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RESEARCH ARTICLE

BROADCAST SPAWNING PATTERN AND PELAGIC LARVAE DURATION OF ACROPORA CYTHEREA AND A. CLATHRATA FROM INSHORE REEF AREA IN KUANTAN COASTAL REGIONMuhammad Faiz Mohd Hanapiah^{a,b*}, Shahbudin Saad^{a,c}, Zuhairi Ahmad^{b,c}, Muhammad Hamizan Yusof^a, Mohd Fikri Akmal Khodzori^a, Muhammad Khairulanwar Rosli^c^a Department of Marine Science, Kulliyah of Science, International Islamic University Malaysia, Jalan Sultan Ahmad Shah, Bandar Indera Mahkota, 25200 Kuantan Pahang^b Remote Sensing, GIS, and Physical Oceanography Modelling Laboratory, Department of Marine Science, Kulliyah of Science, International Islamic University Malaysia, Jalan Sultan Ahmad Shah, Bandar Indera Mahkota, 25200 Kuantan Pahang^c Institute of Oceanography and Maritime Studies, Kulliyah of Science, International Islamic University Malaysia, Jalan Sultan Ahmad Shah, Bandar Indera Mahkota, 25200 Kuantan Pahang*Corresponding Author: faizhanapiah@gmail.com

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ABSTRACT

Acropora sp. is the second-most abundant among the coral genera in the Kuantan coastal region (KCR) located on the east coast of Peninsular Malaysia. This study investigated the timing of coral spawning of two *Acropora* species; *Acropora cytherea* and *Acropora clathrata* through dissection and histological analyses of coral fragments that were collected during predicted spawning months (March until May 2018) from Balok reef, Kuantan. Histological results showed the presence of mature oocytes from a sample collected in April and May 2018, which indicate an extended gamete release pattern for these species within KCR. The gamete maturity coincided with the peak sea surface temperature within KCR from April until May. Both *Acropora* species spawned between 10-11 nights after the full moon. Present results also indicated that both *Acropora* species have optimal pelagic larvae duration (PLD) between 6 – 8 days after spawning. This study contributed to the limited knowledge of coral reproductive biology on the east coast of Peninsular Malaysia. In addition, the timing of coral spawning provides valuable data for population connectivity modelling.

KEYWORDS

Kuantan coastal region, Coral spawning, Pelagic larvae duration, *Acropora*, a Coral reef.

1. INTRODUCTION

Understanding the reproductive biology of coral is among the vital aspects of coral larvae dispersal study. The mode of reproduction (sexual, asexual, hermaphroditism, gonochorism, and brooding) dictates the dispersal pattern of coral larvae. Numerous studies were conducted for the past two decades to describe coral reproduction biology from all over the world (Kolinski and Cox, 2003; Guest et al., 2005; Baird et al., 2009). A group of researcher mentioned that reproductive data were available for about one-third of 1400 known scleractinian species (Baird et al., 2009). Knowledge of coral reproductive strategies is essential in designing conservation approach since coral are vulnerable towards sudden changes in ecosystem environment such as climate change. The timing and onset of coral spawning are among the most critical factors in determining dispersal trajectories of coral larvae in the connectivity framework. Current patterns, especially in Kuantan coastal region, might vary substantially following seasonal patterns even though recent evidence

indicates that tidal forcing was imminent within coral reef areas in this region.

Therefore, determining the timing, duration, and synchrony of coral spawning provides valuable data for population connectivity modelling. The primary aim of this study was to describe broadcast spawning pattern and pelagic larvae duration (PLD) of two *Acropora* species; *Acropora cytherea* and *Acropora clathrata* within Kuantan coastal region (Dana, 1946; Brook, 1891). This coral genus was chosen because it is the second-most abundant among coral genera in Kuantan coastal region, as reported by (Hanapiah et al., 2019). Being a hermaphroditic coral (having both oocytes and spermaries within the same polyps), this coral is often chosen to study reproductive biology and indicator for predicting spawning events in Indo-Pacific reef (Guest et al., 2005; Chelliah et al., 2015; Jamodiong et al., 2018). It is assumed that the broadcast spawning pattern of *Acropora* might be influenced by seasonal variation of sea surface temperature.

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2. METHODOLOGY

2.1 Study sites

Histological sample of coral fragments were collected from Balok reef (3°51'22.26" N, 103°27'8.82" E) during predicted spawning months (March, April, and May) in 2018 while *in situ* coral spawning observation in April 2019 was conducted in Raja Muda reef (3°38'28.36" N, 103°28'3.22" E) in the southern part of Kuantan coastal region as shown in Figure 1.

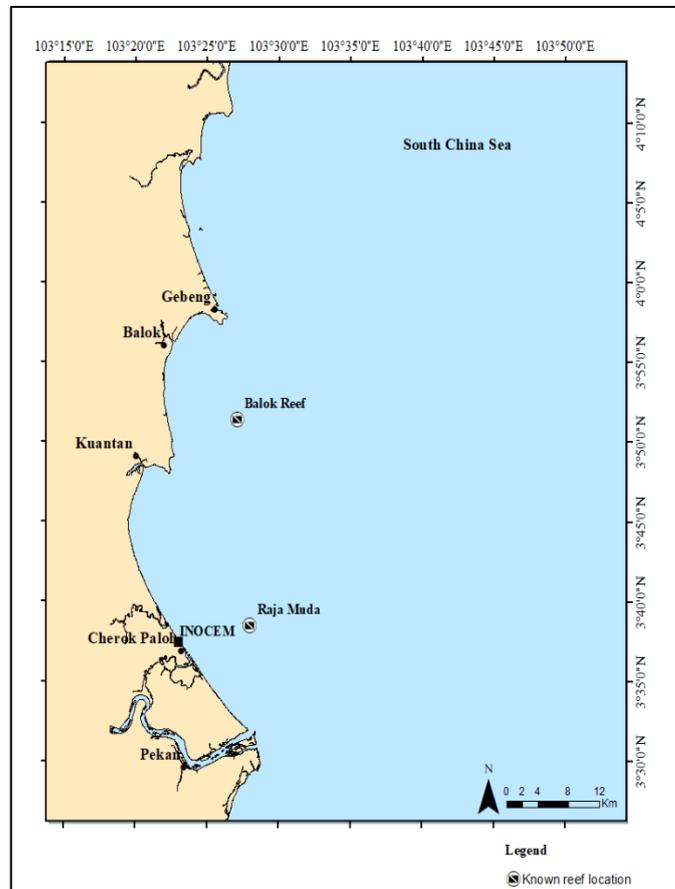


Figure 1: Location of study sites for coral sampling (Balok reef) and coral spawning observation (Raja Muda reef).

2.2 Annual sea surface temperature variation

To observe the seasonal variation of sea surface temperature, satellite image was extracted for the year 2014 until 2018 from Aqua MODIS (Level 3) data. MODIS data provide broader coverage of spatiotemporal data to capture the seasonality pattern of various environmental parameters such as SST, chlorophyll a and photosynthetic active radiation. The SST satellite images were obtained from the OceanColor website (<http://oceancolor.gsfc.nasa.gov/>) provided by NASA.

2.3 Histology analysis for coral spawning prediction

Several fragments (four colonies, each with approximately 10 – 15 cm long) containing several branches of *A. cytherea* and *A. clathrata* (Figure 2) were collected from Balok reef from March to May 2018 by using hammer and chisel. The selection of the months of sampling was based on the previously reported seasonal pattern of other *Acropora* species in Pulau Tioman and the southern part of Singapore who observed broadcast spawning pattern between March and May (Chelliah et al., 2015; Guest et al., 2005). Only a small number of coral fragments were used as a sample since the pattern of gamete development between similar species is highly synchronous, as suggested (Harrison and Wallace, 1990). Therefore, few numbers of samples should suffice in representing coral spawning patterns. Such an approach was also applied by some researchers in describing coral reproduction biology in the Red Sea (Bouwmeester et al., 2016).

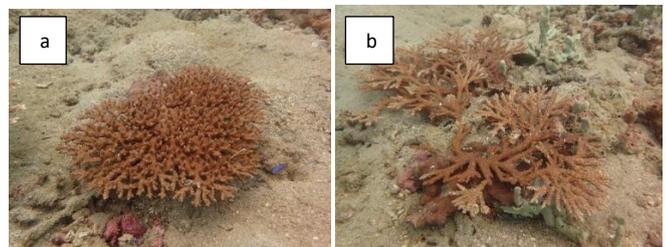


Figure 2: Coral colonies of a) *Acropora cytherea* and b) *Acropora clathrata*

Coral fragments collected from the field were brought back to the lab and fixed in a 10% seawater formalin solution for 24 hours. Then, these fragments were decalcified to remove the coral skeleton by soaking them in 10% buffered HCl for 4 – 24 hours, depending on the dissolution of calcium carbonate structure (Maboloc et al., 2016). For each coral fragment, two branches were cut vertically and loaded into cassettes as replicate. These samples were undergone tissue processing using Thermo Scientific automated tissue processor. Upon completion, the sample was embedded in paraffin wax and sectioned using Thermo Scientific microtome at seven μm thickness. Two sections, approximately 50 μm apart, were mounted on slides for each sample. Sections were then stained using a series of hematoxylin and eosin staining protocol. Slides were viewed using a NIKON digital microscope with NIS Element ver. Three imaging software at a magnification of $\times 10$ to $\times 100$. The presence of oocytes was observed and counted twice (by observing both sectioned samples on each slide) within the mesenteries filament of each sample.

2.4 Coral spawning survey

In order to capture spawning activities in Kuantan coastal region, three approaches were applied; i) *ex situ* coral spawning observation in INOCEM hatchery, ii) *in situ* larvae trap deployment (5 colonies each) and iii) nighttime coral spawning survey following the full moon on 18th April 2019. Adult coral colonies of both *Acropora cytherea* and *Acropora clathrata* were collected from Raja Muda reef (3°38'28.36" N, 103°28'3.22" E) on 10th April 2018. Four colonies (20 – 30 cm) from each species were transferred into an individual 10 L plastic container with filtered seawater (salinity range between 30 – 32 ppt) and maintained under ambient temperature (29 – 30 °C) at INOCEM hatchery. Each container was aerated with an air stone, and seawater was changed daily (70 %) to remove excess nutrients. In addition, each coral colony was feed with approximately 50 mL of zooplankton (*Artemia* sp.) once during dawn. Spawning activities were checked in the tanks at every 30 minutes interval between 8 pm until 12 am.

Larvae traps were installed on selected coral reef colonies from both *Acropora cytherea* and *Acropora clathrata* on 16th April 2019. These traps consist of a funnel made of mosquitos' net with approximately 2 mm mesh size with a transparent 50 mL Falcon tube attached at the mouth of the net. The collecting tube was kept afloat and upright by introducing a small amount of air to the upturned tube. The purpose of installing these larvae trap was to detect any spawning activity occurred in the wild during the spawning period. Nighttime coral surveys were carried out from 17th April 2019 until 24th April 2019. Surveys were conducted on SCUBA by four divers during dawn (approximately between 6 – 7 pm) and night (between 8 – 10 pm). However, due to rough seas condition and safety issues, further spawning observation was done *ex situ* in the INOCEM hatchery on 25th April onwards.

2.5 Pelagic larvae duration estimation

Coral gametes bundles were collected from spawned adults of *A. cytherea* (28th April 2019) and *A. clathrata* (29th April 2019). Gametes bundles for each coral species were transferred into 2 L beaker with filtered seawater and was stirred gently to allow fertilization. Fertilized eggs were rinsed by changing the water in the beaker several times to remove excess sperm as to avoid polyspermy (where more than one sperm try to fertilize one egg). Fertilized eggs were then transferred into three 1 L plastic containers with new filtered seawater and being left overnight.

Crustose coralline algae (*Hydrolithon* sp.) was used to induce coral settlement and metamorphosis. This approach was applied following the experiment by Heyward and Negri (1999) who mentioned the suitability of crustose coralline algae (CCA) as a natural inducer for *Acropora* millepora and *Goniastera retiformis* larvae. To estimate pelagic larvae duration for both *A. cytherea* and *A. clathrata*, 120 larvae were transferred into wells of 6 well culture plates (20 larvae for each well), which filled with 9 ml filtered seawater. The usage of 6 well culture plates for larvae competency assessment could give a reliable estimate on pelagic larvae duration, as suggested (Guest et al., 2010). Therefore, this approach was applied in this study since the number of fertilized embryos obtained was limited. Each well can be considered as one replicate. In this study, two sets of 6 well culture plates were prepared from each *Acropora* species. Larval settlement pattern was observed daily for each coral species. Larvae were counted as competent when they were to either on the surface of CCA or culture plates. The mean percentage of the settlement was plotted into a graph to determine the larval competency pattern for each coral species.

3. RESULTS

3.1 Local annual sea surface temperature

The annual variation of sea surface temperature variation in the Balok reef was demonstrated in Figure 3. Mean sea surface temperature in April was significantly higher in April compared to March, suggesting rapid seasonal rise temperature between both months. Peak SST was observed in May with $31.06\text{ }^{\circ}\text{C} \pm 0.76$ during the first inter-monsoon period and gradually decreased the following months. SST slightly rise between September and October during the second inter-monsoon period.

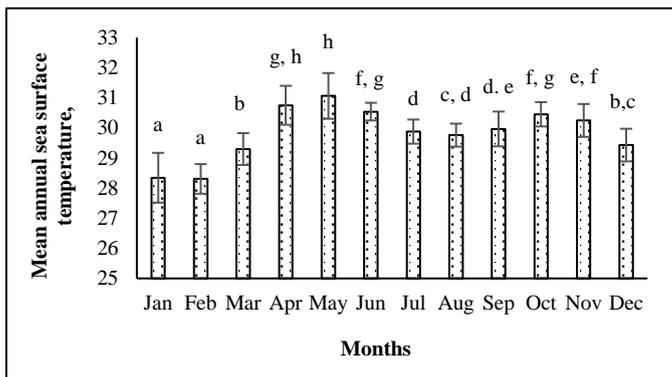


Figure 3: Mean annual sea surface temperature (SST) variation from 2014 until 2018. Non-standard alphabet indicates significant based on the post-hoc Tukey HSD test. Error bar indicating standard deviation.

3.2 Histological analysis

A. cytherea and *A. clathrata* species shared the same pattern of oocytes production in which most mature oocytes were present in April and May. Mature oocytes and spermaries were visible in the mesenteries filament. The highest oocytes count per polyp was recorded in April and lowest in March for both species, as indicated in Figure 4.

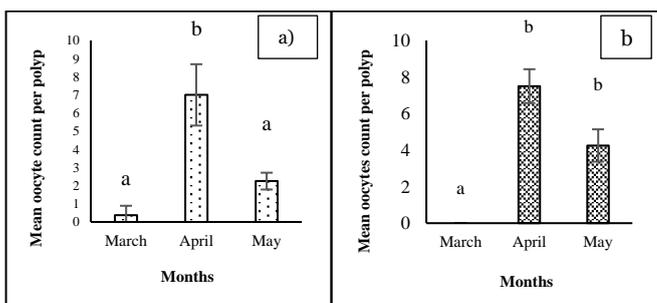


Figure 4: Mean oocytes count per polyp for *A. cytherea* (a) and *A. clathrata* (b) from March until May 2018. Non-standard alphabet indicates significant based on the post-hoc Tukey HSD test. Error bar indicating standard deviation.

3.3 Coral Spawning Survey

Coral colonies of *A. cytherea*, which were maintained in INOCEM hatchery spawned on the night of 28th April 2019, which was ten nights after the full moon (NAFM). Pinkish coral eggs bundle were observed floating in the coral container between 9 to 11 pm, as shown in Figure 5a. The fertilized egg started cell division approximately 1 hour after spawning, as indicated in Figure 5b. In addition, colonies from *A. clathrata* spawned on the 11th NAFM (29th April) in the INOCEM hatchery.

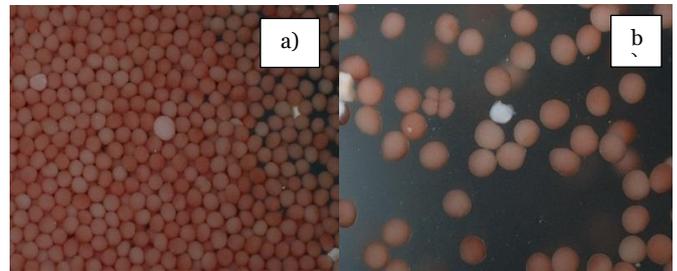


Figure 5: Coral eggs were round and pinkish in a) while some fertilized gametes started cell division after 1-hour post-spawning as indicated by the arrow in b).

3.4 Pelagic larvae duration of A. cytherea and A. clathrate

The pattern of PLD for both *Acropora* species was demonstrated in Figure 6 and Figure 7. It can be noticed that the onset of competency for *A. cytherea* occurred on the 5th DAS compared to *A. clathrata* (4th DAS). The peak settlement of *A. cytherea* occurred between 6th to 8th DAS in which more than 60 % of initially floating larvae have settled with an average new settlement of 4 larvae day⁻¹. In contrast, peak settlement patterns for *A. clathrata* occurred between 5th and 6th DAS with five larvae day⁻¹ settlement rates. Due to the limited number of available coral larvae, the experiments were halted after 10th DAS for both *Acropora* species.

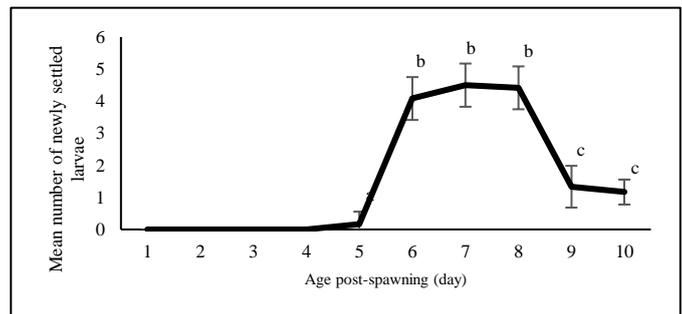


Figure 6: Mean number of newly settled *Acropora cytherea* larvae per day surveyed daily from spawning date (28th April 2019) until 10 DAS (8th May 2019). Non-standard alphabet indicates significant based on the post-hoc Tukey HSD test. Error bar indicating standard deviation.

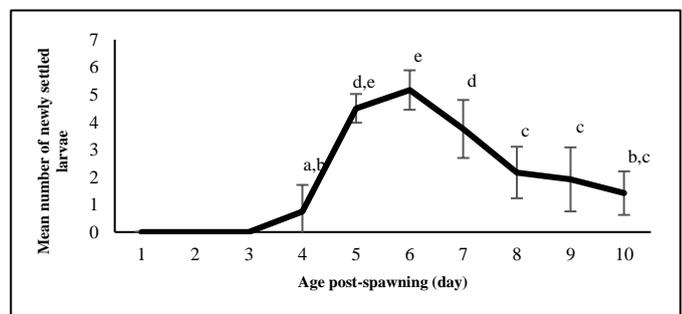


Figure 7: Mean number of newly settled *Acropora clathrata* larvae per day surveyed daily from spawning date (29th April 2019) until 10 DAS (9th May 2019). Non-standard alphabet indicates significant based on the post-hoc Tukey HSD test. Error bar indicating standard deviation.

4. DISCUSSION

The present study indicated the gamete maturity synchrony between *Acropora cytherea* and *Acropora clathrata*. Histological evidence indicated

that the majority of mature oocytes count per polyp for both species were observed in April. Therefore, it can be postulated that the peak spawning months for these species might have also occurred in April. Coral spawning survey later in April 2019 confirmed this prediction and has observed spawning activity between 10 – 11 nights after the full moon (NAFM). This finding was similar to the timing of gamete release of other *Acropora* species (*Acropora nasuta* and *Acropora millepora*) in Tioman Island by who observed pigmented egg in April (Chelliah et al., 2015). Elsewhere, some researchers observed multi-specific spawning synchrony of *Acropora* in April for Singapore (Guest et al., 2005). Since the spawning timing *Acropora* is highly synchronous, it can be suggested that most *Acropora* species found in the Kuantan coastal region might also share the same spawning seasonality. Therefore, this study adds to the increasing knowledge to understand spawning variability, especially along the East Coast of Peninsular Malaysia.

Mature oocytes were occurred in April and May, suggesting spawning in both species was extended over two months. This split-spawning pattern is common among the Indo-pacific coral and has been reported in various reefs location such as Singapore, Northwestern Philippines and Red Sea (Guest et al., 2005; Bouwmeester et al., 2016; Jamodiong et al., 2018). The reason behind this pattern is still unknown though it can be suggested that split-spawning could provide an option for coral to release an egg during favorable environmental conditions and increase the chance of settlement (Harrison et al., 1984). The timing of gamete released for both *A. cytherea* and *A. chlatrata* (10-11 NAFM) was 4-6 days later than the timing of *Acropora* spawning reported in Tioman Island (Chelliah et al., 2015). However, present findings were consistent with the timing of the gamete release of *A. cytherea* in the Philippines in which this coral species was observed to spawn during the last quarter of the moon rather than the full moon (Jamodiong et al., 2016). Some researchers suggested that such a pattern is advantageous for coral since lower tidal amplitude during neap tide could decrease gamete dilution and hence increase the settlement success (Maboloc et al., 2016). A group researchers also suggested that a long dark period around the last quarter of the moon (due to delayed moonrise) might reduce the predation risk on spawned gametes by visual predators (Babcock et al., 1986).

Seasonality of broadcast spawning *Acropora* might be influenced by temporal variation of an environmental condition such as temperature, solar insolation, moonlight, and tidal condition (Willis et al., 1985; Kaniewska et al., 2015). Recent evidence has suggested that the spawning pattern and gamete maturity might be driven by the rate of sea temperature rise prior to spawning (Keith et al., 2016). In Kuantan coastal region, the spawning season for *Acropora* was inferred between April and May, which coincide with the gradual rise of sea surface temperature during the first inter-monsoon period. Previous work has revealed that rising temperatures in a controlled environment might accelerate the rate of gamete maturity and influence spawning timing (Figuerdo et al., 2014). However, higher temperatures might decrease fecundity in the gamete release as suggested by Paxton et al. (2016), who observed egg and sperm count decreased when coral was treated with elevated (2 °C) temperature. Thus, a major release of gametes in April rather than during maximum sea surface temperature (SST) in May could increase the chances of fertilization and survival of coral larvae since coral is often susceptible to temperature-related stress such as coral bleaching. Annual spawning during nearly maximum SST pattern observed in this study was consistent with previous spawning survey in Coral Triangle regions such as in Indonesia, Thailand, the Philippines, and Singapore (Maboloc et al., 2016; Guest et al., 2005; Permata et al., 2012).

Larvae competency pattern for both *A. cytherea* and *A. chlatrata* presented here were comparable with previous works on larvae competency for these genera in the equatorial region (Guest et al., 2005). The onset of competency for both *Acropora* species (4 – 5 DAS) and peak settlement period (6 – 8 DAS) could play a crucial role in estimating larvae dispersal for this broadcast spawning coral. Pelagic larvae duration (PLD) has been used extensively in estimating larvae dispersal in which dispersal distance often scaled proportionally with the duration of larvae in plankton, as suggested (Shanks et al., 2003). Some reports have indicated that

Acroporids larvae have prolonged PLD and high dispersal potential. However, some researchers implied that assuming dispersal distance as a direct function of PLD does not represent actual population connectivity (Sponaugle et al., 2002). Important factors, such as local hydrodynamic patterns, should be considered to estimate the dispersal pattern better since this is the main driving force in larvae transport. Miller and Mundy also suggested that both dispersal and larval competency of these broadcast spawners decrease exponentially with time (Miller and Mundy, 2003).

5. CONCLUSION

In conclusion, this is the first reproductive biology study of *Acropora cytherea* and *Acropora clathrata* in the Kuantan coastal region. The gamete maturity and spawning timing of the *Acropora* genus in this study coincided with the optimal annual sea surface temperature in April. This finding is consistent with the spawning pattern observed during optimum SST in another tropical region. The information of spawning synchrony in this region could be valuable for future ecosystem management and provide baseline information on spawning seasonality in this region. Further work is needed in describing the coral spawning pattern of other coral genera with different such reproductive strategies such as brooders like *Pocillopora* and gonochoric *Porites*.

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REFERENCES

- Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver, J.K., Wallace, C.C., Willis, B.L., 1986. Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef, *Marine Biology*, 90, Pp. 379–394.
- Baird, A.H., Guest, J.R., Willis, B.L., 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology and Evolution System*, 40, Pp. 551–571.
- Bouwmeester, J., Gatins, R., Giles, E.C., Sinclair-Taylor, T.H., Berumen, M.L., 2016. Spawning of coral reef invertebrates and a second spawning season for scleractinian corals in the central Red Sea, *Invertebrate Biology*, 135 (3), Pp. 273–284.
- Chelliah, A., Amar, H., Hyde, J., Yewdall, K., Steinberg, P.D., Guest, J.R., 2015. First record of multi-species synchronous coral spawning from Malaysia, *PeerJ*, 3, Pp. e777.
- Figueredo, J., Baird, A.H., Connolly, S.R., 2013. Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. *Ecology*, 94, Pp. 650–659.
- Guest, J.R., Baird, A.H., Goh, B.P.L., Chou, L.M., 2005. Seasonal reproduction in Equatorial coral reefs, *Invertebrate Reproduction Development*, 48, Pp. 207–218.
- Guest, J.R., Heyward, A., Omori, M., Iwao, K., Morse, A.N.C., Boch, C., 2010. Rearing coral larvae for reef rehabilitation, In: Edwards A (ed) Reef rehabilitation manual. The Coral Reef Targeted Research & Capacity Building for Management Program, St. Lucia, Australia.
- Hanapiah, M.F.M., Saad, S., Ahmad, Z., Yusof, M.H., Khodzori, M.F.A., 2019. Assessment of benthic and coral community structure in an inshore reef in Balok, Pahang, Malaysia. *Biodiversitas Journal of Biological Diversity*, 20 (3), Pp. 872–877.
- Harrison, P.L., Babcock, R.C., Bull, G.D., Oliver, J.K., Wallace, C.C., Willis, B.L., 1984. Mass spawning in tropical reef corals, *Science*, 223, Pp. 1186–1189.
- Harrison, P.L., Wallace, C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals, In: Dubinsky Z (ed) *Ecosystems of the world*, 25, Coral reefs. Elsevier, Amsterdam.

- Heyward, A.J., Negri, A.P., 1999. Natural inducers for coral larval metamorphosis. *Coral Reefs*, 18 (3), Pp. 273–279.
- Jamodiong, E.A., Maboloc, E., Villanueva, R.D., Cabaitan, P.C., 2018. Gametogenesis and Inter-annual variability in the spawning pattern of *Acropora hyacinthus* in Northwestern Philippines. *Zoological Studies*, 57 (46), Pp. 1-10.
- Jamodiong, E.A., Maboloc, E.A., Leriorato, J.C., Tañedo, M.C.S., Diaz, L.A., Tabalanza, T.D., Cabaitan, P.C., Villanueva, R.D., 2016. Coral spawning and spawn-slick observation in the Philippines. *Marine Biodiversity*, 48 (4), Pp. 2187–2192.
- Kaniewska, P., Alon, S., Karako-Lampert, S., Hoegh-Guldberg, O., Levy, O., 2015. Signaling cascades and the importance of moonlight in coral broadcast mass spawning. *eLife*, 4, Pp. e09991.
- Keith, S.A., Maynard, J.A., Edwards, A.J., Guest, J.R., Bauman, A.G., van Hooidek, R., Heron, S.F., Berumen, M.L., Bouwmeester, J., Piromvaragorn, S., Rahbek, C., Baird, A.H., 2016. Coral mass spawning predicted by rapid seasonal rise in ocean temperature. *Proceeding of the Royal Society*, 283, Pp. 20160011.
- Kolinski, S.P., Cox, E.F., 2003. An update on modes and timing of gamete and planula release in Hawaiian scleractinian corals with implications for conservation and management. *Pacific Science*, 57, Pp. 17–27.
- Maboloc, E.A., Jamodiong, E.A., Villanueva, R.D., 2016. Reproductive biology and larval development of the scleractinian corals *Favites colemani* and *Favites abdita* (Faviidae) in northwestern Philippines. *Invertebrate Reproduction & Development*, 60 (1), Pp. 1–11.
- Miller, K., Mundy, C., 2003. Rapid settlement in broadcast spawning corals: implications for larval dispersal. *Coral Reefs*, 22 (2), Pp. 99–106.
- Paxton, C.W., Baria, M.V.B., Weis, V.M., Harii, S., 2016. Effect of elevated temperature on fecundity and reproductive timing in the coral *Acropora digitifera*. *Zygote*, 24 (4), Pp. 511–516.
- Permata, D., Indrayanti, E., Haryanti, D., Fika, L., Arfiyan, H., Achmad, A., 2012. Biannual multispecific spawning in Karimunjawa Archipelago, Indonesia. *Coral Reefs*, 31, Pp. 907.
- Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, 13 (1), Pp. 159–169.
- Sponaugle, S., Cowen, R.K., Shanks, A., Morgan, S.G., Leis, J.M., Pineda, J., Boehlert, G.W., Kingsford, M.J., Kenyon, C., Grimes, C., Munro, J.L., 2002. Predicting Self-Recruitment in Marine Populations: Biophysical Correlates and Mechanisms. *Bulletin of Marine Science*, 70 (1), Pp. 341–375.

