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Patterns in Caribbean Coral Spawning

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Submitted in Partial Fulfillment of the Requirements for the Degree of

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

PATTERNS IN CARIBBEAN CORAL SPAWNING

By

Anna Jordan

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

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Table of Contents

LIST OF FIGURES.....	i
LIST OF TABLES.....	iii
ABSTRACT.....	iv
Chapter 1 – Introduction	1
<i>1.1 Coral Reproduction.....</i>	<i>2</i>
<i>1.2 Factors Influencing Coral Health and Reproduction.....</i>	<i>5</i>
<i>1.3 Objectives.....</i>	<i>9</i>
Chapter 2 – Publication.....	11
2.1 Introduction.....	11
2.2 Methods.....	15
2.3 Results.....	17
<i>2.3.1 Descriptive Statistics for Spawning.....</i>	<i>17</i>
<i>2.3.2 Temporal Trends.....</i>	<i>34</i>
<i>2.3.3 Congener Trends.....</i>	<i>47</i>
<i>2.3.4 Environmental Effects.....</i>	<i>47</i>
2.4 Discussion.....	49
Chapter 3 – Discussion.....	56
<i>Data Limitations.....</i>	<i>56</i>
<i>Stochastic Events.....</i>	<i>59</i>
<i>Congener Trends.....</i>	<i>63</i>
<i>Environmental Effects.....</i>	<i>64</i>
Appendix 1 – Contributors.....	66
Appendix 2 – Supplemental Figures.....	74
References.....	82

List of Figures

Figure 1 Geographic distribution of observations.....	17
Figure 2 Spawning months by species.....	18
Figure 3 Spawning days by species.....	18
Figure 4 Spawning times by species.....	19
Figure 5 <i>Acropora cervicornis</i> spawning scatterplot and moonrise bar graph.....	21
Figure 6 <i>Acropora palmata</i> spawning scatterplot and moonrise bar graph.....	22
Figure 7 <i>Colpophyllia natans</i> spawning scatterplot and moonrise bar graph.....	23
Figure 8 <i>Dendrogyra cylindrus</i> spawning scatterplot and moonrise bar graph.....	24
Figure 9 <i>Diploria Labyrinthiformis</i> spawning scatterplot and moonrise bar graph.....	26
Figure 10 <i>Montastraea cavernosa</i> spawning scatterplot and moonrise bar graph.....	27
Figure 11 <i>Orbicella annularis</i> spawning scatterplot and moonrise bar graph.....	28
Figure 12 <i>Orbicella faveolata</i> spawning scatterplot and moonrise bar graph.....	29
Figure 13 <i>Orbicella franksi</i> spawning scatterplot and moonrise bar graph.....	31
Figure 14 <i>Pseudodiploria strigosa</i> spawning scatterplot and moonrise bar graph.....	32
Figure 15 <i>Stephanocoenia intersepta</i> spawning scatterplot and moonrise bar graph.....	33
Figure 16 <i>Acropora cervicornis</i> spawning time and days by year.....	35
Figure 17 <i>Acropora palmata</i> spawning times and days by year.....	36
Figure 18 <i>Colpophyllia natans</i> spawning times and days by year.....	37
Figure 19 <i>Dendrogyra cylindrus</i> spawning times and days by year.....	38
Figure 20 <i>Diploria labyrinthiformis</i> spawning times and days by year.....	39
Figure 21 <i>Montastraea cavernosa</i> spawning times and days by year.....	41
Figure 22 <i>Orbicella annularis</i> spawning times and days by year.....	42
Figure 23 <i>Orbicella faveolata</i> spawning times and days by year.....	43
Figure 24 <i>Orbicella franksi</i> spawning times and days by year.....	44
Figure 25 <i>Pseudodiploria strigosa</i> spawning times and days by year.....	45

Figure 26 <i>Stephanocoenia intersepta</i> spawning days by year.....	46
Figure 27 Acroporids Survival Analyses.....	48
Figure 28 <i>Orbicella spp.</i> Survival Analyses.....	48
Figure S1 <i>Acropora cervicornis</i> spawning times and days by month.....	75
Figure S2 <i>Acropora palmata</i> spawning times and days by month.....	75
Figure S3 <i>Colpophyllia natans</i> spawning times and days by month.....	76
Figure S4 <i>Dendrogyra cylindrus</i> spawning times and days by month.....	76
Figure S5 <i>Dendrogyra cylindrus</i> spawning times and days by gender.....	77
Figure S6 <i>Diploria labyrinthiformis</i> spawning times and days by month.....	77
Figure S7 <i>Montastraea cavernosa</i> spawning days by month.....	78
Figure S8 <i>Montastraea cavernosa</i> spawning times by month.....	78
Figure S9 <i>Montastraea cavernosa</i> spawning times and days by gender.....	78
Figure S10 <i>Orbicella annularis</i> spawning times and days by month.....	79
Figure S11 <i>Orbicella faveolata</i> spawning times and days by month.....	79
Figure S12 <i>Orbicella franksi</i> spawning times and days by month.....	80
Figure S13 <i>Pseudodiploria strigosa</i> spawning times and days by month.....	80
Figure S14 <i>Stephanocoenia intersepta</i> spawning days by month.....	81
Figure S15 <i>Stephanocoenia intersepta</i> spawning days by gender.....	81

List of Tables

Table 1 Split Spawning Observations.....	20
Table S1 Summary of Spawning Observations.....	74

Abstract

Most corals worldwide are broadcast spawners that rely on synchronous gamete release for successful fertilization. Spawning synchrony may also decrease the probability of heterospecific fertilization that may produce maladaptive hybrids. Despite the importance of reproductive timing, researchers have only recently begun to collect spawning data across coral species in the Caribbean, but these data remain to be analyzed. This study investigates interannual, seasonal, and environmental patterns that may influence Caribbean scleractinian spawning times. The number of spawning observations varies widely among location and species. Most spawning observations were collected in Florida, Curaçao, and Flower Garden Banks National Marine Sanctuary. *Acropora palmata*, *A. cervicornis*, and *Orbicella* species were the most documented. The *Orbicella* spp. were very consistent for spawning day annually, while the acroporids were less reliable. However, the acroporids were more consistent for spawning time in minutes after sunset between years. Season and moon cycles were obvious proximate cues for spawning, but a strong influence from wind and tides was absent. *Acropora cervicornis* was the only species in this study which spawning was significantly affected by water temperature. For some scleractinians, the day of spawning was significantly affected by mass bleaching events; spawning could occur on earlier days than in previous years for up to two years after the event. This study highlights existing data gaps for *Pseudodiploria clivosa*, *A. prolifera* and *Siderastrea siderea*. Documenting spawning patterns is crucial to better understand the potential impacts of future threats on the already imperiled Caribbean corals at risk from reproductive failure.

Keywords: Caribbean, Broadcast spawner, *Orbicella*, *Acropora*, Temporal isolation, coral, Spawning times

Chapter 1

Coral reefs' structural intricacy provides significant commercial value, primarily through tourism, shoreline protection, and fishing (Hughes 1994; Park *et al.* 2002; Hawkins and Roberts 2004). Many coral reef organisms contain compounds that have been used in pharmaceuticals and for advancing medical research (Knowlton *et al.* 2010). In 2003, over half of all new medical research for cancer drugs involved marine organisms (Cesar *et al.* 2003). The economic value of tropical coral reefs through pharmaceuticals, shoreline protection, recreation, seafood, and tourism is estimated at US \$797.359 billion worldwide (Cesar *et al.* 2003). However, human use can also cause great harm, *e.g.* coastal development to support tourism, interfering diving behavior, boat anchoring, and destructive or overfishing practices (Cesar *et al.* 2003). For decades coral reefs have been declining worldwide from these practices and other anthropogenic influences, such as disease outbreaks, pollution, and bleaching events, *i.e.*, where corals lose their symbiotic dinoflagellate that gives the tissue its color (Hoegh-Guldberg *et al.* 2017; Hughes *et al.* 2018). These factors have led researchers to suggest that coral reefs will not survive more than a few decades without immediate protection from human exploitation (Pandolfi *et al.* 2003; Gattuso *et al.* 2015).

The Atlantic and Caribbean have 7.6% of coral cover worldwide (Spalding *et al.* 2001) and in 2003, the net value of coral reefs for the Caribbean and United States was almost US \$80 billion (Cesar *et al.* 2003). Regardless of their value, Caribbean corals are particularly vulnerable to overfishing and pollution due to a lack of (or at least insufficient) protective measures (Jackson *et al.* 2014). In 2012, the mean live coral cover found in the Caribbean was 16.8%, which represents almost a 20% absolute decrease since 1973 (Jackson *et al.* 2014). In the Florida Reef Tract, the combination of a growing human population, lower quality and quantity of fresh water input from the Everglades makes this coral reef ecosystem unique in the Western Atlantic and Caribbean, as it is one of the most studied but also heavily used reef systems in the Caribbean (Spalding *et al.* 2001; Keller and Causey 2005).

Scientists are researching techniques to restore coral populations in areas that have been affected by direct and indirect anthropogenic stressors. One strategy uses the

natural process of fragmentation, where a piece of coral breaks off from the parent colony, reattaches to the substrate, and continues to grow (Highsmith 1982). Scientists are using fragmentation methods to grow and transplant corals to areas where high coral mortality has occurred from disease and predator outbreaks, bleaching, or ship groundings (Yeemin *et al.* 2006). Asexual reproduction is beneficial for corals because it only requires one coral, it requires less energy, is quick, and because fragments do not disperse over a large distance, the coral has a genotype adapted to the local environment (Williams 1975). However, scientists are also attempting to use sexual propagation to generate larvae and re-seed the reefs (Marhaver *et al.* 2015). In areas affected by multiple anthropogenic stressors, natural coral recruitment can be limited; therefore, in highly disturbed areas, restoration efforts may be the most effective and rapid way to increase coral biomass, and thus guarantee the success of sexual reproduction, and restoration of ecosystem function (Yeemin *et al.* 2006).

1.1 Coral Reproduction

There are two forms of sexual reproduction in corals, brooding and broadcast spawning (Marshall and Stephenson 1933; Szmant-Froelich *et al.* 1980). The main difference between these two reproductive strategies is that fertilization and embryonic development occur internally in brooders, and externally in broadcast spawners (Lacaze-Duthiers 1873; Marshall and Stephenson 1933; Szmant-Froelich *et al.* 1980; Fadlallah and Pearse 1982). The embryo develops into a planula larva that settles on the benthos, undergoes metamorphosis, and if it survives to an adequate size will reproduce, completing the life cycle (Fadlallah 1983). In the Indo-Pacific, tens to hundreds of species can spawn in a highly synchronized mass spawning event. Yet, scientists first observed this phenomenon only a few decades ago (Babcock *et al.* 1986; Richmond and Hunter 1990; McGuire 1998). Worldwide most coral species (84%) are broadcast spawners (Baird *et al.* 2009); however, in the Caribbean broadcast spawning and brooding species are about equally represented (Harrison and Wallace 1990). Broadcast spawners typically reproduce once or twice per year while brooders reproduce several times per year, as frequently as every month (Richmond and Hunter 1990; McGuire 1998). Regardless of their mating strategy, approximately 73% of coral species are

hermaphrodites, where one coral has both female and male sex organs, while other coral species have separate sexes, *i.e.*, gonochores (Harrison and Wallace 1990; Richmond and Hunter 1990; Fine *et al.* 2001). Due to the exchange of genetic material between eggs and sperm from separate colonies and the recombination of their genetic material, sexual reproduction leads to increased genetic diversity (Crow 1994). Selfing, where sperm and eggs from an individual colony or clone successfully fertilize (Carlson 1999), is relatively rare, and it is unclear if the resulting larvae are viable.

Mass spawning events aid the reproductive success of the coral species that participate in this event. These advantages include increasing genetic diversity through cross fertilization of multiple synchronized genotypes and promoting higher larval survival rate due to predator satiation (Harrison *et al.* 1984). Fish and reef invertebrates, from brittle stars to whale sharks, will consume coral gametes and embryos until they are satiated (Westneat and Resing 1988). If corals are present in high densities and spawning is highly synchronous, predators become satiated before all coral gametes and embryos are consumed (Harrison *et al.* 1984). This allows the population to have higher fertilization and larval survival. However, spawning synchrony does not come without a cost, *i.e.*, increased chance of polyspermy and thus egg death (Styan 1998). There is also the chance of a single catastrophic event during spawning reducing reproductive success (Harrison *et al.* 1984; Richmond and Hunter 1990) and the potential of maladaptive or infertile hybrid formation leading to gamete wastage (Willis *et al.* 1997). Nevertheless, spawning is overall an effective means to reproduce.

Like many other marine species (Kojis and Quinn 1981; Caspers 1984; Hoppe and Reichert 1987; Babcock *et al.* 1992), for corals, a precise combination of environmental conditions is required to induce mass spawning events (Shlesinger and Loya 1985), including temperature (van Woesik *et al.* 2006), light (Shlesinger and Loya 1985; Babcock *et al.* 1994), wind (Mangubhai and Harrison 2006; van Woesik 2009), tides (Babcock *et al.* 1986), genetics (Knowlton *et al.* 1997; Levitan *et al.* 2011), and chemical cues (Atkinson and Atkinson 1992; Van Veghel 1994; Slattery *et al.* 1999). Levitan *et al.* (2011) found that *Orbicella spp.* (formerly *Montastraea*) have very precise interannual spawning times, but spawning becomes less precise when corals release

gametes later after the full moon and sunset. If these corals do not release gametes within 15 minutes of peak spawning, fertilization is reduced (Levitan *et al.* 2004). In other marine invertebrates, like sea urchins, when sperm are competing, spawning precision on the scale of tens of seconds can affect which individuals mate and which do not (Levitan 2005).

Corals use seawater temperature and solar insolation cycles to synchronize reproduction to the same season (van Woesik *et al.* 2006). Temperature can be influenced by sunlight and seasonal cycles and generally affects the season that corals will spawn. The monthly average sea surface temperature significantly correlates with the timing of spawning for 12 species of Caribbean broadcast spawners (van Woesik *et al.* 2006). Others suggest that the rate of change in sea surface temperature, not the monthly average is the proximate cue for mass spawning events (Keith *et al.* 2016). There are arguments that solar insolation cycles are better predictors of coral spawning in the Caribbean (van Woesik *et al.* 2006). Others hypothesize that spawning day is influenced by lunar factors such as the coincidence of the third quarter of the lunar cycle and the movement of the moon over the equator (Wolstenholme *et al.* 2018). Lin and Nozawa (2017) monitored 42 scleractinian species, including *Acropora spp.*, at the same locations in the Indo-Pacific for seven years, allowing them to identify variability in spawning time or date that occurred between years. They found that different species follow different biological clock models. For example, acroporids are more sensitive to changes in the environment because they follow an hourglass biological clock model, which can increase the variability in spawning time for this genus (Lin *et al.* 2013; Lin and Nozawa 2017).

Coral spawning has been found to coincide with calm periods in regional wind fields and low-amplitude tides. This enables the corals to have maximum fertilization success and retain larvae (van Woesik 2009). If the corals spawn during periods of high winds, their larvae could be transported to unsuitable habitats. Mangubhai and Harrison (2006) observed multiple species of corals spawning during calm periods in regional wind fields on a reef near the equator off the coast of Kenya. Tides influence the direction that the gametes disperse and therefore impact fertilization success. Babcock *et al.* (1986) found that mass spawning most often coincides with low-amplitude tides.

The seasonal photoperiod may influence the month corals spawn (Babcock *et al.* 1994) and sunlight and moonlight may influence the time corals spawn (Babcock *et al.* 1992). Light, including moonlight and sunlight, is the most commonly recorded cue to influence coral spawning. Light cues have been found to dictate which night the corals will spawn, usually measured in the number of days before or after the full moon (Babcock *et al.* 1994). In the Caribbean, broadcast spawners typically reproduce three to six days after the full moon and two to four hours after sunset. Brooding corals, such as *Porites astreoides*, reproduce in relation to the new moon (Babcock *et al.* 1986; Chornesky and Peters 1987). Light also has an influence on predation during coral spawning. If there is less light (*i.e.*, before moonrise), visual predators may not be as successful at preying on coral gametes and embryos (Babcock *et al.* 1992).

Lastly, genetics and chemical cues appear to play a role in fine scale spawning synchrony and fertilization success of corals. Gametes could be genetically incompatible and lead to fertilization failure (Knowlton *et al.* 1997). Individual corals with the same genotype (ramets) tend to have similar spawning times, but unique genotypes can have significantly different spawning times (Levitan *et al.* 2011). Hormones also influence the timing of gametogenesis and spawning *e.g.*, soft corals have an increase in testosterone before spawning events, and increases in progesterone were correlated with female gametogenesis (Slattery *et al.* 1999). Neighboring corals, regardless of genotype, spawn more synchronously than corals with the same genotype that were spaced further apart, suggesting that hormones may be a cue for mass spawning events (Levitan *et al.* 2011). Estradiol-17 β was found to be present during mass spawning of scleractinian corals in Australia (Atkinson and Atkinson 1992). It was hypothesized that the presence of this steroid suggests that it is involved in spawning synchrony or the final maturation of the eggs (Atkinson and Atkinson 1992).

1.2 Factors influencing coral health and reproduction

Direct and indirect anthropogenic stressors are a threat to the continued existence of corals. The most prevalent threat to corals is ocean warming and acidification (Hoegh-Guldberg *et al.* 2017). An increase in the amount of carbon dioxide in the atmosphere causes an increase in the amount of carbon dioxide in the ocean (Raven *et al.* 2005). The

carbon dioxide in the ocean reacts with the water resulting in an increased concentration of hydrogen ions. This increase in hydrogen ions lowers the pH of the water, thus making the ocean more acidic (Raven *et al.* 2005). Since coral skeletons are composed/built of calcium carbonate, the increase in ocean acidity weakens their skeletons and forces corals to allocate their metabolic energy differently (Kleypas and Langdon 2006). In acidic conditions, corals need to allot more energy to build their skeletons, leading to a reduction in the energy available for other important processes, such as reproduction (Hoegh-Guldberg *et al.* 2007). Reduced energy allocation can cause corals to produce smaller or less viable eggs and sperm, halt reproduction in order to conserve energy, or reabsorb gametes (Szmant and Gassman 1990). The detrimental effects of ocean acidification are found to increase in sperm-limited circumstances. Albright *et al.* (2010) found a compounded decrease of 73% in the number of settled larvae under ocean acidification conditions.

The increased carbon dioxide in the atmosphere can also cause warming (Callendar 1938). When heat leaves the earth's surface and travels through the atmosphere, the increased levels of carbon dioxide gas trap the heat in our atmosphere causing the temperature in our atmosphere to increase (Callendar 1938). Changes in temperature cause coral stress which can lead to a number of different reactions from the coral. One reaction could be that the corals may expel their endosymbionts and thus lose their color. The white calcium carbonate skeleton can be seen through their translucent tissue; therefore, this process is called "coral bleaching." The endosymbionts provide enough nutrition through the process of photosynthesis to meet the requirements for the coral's metabolic respiration (Muller-Parker *et al.* 2015). Bleaching therefore contributes to a reduction of energy reserves which will ultimately limit sexual reproduction. The reduced energy prevents or reduces the production of gametes for up to two years after the bleaching event causing a significant decrease in reproduction (Szmant and Gassman 1990; Omori *et al.* 2001; Levitan *et al.* 2014). If the corals have enough energy for gametogenesis to occur, the gametes produced could be of lesser quality, for example sperm with decreased motility (Omori *et al.* 2001) or eggs have less lipids (Michalek-Wagner and Willis 2001) which can reduce fertilization success and dispersal distances. Bleached corals may be able to spawn but only if they have enough energy stores (Fitt *et*

al. 2000). After a bleaching event, there can be a decrease in spawning synchrony for up to two years (Levitan *et al.* 2014). Paxton *et al.* (2015) found that when corals are experiencing increased temperatures, even before bleaching occurs, egg volume and sperm number decrease. Elevated temperatures can also cause corals to reproduce earlier in the lunar cycle (Crowder *et al.* 2014; Paxton *et al.* 2015).

Direct anthropogenic influences, including pollution, physical contact with corals, and sedimentation can also reduce coral reproductive success. Nutrient enrichment and pollution have been found to decrease coral reproduction and growth rates (Richmond 1993). Even low levels of pollutants, for example oil, runoff, or sewage, can have a severe impact on the ecosystem over time, by causing mortality, reducing gamete production, larval recruitment, and therefore recovery (Richmond 1993). Some of the toxic substances from runoff, such as oil, have been shown to shrink the gonad size of scleractinian corals and further decrease the coral population's ability to recover from other stressors (Rinkevich and Loya 1979). Macroalgae thrive in nutrient-rich water, including coastal environments with heavy runoff containing fertilizers from agriculture and residential lawns. This in addition to the loss of important herbivores through disease and overfishing has led to an overabundance in macroalgae (Carpenter 1990; Hughes 1994). It was also found that corals in the presence of macroalgae have lower larval output. Tanner (1995) found that corals that were cleared of macroalgae produced over twice as many larvae as the corals that were naturally overgrown. Direct diver contact causes coral injuries, potentially increasing the prevalence of disease and decreasing their reproductive potential (Lamb *et al.* 2014). Sedimentation from dredging and runoff also poses a threat to coral settlement, growth, and reproduction (Fabricius 2005; Fourney and Figueiredo 2017). Low light and sedimentation have been proven to reduce coral fecundity and recruitment (Fabricius 2005). Fertilization occurs more slowly, and eggs and sperm are produced in lower quantities when adults are exposed to sedimentation (Gilmour 1999). It should be noted that when studying these stressors and their influence on a community, that there is rarely only one stressor acting on the community.

Coral diseases occur as a response to stress acting on the corals which can have a detrimental effect on coral reproduction. White-band disease is one of the most prevalent

coral diseases and causes more than 90% mortality in Caribbean acroporids. The disease kills coral tissue as it spreads from base to tip (Aronson and Precht 2001). Aronson and Precht (2001) found that *Acropora* species in the Caribbean exhibit a lack of genetic diversity due to the mortality from white-band disease. The lack of genetic diversity is then further magnified by their primarily asexual reproduction (Aronson and Precht 2001). This loss of *A. palmata* genetic diversity sometimes leads to the domination of one clone on a reef (Baums *et al.* 2006), thus reducing the ability for successful fertilization because selfing is limited (Fogarty, Vollmer, *et al.* 2012). Additionally, *A. palmata* contracts white pox disease. This disease causes circular lesions to form on the coral and eventually results in tissue loss and colony mortality. The high likelihood of mortality makes it challenging for *A. palmata* populations to recover from white pox outbreaks because this species relies heavily on asexual fragmentation (Patterson *et al.* 2002). Yellow band disease is caused by a bacterial pathogen that primarily affects *Orbicella* species. This disease seems to mainly affect the corals' endosymbionts. It has been found that polyps infected with yellow band disease have significantly fewer eggs than polyps without the disease, which could decrease fertilization success (Weil *et al.* 2009). Lastly, Borger and Colley (2010) found that *O. faveolata* colonies affected by white plague disease have fewer reproductive polyps, lower reproductive mesenteries, lower oocyte volume, a lower quantity of oocytes, and lower fecundity than healthy colonies.

Fish are both predators and protectors of corals. While some fish species help the corals by eating algae, others eat coral polyps (Francini-Filho *et al.* 2008) and/or gametes. In Australia, *Acanthochromis polyacanthus* and *Abudefduf bengalensis* prey upon coral gametes their stomachs can be over 90% full of gametes (Westneat and Resing 1988), likely reducing coral fertilization. Parrotfish are known to selectively feed on adult corals in the Caribbean (Francini-Filho *et al.* 2008), particularly *O. annularis* polyps with greater reproductive potential, as defined by the number of gonads, number of eggs, and number of eggs per gonad between polyps (Rotjan 2007). Additionally, because parrotfish tend to graze on the same coral polyps repeatedly, the corals need to constantly regenerate these parts likely leading to decreased reproductive rates. On the other hand, parrotfish algal grazing may have a significant positive affect on coral health by removing algal cover with historical evidence showing the potential of grazing to reduce

disease for corals (Jackson 2001). Despite the dichotomy between the positive and negative effects of parrotfish on corals, it has been suggested that overall parrotfish are helpful to coral health, and conservation efforts should focus on the parrotfish protection to stabilize coral populations (Mumby *et al.* 2007). If corals are undisturbed, they will grow faster than predators can eat them (Jackson 1977; Jackson 2001). Parrotfish have been overfished in many Caribbean locations leading to an inverse relationship between coral and algal cover (Mumby 2006).

While several studies have compiled spawning data on scleractinian species in the Caribbean and Western Atlantic, there has not been a statistical analysis of this data. Most of the studies with compiled spawning data include scleractinian species from across the world (Richmond and Hunter 1990; Baird *et al.* 2009; Harrison 2011). Some of these studies examine general patterns in the reproductive biology or evolution of the species (Baird *et al.* 2009; Harrison 2011). While the spawning of several Caribbean species has been recorded, there is no broad analysis of species-specific proximate cues for spawning. It is important to establish trends in coral reproduction prior to further coral mortality and environmental changes in order to implement the best protective measures and restoration strategies.

1.3 Objectives

The main objectives of this paper were to create a database of Caribbean, Western Atlantic, and Gulf of Mexico scleractinian spawning data, and then to identify potential proximate cues for spawning on regional scales within individual species and among congeners. This project aimed to answer three questions:

1. Is there a species-specific temporal pattern of spawning?

I analyzed annual, monthly, and daily patterns in the moon cycle and day cycle.

2. Do congeners exhibit similar spawning patterns?

I analyzed daily differences in spawning among congeners relative to moon cycle and day cycle in *Acropora spp.* and *Orbicella spp.*

3. What are the environmental proximate cues for spawning?

I determined if water temperature, wind speed, and moonrise time cued spawning.

Chapter 2

2.1 Introduction

The Atlantic Ocean and Caribbean Sea have an estimated 21,600 km² of coral reef, equaling 7.6% of the total reef cover in the world (Spalding *et al.* 2001). The structural complexity of these reefs hosts immense biodiversity, providing significant commercial value through tourism, shoreline protection, and fishing (Hughes 1994; Park *et al.* 2002; Hawkins and Roberts 2004). Since the 1970s, the Caribbean has decreased in coral cover almost 20% (Côté *et al.* 2005; Jackson *et al.* 2014). Overpopulation and tourism, in combination with unenforced or absent measures of protection, overfishing, loss of herbivores, disease, and coastal pollution were found to be the main drivers behind coral habitat loss (Jackson *et al.* 2014). These factors led to a phase shift from a coral dominated benthos to a macroalgal domination (Côté *et al.* 2005). Successful coral reproduction through asexual propagation or larval reseeded coupled with increased herbivory would help to reverse this trend and restore coral reefs to their former coral dominated state.

There are two ways corals can sexually reproduce, broadcast spawning and brooding (Marshall and Stephenson 1933; Szmant-Froelich *et al.* 1980). The main difference between these two reproductive strategies is that fertilization and embryonic development occur internally in brooders and externally in broadcast spawners (Lacaze-Duthiers 1873; Marshall and Stephenson 1933; Szmant-Froelich *et al.* 1980; Fadlallah and Pearse 1982). Worldwide most coral species (84%) are broadcast spawners (Baird *et al.* 2009); however, in the Caribbean broadcast spawning and brooding species are about equally represented (Harrison and Wallace 1990). Broadcast spawners only reproduce once or twice per year, while brooders reproduce several times per year (Richmond and Hunter 1990; McGuire 1998). A majority of corals (73%) are hermaphrodites, where one coral will have both male and female sex organs, while other corals have separate sexes, *i.e.*, gonochores (Harrison and Wallace 1990; Richmond and Hunter 1990; Fine *et al.* 2001). Due to the exchange of genetic material between eggs and sperm from separate colonies and recombination, sexual reproduction leads to increased genetic diversity (Crow 1994).

Some species of corals are known for their precise spawning times. For example *Orbicella* species (Levitan *et al.* 2011) have an interannual standard deviation in spawning times of as little as 7 minutes. However, spawning becomes less precise when corals release gametes later after the full moon and sunset (Levitan *et al.* 2011). Fertilization is reduced if corals do not release gametes within 15 minutes of peak spawning (Levitan *et al.* 2004); therefore, spawning synchrony is crucial to reproductive success. Shlesinger and Loya (1985) suggested that a precise combination of environmental conditions is required to induce mass spawning events, including temperature (van Woesik *et al.* 2006), light (Shlesinger and Loya 1985; Babcock *et al.* 1994), wind (Mangubhai and Harrison 2006; van Woesik 2009), tides (Babcock *et al.* 1986), genetics (Knowlton *et al.* 1997; Levitan *et al.* 2011), and chemical cues (Atkinson and Atkinson 1992; Van Veghel 1994; Slattery *et al.* 1999).

For many broadcast spawning corals, the monthly average sea surface temperature, which is influenced by sunlight and seasonal cycles, is the best predictor of which month corals will spawn (van Woesik *et al.* 2006). Yet, it has been found that the rate of change in sea surface temperature, not the monthly average, is the proximate cue for mass spawning events (Keith *et al.* 2016). However, solar insolation cycles have been suggested to be better predictors of coral spawning in the Caribbean (van Woesik *et al.* 2006). Solar insolation is the quantity of electromagnetic energy incident to earth's surface (van Woesik *et al.* 2006). Others hypothesize that spawning day is influenced by lunar factors such as the coincidence of the third quarter of the lunar cycle and the movement of the moon over the equator (Wolstenholme *et al.* 2018). Multiple coral species spawn during calm periods in regional wind fields, and mass spawning frequently coincides with low-amplitude tides (Babcock *et al.* 1986; Mangubhai and Harrison 2006). Spawning under both of these conditions enables the corals to have maximum fertilization success and retain larvae (van Woesik 2009). Lunar light cues dictate which night corals will spawn and also influences predation (Babcock *et al.* 1994). A majority of spawning observations also occur before the moon rises to reduce predation on coral gametes and embryos during mass spawning events (Babcock *et al.* 1994). Spawning for most species of scleractinians in the Caribbean occurs after sunset, the exception being *Diploria labyrinthiformis*, which spawns before sunset. Lastly, genetics and chemical

cues appear to play a role in fine scale spawning synchrony and fertilization success of corals. Individual corals with the same genotype (ramets) have similar spawning times, but unique genotypes have significantly different spawning times (Levitan *et al.* 2011). Hormones also influence the timing of gametogenesis and spawning (Slattery *et al.* 1999). Neighboring corals, regardless of genotype, spawn more synchronously than corals with the same genotype that were spaced further apart, suggesting that hormones may be a cue for mass spawning events (Levitan *et al.* 2011).

There are many environmental and anthropogenic factors that threaten coral reproductive success; among the most detrimental is thermal stress. Coral bleaching often occurs under thermal stress and causes the coral to expel its endosymbionts (*Symbiodinium* spp.) and lose its color. These endosymbionts produce most of the coral's nutrition, and their loss can have devastating effects on the coral (Muller-Parker *et al.* 2015). If the coral does not have sufficient metabolic energy, they will reallocate their energy in order to survive. The reduced energy from bleaching can prevent or reduce production of gametes for up to two years after the bleaching event, causing a substantial decrease in reproductive output (Szmant and Gassman 1990; Omori *et al.* 2001; Levitan *et al.* 2014). If the corals have enough energy for gametogenesis to occur, the gametes produced could be of lesser quality, for example fewer sperm with decreased motility (Omori *et al.* 2001) and reduced egg volume including decreased lipids in eggs (Michalek-Wagner and Willis 2001; Paxton *et al.* 2015). Broadcast spawners reproduce earlier under increased sea surface temperature. Furthermore, after a bleaching event, there can be a decrease in spawning synchrony for up to two years (Levitan *et al.* 2014; Paxton *et al.* 2015). Brooders are not immune to the effects of thermal stress. Elevated temperatures likely caused *Pocillopora damicornis* to release planulae earlier in the lunar cycle, and the shifts can occur quickly, in as little as one reproductive cycle (Crowder *et al.* 2014; Levitan *et al.* 2014; Paxton *et al.* 2015).

Disease outbreaks and predation have detrimental effects on coral reproduction. White plague disease and yellow band disease reduce the number of reproductive polyps in *Orbicella* species (Weil *et al.* 2009; Borger and Colley 2010). Polyps infected with yellow band disease have significantly less eggs than polyps without the disease (Weil *et*

al. 2009). *Orbicella* (formerly *Montastraea*) *faveolata* colonies infected with white plague disease had lower oocyte volume, less oocytes, and lower fecundity than healthy colonies (Borger and Colley 2010). Parrotfish have been found to selectively graze on corals in the Caribbean (Francini-Filho *et al.* 2008), specifically grazing on *O. annularis* polyps with higher reproductive potential, defined as number of gonads and number of eggs (Rotjan 2007). *Acanthochromis polyacanthus* and *Abudefduf bengalensis* have been found to eat until their stomachs are over 90% full of gametes (Westneat and Resing 1988), likely reducing coral fertilization. This is why coral mass spawning events usually occur after sunset and before moonrise; the darkness reduces predation on coral gametes and embryos (Babcock *et al.* 1994).

To implement the best protective measures and restoration strategies, it is important to establish trends in coral reproduction prior to further coral mortality and environmental changes. Several studies have compiled spawning data on scleractinian species, but an emphasis on the Caribbean is lacking. Most of the studies with compiled spawning data include scleractinian species from across the world (Richmond and Hunter 1990; Baird *et al.* 2009; Harrison 2011). Some of these studies examine general patterns in the reproductive biology or evolution of the species (Baird *et al.* 2009; Harrison 2011). While compiled spawning data exists for some Caribbean species, no broad analysis of spawning data or the environmental factors that may influence spawning exists for Caribbean scleractinians.

The main objectives of this study were to create a database of Caribbean, Western Atlantic, and Gulf of Mexico scleractinian spawning information to determine which spawning cues and environmental factors influence spawning within a species and among congeners. Specifically, I tested whether water temperature, wind speed, or time of moonrise affected the absence or presence of spawning.

2.2 Methods

Data was compiled from peer-reviewed publications, NOAA's Coral Health and Monitoring Program Coral ListServer, posts to the coral spawning research Facebook page (created and managed by N. Fogarty), and contributing researchers (see Appendix 1) across the Western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico for every species of scleractinian coral for which data was available. The information collected from these sources included date and time of spawning, proportion of corals observed that spawned, and environmental data at the time of the spawning event, including sea surface temperature, time of moonrise, wind speed, and tides. If environmental data was not provided, it was obtained from other sources. Sunset and moonrise data was gathered from the United States Naval Observatory Astronomical Applications Department website, http://aa.usno.navy.mil/data/docs/RS_OneDay.php. Temperature data was obtained from Rutgers University Coastal Ocean Observation Lab website, https://marine.rutgers.edu/cool/sat_data/?product=sst®ion=floridacoast¬humbs=0. Wind data was obtained from the Weather Underground website, <https://www.wunderground.com>. Tide data was sourced from NOAA's Tides and Currents database https://tidesandcurrents.noaa.gov/historic_tide_tables.html.

Data Analysis

Statistical tests were chosen by the distribution of data being tested to explore patterns that might exist with Western Atlantic scleractinian coral spawning times. To assess species-specific temporal patterns, I used Mantel-Haenszel survival analyses and Mann-Whitney Wilcoxon tests. The Mantel-Haenszel tests were run for each individual species that had at least 20 spawning observations and across genera. Survival analyses were used to compare day cycle, defined as spawning minutes after sunset, or moon cycle, defined as spawning days after the full moon, by month and by year. I also tested if there were patterns found between males and females for spawning day or spawning time for the gonochoric species in this study. I used a survival analysis because it tests the time leading up to an event (*i.e.*, spawning), which does not have to be death. The test analyzes the time in minutes or days leading up to spawning. Each individual curve represented a different month or year, in order to compare trends between these factors.

Data quality control was performed before tests were run, which involved removing invalid data points. The Mann-Whitney Wilcoxon test was used to analyze whether bleaching events affected spawning day for individual species of corals. The year in which a mass bleaching event occurred (*i.e.*, 1998, 2005, and 2010) and the two years following the bleaching year were tested against other years to determine if the spawning day was significantly different during this time.

To determine whether congeners exhibit similar spawning patterns, I used Mantel-Haenszel survival analyses as well. These tests analyzed moon cycles and day cycles for the acroporid and *Orbicella spp.* congeners. For these survival analyses, each individual curve represented a different congener. Data quality control was performed before these tests were run also.

To analyze the environmental proximate cues for spawning, I used Generalized Linear Models (GLMs). These were run on adequate environmental data and adequate negative spawning observations, *i.e.*, a minimum of 20 observations with all variables present, to test whether water temperature, wind speed, or moonrise time affected the presence or absence of spawning. The species tested were *A. cervicornis*, *A. palmata*, *O. faveolata*, *O. franksi*, and *P. strigosa*.

2.3 Results

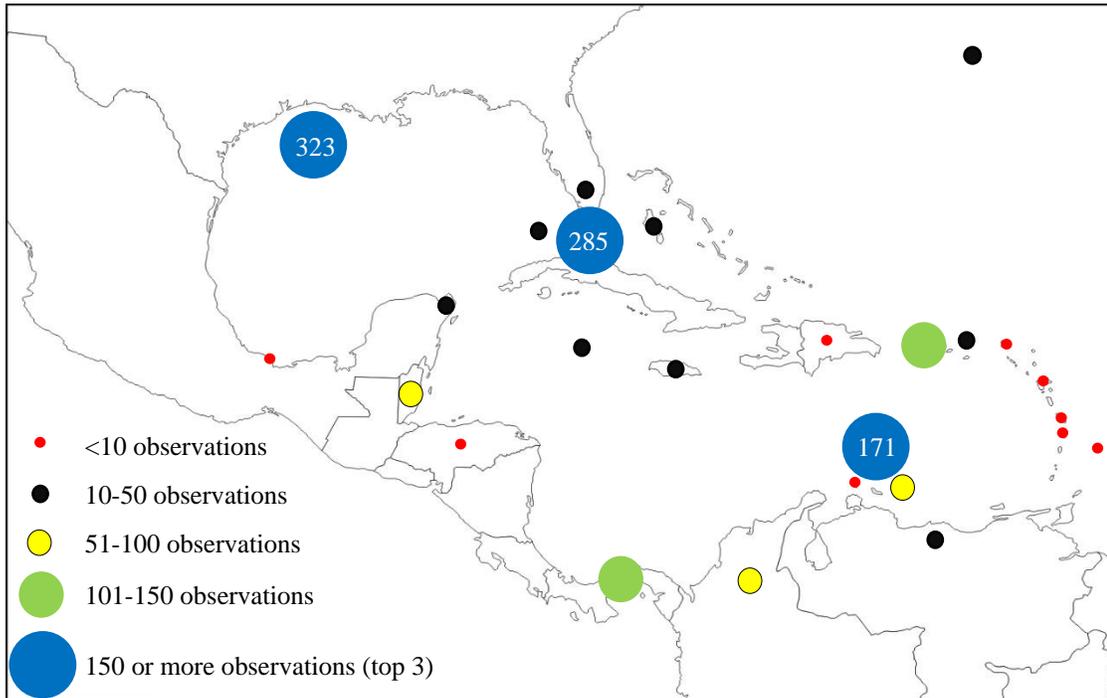


Figure 1. Geographic distribution of observations. The dots represent regions where observations were recorded.

2.3.1 Descriptive Statistics for Spawning

The data spanned 26 different regions across the Caribbean, Gulf of Mexico, and Western Atlantic (Fig. 1). The top three regions with the most spawning observations in the dataset were Curaçao, the Florida Keys, and Flower Garden Banks National Marine Sanctuary. There was a sufficient amount of data to run analyses on 11 species of broadcast spawning scleractinians. Of these species, three were gonochores and eight were hermaphrodites (Table S1). For some species, data goes back to 1983, while the most recent observations are from 2016. Spawning month refers to the month that spawning occurs. In this dataset spawning occurs from May to November, with all 11 species having August as a peak spawning month (Fig. 2, Table S1). *Diploria labyrinthiformis* had the broadest spawning window from May to November (Table S1). Spawning day refers to the day spawning occurred and is recorded as days before or after the full moon. Spawning day ranged from the day of the full moon to 18 days after the full moon for the species in this study (Fig. 3). Spawning time refers to the precise time

	May	June	July	August	September	October	November
<i>A. cervicornis</i>							
<i>A. palmata</i>							
<i>A. prolifera</i>							
<i>O. annularis</i>							
<i>O. faveolata</i>							
<i>O. franksi</i>							
<i>C. natans</i>							
<i>D. labyrinthiformis</i>							
<i>P. strigosa</i>							
<i>D. cylindrus</i>							
<i>M. cavernosa</i>							
<i>S. intersepta</i>							

Figure 2. Spawning months by species. Gray represents a month in which spawning occurs. Black represents the peak spawning month(s).

(hours and minutes) spawning occurred, and it was recorded as minutes before or after sunset or moonrise. Most species spawned between 30 and 300 minutes after sunset; exceptions were *D. labyrinthiformis* and *Montastraea cavernosa* because they also spawned before sunset (Fig. 4). Seven species displayed “split-spawn”, *i.e.* spawned after two consecutive full moons within the same region (Table 1).

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>A. cervicornis</i>																			
<i>A. palmata</i>																			
<i>A. prolifera</i>																			
<i>O. annularis</i>																			
<i>O. faveolata</i>																			
<i>O. franksi</i>																			
<i>C. natans</i>																			
<i>D. labyrinthiformis</i>																			
<i>P. strigosa</i>																			
<i>D. cylindrus</i>																			
<i>M. cavernosa</i>																			
<i>S. intersepta</i>																			

Figure 3. Spawning days by species. The numbers correspond to the date after the full moon with day 0 referring to the date of the full moon. Gray represents a day in which spawning occurs. Black represents the peak spawning days. Peak spawning day was not included for *A. prolifera* because there were not enough observations to calculate.

	-120 -> -91	-90 -> -61	-60 -> -31	-30 -> -1	0-29	30-59	60-89	90-119	120-149	150-179	180-209	210-239	240-269	270-299	300-329
<i>A. cervicornis</i>						█	█	█	█	█	█	█	█	█	█
<i>A. palmata</i>						█	█	█	█	█	█	█	█	█	█
<i>A. prolifera</i>										█	█	█	█	█	█
<i>O. annularis</i>								█	█	█	█	█	█	█	█
<i>O. faveolata</i>						█	█	█	█	█	█	█	█	█	█
<i>O. franksi</i>						█	█	█	█	█	█	█	█	█	█
<i>C. natans</i>						█	█	█	█	█	█	█	█	█	█
<i>D. labyrinthiformis</i>	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
<i>P. strigosa</i>						█	█	█	█	█	█	█	█	█	█
<i>D. cylindrus</i>						█	█	█	█	█	█	█	█	█	█
<i>M. cavernosa</i>						█	█	█	█	█	█	█	█	█	█
<i>S. intersepta</i>						█	█	█	█	█	█	█	█	█	█

Figure 4. Spawning times by species. The numbers correspond to the minutes after sunset that spawning occurred with negative numbers referring to the minutes before sunset. Gray represents that spawning was observed within that 30 minute time frame.

Acropora cervicornis spawning occurred from July to September, peaking in August, and varied greatly across spawning day and time (Figs. 5a, S1). Spawning varied across days after the full moon for all three months where spawning was observed (Fig. 5a). July and August had more variability in spawning day than September (Fig. 5a). Days 3, 5, and 6 after the full moon had more variance in spawning time than other days where spawning was observed. Observations for *A. cervicornis* spawning ranged from 30 to 257 minutes after sunset and 1 to 15 days after the full moon (Figs. 5a, S1). Spawning peaked between 150 and 165 minutes after sunset on days 3 to 6 after the full moon. The variability in spawning time changed from day to day (Fig. 5a). Most *A. cervicornis* spawning (75%) was observed prior to 30 minutes post-moonrise. The variability, however, was high, ranging from 536 minutes before moonrise to 307 minutes after moonrise (Fig. 5b). One split spawn was observed for *A. cervicornis*, in July and August 1985 (Table 1).

Acropora palmata spawned from July to September and had high variability for both spawning day and spawning time for all three months (Figs. 6a, Table S1). Peak

Table 1. Summary of observed split spawns for 7 species across Florida, the Gulf of Mexico, and the Caribbean from data collected for this study.

Species	Site	Month	Year	Days After Full Moon	Full Moon Date
<i>Acropora cervicornis</i>	La Parguera, Puerto Rico	July	1985	7,8	7/2/85
		August		7/31/85	
<i>Acropora palmata</i>	Key Largo, FL	August	1997	13	7/19/97
				6,8	8/18/97
	Tres Palmas, Puerto Rico	August	2007	4	7/30/07
				3	8/28/07
	Elbow Reef, Florida	August	2012	2	8/2/12
		Keys		September	2,3
La Bocana Chica, Mexico	July	2013	4	7/22/13	
	August		3	8/20/13	
Carrie Bow, Belize	July	2013	5,6,7	7/22/13	
	August		2,3	8/20/13	
<i>Montastraea cavernosa</i>	Flower Garden Banks	August	1995	6,7,12	8/10/95
		September		8	9/8/95
<i>Orbicella annularis</i>	Key Largo, FL	August	1997	13	7/19/97
				6,8	8/18/97
	Seaquarium, Curaçao	September	2015	6	8/29/15
		October		9/27/15	
<i>Orbicella faveolata</i>	Flower Garden Banks	August	1995	7,8	8/10/95
		September		8	9/8/95
	Flat Cay, USVI St. Thomas	August	2012	8	8/2/12
		September		7	8/31/12
	Hind Bank, USVI St. Thomas	August	2012	8	8/2/12
		September		7	8/31/12
Horseshoe Reef, Florida	August	2014	6,7	8/10/14	
	Keys		September	6	9/9/14
	Seaquarium, Curaçao	September	2015	6	8/29/15
		October		9/27/15	
<i>Orbicella franksi</i>	Key Largo, FL	August	1997	13	7/19/97
				6,8	8/18/97
	Flower Garden Banks	August	2001	5,6,7	8/4/01
		September		7,8	9/2/01
<i>Pseudodiploria strigosa</i>	Flower Garden Banks	August	1995	7,8,11	8/10/95
		September		8	9/8/95

spawning for *A. palmata* occurred in August. July had less variability in spawning time than August or September (Fig. 6a). Days 3 and 4 after the full moon had more variance

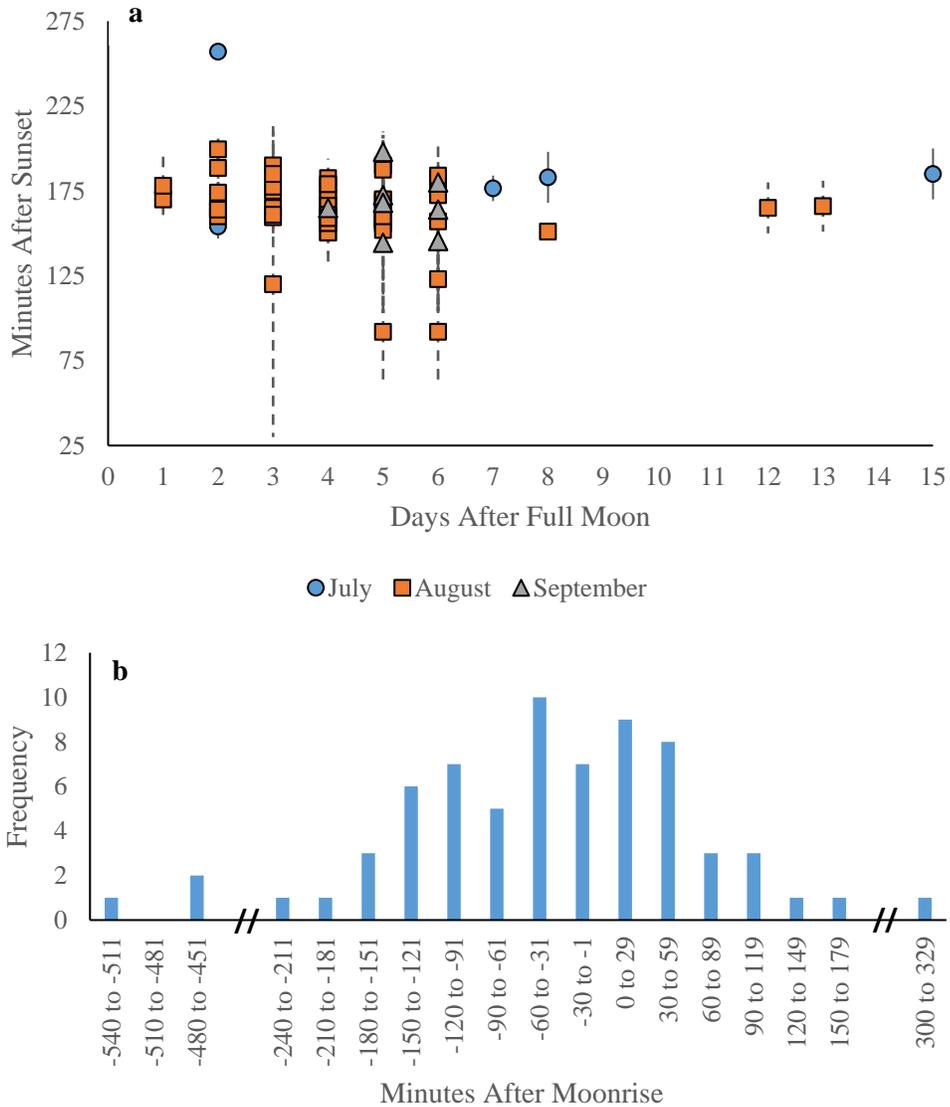


Figure 5. *Acropora cervicornis* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

in spawning time than other days where spawning was observed. *Acropora palmata* had the greatest range of observed spawning days of any species in this study, with observations recorded from the day of the full moon to 18 days after the full moon (Figs. 6a, S2a). Spawning time also varied from 50 to 260 minutes after sunset (Figs. 6a, S2b). Peak spawning occurred 3 to 5 days after the full moon from 136 to 157 minutes after sunset, but had the highest variability in spawning times for *A. palmata* (Figs. 6a). There was also high variability in spawning in relation to moonrise (Fig. 6b). Spawning had been observed starting at 611 minutes before moonrise until 138 minutes after moonrise

(Fig. 6b). Three-quarters of spawning observations occurred prior to 7 minutes after moonrise (Fig. 6b). There were five split spawns observed for *A. palmata* (Table 1). These occurred in 1997, 2007, 2012, and at two locations in 2013 (Table 1).

Colpophyllia natans was observed spawning from August to November and with limited variance in spawning days and times (Fig. 7a, Table S1). August had the highest variability in spawning time, but the most data points (Figs. 7a, S3b). Spawning was observed from 38 to 170 minutes after sunset and 6 to 10 days after the full moon (Figs.

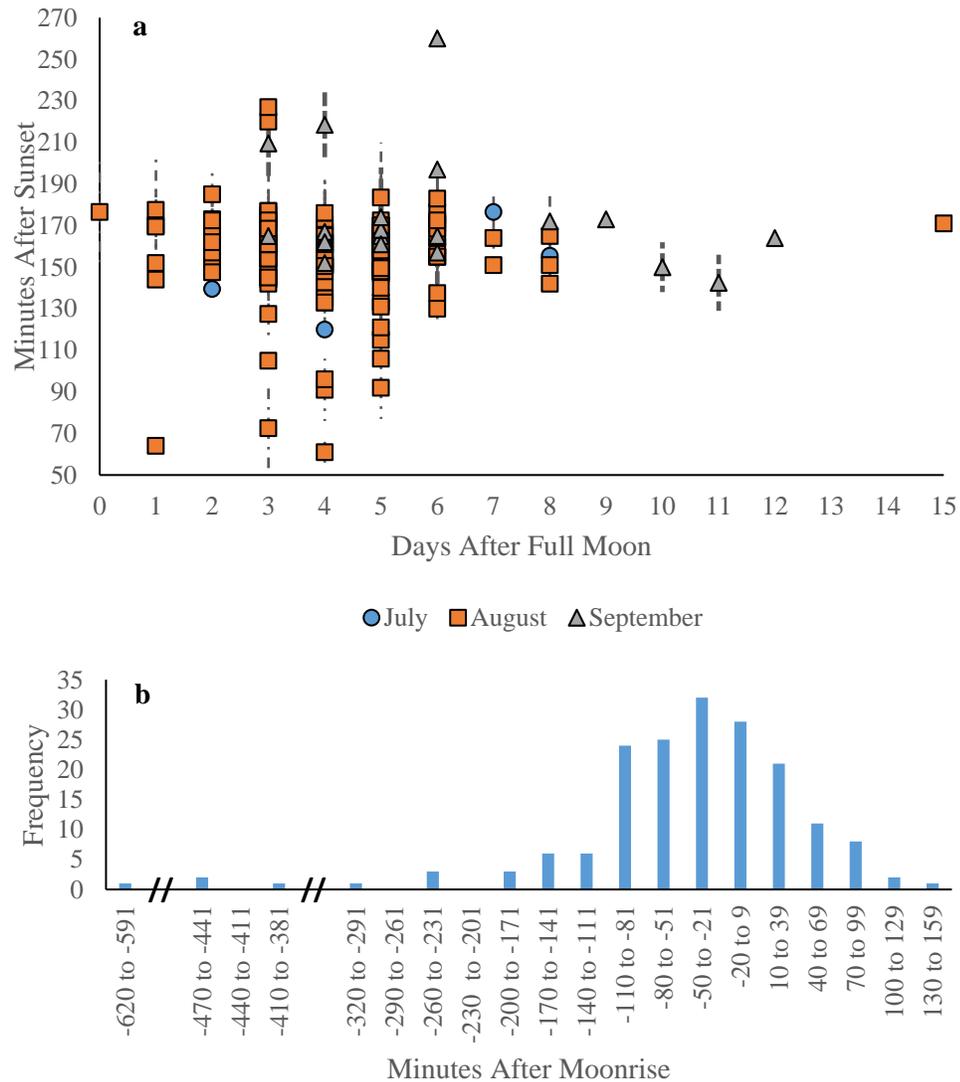


Figure 6. *Acropora palmata* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

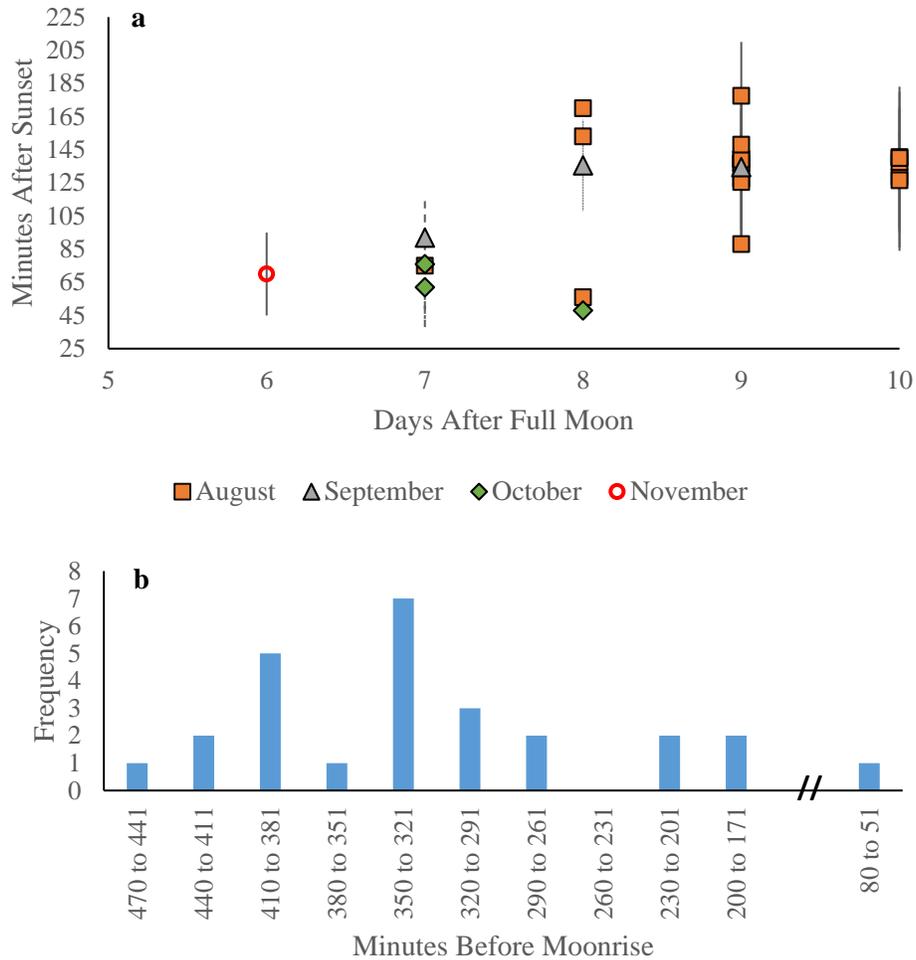


Figure 7. *Colpophyllia natans* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise.

7a, S3, Table S1). Peak spawning was on days 8 and 9 after the full moon from 83 to 123 minutes after sunset (Figs. 7a, Table S1). *Colpophyllia natans* was one of two species in this study to have all of their spawning observations occur before moonrise (Fig. 7b) and a majority (75%) of the observations occurred more than 287 minutes before moonrise (Fig. 7b). Split spawning was not recorded for *C. natans*.

Dendrogyra cylindrus is a gonochore and was observed spawning from August to October, with the majority of the observations in August and September (Fig. 8a, Table S1). The spawning days and times varied the least of the 11 species studied here (Fig. S4). Male *D. cylindrus* were observed spawning from 2 to 5 days after the full moon, and

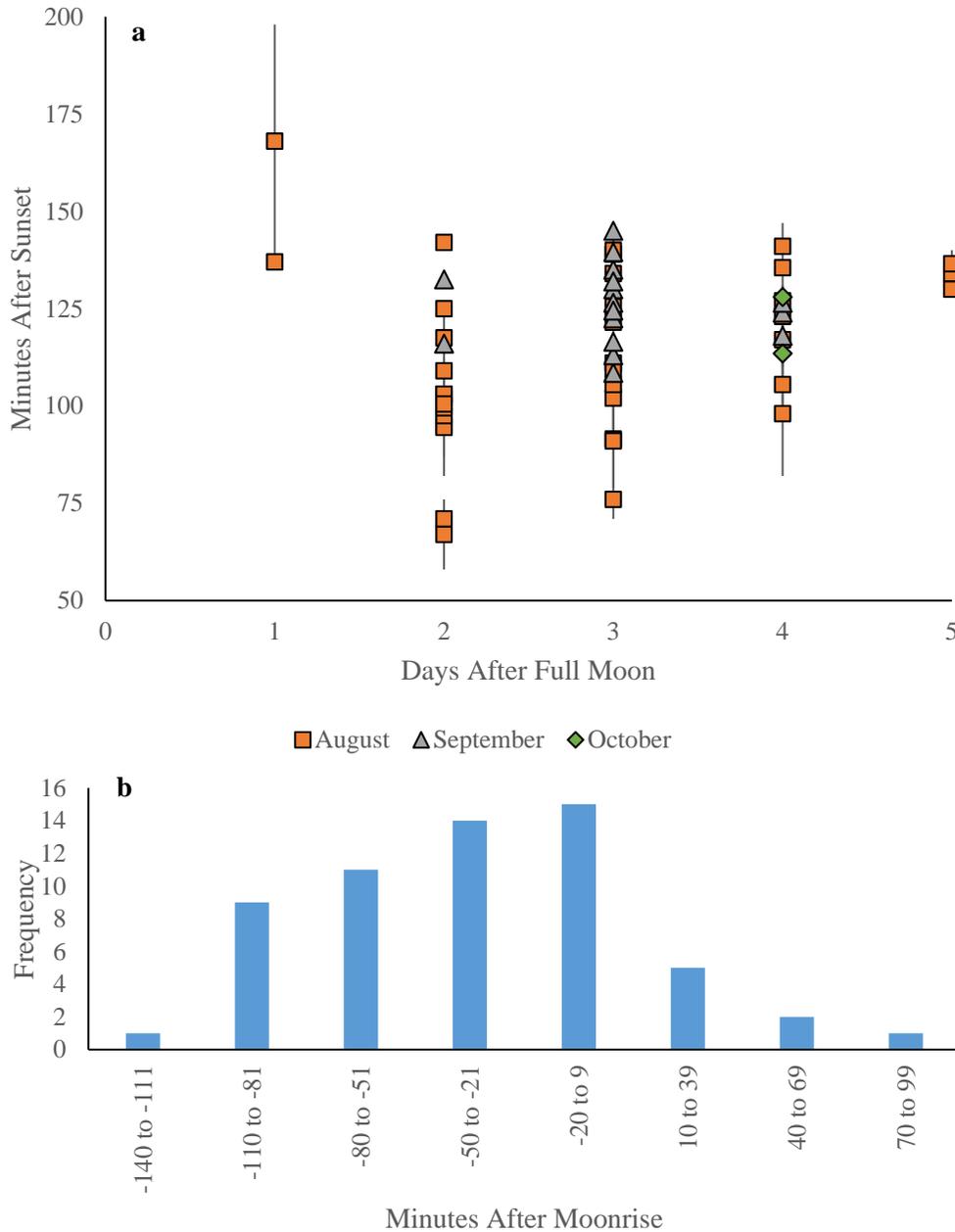


Figure 8. *Dendrogyra cylindrus* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. **b)** Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

females were observed spawning from 1 to 5 days after the full moon (Figs. 8a, S5a, Table S1). Peak spawning days occurred for males from 2 to 4 days after the full moon and females from 2 to 3 days after the full moon. Males spawned from 58 to 134 minutes after sunset while females spawned from 58 to 142 minutes after sunset (Fig. 8a, Table

S1). Peak spawning time for males was from 93 to 119 minutes after sunset and females from 102 to 134 minutes after sunset. *Dendrogyra cylindrus* was the only gonochore in this study with significantly different spawning times between males and females (Mantel-Haenszel test $p = 0.0451$; Fig. S5b). Spawning in relation to moonrise for *D. cylindrus* occurred from 132 minutes before moonrise to 73 minutes after moonrise (Fig. 8b). Three-quarters of spawning observations occurred prior to 5 minutes before moonrise (Fig. 8b). No split spawn was recorded for *D. cylindrus*.

Diploria labyrinthiformis had one of the smallest ranges of spawning times and days in this study, but the largest range of spawning months (Figs. 2, 9a, S6, Table S1). This was also the only species of scleractinian in this study to spawn exclusively before sunset. *Diploria labyrinthiformis* spawned from May to September, with peak spawning occurring in June and August (Fig. 2). All of the months seemed to have similar variability in spawning days and times (Figs. 9a, S6). Spawning occurred from 7 to 13 days after the full moon and 117 minutes before sunset until the time of sunset (Fig. 9a, Table S1). Day 13 after the full moon had the most variability for spawning time, while the other spawning days had consistent spawning times (Fig. 9a). Peak spawning for *D. labyrinthiformis* occurred on days 11 and 12 after the full moon from 52 to 40 minutes before sunset (Fig. 9a, Table S1). Due to the early spawning times, all colonies spawned before moonrise (Fig. 9b). Spawning was observed from 677 to 140 minutes before moonrise, with three-quarters of the observations occurring prior to 544 minutes before moonrise (Fig. 9b). No split spawning observations were recorded for *D. labyrinthiformis*.

Gonochore, *Montastraea cavernosa*, demonstrated high variance in spawning months, days, and times. Spawning was observed from June to November, with most of the observations occurring in August and September (Figs. 2, 10a, Table S1). All of the months of spawning had high variability in spawning times and days (Figs. 10a, S7, S8). There were observations from day 1 to 12 after the full moon for both males and females (Figs. 10a, S9a, Table S1). Days 4 and 9 after the full moon had less variability in spawning times than the other spawning days (Fig. 10a). Days 6 and 7 after the full moon were the peak spawning days for both males and females. This was the only species in

this study that had spawning times both before and after sunset. Males spawned from 19 minutes before sunset to 259 minutes after sunset, while females spawned from 9 minutes before sunset to 245 minutes after sunset (Fig. 10a, Table S1). Males had peak spawning from 62 to 154 minutes after sunset, while for females spawning peaked from 62 to 147 minutes after sunset (Fig. 10a, Table S1). Males and females did not have significantly different spawning times (Mantel-Haenszel test $p = 0.824$; Fig. S9b). There were spawning observations from 349 minutes before moonrise to 75 minutes after moonrise

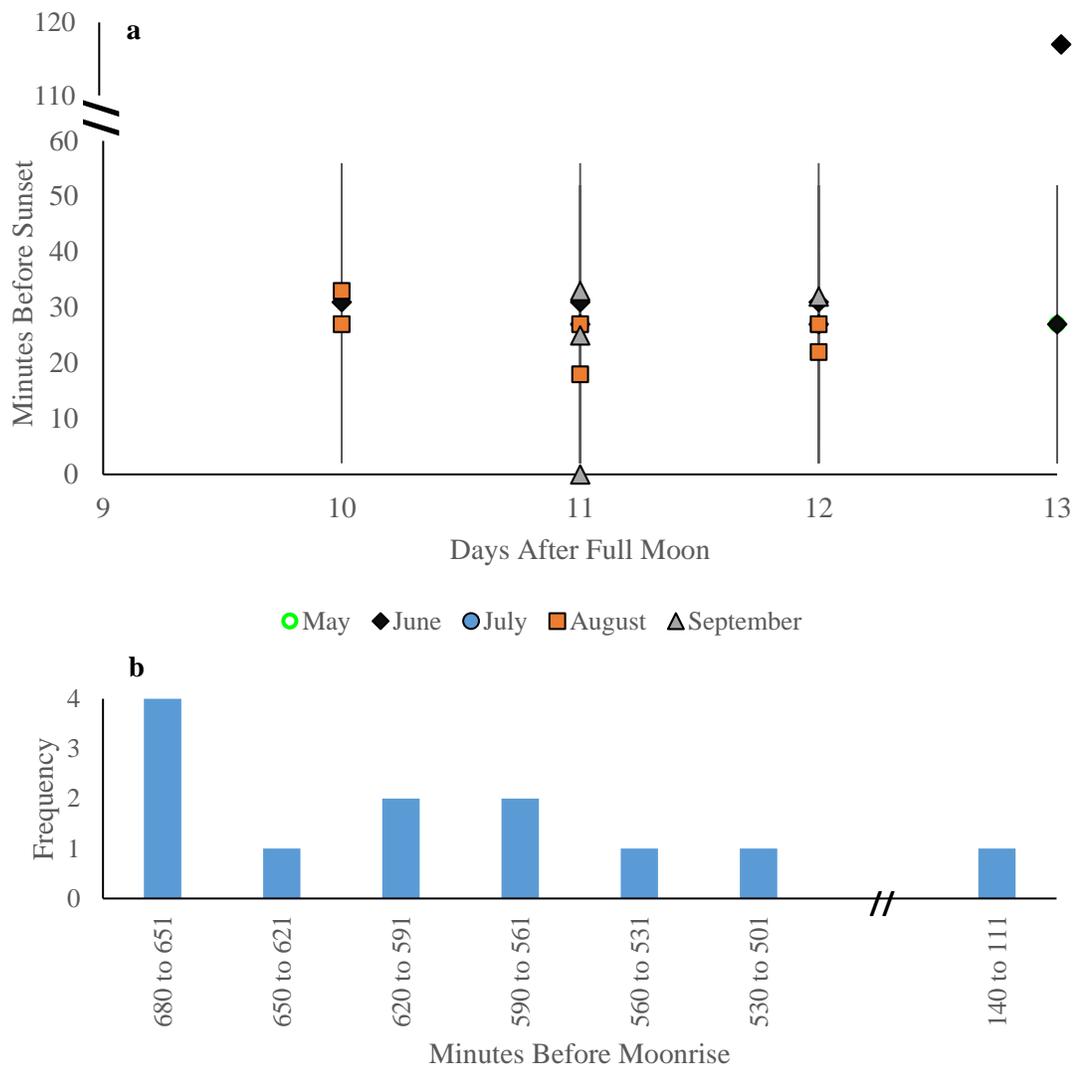


Figure 9. *Diploria labyrinthiformis* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise.

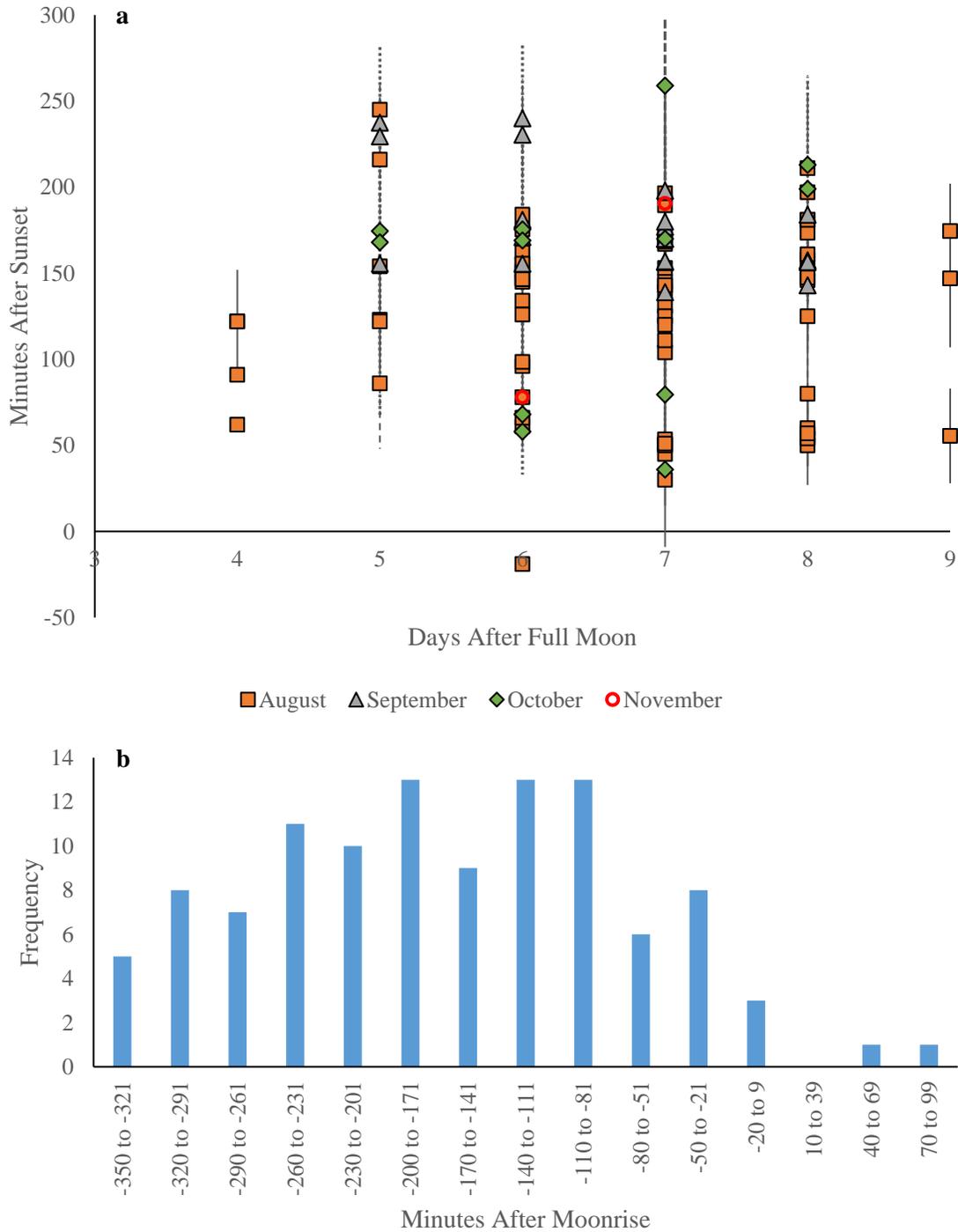


Figure 10. *Montastraea cavernosa* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

(Fig. 10b). A majority (75%) of the spawning observations occurred prior to 91 minutes before moonrise (Fig. 10b). There was one observation of split spawning for *M.*

cavernosa in the dataset, occurring in August and September of 1995 (Table 1).

The spawning months for *O. annularis* across the Caribbean were August to November (Fig. 11a, Table S1). Spawning peaked in September. November was the most consistent for spawning month out of all the months (Fig. 11a). October and November had more consistent spawning times than August or September (Figs. 11a, S10b).

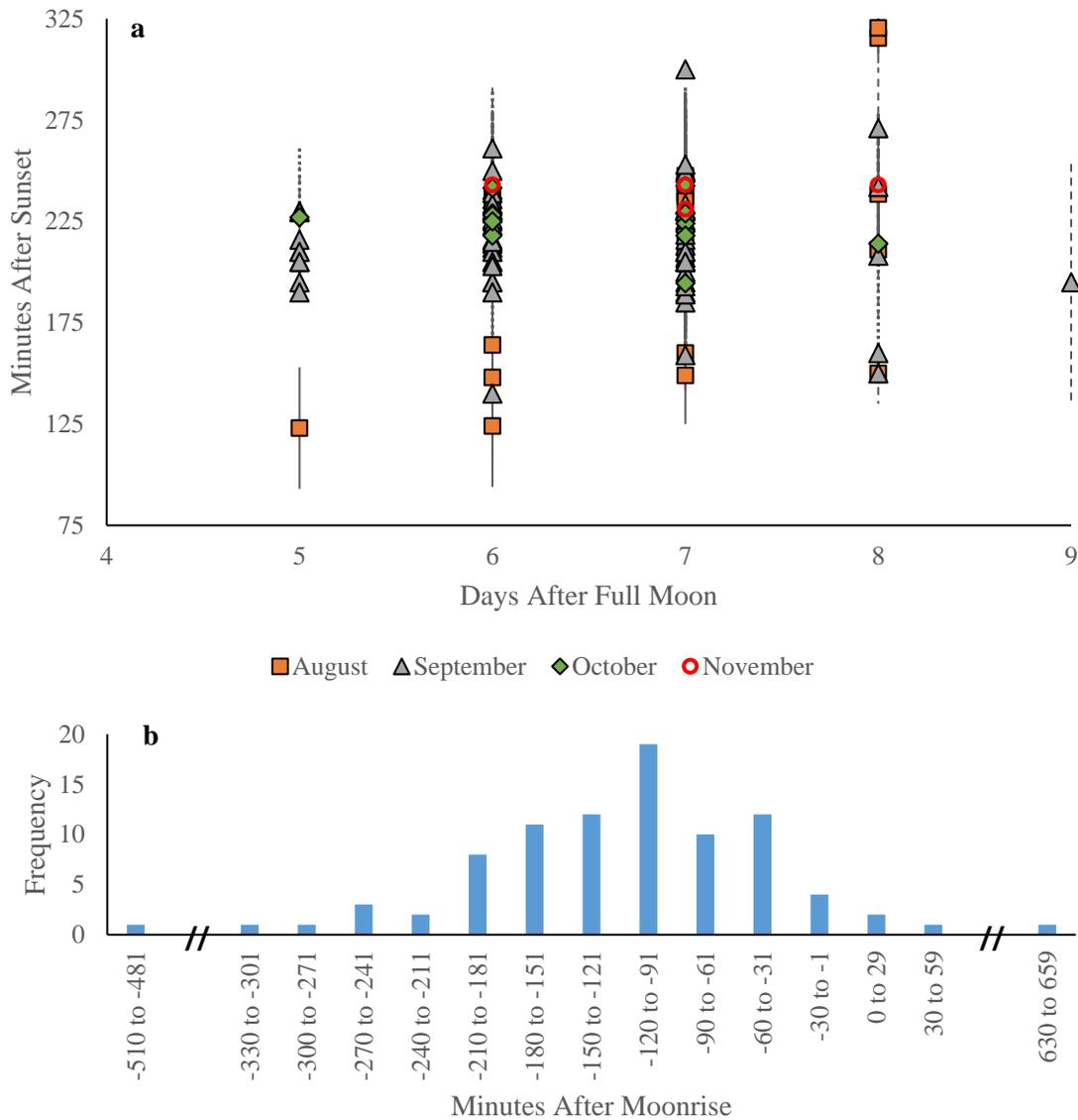


Figure 11. *Orbicella annularis* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

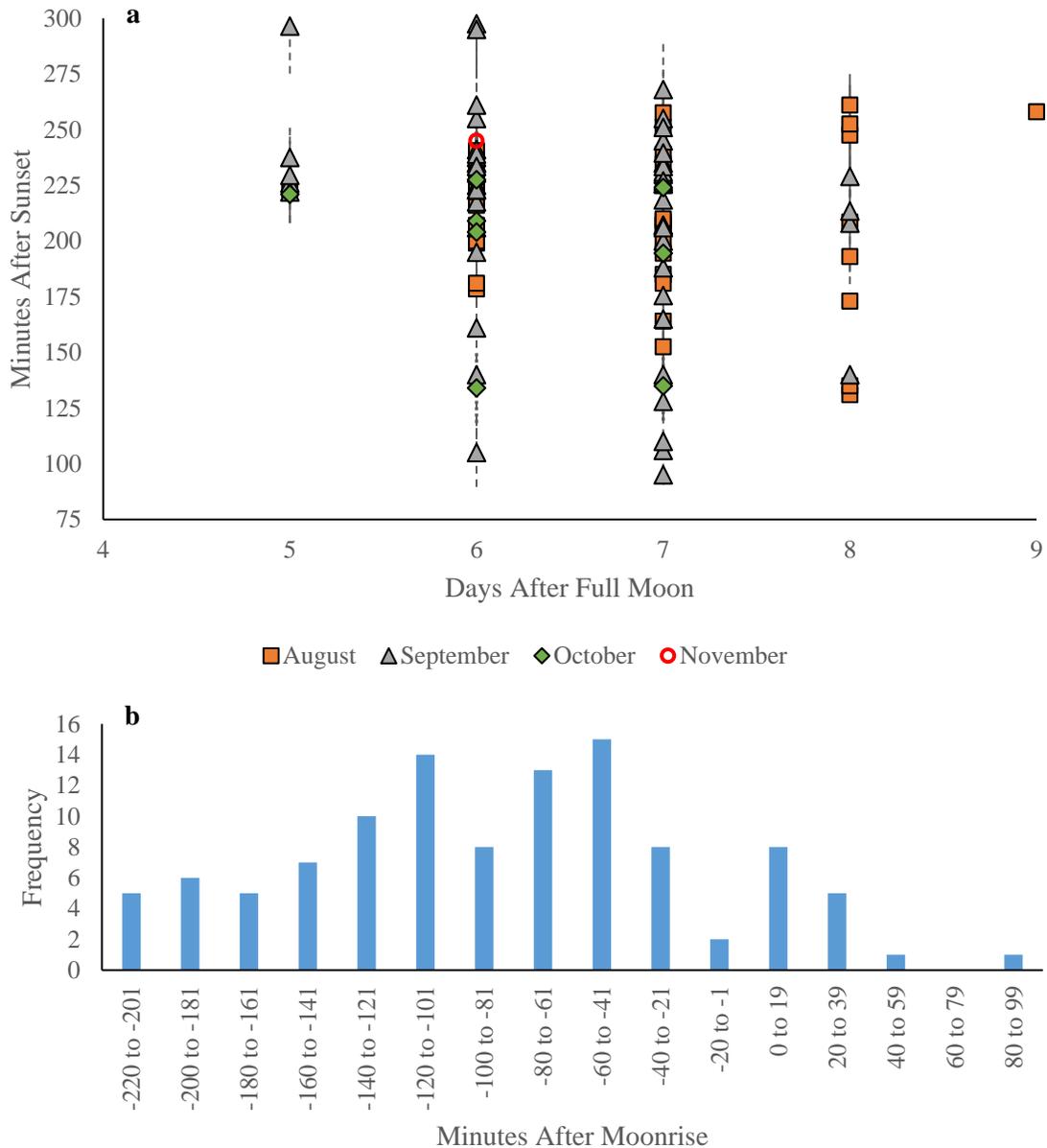


Figure 12. *Orbicella faveolata* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

Spawning was observed from 4 to 13 days after the full moon and 93 to 308 minutes after sunset (Figs. 11a, S10, Table S1). Peak spawning occurred on days 6 and 7 after the full moon from 180 to 220 minutes after sunset (Fig. 11a, Table S1). All of the days appeared to have similar variability in spawning times from the data used for this study (Fig. 11a). *Orbicella annularis* had a wide range of spawning times in relation to moonrise time,

with observations recorded from 508 minutes before moonrise until 639 minutes after moonrise (Fig. 11b). Three-quarters of the spawning observations occurred prior to 72 minutes before moonrise (Fig. 11b). Split spawning was recorded twice for *O. annularis* (Table 1). These occurred in August of 1997 and September and October of 2015.

Orbicella faveolata had similar spawning days, times, and months to its congener, *O. annularis*. August to November were the spawning months for *O. faveolata*, with spawning peaking in September (Fig. 12a, Table S1). All of the spawning months seemed to have variability in their spawning times and days, with September having the most variability in spawning times (Figs. 12a, S11). Spawning occurred from day 4 to 9 after the full moon from 88 to 275 minutes after sunset (Fig. 12a, Table S1). The days with the least variability in spawning time were days 5 and 9 after the full moon (Fig. 12a). The peak spawning time was observed from 181 to 223 minutes after sunset on days 6 and 7 after the full moon, similar to *O. annularis* (Fig. 12a, Table S1). *Orbicella faveolata* had a smaller range of spawning times in relation to moonrise than *O. annularis* (Fig. 12b). The spawning observations ranged from 220 minutes before moonrise to 81 minutes after moonrise (Fig. 12b). Three-quarters of the spawning observations happened prior to 44 minutes before moonrise (Fig. 12b). *Orbicella faveolata*, along with *A. palmata*, had the highest number of split spawns found in the dataset (Table 1). These occurred in August and September of 1995, at two locations in August and September of 2012, August and September of 2014, and September and October of 2015 (Table 1).

While *Orbicella franksi* had similar spawning days and months to its congeners, it had significantly earlier spawning times than the other congeners (Fig. 13a, Table S1). The observed spawning days were similar to *O. annularis*, occurring from day 4 to 13 after the full moon with the peak spawning days being 6 to 8 (Figs. 13a, S12a, Table S1). All of the spawning days had high variability for spawning time with day 7 having the most variability (Fig. 13a). *Orbicella franksi* was observed spawning from 44 to 265 minutes after sunset, slightly earlier than its congeners, with the peak occurring from 109 to 159 minutes after sunset (Figs. 13a, S12b, Table S1). Spawning in relation to moonrise occurred from 379 minutes before moonrise to 123 minutes after moonrise, with three-

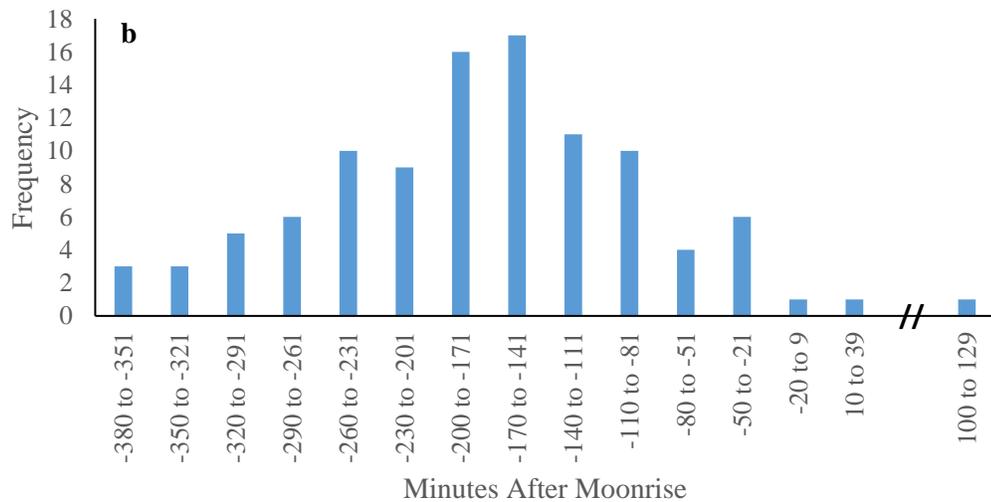
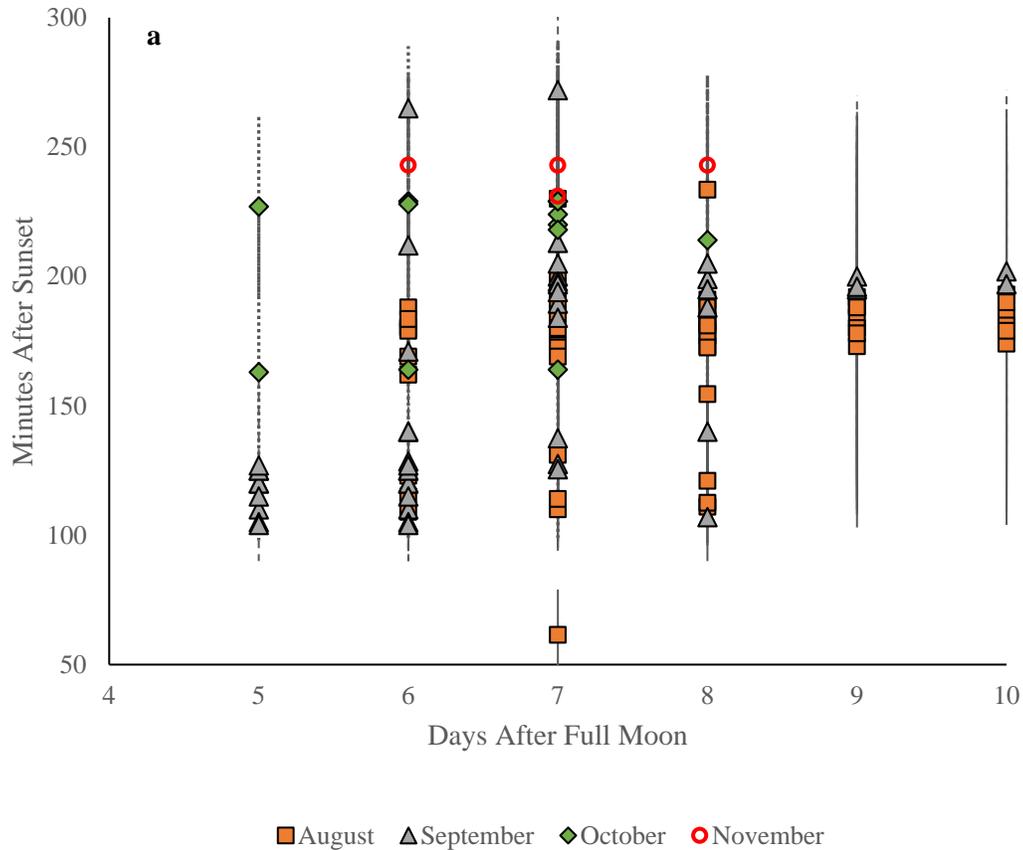


Figure 13. *Orbicella franksi* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

quarters of the observations occurring prior to 114 minutes before moonrise (Fig. 13b).

Orbicella franksi had two split spawning observations recorded in the dataset, one in August of 1997 and one in August and September of 2001 (Table 1).

Pseudodiploria strigosa is a hermaphroditic broadcast spawner and had a wide range of spawning times and days. Spawning was recorded from July to October (Fig. 14a, Table S1). Peak spawning occurred in August and September. Spawning observations were recorded for 5 to 14 days after the full moon from 37 to 313 minutes after sunset (Figs. 14a, S13, Table S1). Peak spawning occurred on days 6 through 8 after the full moon from 108 to 173 minutes after sunset (Fig. 14a, Table S1). Spawning occurred from 395 minutes before moonrise to 47 minutes after moonrise (Fig. 14b). A

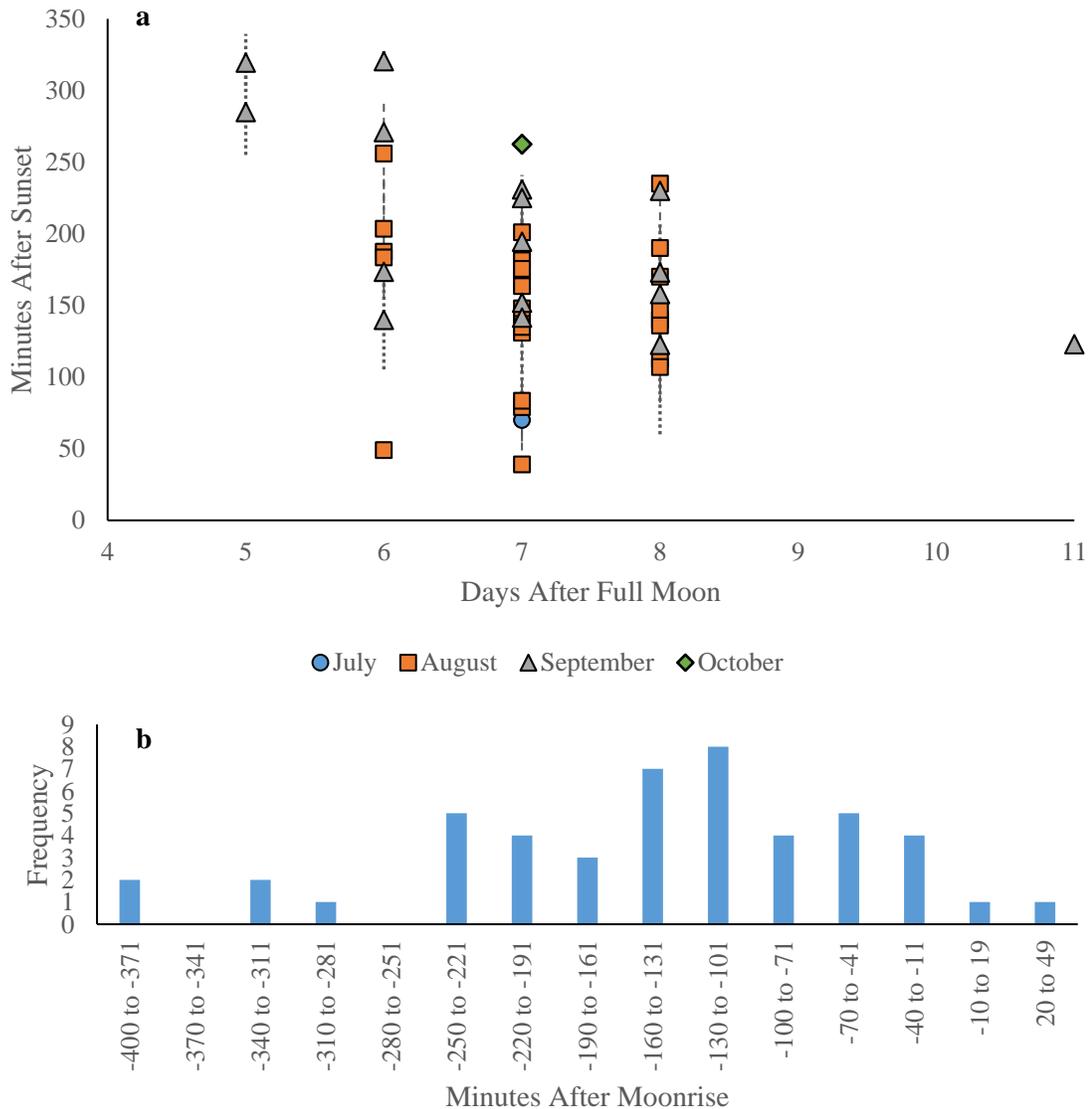


Figure 14. *Pseudodiploria strigosa* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

majority (75%) of the spawning observations occurred prior to 81 minutes before moonrise (Fig. 14b). There is one split spawning record for *P. strigosa* in August and September of 1995 (Table 1).

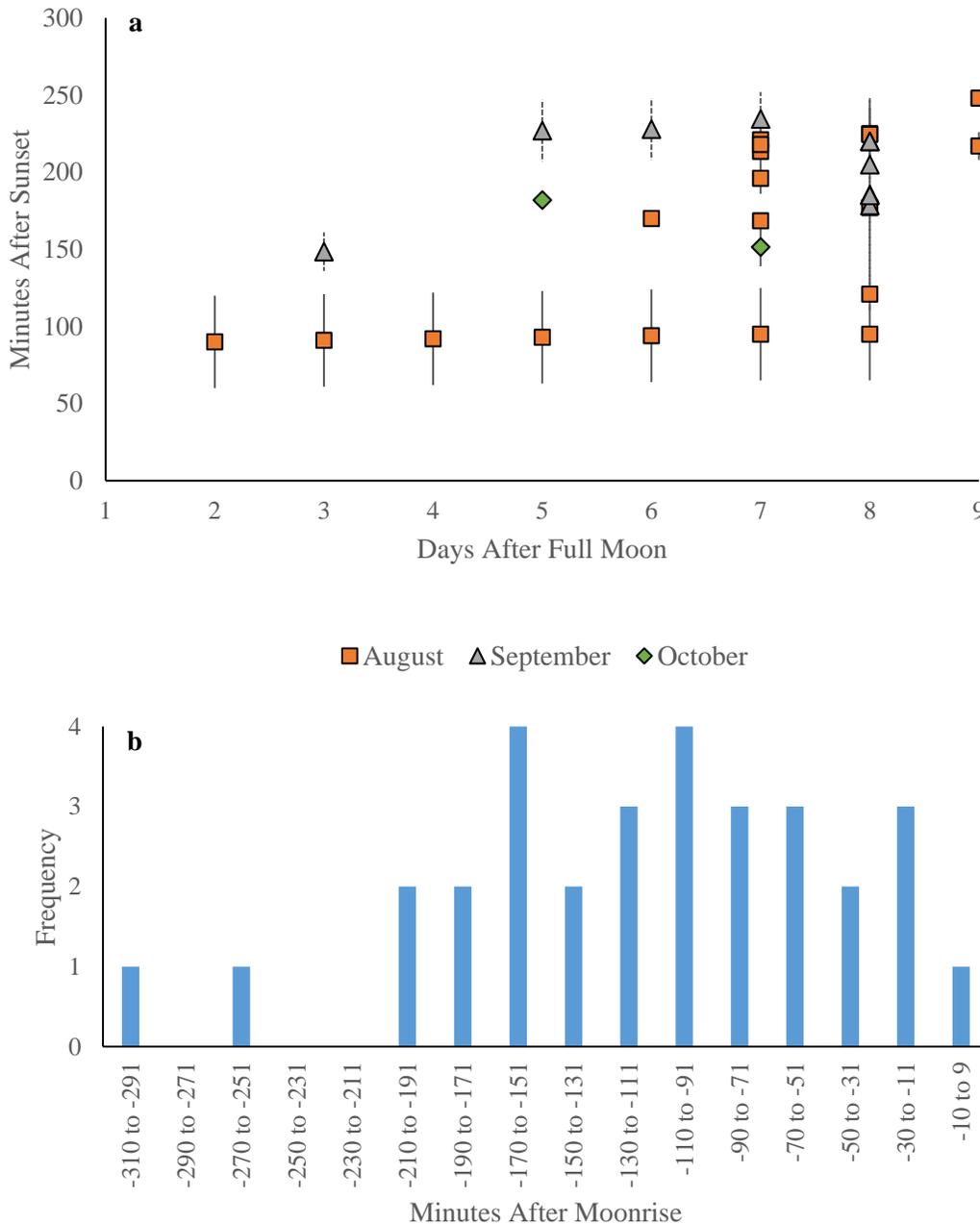


Figure 15. *Stephanocoenia intersepta* spawning in Western Atlantic. a) Average spawning times for a specific site, error bars denote range of spawning time for that evening. b) Number of spawning observations for 30 min time block after moonrise (negative values indicate spawning before moonrise).

Stephanocoenia intersepta is a gonochoric broadcast spawner in this study. Spawning observations occurred from August to October for *S. intersepta*, with the most observations recorded in August. Both August and September had high variability in spawning times and days (Figs. 15a, S14). Spawning occurred from 2 to 10 days after the full moon for both males and females (Figs. 15a, S15, Table S1). Males and females had slightly different spawning time ranges with males spawning from 60 to 225 minutes after sunset and females spawning from 60 to 248 minutes after sunset (Fig. 15a, Table S1). Spawning peaked on days 7 and 8 after the full moon for both males and females from 65 to 207 minutes after sunset (Fig. 15a, Table S1). Most of the spawning observations for *S. intersepta* occurred before moonrise, ranging from 305 minutes before moonrise to 1 minute after moonrise (Fig. 15b). Three-quarters of the spawning observations happened prior to 65 minutes before moonrise (Fig. 15b). There were no observations of split spawning recorded in the dataset for *S. intersepta*.

2.3.2 Temporal Trends

Many species had significant differences in their spawning times and days over years and months. For every species, significant differences were found between years and for both spawning minutes in relation to sunset and spawning days after the full moon (Mantel-Haenszel tests $p < 0.05$). *Stephanocoenia intersepta* did not have enough recorded spawning times to run an analysis, but there were enough recorded spawning days to analyze. Five species had significant differences between months for spawning minutes after sunset: *A. palmata*, *C. natans*, *O. franksi*, *P. strigosa*, and *M. cavernosa* (Mantel-Haenszel tests $p < 0.05$; Figs. S2a; S3a; S12a; S13a; S7). Four species had significant differences in spawning days after the full moon between months: *A. cervicornis*, *A. palmata*, *C. natans*, and *O. franksi* (Mantel-Haenszel tests $p < 0.05$; Figs. S1b-S3b; S12b). For the gonochoristic species tested, only *Dendrogyra cylindrus* had a significant difference between males and females for spawning minutes after sunset (Mantel-Haenszel test $p = 0.0451$; Fig. S5a).

The variability in spawning time and days was examined for each species as well. Most species had noticeable variation between years for both spawning time and days

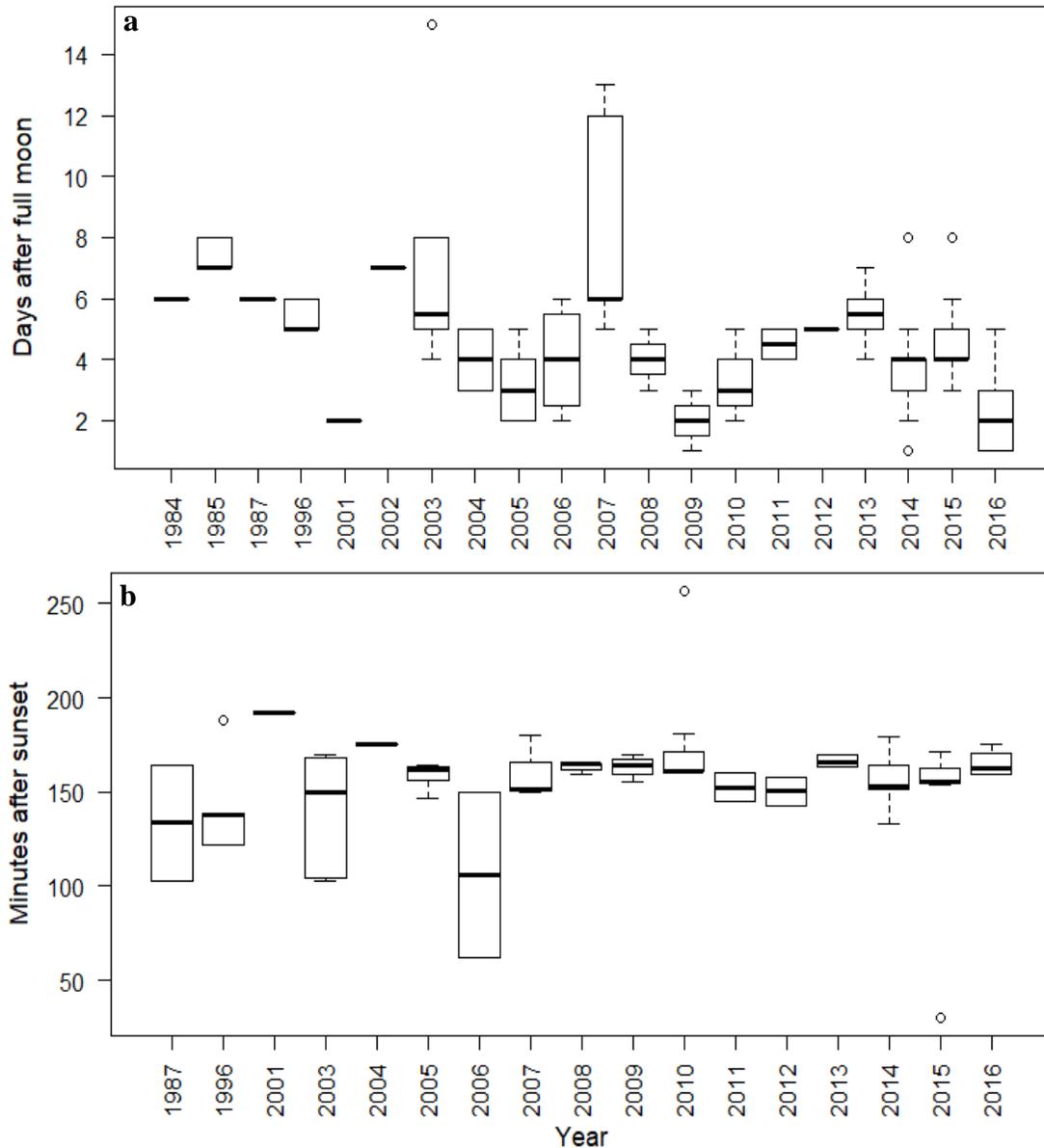


Figure 16. *Acropora cervicornis* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

(Figs. 16-26). *Acropora cervicornis* had high variability in spawning days over years (Fig. 16a). The spawning days seemed to vary from year to year, with no clear pattern. Some years had wider ranges of days within that year than others, such as 2003, 2006, and 2007 (Fig. 16a). The spawning time over years was more precise, with only a few years having higher variability in spawning time overall (Fig. 16b). The years 1987, 2003, and 2006 had the largest ranges of spawning times (Fig. 16b). Starting in 2007, the spawning times seemed to stabilize and spawning seemed to occur consistently at the

same time annually (Fig. 16b), but this could be due to a more robust dataset, meaning that there were more data points for more recent years. The years 2003 and 2006 had wide ranges for both spawning times and days.

Acropora palmata had similar results to *A. cervicornis*. The spawning days had high variability among years, though it seemed to stabilize starting in 2009 (Fig. 17a). Multiple years had large ranges of spawning days including 1998, 2007, 2008, and 2015 (Fig. 17a). The spawning time by year was fairly consistent annually (Fig. 17b). There

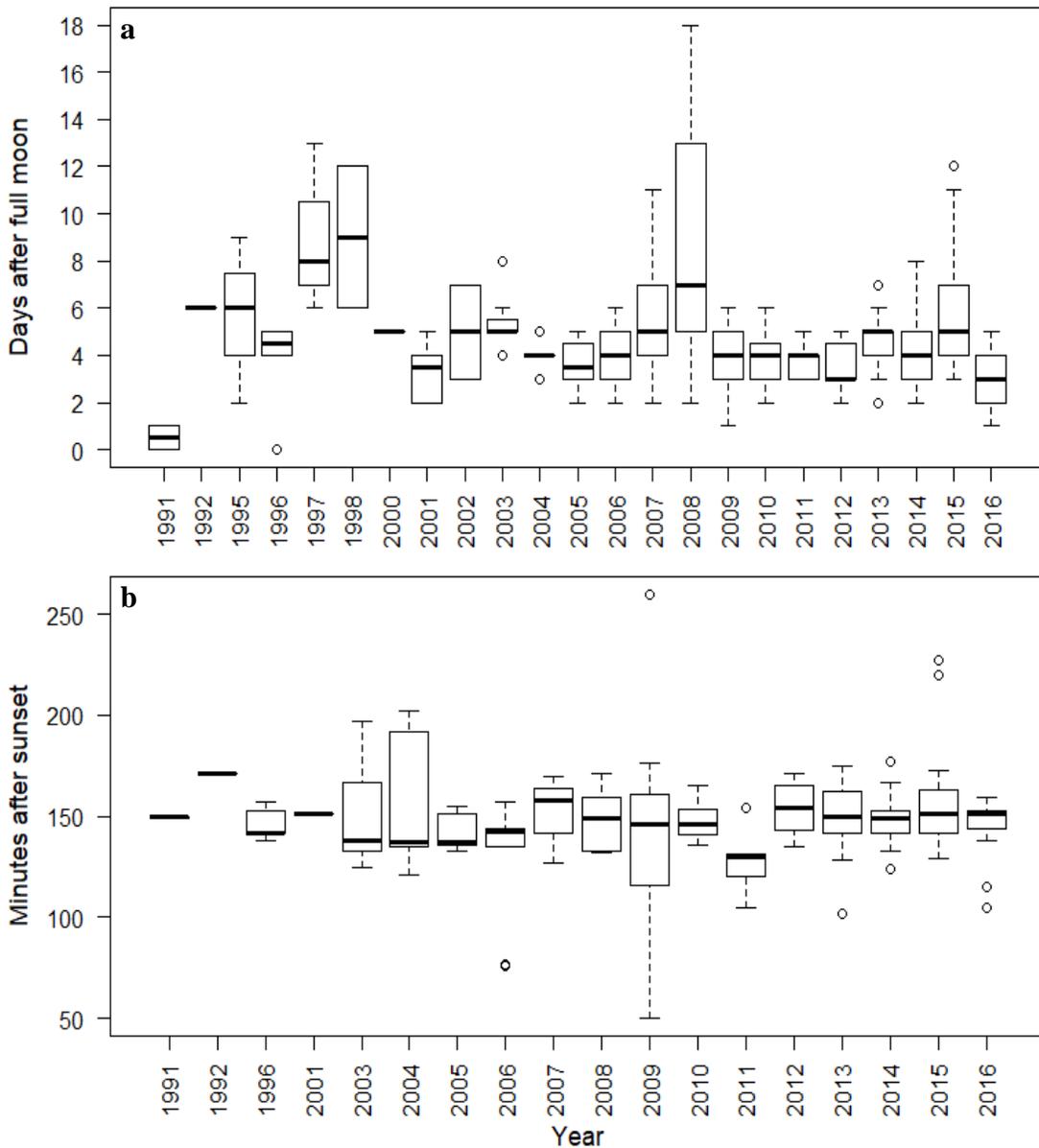


Figure 17. *Acropora palmata* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

were a few years with large ranges of spawning times, 2003, 2004, and 2009 (Fig. 17b). The years with wide ranges for either spawning time or day did not have a wide range for the other variable, unlike the data for *A. cervicornis*.

The spawning times for *C. natans* were consistent annually, but the spawning days had some variability. For spawning times, most years had about equal ranges, though 2010 had the largest range in spawning times (Fig. 18b). In 2015, spawning occurred earlier than it had in any other year spawning was recorded (Fig. 18b). From

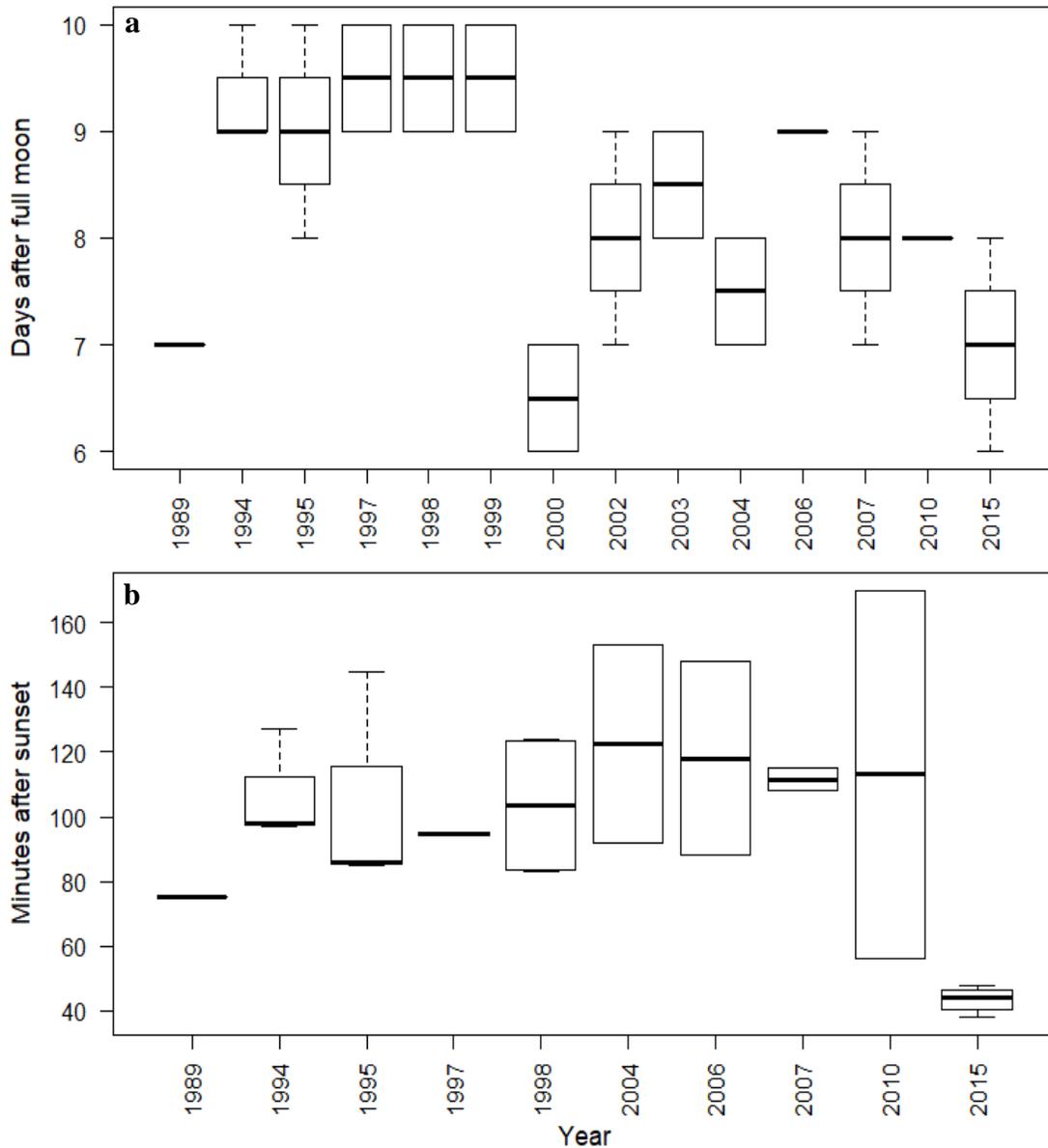


Figure 18. *Colpophyllia natans* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

1994 to 1999, spawning day was consistent (Fig. 18a). In 2000, spawning occurred 2 and 3 days earlier than it had been the past five years. After 2000, there was no consistent spawning days from year to year (Fig. 18a). Spawning occurred on earlier days than other years in 1989, 2000, and 2015. Spawning occurred on earlier days and at earlier times in 2015.

Dendrogyra cylindrus was consistent in annual spawning times, but had some variability in annual spawning days. The annual spawning times for *D. cylindrus* were

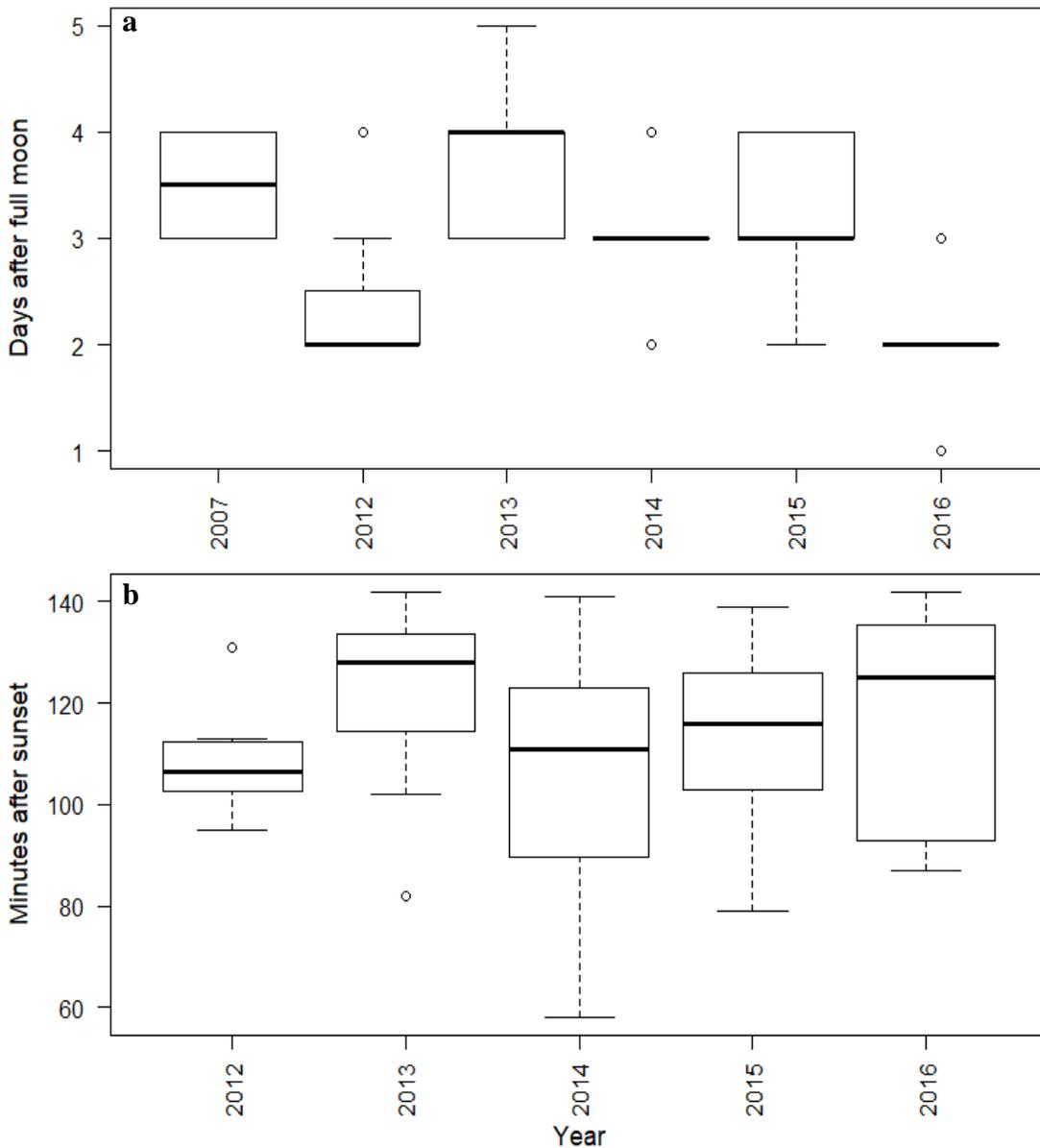


Figure 19. *Dendrogyra cylindrus* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

consistent, with 2014 having the largest range of spawning time (Fig. 19b). For spawning day, 2007, 2013, and 2015 had similar spawning days, while 2012, 2014, and 2016 had similar spawning days that were slightly earlier than the other years (Fig. 19a). While 2014 had a large range of spawning times, it had a small range of spawning days.

Diploria labyrinthiformis had variability for both spawning times and days by year. Spawning times started in 2010 with the earliest spawning times in the dataset (Fig. 20b). There was then a large shift of more than an hour in 2012 to later spawning times,

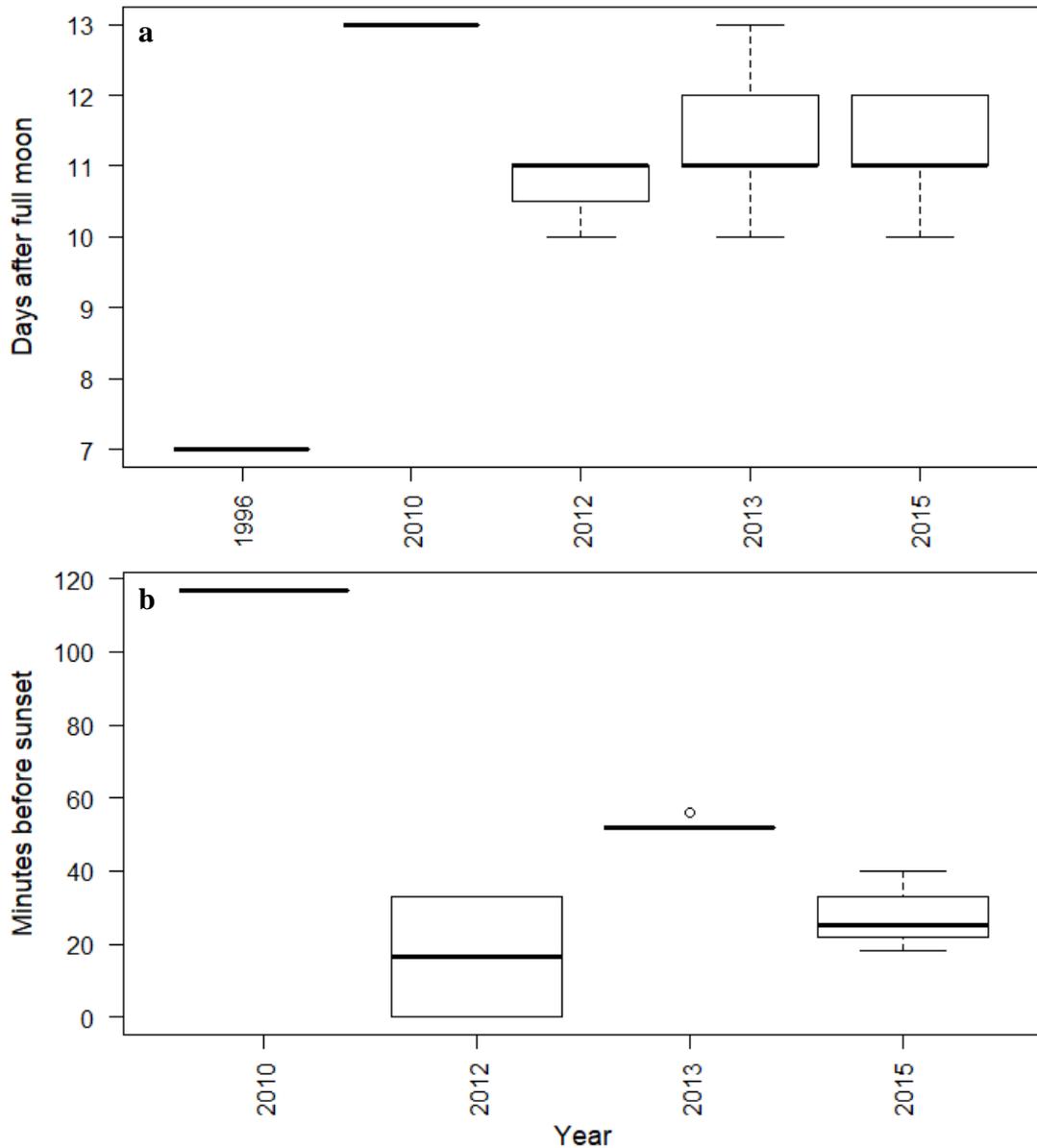


Figure 20. *Diploria labyrinthiformis* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes before sunset by year.

with these times occurring for 2013 and 2015 also (Fig. 20b). For spawning day, the data started in 1996 with the earliest spawning day of the dataset (Fig. 20a). Then in 2010, there was a large shift to spawning six days later. The next three years in the data set stabilized in between the earliest and latest date of spawning (Fig. 20a). In 2010, there was the earliest spawning time and the latest spawning day observed in the dataset.

Montastraea cavernosa had high variability in annual spawning times but more consistent annual spawning days. The spawning times seemed to shift each year with no visible pattern (Fig. 21b). There were multiple years with large ranges of spawning times including 2004, 2006, 2008, 2010, 2012, and 2013 (Fig. 21b). The spawning days were consistent from year to year with the most noticeable shifts to earlier spawning days in 2014 and 2016 (Fig. 21a). The year with the largest range in spawning days was 2007 but was not reflected in the spawning times (Fig. 21b).

Orbicella annularis, which is known for its precision, had some variability in spawning times by year and was fairly consistent for spawning day by year. At the start of the dataset, the spawning times were early (Fig. 22b). Each year after the first year, the spawning times shifted slightly later than the year before. This pattern continued until 1997. Starting in 2002, the spawning times were more consistent, though there were multiple years with large ranges in spawning times, including 2006 and 2013 (Fig. 22b). For the spawning days, there was consistency between years with only slight shifts seen (Fig. 22a). The most noticeable shift occurred in 1999 and 2000, where spawning was observed on earlier days than 1998 and 2001 (Fig. 22a). This shift may be caused by a bleaching event that occurred in 1998. A Mann-Whitney Wilcoxon test showed that the spawning day for bleaching years and two years after the bleaching year was significantly earlier than the spawning day in other years ($p = 1.825 \times 10^{-4}$). The largest range in spawning day occurred in 2004.

Orbicella faveolata had fairly consistent spawning times and days by year. The spawning times for years prior to 2004 were inconsistent (Fig. 23b). The year 1997 had much earlier spawning times than the year before or after (Fig. 23b). In 2004, the spawning times started to become more consistent, with a few years with large ranges of spawning times. The years with large ranges of spawning times were 2005, 2007, 2012,

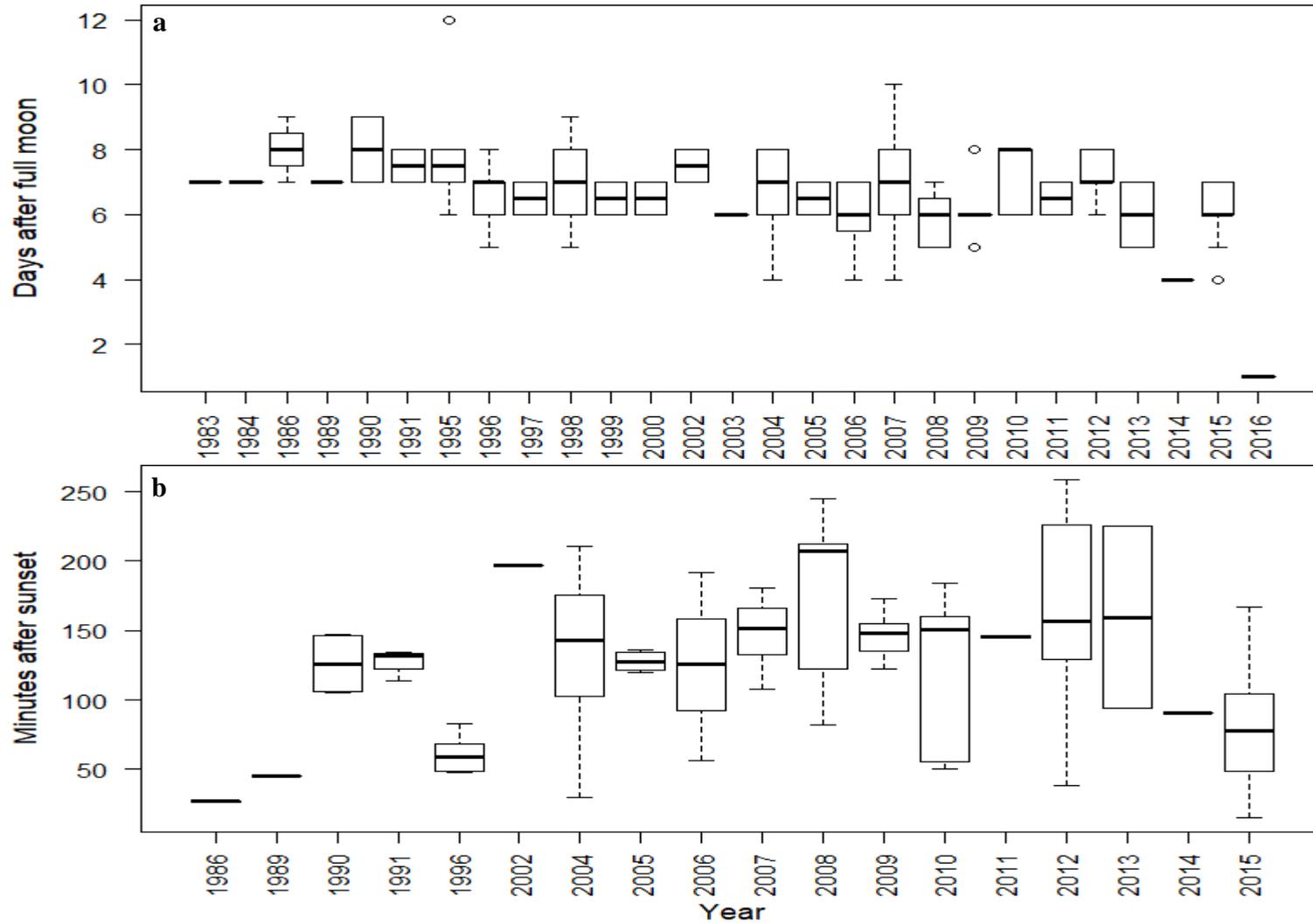


Figure 21. *Montastraea cavernosa* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

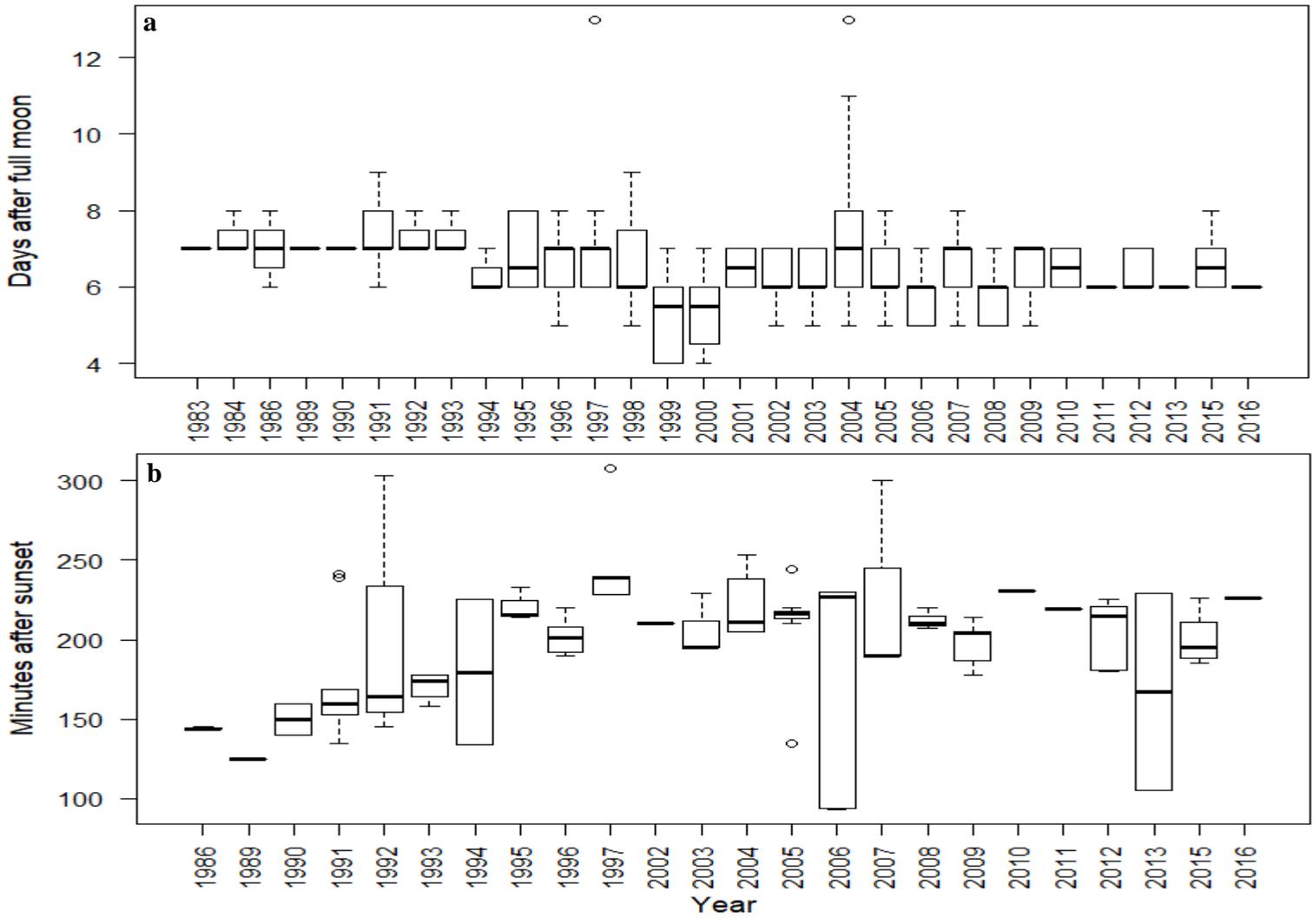


Figure 22. *Orbicella annularis* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

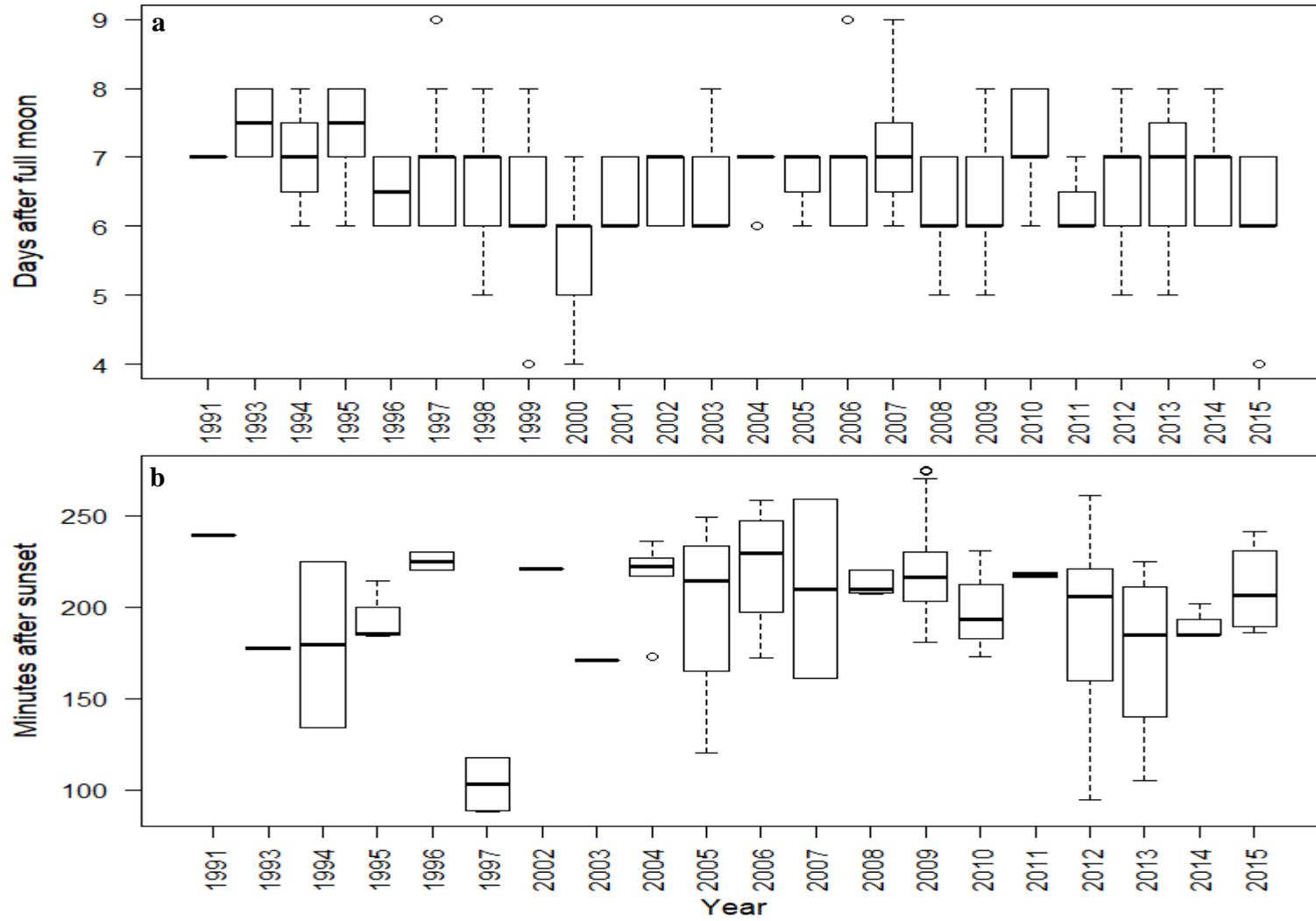


Figure 23. *Orbicella faveolata* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

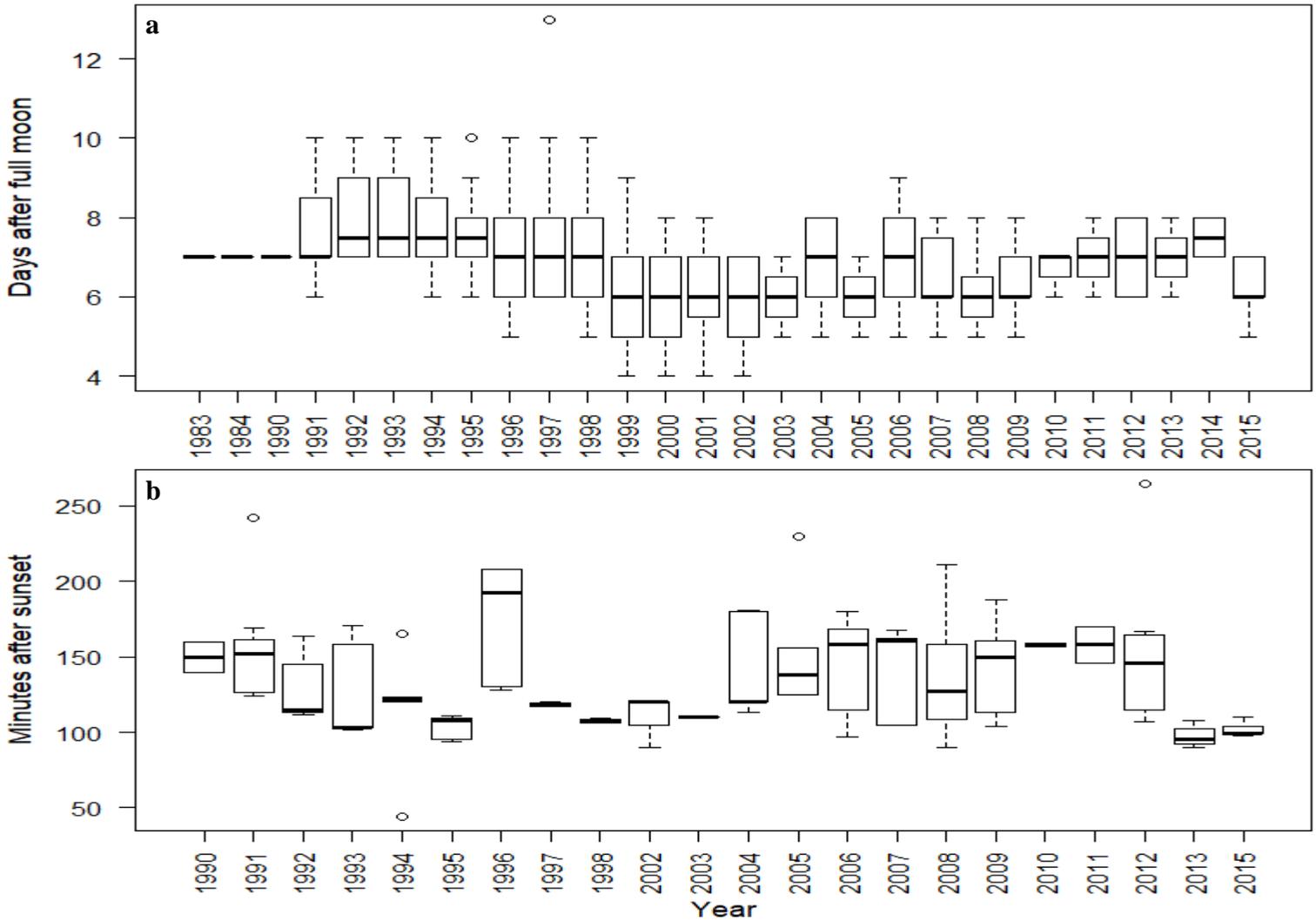


Figure 24. *Orbicella franksi* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

and 2013 (Fig. 23b). The spawning days were more consistent than the spawning times (Fig. 23a). The most noticeable shifts occurred in 2000 and 2010.

Orbicella franksi had the most consistent spawning times and days by year of the *Orbicella spp.* with only slight shifts between years. The spawning times were consistent from year to year with the largest ranges in time in 1993, 1996, and 2008 (Fig. 24b). The spawning days were also fairly consistent by year. Starting in 1996, the spawning day began to shift earlier each year reaching the earliest spawning days in 1999, 2000, 2001,

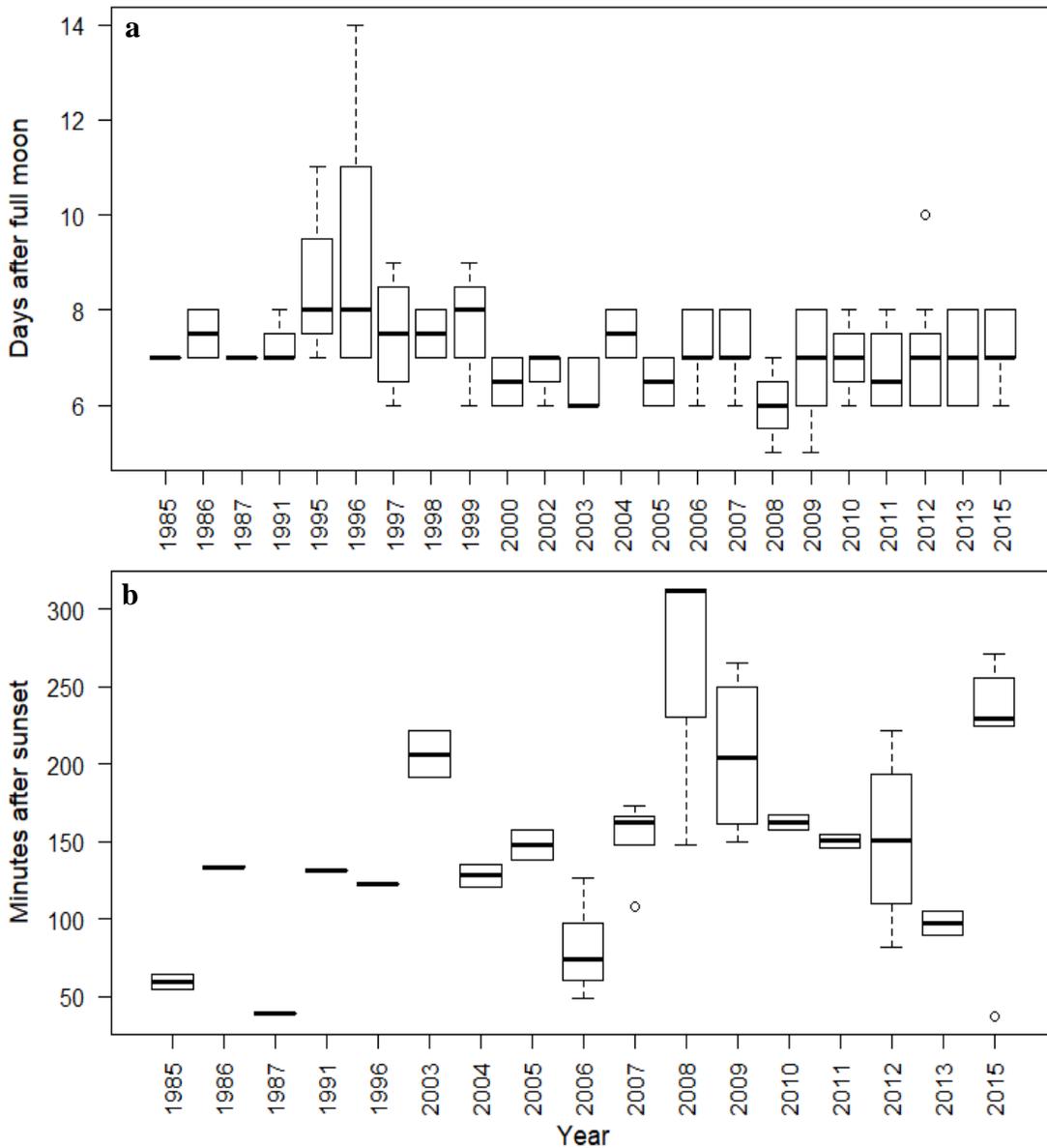


Figure 25. *Pseudodiploria strigosa* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

and 2002. The shift in spawning day may have been caused by a bleaching event that occurred in 1998. The spawning days during bleaching years and the two years after a bleaching year were significantly earlier than the spawning days in non-bleaching years (Mann-Whitney Wilcoxon, $p = 0.007134$).

Pseudodiploria strigosa had the most variability in spawning time by year of any species in this study. There were many large shifts, of more than an hour, in time from year to year (Fig. 25b). There was also high variability of spawning times within years.

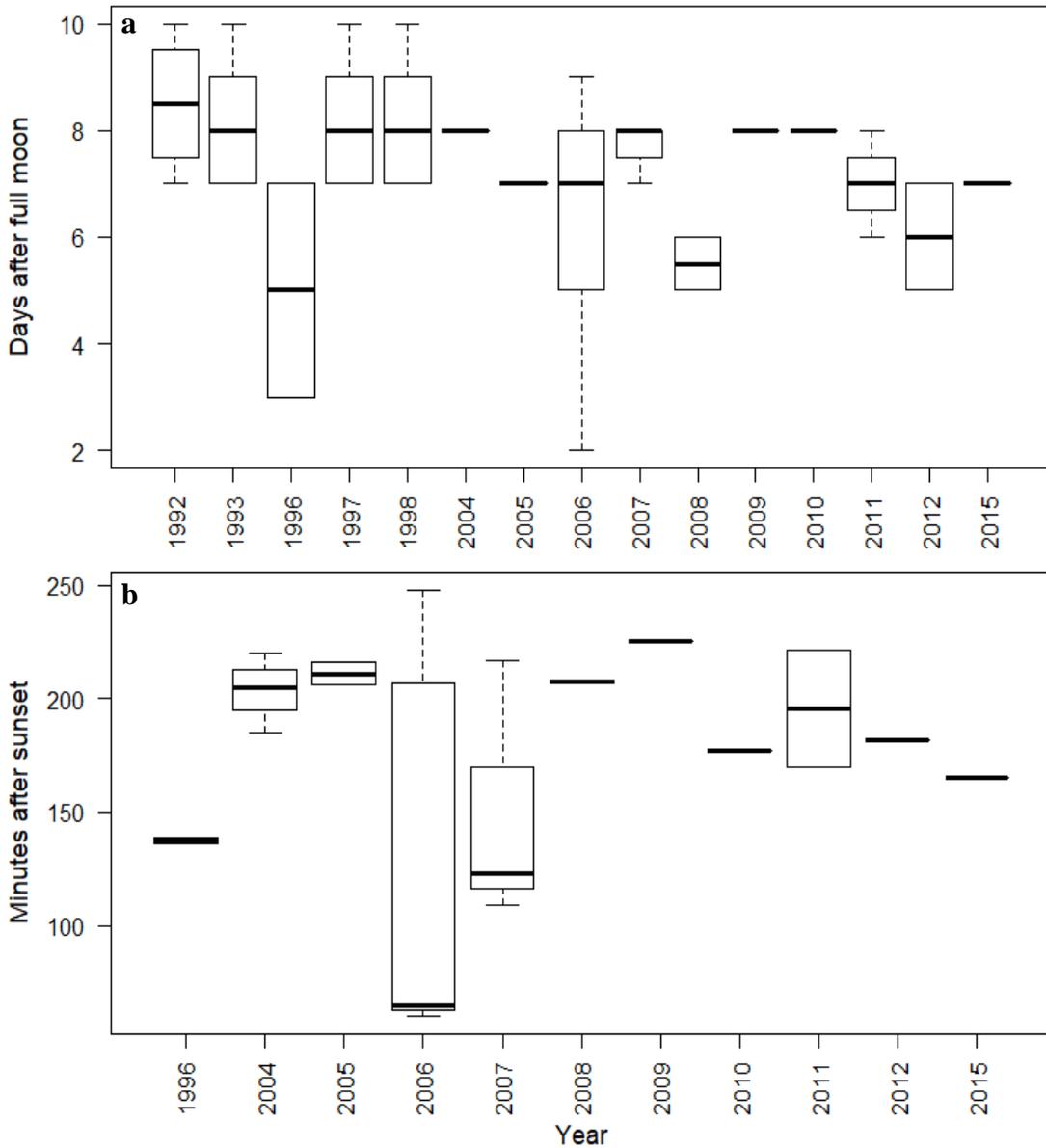


Figure 26. *Stephanocoenia intersepta* annual spawning data. a) Spawning days after the full moon by year. b) Spawning minutes after sunset by year.

The years with the largest ranges in time were 2006, 2008, 2009, and 2012 (Fig. 25b). The spawning days by year were more consistent (Fig. 25a). The most noticeable shifts occurred between 2004 and 2009, though these are shifts of only one day (Fig. 25a). The year with the largest range in spawning days was 1996, which was not reflected in the spawning times for that year.

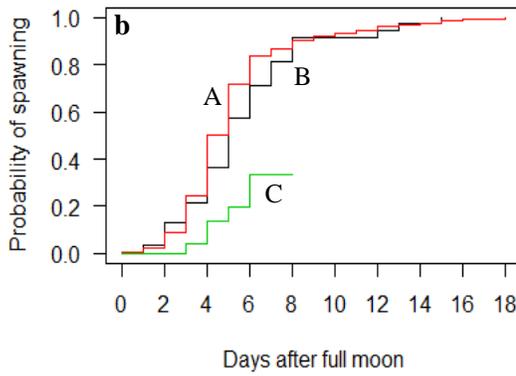
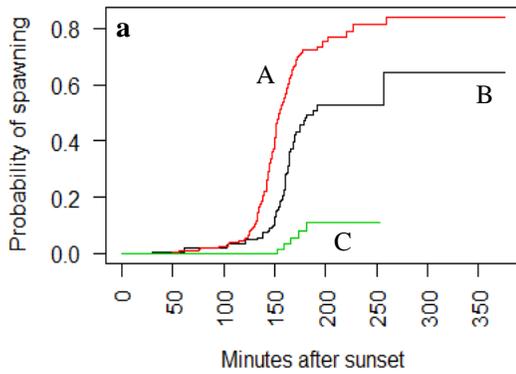
Stephanocoenia intersepta had some variability in both spawning times and days by year. There were a few shifts in spawning times by year, with the most noticeable shift occurring after 1996, when there was a shift to later spawning times (Fig. 26b). Most years did not have much variability in spawning time, but the year with the largest range in spawning times was 2006 (Fig. 26b). There were some changes seen in spawning day by year as well (Fig. 26a). In 1996, there were earlier spawning times and days observed. The years with the largest range of spawning days were 1996 and 2006 (Fig. 26a).

2.3.3 Congener Trends

There were two groups of congeners tested in this study, the acroporids and the *Orbicella spp.* For the acroporids, Mantel-Haenszel tests showed that each congener had a significantly different spawning time in minutes after sunset and days after the full moon from the other congeners (Mantel-Haenszel $p < 0.05$; Fig. 27). For the *Orbicella spp.*, Mantel-Haenszel tests showed that *O. annularis* and *O. faveolata* had significantly different spawning times in minutes after sunset and days after the full moon from *O. franksi* (Mantel-Haenszel $p < 0.05$; Fig. 28).

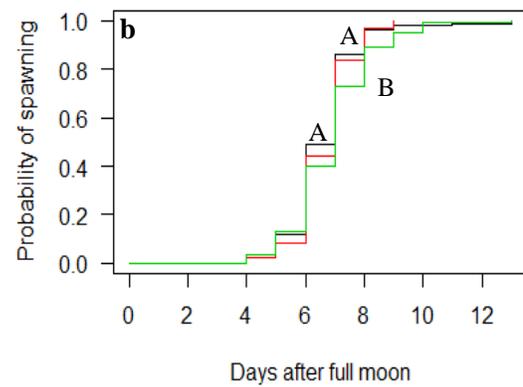
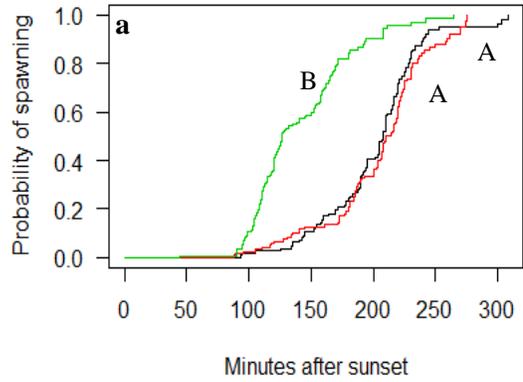
2.3.4 Environmental Effects

Water temperature did have a significant effect on the probability of spawning for *A. cervicornis* (GLM $p = 0.0121$). For every one degree Celsius increase in water temperature, the odds of spawning decreased by a factor of 0.2714295. *Acropora palmata*, *O. faveolata*, *O. franksi*, and *P. strigosa* spawning were not significantly affected by moonrise time, wind speed, or water temperature environmental variables (GLM $p > 0.05$).



— *Acropora palmata* A
— *Acropora cervicornis* B
— *Acropora prolifera* C

Figure 27. Survival analyses for acroporid spawning. a) Minutes after sunset (Mantel-Haenszel $p=0$). b) Days after full moon (Mantel-Haenszel $p=3.19 \times 10^{-5}$).



— *Orbicella faveolata* A
— *Orbicella annularis* A
— *Orbicella franksi* B

Figure 28. Survival analyses for *Orbicella* spp. a) Minutes after sunset (Mantel-Haenszel $p=0$). b) Days after full moon (Mantel-Haenszel $p=0.0109$).

2.4 Discussion

The patterns found for Caribbean scleractinian spawning times give some insight into how different factors affect coral spawning times. The corals in this study consistently spawned during the same season each year. Most species spawned after sunset and before moonrise or shortly thereafter. Wind was found to be a poor predictor of spawning, with spawning occurring regardless of the wind speed. There were statistical significances found for spawning times and days among years, with some species having more interannual variation than others. There were interesting patterns found in the two groups of congeners tested; the acroporids had significantly different spawning days and times, while *O. franksi* had significantly different spawning days and times than the other *Orbicella* species. Wind speed and time of moonrise did not affect whether spawning occurred, and water temperature only affected whether spawning occurred for *A. cervicornis*.

Data Limitations

While being the most complete compilation of spawning data for the Caribbean, there were still multiple limitations with this dataset. First, the limited data available for some broadcast spawners (*Acropora prolifera*, *Dichocoenia stokesi*, *Pseudodiploria clivosa*, and *Siderastrea siderea*) made some analyses impossible. Other species whose analyses could have benefited from more observations in order to draw additional conclusions were *Colpophyllia natans*, *Diploria labyrinthiformis*, and *Stephanocoenia intersepta*. Obtaining more spawning data on these species should be a priority for the research community.

There was also an uneven distribution of data for spawning months and years. Because most broadcast spawners only reproduce once or twice a year, if a species had observations from more than two months, the other months would have far fewer observations than the peak spawning months. For example, *A. cervicornis* spawned from July through September, with spawning peaking in August. Therefore, there are fewer observations in July and September and only corals at the lower latitudes in the Caribbean (*e.g.*, Curaçao) spawn in September. Spawning in July is unusual, though it does occur. This makes the distribution of observations over the months unequal. While a

survival analysis can compare unequal sample sizes, the analysis would be more robust if the sample sizes were more similar. An uneven distribution of annual data also occurs. Earlier years in the records, such as the 1980s and early 1990s, have minimal observations. While in more recent years, species like *A. palmata* will have over thirty spawning observations in a single year. Unequal data distribution for spawning days, months, and/or years could account for some of the variance seen in the results. For example, if a particular spawning day had more observations than the other days for that species that could result in a high variance. Attempting to test data with vastly unequal sample sizes could impede the ability to acquire accurate results.

There is also some bias present in the dataset from unequal distribution over spawning locations. Most species in the analyses have one location with observations that far exceed the number elsewhere. The uneven distribution of data across regions becomes problematic if an environmental stressor occurs at the location where most of the observations were recorded. If the region with the most spawning observations is prone to bleaching events, it could cause a shift in the spawning data. This shift could then be misinterpreted as a change in spawning across the entire Caribbean basin when that may not be accurate. For example, 75% of the spawning observations for *C. natans* came from Flower Garden Banks. Any catastrophic events or environmental stressors that affect this region could cause a change in the dataset since a majority of the observations originate from that location. Likewise, because the Flower Garden Banks is a unique, high-latitude reef, it may have different spawning times than locations in the Caribbean. Some of the variance for days, months, or years of spawning could have arose from the distribution of spawning locations also. For example, if the spawning observations for one day were recorded across many regions, it could have caused a larger variance for that particular day. As previously mentioned, for some species in this study, the spawning observations recorded after the peak spawning month all originate from lower latitude regions. Some of the spawning observations for *A. palmata* and *C. natans* after the peak spawning month of August come from higher latitudes, but for a majority of the species in this study, the observations recorded after the peak spawning months are from lower latitudes.

Stochastic Events

Stochastic factors that influence coral health, *i.e.*, coral bleaching, disease, and hurricanes, may also influence spawning synchrony. Multiple bleaching events occurred over the span of time of these records. Bleaching events can reduce coral spawning for up to two years after the event (Levitan *et al.* 2014). Specifically, a bleaching event may not alter the timing of spawning, only whether or not spawning occurs. For example, Levitan *et al.* (2014) observed *Orbicella spp.* spawning in Panama after bleaching events in 2005 and 2010 (Levitan *et al.* 2011). In this study, no anomalies in spawning times during bleaching years were found, yet *O. annularis* displayed a slight shift in spawning day the years after bleaching events. More observations of spawning were recorded on earlier days in 2006 and 2011 than in previous years, both one year after each of the bleaching events. This pattern continues with other sites of bleaching in the Caribbean. In 1998, there was a global bleaching event that likely also affected sites in the Caribbean (Goreau *et al.* 2000; Mumby 1999). In 1999 and 2000, *O. annularis* and *O. franksi* spawned on earlier days than in previous years. Both *O. annularis* and *O. franksi* had significantly earlier spawning days in bleaching years and the two years following bleaching years than in other years (Mann-Whitney Wilcoxon test $p < 0.05$). Bleaching events may not affect the timing of spawning after sunset for *O. annularis* and *O. franksi*, but it may affect the spawning day. Other species showed shifts in spawning days during or after bleaching events, but these were not found to be statistically significant (Mann-Whitney Wilcoxon test $p > 0.05$).

In 2005, after the Caribbean-wide bleaching event, the incidence of disease in *A. palmata* was found to increase significantly when water temperature increased (Muller *et al.* 2008). Coral diseases have been prevalent in the Caribbean and caused high rates of mortality and a decrease in genetic diversity for some species (Aronson and Precht 2001). There were no obvious trends found in the spawning data relating to coral disease outbreak, but the effects of the disease combined with the bleaching may affect coral reproduction.

Tropical storms and hurricanes could have prevented researchers from being able to observe coral spawning some months. Hurricane Mitch had severe effects on corals in

Belize in 1998 (Mumby 1999). Not only did it remove 90% of living *A. palmata* colonies at some sites, but 85% of large *O. annularis* colonies experienced partial mortality (Mumby 1999). In 2004 and 2005, the Caribbean was hit with multiple hurricanes (National Hurricane Center 2017). It is unclear why there are no spawning observations for some locations or nights because there is a lack of negative observations recorded, (*i.e.*, when researchers monitored the corals but no spawning was observed). If more negative observations were recorded for different species, the analysis could have been more complete.

Spawning synchrony is important for maximum fertilization success (Levitan *et al.* 2011). If the spawning is not synchronized, it could lead to gamete wastage. For gonochores, males typically spawn first across broadcast spawning organisms (Campbell 1974). In this study, two of the three gonochores spawned on the same days, the exception being *D. cylindrus*. The males for this species spawned from 2 to 5 days after the full moon while the females spawned from days 1 to 5. This means that there was gamete wastage on day 1 for this species. *Dendrogyra cylindrus* was also the only gonochore to have significantly different spawning times in minutes after sunset for males and females. Some scleractinians are known for their spawning precision, such as the *Orbicella* species, though it is known that the standard deviation of spawning time increases as you get farther from the cue, such as sunset or the full moon (Levitan *et al.* 2011). This could account for some of the variance in spawning days seen; spawning was occurring later, so it was less precise.

Split spawning occurred for multiple species of scleractinians in the Caribbean. This phenomenon is related to when an early full moon causes a split spawning between two or more months and was first noted on the Great Barrier Reef (Willis *et al.* 1985; Bastidas *et al.* 2005). This can occur on a population level, or even on the individual level, where half of an individual coral spawns one month and the other half spawns the next month (Willis *et al.* 1985; Bastidas *et al.* 2005). Spawning more than once per year could be an advantageous reproductive strategy. A single catastrophic event could significantly decrease the reproductive success at both a genotypic and population level (Richmond and Hunter 1990). Seven different species were observed split spawning in

the dataset. The split spawning observations in this study did not only associate with an early full moon, occurring in the first half of the month (Willis *et al.* 1985; Bastidas *et al.* 2005). However, they did seem to correlate with full moons in the very beginning or end of the month, but there were a few exceptions. For example, in 1997, the full moon fell on July 19th, and *A. palmata*, *O. annularis*, and *O. franksi* all split spawn in the month of August. At Flower Garden Banks in 1995, *M. cavernosa*, *O. faveolata*, and *P. strigosa* spawned in both August and September after an early full moon on August 10th. In 2015, *O. annularis* and *O. faveolata* split spawn in Curaçao in September and October after a late full moon on August 29th. Perhaps there are other factors causing split spawns to occur in the middle of the month, such as spawning synchrony cues disrupted by weather events. The frequency of split spawning did not seem to be affected by bleaching events, with only three of the seventeen observations occurring during a recorded bleaching year in the Caribbean. No other environmental factors seem to affect the timing of the split spawns found in the dataset.

Congener Trends

Different biological clock models can explain why spawning days are highly variable for acroporids, but consistent for *Orbicella* species. It has been suggested that Indo-Pacific acroporids follow an hourglass biological clock model (Lin and Nozawa 2017). This means that their reproductive rhythm is maintained due to the presence of fluctuations of environmental cues that trigger an event to occur, in this case spawning (Rensing *et al.* 2001; Lin *et al.* 2013). This causes the spawning days of acroporids to be more sensitive to changes in the environment (Lin *et al.* 2013; Lin and Nozawa 2017). The Caribbean acroporids were found to have large variance in spawning days, ranging from the day of the full moon to 18 days after the full moon. The *Orbicella spp.* follow an oscillation biological clock model, meaning the rhythm of the clock is endogenous, so no trigger is required (Lin *et al.* 2013; Lin and Nozawa 2017). Therefore, *Orbicella spp.* are less sensitive to changes in the environment than the acroporids (Lin and Nozawa 2017). The *Orbicella spp.* did not have as large of a variance for spawning days as the acroporids; they spawned between 4 and 13 days after the full moon. The significant difference found in the congener spawning times for the *Orbicella spp.* was expected. *O.*

franksi typically spawns earlier than *O. annularis* and *O. faveolata* (Levitan *et al.* 2004). The significant differences found for acroporids were unexpected because acroporids on a specific reef typically have overlapping spawning times (Fogarty, Vollmer, *et al.* 2012). This discrepancy could be explained by the large geographic range of spawning observations and/or the influence of localized environmental cues.

Environmental Effects

Of the five species which had more complete records, only *A. cervicornis* was found to have a significant relationship with an environmental factor. The chances of spawning decreased for *A. cervicornis* with an increase in temperature. It is unclear why this was the only species affected. It could be that the actual temperature does not affect spawning as much as the rate of increase of temperature, which has been found to be a good predictor of spawning times (Keith *et al.* 2016). Because the probability of spawning for most of the species tested seems unaffected by temperature, this could be a positive result with increasing sea surface temperatures due to climate change. Since none of the species' spawning probability was significantly affected by wind speed, it could be that wind speed the night of spawning does not affect the probability of spawning as much as calm periods in regional wind fields during months of spawning (van Woessik 2009). The time of moonrise may not have had a significant affect because there could have been other factors masking this cue such as bad weather or cloud cover. The time of moonrise does not necessarily inform how much light was present, which is known to be a cue for spawning. Other lunar cues that were not investigated in this study may be better predictors of spawning, such as the coincidence of the lunar third quarter and the movement of the moon over the equator (Wolstenholme *et al.* 2018). My findings may also been affected by the lack of negative observations.

Conclusions

This study highlights spawning patterns for major species of scleractinians in the Caribbean. Elevated temperatures that cause bleaching events may cause coral spawning to occur on earlier days than in previous years. This effect can occur the year of a bleaching event and up to two years after the event. Temperature was found to significantly affect whether spawning occurred in only one species in the Caribbean, *A.*

cervicornis. This data for environmental influences on coral spawning could benefit coral managers and scientists by informing them how temperature affects coral spawning. A better understanding of how temperature could shift coral spawning could allow for scientists to be able to predict when coral spawning will occur more accurately, and therefore lead to more research. Coral managers could employ better protection strategies for corals around the time of spawning or to try to combat rising sea surface temperatures.

Future directions

There is still much we do not know about spawning behavior of Caribbean corals. Additional data on the proportion of colonies that spawned, records of negative spawning observations, and data on *A. prolifera*, *D. stokesi*, *P. clivosa*, and *S. siderea* would help address existing research gaps. Additional information on how bleaching and disease influence if and when corals spawn is also needed.

Chapter 3

The goal of this project was to collate Caribbean scleractinian spawning observations to identify trends in spawning times within a species, among congeners, and across environmental factors. I gathered enough data to statistically analyze eleven scleractinian species at locations across the Caribbean, Gulf of Mexico, and Western Atlantic. The patterns found give some insight into how different factors affect coral spawning times. The corals in this study consistently spawned during the same season each year. Most species spawned after sunset and before moonrise or shortly thereafter. Spawning occurred regardless of wind conditions. There were statistical significances found for spawning times and days among years, with some species having more interannual variability than others. There were patterns found in the two groups of congeners tested; the acroporids all had significantly different spawning days and times, while *O. franksi* had significantly different spawning days and times than the other *Orbicella* species. The GLMs showed that wind speed and time of moonrise did not affect whether spawning occurred, and water temperature only affected whether spawning occurred for one of the species tested. There were some challenges with the dataset that made it difficult to run some analyses and to ascertain the reason behind some of the trends observed. The species with the most robust datasets were *Acropora palmata*, *Orbicella annularis*, *O. faveolata*, and *O. franksi*. Even though these species had many recorded spawning observations, there were still parts of the dataset that were not ideal for statistical analysis. This could explain some of the results obtained from the analyses and increased variation. Some of the variation seen in the data could be a result of limitations with the dataset, but some could be explained by different biological clock models.

Data Limitations

There were major limitations with this dataset. First, the limited data available for some broadcast spawners (*Acropora prolifera*, *Dichocoenia stokesi*, *Pseudodiploria clivosa*, and *Siderastrea siderea*) made certain analyses impossible. Other species whose analyses could have benefited from more observations to draw additional conclusions were *Colpophyllia natans*, *Diploria labyrinthiformis*, and *Stephanocoenia intersepta*.

Obtaining more spawning data on these species should be a priority for the coral spawning research community. The survival analysis test can misinterpret a dataset with insufficient data points by producing a curve that appears to be significantly different, but the test then gives a result of no significance. If there were a larger, more robust dataset that produced a similar curve, the test may produce a result of significance. The more observations there are, the better that dataset will reflect the actual events. Limited data also affected the acroporid congener survival analyses. *Acropora palmata* had the most data with approximately 280 observations, *A. cervicornis* had the second most with approximately 100 observations, and *A. prolifera* had the least with only 5 observations. Since there was only a small amount of data available for *A. prolifera*, it suggests that few people have monitored this taxon or that it rarely or unreliably spawns.

Another factor that affected the dataset was the limited monthly and/or yearly data within certain species. If the dataset included more than two months (*i.e.*, split spawns or geography variation in spawning months), there was not an even distribution of observations over all months. This affected both *A. cervicornis* and *A. palmata* which have peak spawning in August. There were recorded observations from July and September for both species, but the number of observations for these two months combined were less than the number of observations from August. It should be noted that *A. cervicornis* has only been observed spawning in September at lower latitudes in the Caribbean. For *Orbicella spp.*, peak spawning occurs in August and September, but there were also some observations from October and November. The number of observations for October and November combined were less than one month's observations for either August or September. An uneven distribution also occurs for annual data, where some years have few observations. This includes data from the 1980s and early 1990s, when there were less recorded observations of coral spawning. The number of total spawning observations, both positive and negative, started to grow in 1995, peaking in recent years. Unequal distribution of data could have affected the variance in spawning days, month, or years; for example, if there were more observations on one spawning day than the other spawning days, it could cause that day to have higher variance in spawning time. For *D. labyrinthiformis*, there is a shift in spawning days from 1996 to 2010. This is most likely due to the limited number of observations for these years, as each year only had

one observation. If there were more observations, the variance could increase for either year, which could decrease or eliminate the difference between the years. Attempting to test data with vastly unequal sample sizes would impede the ability to acquire accurate results from an analysis.

There is additionally some bias present in the dataset from unequal distribution over spawning locations. Most species in the analyses have one location with observations that far exceed the number at other locations. *Acropora cervicornis* and *O. annularis* have observations that are evenly dispersed across all of the sites of spawning. An uneven distribution of data across regions becomes problematic if an environmental stressor, such as bleaching, occurs at the location where most of the observations were recorded which could cause a shift in the spawning data. For example, 75% of the observations for *C. natans* come from Flower Garden Banks. Any catastrophic events or environmental stressors that affect this region could cause a noticeable change in the dataset since a majority of the observations come from that location. That change may not be an accurate representation of spawning for that species across the entire Caribbean. This location bias could also cause some of the variation in the spawning days, months, or years. The variance could have been affected by the number of regions with recorded spawning observations for that time period. For example, if one day had observations across more regions than other days, it could cause greater variance in spawning times for that day. As previously mentioned, for some species in this study, the spawning observations recorded after the peak spawning month are all from lower latitude regions. Some of the spawning observations for *A. palmata* and *C. natans* after the peak spawning month of August came from higher latitudes, but for a majority of the species in this study, the observations recorded after the peak spawning months are from lower latitudes.

Some of the increased variability in spawning days may be due to the numbering of the spawning day. There is some discussion for numbering the days after the full moon in accordance to what time the full moon occurs. Some parties believe that if the full moon occurs before a certain time in the morning, typically 4:00 am, this means that the day of the full moon should be counted as day 1. For this study, I counted all of the days

of the full moon as day 0 regardless of the time of the full moon. This may have led to increased variability in spawning days seen.

Stochastic Events

Stochastic factors that influence coral health, *i.e.*, coral bleaching, disease, and hurricanes, may also influence spawning synchrony. Bleaching has been proven to prevent corals from spawning the year a bleaching event occurs and may limit spawning up to two years after the event (Levitan *et al.* 2014). Levitan *et al.* (2014) found that bleaching did not affect the timing in minutes after sunset of spawning for *Orbicella spp.* in Panama, only whether spawning occurred. In this study, I found a shift in spawning days after the full moon following the bleaching event in 2005 and 2010 for *O. annularis*. A majority of observations for *O. annularis* were from Panama. In 2006 and 2011, spawning days after the full moon for *O. annularis* were slightly earlier than in previous years, though there were few spawning observations in 2011. This probably did not cause the high variation in spawning times in 2006 since Levitan *et al.* (2014) found that bleaching events did not affect the timing of spawning. It is unknown if bleaching events could affect the timing of other species of corals in the Caribbean. Due to the location bias present in the dataset, a severe bleaching event could significantly affect any of the species.

There were many other bleaching events in the Caribbean during the span of the dataset including mass bleaching events in the Caribbean in 1983 and 1987 (Glynn 1993). Unfortunately there are not many published spawning observations from this time, so it is difficult to determine whether or not these bleaching events affected spawning. There is also a lack of published observations of negative spawning, when observers went into the field in the hopes of observing spawning and did not see spawning occur during their observation window. Documented negative observations help us to understand why there are no published spawning observations for some years. Without the knowledge of negative observations, it is impossible to tell if researchers went into the field and did not witness spawning or if no one attempted to observe spawning. With more negative observations, more GLMs could have been run in this study.

A global bleaching event occurred in 1998 which caused severe bleaching in Belize and the southern Caribbean (Mumby 1999; Goreau *et al.* 2000). This could have affected the spawning data for *O. annularis* which has most of its observations from Panama and *A. cervicornis* which has Belize as one of the two top locations for its observations. *Orbicella faveolata* and *O. franksi* also have many observations published from Panama. It can be seen that there is a shift in spawning days after the full moon starting in 1999 or 2000 for all three species of *Orbicella*. Although Levitan *et al.* (2014) found that the timing of spawning was not affected in Panama for *Orbicella spp.* after the bleaching events in 2005 and 2010, the severity of the bleaching event in 1998 potentially caused a shift in the spawning day. *Orbicella annularis* and *O. franksi* had significantly different spawning days during bleaching years and the two years following bleaching years than in non-bleaching years (Mann-Whitney Wilcoxon test $p < 0.05$). There are no observations for *A. cervicornis* in 1998, 1999, or 2000 in this study, so it is impossible to say whether this bleaching event affected the spawning day for this species. While other species experienced some shift in spawning days around bleaching events, these shifts were not found to be significant (Mann-Whitney Wilcoxon test $p > 0.05$). Other factors could have also contributed to this shift, including mortality from Hurricane Mitch (Mumby 1999).

The Florida Keys also endured a significant bleaching event from high temperatures in 2005 (Ritchie 2006). In 2005, after the Caribbean-wide bleaching event, the incidence of disease in *A. palmata* was found to increase significantly when water temperature increased (Muller *et al.* 2008). Coral diseases have been prevalent in the Caribbean and caused high rates of mortality and a decrease in genetic diversity for some species (Aronson and Precht 2001). This shows that bleaching events could have a more significant effect on coral spawning because bleaching could also cause disease outbreaks that further hinder the coral's ability to reproduce.

Coral disease outbreaks could have also affected the dataset due to reduced fertility of corals and potential mass mortality. *Acropora palmata* colonies were affected by white pox in the Florida Keys in 1998 (Patterson *et al.* 2002). There are no spawning observations for *A. palmata* from 1999 included in the dataset so it is impossible to say

whether or not this disease outbreak affected spawning. The absence of spawning observations that year may not be explained by the disease outbreak, since there is also a lack of negative observations. If the disease only affected part of the coral colony, the unaffected part of the colony may have spawned. In the dataset, not many observers recorded what proportion spawned, for either individual colonies or the population. If this data had been recorded, more analyses could have been run, and it may have been easier to determine what outside stressors affected spawning. This is a factor I was hoping to gather more data for, but it does not seem to be recorded frequently.

It has been suggested that *A. cervicornis* mortality at Carrie Bow Cay, Belize has been caused primarily by white-band disease, not hurricanes, from the 1980s to 2001 (Aronson and Precht 2001). Since Belize is one of the top two sites for *A. cervicornis* spawning observations, this could have had an effect on its data. *Acropora cervicornis* does not have many spawning observations before 2001, so it is difficult to say whether or not this affected the data. Following the mass bleaching across the Caribbean basin in 2005, there were multiple disease outbreaks in 2006 (Cróquer and Weil 2009). Cróquer and Weil (2009) monitored coral disease outbreaks at six different locations with two sites each across the Caribbean following the 2005 bleaching events and found that there was significantly more white plague disease following the bleaching event in Curaçao, Panama, and Puerto Rico. Perhaps the increase in disease could have contributed to the shift in spawning days for *O. annularis* in 2006 due to limited spawning observations.

As previously stated, another environmental factor that could have affected the dataset is tropical storms and hurricanes. If a significant weather event occurred during spawning season it could have prevented researchers from obtaining spawning observations during that time. In the Caribbean, spawning season does coincide with hurricane season. Hurricane Mitch caused destruction to corals in Belize in October of 1998 removing as much as 90% of living *A. palmata* at some locations (Mumby 1999). The storm also caused severe damage to *O. annularis* colonies with 85% of large colonies showing partial mortality after the hurricane (Mumby 1999). Hurricane Mitch occurred the same year as a severe bleaching event in the area (Mumby 1999); the high coral mortality in the area due to both events could have had an effect on the dataset. The

Caribbean had a high number of hurricanes compared to previous years during spawning season in both 2004 and 2005 that could have affected spawning observations from sites crucial to the dataset including the Florida Keys, Curaçao, and Flower Garden Banks (National Hurricane Center 2017). Not only could these storms have reduced the number of spawning observations gathered during the time of the storm, they could have caused high mortality rates that affected observations at the affected sites for years. The affects could include limited total observations from the sites or reduced numbers of genotypes spawning at the sites, both of which could affect the spawning times observed.

Split spawning occurs for multiple species of scleractinians in the Caribbean. The term split spawning refers to spawning in consecutive moon cycles and has been found to be related to when the full moon occurs during the month of spawning, with an early full moon occurring during the first half of the month causing split spawning on the Great Barrier Reef (Willis *et al.* 1985; Bastidas *et al.* 2005). This can occur on a population level, or even on the individual level, where half of an individual coral spawns one month and the other half spawns the next month (Willis *et al.* 1985; Bastidas *et al.* 2005). Spawning more than once per year could be an advantageous reproductive strategy; if spawning only occurs once per year, a single catastrophic event could significantly decrease reproductive success at both an individual and population level (Richmond and Hunter 1990). Baird *et al.* (2009) suggested that the occurrence of split spawning depends on the number of lunar months in successive years and therefore, split spawning helps to maintain a consistent spawning season for scleractinians on the Great Barrier Reef. Seven different species were observed split spawning in the dataset. The split spawning observations in this study seem to occur when there is an early full moon or a late full moon, with a few exceptions. For example, in La Parguera, Puerto Rico in 1985, *A. cervicornis* spawned in both July and August after an early full moon on July 2nd. At Seaquarium Reef in Curaçao in 2015, *O. annularis* and *O. faveolata* split spawned in September and October after a late full moon on August 29th. In 1997, the full moon fell on July 19th, and *A. palmata*, *O. annularis*, and *O. franksi* all split spawn in the month of August. Since the split spawning observations for the Caribbean do not seem as strongly associated with the timing of the full moon as those in the Pacific, potentially there are other factors causing split spawns to occur, such as spawning synchrony cues being

thrown off by weather events. No other environmental factors seem to affect the timing of the split spawns found in the dataset.

Spawning synchrony is important for maximum fertilization success (Levitan *et al.* 2011). If spawning is not synchronized, it could lead to gamete wastage. For gonochores, males typically spawn first across broadcast spawning organisms (Campbell 1974). In this study, two of the three gonochores spawned on the same days, the exception being *D. cylindrus*. The males for this species spawned from 2 to 5 days after the full moon while the females spawned from days 1 to 5. This means that there would be gamete wastage on day 1 for this species. *Dendrogyra cylindrus* was also the only gonochore to have significantly different spawning times in minutes after sunset for males and females. Some scleractinians are known for their spawning precision, such as the *Orbicella* species. However, it is known that the standard deviation of spawning time increases the later after a cue, such as sunset or the full moon, that spawning occurs (Levitan *et al.* 2011). This could account for some of the variance in spawning days seen; spawning was occurring later, so it was less precise.

Congener Trends

Unpredictable spawning behaviors for some species of scleractinians might be caused by an hourglass biological clock model (Lin *et al.* 2013; Lin and Nozawa 2017). The hourglass model is when a biological rhythm is maintained due to the presence of fluctuations of environmental cues which trigger an event, in this case spawning (Rensing *et al.* 2001; Lin *et al.* 2013). During a seven year study, acroporids in the Indo-Pacific were found to have inconsistent spawning days from year to year (Lin and Nozawa 2017). The monitored *Acropora* species all spawned on the same night but on different days each year ranging from one to eleven days after the full moon (Lin and Nozawa 2017). Since the reproduction of this genus fits an hourglass biological clock model, it could be expected that spawning would be more sensitive to temporal variations in environmental cues, such as temperature or light (Lin *et al.* 2013; Lin and Nozawa 2017). The GLM run on *A. cervicornis* did show a significant difference for temperature in whether or not spawning occurred (GLM $p = 0.0103$). The Caribbean acroporids were also found to have high variability in spawning day in this study. Spawning was observed

between 0 to 18 days after the full moon. *Acropora cervicornis* and *A. palmata* both had significant differences in spawning days by month (Mantel-Haenszel $p < 0.05$). I believe that *A. cervicornis*, *A. palmata*, and *A. prolifera* follow this biological clock model, similar to the Indo-Pacific acroporids.

Other species that have more predictable spawning days follow a different model called an oscillator biological clock model (Lin *et al.* 2013; Lin and Nozawa 2017). In this model, the rhythm of the clock is endogenous; a trigger is not required (Lin *et al.* 2013; Lin and Nozawa 2017). Corals that follow this model for spawning include *Orbicella spp.* and *D. labyrinthiformis*, which are known for their precise spawning times and days (Levitan *et al.* 2011; Lin and Nozawa 2017). Spawning that fits this model is less likely to have shifts in spawning times with variation of environmental cues (Lin and Nozawa 2017). In the Caribbean, *Orbicella spp.* were observed spawning from 4 to 11, and 13 days after the full moon but were very consistent with spawning days annually. *Orbicella annularis* and *O. faveolata* were found to have no significant difference in spawning times or days by month in Mantel-Haenszel analyses. *Orbicella franksi* did have significant differences in spawning times and days by month (Mantel-Haenszel $p < 0.05$), so it may not follow this model as well as *O. annularis* and *O. faveolata*. *Montastraea cavernosa*, *D. cylindrus*, and *P. strigosa* may also follow this biological clock model as their spawning days seemed consistent annually. The other species in this study did not have as robust datasets as the acroporids or *Orbicella spp.*; therefore, it is difficult to say with certainty which biological clock model these species' spawning patterns follow.

Environmental Effects

The only species that was found to be affected by an environmental factor was *A. cervicornis*. It was found that the probability of spawning for *A. cervicornis* decreases by a factor of 0.27 for every one degree Celsius increase in water temperature. It is unclear why this was the only species affected. It could be that the actual temperature does not affect spawning as much as the rate of increase of temperature, which has been found to be a good predictor of spawning times (Keith *et al.* 2016). Because the probability of spawning for most of the species tested seems unaffected by temperature, this could be a

positive result with increasing sea surface temperatures due to climate change. Since none of the species' spawning probability was significantly affected by wind speed, it could be that a better predictor is calm periods in regional wind fields during the month of spawning (van Woesik 2009). The time of moonrise may not have had a significant affect because there could have been other factors masking this cue such as bad weather or cloud cover. The time of moonrise does not necessarily inform how much light was present, which is known to be a cue for spawning. Other lunar cues that were not investigated in this study may be better predictors of spawning such as the coincidence of the lunar third quarter and the movement of the moon over the equator (Wolstenholme *et al.* 2018). My findings could have also been affected by the lack of negative observations.

This study highlighted gaps in Caribbean scleractinian spawning knowledge. More observations are needed for *Acropora prolifera*, *Dichocoenia stokesi*, *Pseudodiploria clivosa*, and *Siderastrea siderea*. More observations of other factors surrounding spawning events could give more information about how environmental factors affect spawning. These include proportion of colonies that spawned and negative spawning observations. Other studies could focus on the effect of bleaching on the timing of spawning and spawning days for other species of corals in the Caribbean other than the *Orbicella spp.* These additional studies could give valuable insight into which environmental factor has the greatest impact on coral reproduction and threatens the continued survival of corals in the Caribbean and worldwide.

Appendix 1

Data Contributors

Observer	Region	Site	Species	Year	# of Observations	Email	Additional Observers
Robert Brewer	USVI	Flat Cay	<i>A. cervicornis</i> , <i>A. palmata</i> , <i>A. prolifera</i>	2013	9	Robert.brewer@cune.org	
Robert Brewer	USVI	Flat Cay	<i>A. palmata</i> , <i>A. prolifera</i>	2016	6	Robert.brewer@cune.org	Brown, Cassell, Howe, Gutting, Ewen, Egan, Spathias
Valérie Chamberland	Curaçao	Seaquarium, Holiday Beach, Waterfactor y	<i>D. cylindrus</i> , <i>A. palmata</i> , <i>P. (D.) strigosa</i> , <i>D. labyrinthiformis</i> , <i>S. siderea</i> , <i>M. cavernosa</i> , <i>O. (M.) faveolata</i> , <i>O. (M.) annularis</i> , <i>C. natans</i>	2015	351	Chamberland.f.valerie@gmail.com	SECORE/Carmabi, Dirk Petersen, Kristen Marhaver, Mark Vermeij
Mary Hagedorn	Puerto Rico	Trés Palmas Reserve	<i>A. palmata</i>	2009	1	HAGEDORNM@si.edu	
Emma Hickerson	Flower Garden Banks	East FGB	<i>M. cavernosa</i> , <i>P. (D.) strigosa</i> , <i>O. (M.) franksi</i> , <i>C. natans</i> , <i>O. (M.) annularis</i>	2004	14	emma.hickerson@noaa.gov	
Emma Hickerson	Flower Garden Banks		<i>O. (M.) franksi</i> , <i>O. (M.) faveolata</i> , <i>O. (M.) annularis</i> , <i>M. cavernosa</i> , <i>P. (D.) strigosa</i> , <i>S. intersepta</i>	2005	14	emma.hickerson@noaa.gov	G. P. Schmahl, Doug Weaver, Dr. Peter Vize, Jennifer DeBose, Eric Borneman

Emma Hickerson	Flower Garden Banks		<i>M. cavernosa</i> , <i>O. (M.) franksi</i> , <i>P. (D.) strigosa</i> , <i>S. intersepta</i> , <i>O. (M.) faveolata</i> , <i>C. natans</i>	2006	26	emma.hickerson@noaa.gov	G. P. Schmahl, Doug Weaver, Kyle Byers, Lindsay Kurelja, Dr. Peter Vize and team, Bob Cranston, Peter Craig, Kaile Tsapis, Gary Merritt, Emily Platzer, Andy Bruckner, Eric Borneman, Craig Burnside, Joyce Burek, Frank Burek, Chris Parsons, Neal Baltz
Emma Hickerson	Flower Garden Banks		<i>O. (M.) faveolata</i> , <i>P. (D.) strigosa</i> , <i>M. cavernosa</i> , <i>O. (M.) franksi</i> , <i>S. intersepta</i> , <i>O. (M.) annularis</i> , <i>C. natans</i>	2007	20	emma.hickerson@noaa.gov	Dr. Peter Vize, Sarah Davies, Dan Hilton
Emma Hickerson	Flower Garden Banks		<i>M. cavernosa</i> , <i>O. (M.) franksi</i> , <i>P. (D.) strigosa</i> , <i>O. (M.) faveolata</i> , <i>C. natans</i>	2008	12	emma.hickerson@noaa.gov	G. P. Schmahl, Jennifer DeBose, Marissa Nuttall, Dr. Peter Vize, Sarah Davies, Jay Reichman
Emma Hickerson	Flower Garden Banks	West Bank Buoys #1 & 4, East Bank Buoys # 1, 3, 4, 5, & 6	<i>M. cavernosa</i> , <i>O. (M.) franksi</i> , <i>P. (D.) strigosa</i>	2009	13	emma.hickerson@noaa.gov	Neal Baltz, JT Tyler, Fling guests and crew, Scot, Tom Patterson, Marissa, Penny Hammer,

							Todd Richard, Jeremy Rodriguez, Frank Zavalla
Emma Hickerson	Flower Garden Banks	East Buoy #4	<i>M. cavernosa, O. (M.) franksi, P. (D.) strigosa, C. natans, O. (M.) faveolata, S. intersepta</i>	2010	15	emma.hickerson@noaa.gov	G. P. Schmahl, Marissa Nuttall, Dan Basta, Tom Moore, Sarah Davies, Eli Meyer
Emma Hickerson	Flower Garden Banks	East	<i>O. (M.) franksi, P. (D.) strigosa, M. cavernosa, S. intersepta, O. (M.) faveolata</i>	2011	9	emma.hickerson@noaa.gov	Sarah Davies, Eli Meyers, Dr. Misha Matz, John Embesi, Ryan Eckert, Marissa Nuttall
Emma Hickerson	Flower Garden Banks	West Buoy #4, East Buoys #5 & 7	<i>P. (D.) strigosa, O. (M.) franksi, M. cavernosa, O. (M.) faveolata</i>	2012	15	emma.hickerson@noaa.gov	G. P. Schmahl, Marissa Nuttall, John Embesi, Ryan Eckert, Michelle Johnston, Sarah Davies, Damien Caillaud, Carly Kenkel, Eli Meyer
Emma Hickerson	Flower Garden Banks	East	<i>O. franksi, M. cavernosa, P. (D.) strigosa, O. faveolata, O. annularis</i>	2013	8	emma.hickerson@noaa.gov	Marissa Nuttall, G. P. Schmahl, Misha Matz, Marie Strader, Carly Kenkel, Sarah Davies, Eli Meyer, Sarah Guermond
Emma Hickerson	Flower Garden Banks	East	<i>M. cavernosa, O. franksi, P. strigosa, S. intersepta</i>	2015	6	emma.hickerson@noaa.gov	Ryan Eckert, John Embesi, Michelle Johnston, Marissa Nuttall,

							G. P. Schmahl, Travis Sterne
Ilsa Kuffner	Bermuda		<i>A. fragilis, S. radians, F. fragum, P. asteroides</i>	1993	210	ikuffner@usgs.gov	
Lauri MacLaughlin	Florida Keys	Looe Key	<i>A. cervicornis, A. palmata, D. cylindrus, M. cavernosa, O. (M.) annularis, O. (M.) faveolata, P. (D.) strigosa, D. labyrinthiformis</i>	2006	20	Lauri.maclaughlin@noaa.gov	Kim Ritchie, Mikhail Matz, Max Teplitski, Andrea Hayland, Cory Krediet, Billy Causey, Steve Baumgartner, Dave Score, Alex Score, Cory Walter, Erich Bartels, Sandra Brooke, Carl Beaver, Jan Blackman, Genelle Harrison, Carly Kenkel, Jon Onufryk, Nadine Slimak, Leigh Espy, Rusty Mason, Alex Creedon, Robert Keeley, Bruce Reygoudt, Noel Kartman
Lauri MacLaughlin	Florida Keys	Looe Key	<i>A. palmata, D. cylindrus, M. cavernosa, O. (M.) franksi, O. (M.) faveolata, O. (M.) annularis, S. siderea, C. natans,</i>	2007	125	Lauri.maclaughlin@noaa.gov	Ross Cunning, Carly Kenkel, Jon Onufryk, Erich Bartels, Koty Sharp, Kim Ritchie, Cecelia

			<i>P. (D.) strigosa, D. labyrinthiformis, S. intersepta</i>				Weaver, Trish, Lyn Cox, Roberty Keeley, Shannon Keenon, Susan Leser, Genelle Harrison, Sandra Brooke, Shelli Braynard, Paul Fitzgerald, Pat Haney, Joe Borowicz
Lauri MacLaughlin	Florida Keys	Horseshoe Reef	<i>D. stokesii</i>	2009	1	Lauri.maclaughlin@noaa.gov	Not listed
Lauri MacLaughlin	Florida Keys	Horseshoe Reef	<i>S. siderea</i>	2015	1	Lauri.maclaughlin@noaa.gov	Margaret, Chris
Margaret Miller	Florida Keys	Key Largo Dry Rocks	<i>O. faveolata</i>	2000	1	m.miller@secore.org	
Margaret Miller	Florida Keys	Key Largo Dry Rocks	<i>O. faveolata</i>	2001	2	m.miller@secore.org	
Margaret Miller	Florida Keys	Key Largo Dry Rocks	<i>O. faveolata</i>	2002	2	m.miller@secore.org	
Margaret Miller	Florida Keys	Key Largo Dry Rocks	<i>O. faveolata</i>	2003	1	m.miller@secore.org	
Margaret Miller	Florida Keys	Key Largo Dry Rocks, Grecian Rocks	<i>O. faveolata, P. (D.) strigosa</i>	2006	8	m.miller@secore.org	

Margaret Miller	Florida Keys	Grecian Rocks	<i>O. faveolata</i>	2007	1	m.miller@secore.org	
Margaret Miller	Florida Keys	White Banks	<i>O. faveolata</i>	2010	1	m.miller@secore.org	
Margaret Miller	Florida Keys	Grecian Rocks	<i>O. faveolata</i>	2011	1	m.miller@secore.org	
Margaret Miller	Florida Keys	Horseshoe	<i>O. faveolata</i>	2012	2	m.miller@secore.org	
Margaret Miller	Florida Keys	Sand Island, Grecian Rocks, Horseshoe	<i>O. faveolata</i>	2013	3	m.miller@secore.org	
Margaret Miller	Florida Keys	Horseshoe, Grecian Rocks	<i>O. faveolata</i>	2014	7	m.miller@secore.org	

Publications

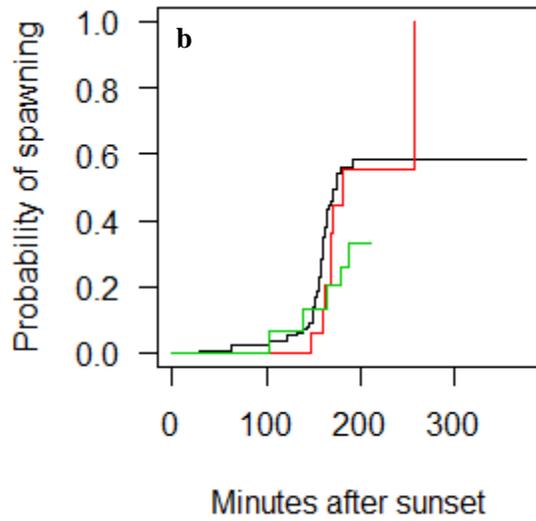
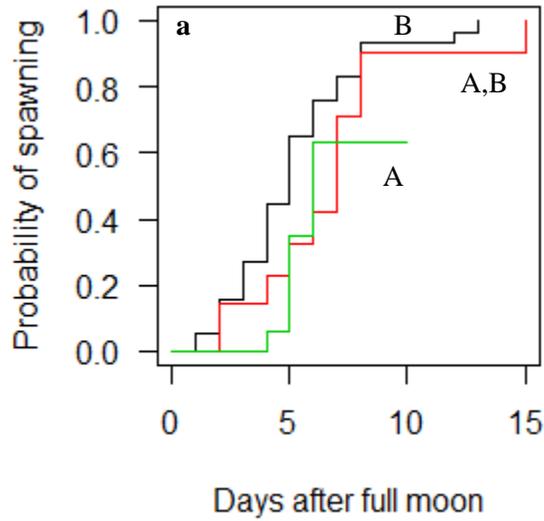
Source	Region	Journal
(Acosta and Zea 1997)	Colombia	<i>Marine Biology</i>
(Albright <i>et al.</i> 2010)	Florida Keys	<i>Proceedings of the National Academy of Sciences</i>
(Bassim <i>et al.</i> 2002)	Flower Garden Banks	<i>Marine Biology</i>
(Bastidas <i>et al.</i> 2005)	Venezuela	<i>Hydrobiologia</i>
(Baums <i>et al.</i> 2005)	Florida Keys, Bahamas	<i>Marine Ecology Progress Series</i>
(Baums <i>et al.</i> 2013)	Puerto Rico	<i>Coral Reefs</i>
(Beaver <i>et al.</i> 2004)	Mexico	<i>Coral Reefs</i>
(Chamberland <i>et al.</i> 2017)	Curacao	<i>Coral Reefs</i>
(De Graaf <i>et al.</i> 1999)	Bonaire	<i>Bulletin of Marine Science</i>
(Duerden 1902)	Jamaica	
(Fogarty, Lowenberg, <i>et al.</i> 2012)	Panama	<i>PLOS One</i>
(Gittings <i>et al.</i> 1992)	Flower Garden Banks	<i>Bulleting of Marine Science</i>
(Hagedorn <i>et al.</i> 2012)	Puerto Rico	<i>PLOS One</i>
(Hagman <i>et al.</i> 1998)	Flower Garden Banks	<i>Gulf of Mexico Science</i>
(Kirk <i>et al.</i> 2013)	Belize	<i>PLOS One</i>
(Levitan <i>et al.</i> 2004)	Panama, Curacao, Bahamas	<i>Evolution</i>
(Levitan <i>et al.</i> 2011)	Panama	<i>Evolution</i>
(Lopez <i>et al.</i> 1999)	Panama	<i>The Biological Bulletin</i>
(Marhaver <i>et al.</i> 2015)	Curacao	<i>BMC Ecology</i>
(Mendes and Woodley 2002)	Jamaica	<i>Marine Ecology Progress Series</i>
(Miller 2014)	Florida Keys	<i>Coral Reefs</i>
(Randall and Szmant 2009)	Mexico, Puerto Rico	<i>The Biological Bulletin</i>
(Ritson-Williams <i>et al.</i> 2014)	Belize	<i>Coral Reefs</i>
(Sánchez <i>et al.</i> 1999)	Colombia	<i>Bulletin of Marine Science</i>
(Sneed <i>et al.</i> 2014)	Belize	<i>Proceedings of the Royal Society B: Biological Sciences</i>
(Soong 1991)	Panama	<i>Bulletin of Marine Science</i>
(Steiner 1995)	Puerto Rico	<i>Bulletin of Marine Science</i>
(Szmant 1986)	Puerto Rico	<i>Coral Reefs</i>
(Szmant 1991)	Puerto Rico	<i>Marine Ecology Progress Series</i>
(Szmant <i>et al.</i> 1997)	Florida Keys, Bahamas	<i>10th International Coral Reef Symposium</i>
(Szmant and Miller 2006)	Florida Keys	<i>Marine Biology</i>
(van Woesik <i>et al.</i> 2006)	Various	<i>Ecology Letters</i>
(Vargas-Ángel and Thomas 2002)	Florida	<i>Coral Reefs</i>
(Vargas-Ángel <i>et al.</i> 2003)	Florida	<i>Coral Reefs</i>

(Vargas-Ángel <i>et al.</i> 2006)	Florida	<i>Coral Reefs</i>
(Villinski 2003)	Florida Keys	<i>Marine Biology</i>
(Wyers <i>et al.</i> 1991)	Bermuda	<i>Hydrobiologia</i>

Appendix 2: Supplemental Figures

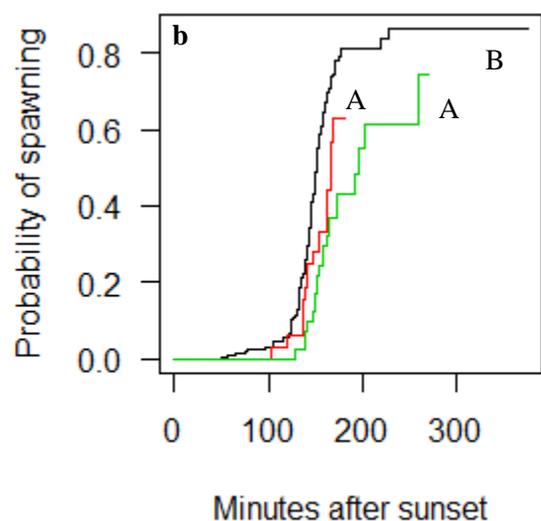
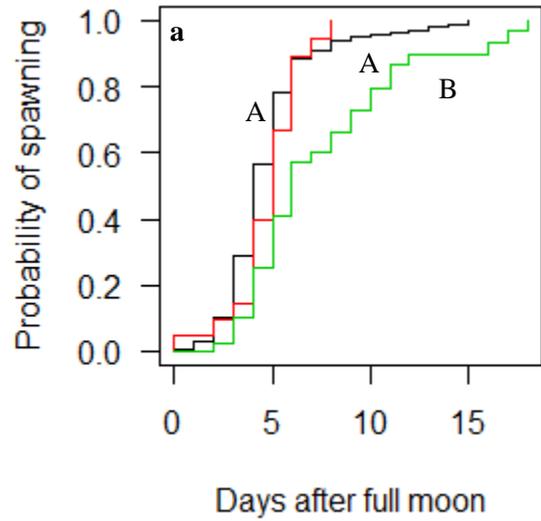
Table S1 Summary of spawning observations for 11 species of scleractinians in the Caribbean from data collected for this study. H stands for hermaphrodite and G stands for gonochore. M stands for male and F stands for female. If a gender is not specified for a variable for a gonochore, the value given is for both males and females. If one of the values for day, time, or month listed is not present in the scatterplot for that species, it is because that observation did not have the other variable with it (Figures 1-11). For *D. labyrinthiformis*, spawning times are negative to indicate that spawning occurs before sunset. Citations for sexuality: 1. (Szmant 1986) 2. (Gittings *et al.* 1994) 3. (Hagman *et al.* 1998) 4. (Szmant-Froelich 1984) 5. (Wyers *et al.* 1991) 6. (De Graaf *et al.* 1999)

Species	Month	Days After the Full Moon	Peak Spawning Days	Minutes After Sunset	Peak Spawning Time	Sexuality
<i>Acropora cervicornis</i>	July – September	1-8, 12, 13, 15	3-6	30-257	150-165	H ¹
<i>Acropora palmata</i>	July – September	0-18	3-5	50-260	136-157	H ¹
<i>Colpophyllia natans</i>	August – November	6-10	8-9	38-170	83-123	H ^{2,3}
<i>Dendrogyra cylindrus</i>	August – October	M 2-5 F 1-5	M 2-4 F 2-3	M 58-134 F 58-142	M 93-119 F 102-134	G ⁴
<i>Diploria labyrinthiformis</i>	May – September	7, 10-13	11-12	-117 - 0	-52 - -40	H ⁵
<i>Montastraea cavernosa</i>	June – November	1, 4-10, 12	6-7	M -19-259 F -9-245	M 62-154 F 62-147	G ⁴
<i>Orbicella annularis</i>	August – November	4-9, 11, 13	6-7	93-308	180-220	H ¹
<i>Orbicella faveolata</i>	August – November	4-9	6-7	88-275	181-223	H ¹
<i>Orbicella franksi</i>	August – November	4-10, 13	6-8	44-265	109-159	H ¹
<i>Pseudodiploria strigosa</i>	July – October	5-11, 14	6-8	37-313	108-173	H ⁴
<i>Stephanocoenia intersepta</i>	August – October	2-10	7-8	M 60-225 F 60-248	65-207	G ⁶



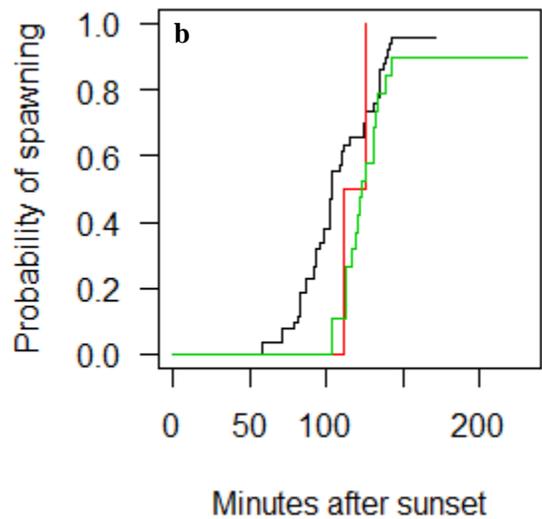
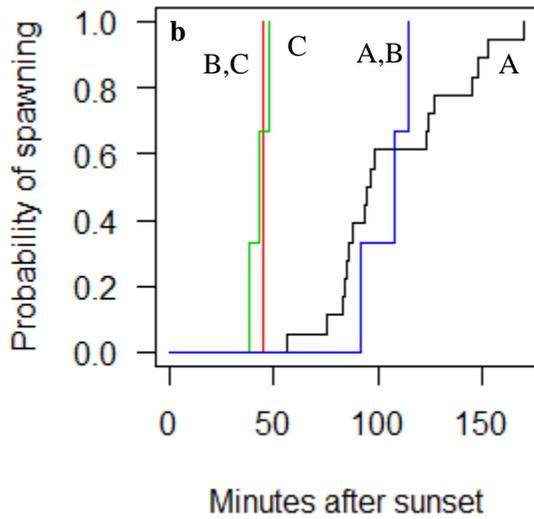
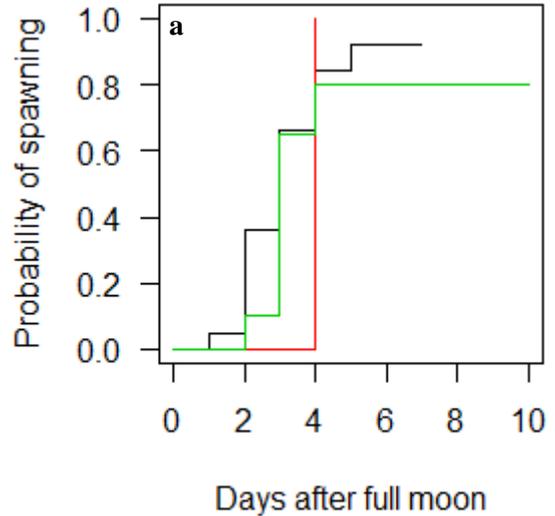
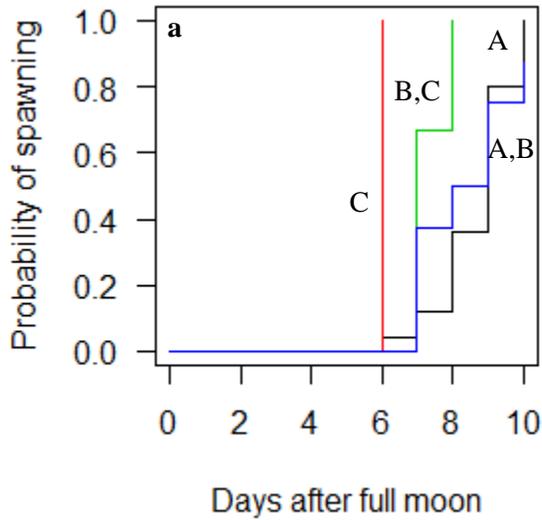
— July
 — August
 — September

Figure S1. Survival analyses for *Acropora cervicornis* month of spawning. a) Days after full moon (Mantel-Haenszel $p=0.0178$). b) Minutes after sunset.



— July
 — August
 — September

Figure S2. Survival analyses for *Acropora palmata* month of spawning. a) Days after full moon (Mantel-Haenszel $p=1.73 \times 10^{-6}$). b) Minutes after sunset (Mantel-Haenszel $p=4.47 \times 10^{-5}$).

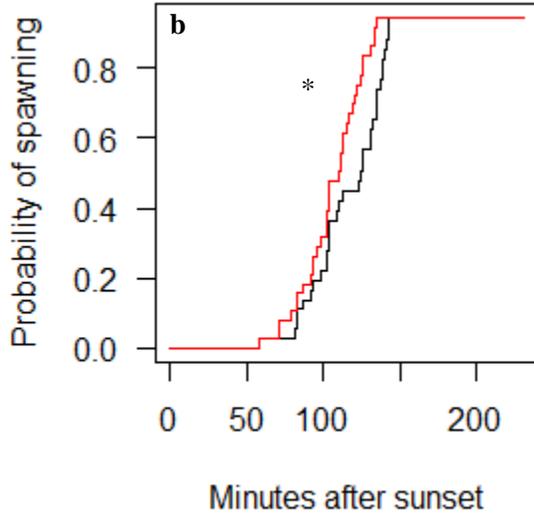
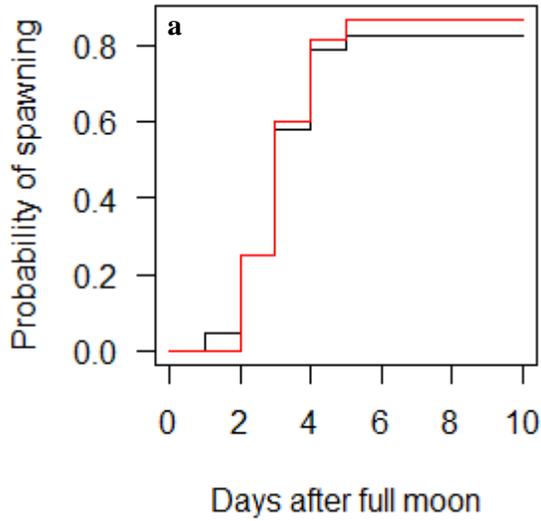


— August
 — September
 — October
 — November

— August
 — September
 — October

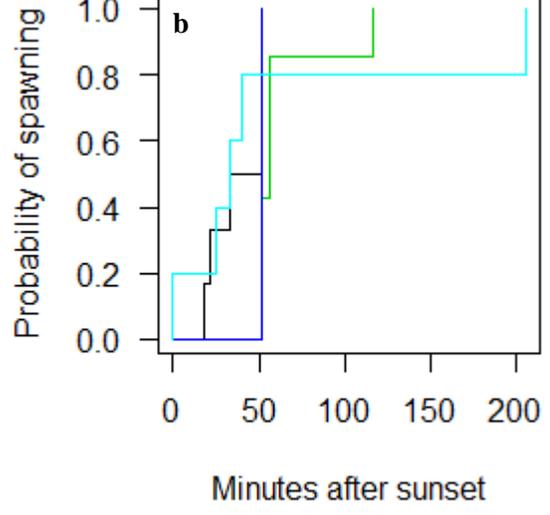
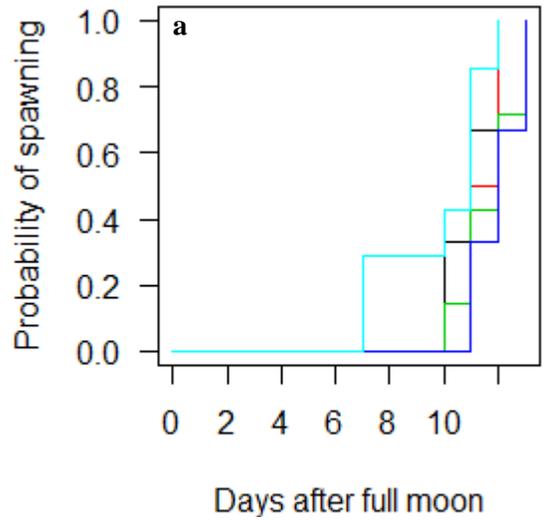
Figure S3. Survival analyses for *Colpophyllia natans* month of spawning. a) Days after full moon (Mantel-Haenszel $p=4.76 \times 10^{-5}$). b) Minutes after sunset (Mantel-Haenszel $p=9.14 \times 10^{-8}$).

Figure S4. Survival analyses for *Dendrogyra cylindrus* month of spawning. a) Days after full moon. b) Minutes after sunset.



— Male
— Female

Figure S5. Survival analyses for *Dendrogyra cylindrus* gender. a) Days after full moon. b) Minutes after sunset (Mantel-Haenszel $p=0.0451$).



— May
— June
— July
— August
— September

Figure S6. Survival analyses for *Diploria labyrinthiformis* month of spawning. a) Days after full moon. b) Minutes before sunset.

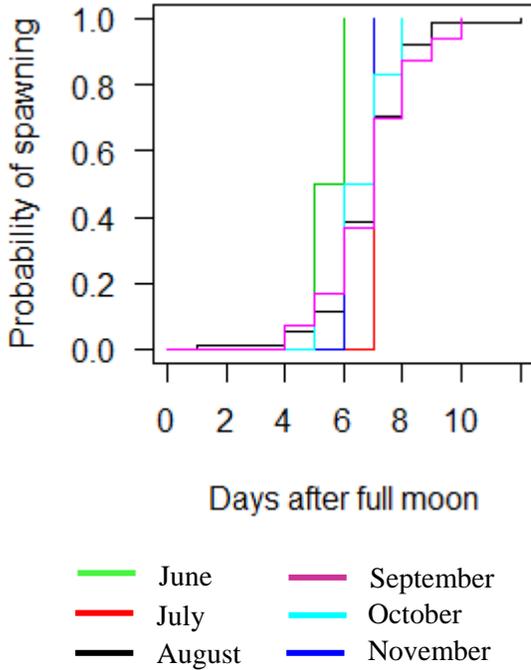


Figure S7. Survival analysis for *Montastraea cavernosa* month of spawning. Days after the full moon.

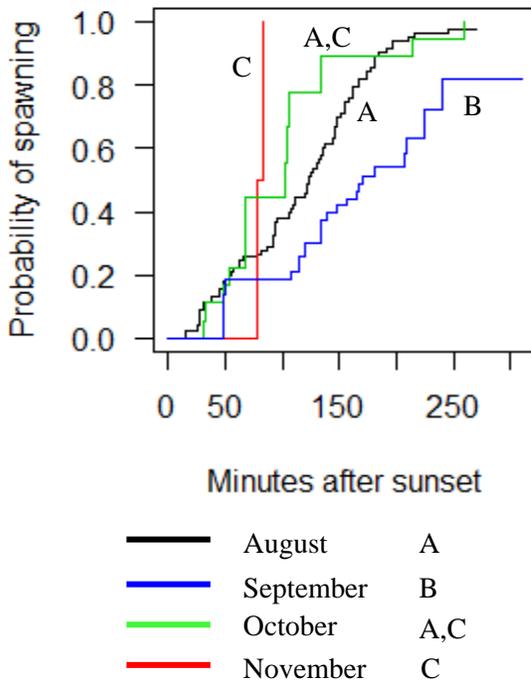


Figure S8. Survival analysis for *Montastraea cavernosa* month of spawning. Minutes after sunset (Mantel-Haenszel $p=4.4 \times 10^{-6}$).

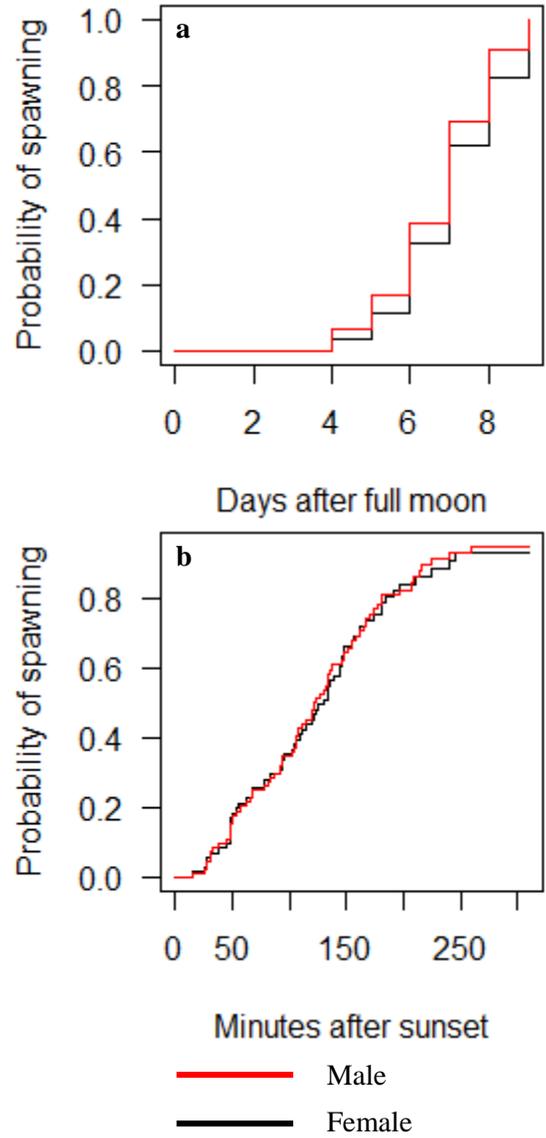
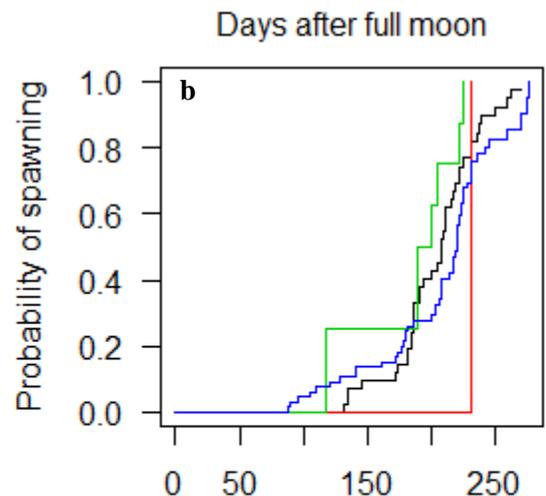
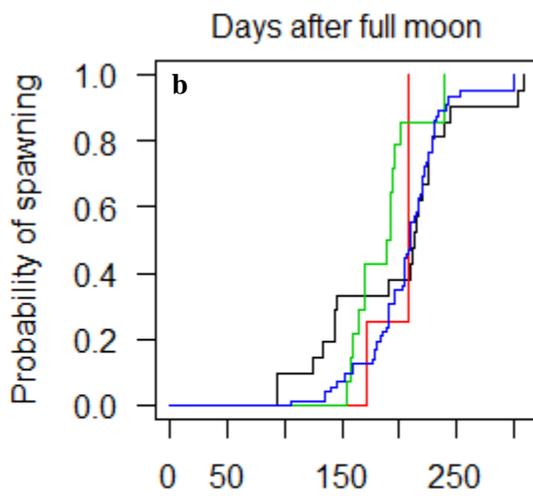
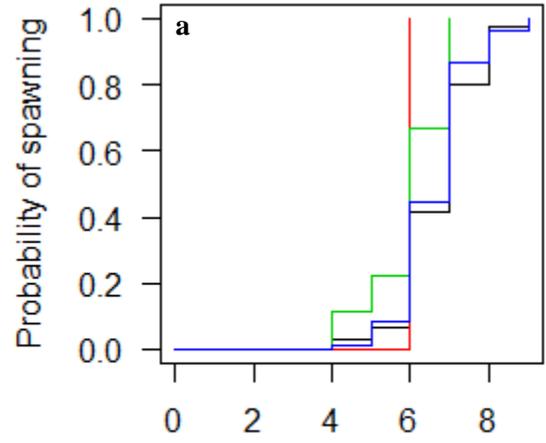
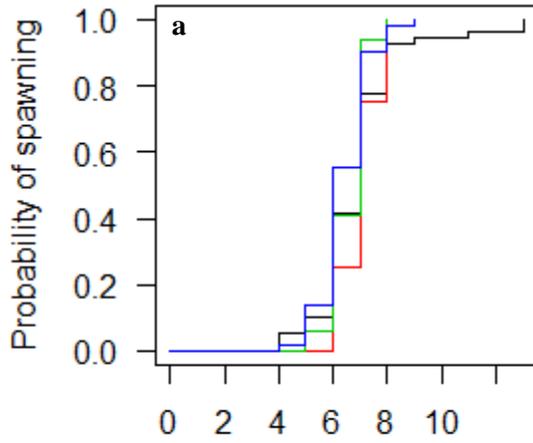


Figure S9. Survival analyses for *Montastraea cavernosa* gender. a) Days after full moon. b) Minutes after sunset.



Minutes after sunset

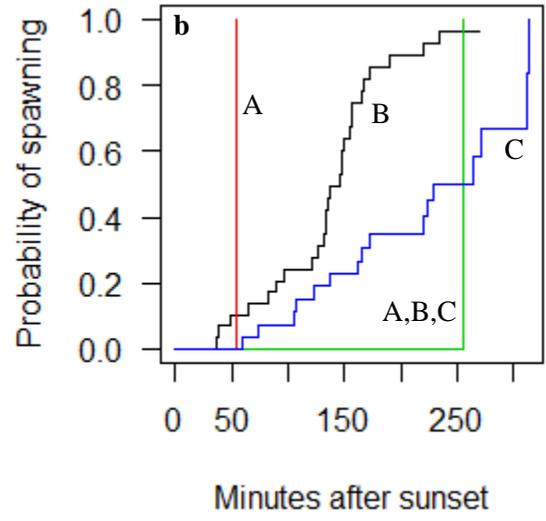
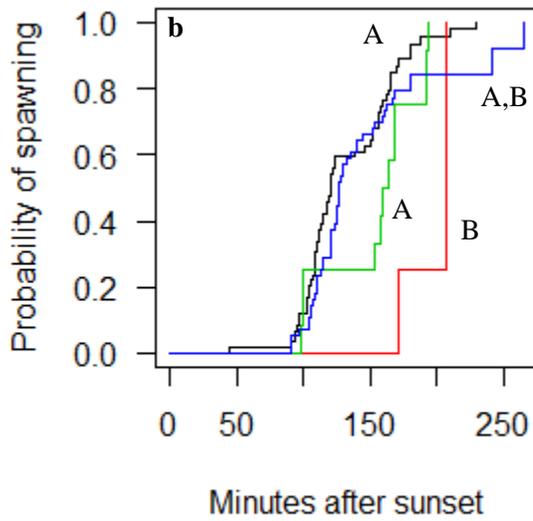
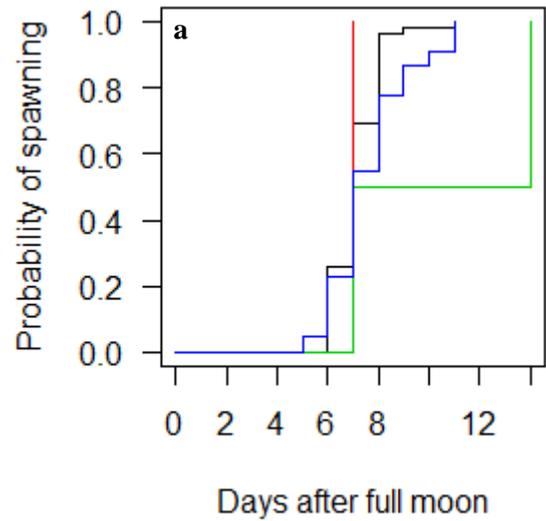
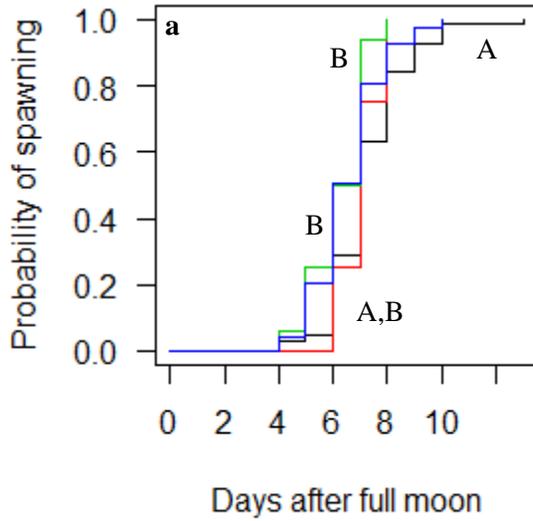
- August
- September
- October
- November

Minutes after sunset

- August
- September
- October
- November

Figure S10. Survival analyses for *Orbicella annularis* month of spawning. a) Days after full moon. b) Minutes after sunset.

Figure S11. Survival analyses for *Orbicella faveolata* month of spawning. a) Days after full moon. b) Minutes after sunset.



— August
 — September
 — October
 — November

— July
 — August
 — September
 — October

Figure S12. Survival analyses for *Orbicella franksi* month of spawning. a) Days after full moon (Mantel-Haenszel $p=0.000907$). b) Minutes after sunset (Mantel-Haenszel $p=0.0414$).

Figure S13. Survival analyses for *Pseudodiploria strigosa* month of spawning. a) Days after full moon. b) Minutes after sunset (Mantel-Haenszel $p=1.25 \times 10^{-6}$).

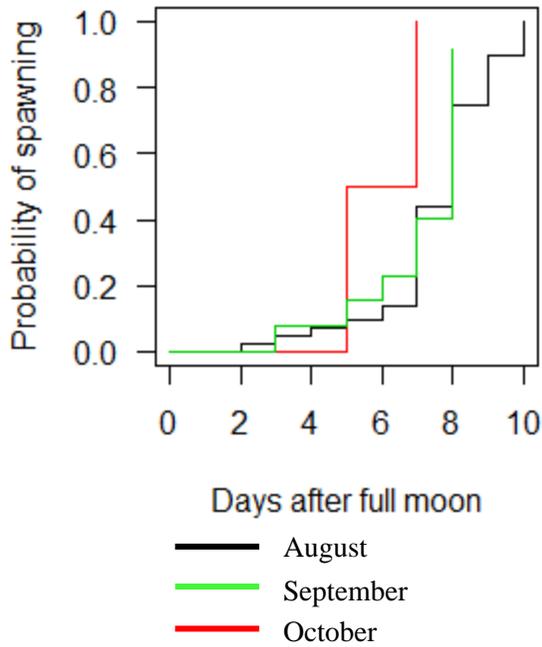


Figure S14. Survival analysis for *Stephanocoenia intersepta* month of spawning. Days after the full moon.

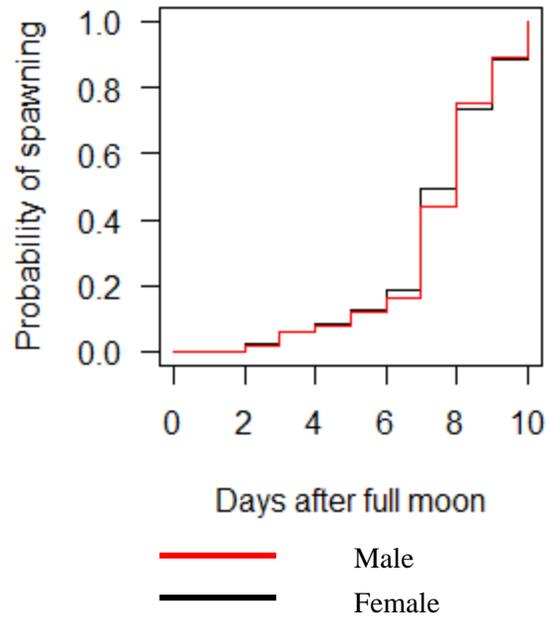


Figure S15. Survival analysis for *Stephanocoenia intersepta* gender. Days after the full moon.

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