

Reproduction Pattern and Multispecific Spawning of *Acropora* spp. in Spermonde Islands Reef, Indonesia

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Abstrak

Pola Reproduksi dan Pemijahan Multispecific *Acropora* spp. di Kepulauan Spermonde, Indonesia

Perairan laut tropis Indonesia yang memiliki variasi lingkungan yang hampir konstan, diduga periode pemijahan karang melebar sampai beberapa bulan dan pada fase bulan yang berbeda, sehingga sulit menentukan waktu pemijahannya dalam skala bulan, hari dan jam. Penelitian ini memberikan informasi pola reproduksi dan sinkronisasi pemijahan beberapa jenis karang *Acropora* spp di Kepulauan Spermonde, Makassar. Sebanyak tujuh jenis karang *Acropora* spp. diamati kematangan atau kemunculan gonad dan pemijahannya di alam (*in situ*) dan atau di laboratorium (*ex situ*) di Marine Station Universitas Hasanuddin. Pola reproduksi menunjukkan pemijahan berlangsung setiap musim hujan pada bulan Februari-Maret selama tiga tahun berturut-turut. Pemijahan berlangsung secara sinkron dan broadcasting pada awal bulan purnama (0 BP sampai +2 BP), pada jam 18:10–19:00. Bersamaan dengan itu, kondisi lingkungan pemijahan berlangsung saat puncak pasang tinggi dengan suhu rata-rata harian perairan 30,3°C dan curah hujan yang masih tinggi di bulan Maret. Informasi ilmiah ini bermanfaat untuk mengembangkan riset dan tehnik reproduksi karang di alam dan laboratorium sebagai upaya merestorasi dan merepopulasi jenis karang tertentu.

Kata kunci : *Acropora* spp, reproduksi seksual, Kepulauan Spermonde

Abstract

It has been thought that Indonesian marine tropical waters have less environmental variability, so that spawning period of coral extend for several months and occurred during different lunar phases. Therefore the timing of coral spawning in a year cannot be predicted especially for monthly, daily and hourly scales. This study was aimed to investigate the reproductive pattern, and the environmental cues of *Acropora* spp. in Spermonde Islands reefs of Makassar. Spawning corals have been determined the presence of mature gonad and spawning event in their habitats (*in situ*) and in the laboratory (*ex situ*) of Marine Station of Barrang Lompo Island, Hasanuddin University. Here we showed that seven species of *Acropora* spp. spawned in February and March of rainy season for consecutive three years (2010, 2011, 2012). The multispecific broadcasting spawning took place in lunar period (0–2 AFM) at 06:10–07:00 pm). The spawning time occurred in high tide and the temperature was 30,3°C. This study will be useful for development of coral reproduction research and technique in both field and laboratory as an effort to restore coral reef and enhance coral population in particular.

Keywords: *Acropora* spp, sexual reproduction, Spermonde Islands

Introduction

Studies on coral reproduction have been initiated in the 1930s by Abe in 1937. In the 1980s, study of coral reproduction has been developed in the Great Barrier Reef Australia, Red Sea and the Caribbean. During this period, they have discovered coral spawning phenomenon (Poinski, 2004). Willis *et al.* (1985) examined the synchronous of mass reproduction of corals in the Great Barrier Reef as a

unique phenomenon, the same thing happen to many recorded cases in Japan (Loya *et al.*, 2009) and the Red Sea (Shlesinger and Loya, 1985).

Sexual reproduction pattern is determined partly by coral species and location of latitude, geographical isolation, season, local and regional oceanographic conditions where reefs extend (Mendes and Woodley, 2002). Indonesian reefs within the low latitude region are located in true

tropical marine waters. It has two different climates consist of rainy and dry seasons.

Environmental factors that influence sexual reproduction and the eventual spawning have been studied for 20th years. The coral spawning pattern is influenced by biological, chemical and physical environmental cues. These generally considered to operate on at least three inter-related temporal levels: time of year, the lunar cycle and the time of night (Willis *et al.*, 1985; Van Woesik *et al.*, 2006). Clearly, gametes is usually released at night, but a consistent relationship between lunar phase and the time of spawning is different throughout the world reefs. However, it is easy to observe the time of spawning around the full moon and new moon, therefore, the lunar cycle can be used to accurately predict the broadcast spawning night in many location (Willis *et al.*, 1985). Some researches in high latitudes suggest that some coral spawning took place at the full moon, and others were found while the new moon or dark as observed in the GBR (Willis *et al.*, 1985). In areas with relatively constant environmental conditions such as the tropics, the coral spawning extends to several months and the release of gametes occurs at different phases of the moon (Shlesinger and Loya, 1985; Szmant, 1986). Another study determined the key of environmental variable is solar insolation cycles which correlated with the selection of the month of spawning (Van Woesik *et al.*, 2006)

Several researches on coral reproduction revealed that the genus *Acropora* is the most common group of reproduction that has been studied. This coral group has high species diversity in many coral reef habitats and so wide distribution in coral reefs throughout Indonesia and Indo Pacific (Wallace, 1999). Inventory data and taxonomy of the Indonesian genus of *Acropora* recorded 91 species (Wallace and Walstenholme, 1998; Wallace, 1999). Furthermore, the coral of genus *Acropora* is well contains the greatest number of species of any extant coral genera and it occurs in all tropical oceans as well as most reef habitats (Wallace, 1999).

Study of coral reproduction in Indonesia is still limited, e.g. Bahtiar (2002) in Lombok Strait, Munasik (2002) in Jepara Central of Java, Rani and Jompa (2005) and Romawanti (2006) in Spermonde Islands Makassar, Baird *et al.* (2005) in Aceh, Baird *et al.* (2009a) in Manado just done locally and limited species. From these researches, it is not clearly known if reproduction pattern synchronized? This question had been answered by Edinger *et al.* in Tomascik *et al.* (1997) and Permata *et al.* (2012) found the multispecific synchronized spawning in the Karimunjawa reefs in Indonesia. The coral spawned

in October 1995 (Edinger *et al.* in Tomascik *et al.*, 1997) and in March 2009 (Permata *et al.*, 2012). It can be said that Karimunjawa corals had the multispecific spawning within bianual. How is the Spermonde'corals reproductoin as part of the eastern Indonesian Coral in Coral Triangle Area. Therefore, this research will add information on the pattern of Acroporoid reproduction. It will be useful as an initial step to develop the sexual reproduction of Indonesian corals, especially in Makassar Spermonde Reefs.

Material and Methods

This study was conducted in Spermonde Islands within the Makassar Strait for three years (2010-2012). Coral spawning observation and gonad *in situ* checks were carried out on the reefs of Bone Tambu Island, Langkai Island and Badi Island. In the first year (2010), maturity gonad of *Acropora loripes* colonies were initially observed in Langkai Island reef (no GPS, in northwest side). The second year (2011), colonies of *A. digitifera*, *A. cerealis*, *A. nasuta* and *A. aculeus* were observed in Bone Tambu Island reef (S 04° 55' 30" E 119° 18' 58") of gonad maturation and their spawning on laboratory. The third year (2012) was observed for *Acropora sp* in Badi Island reef (S 04° 57' 86" E 119° 17' 14") for the gonad maturity in reef habitat.

The observation of gonad maturity was carried out at corals in nature (*in situ*) and in laboratory (*ex situ*) (Willis *et al.*, 1985). Gonad maturity of coral can be observed by *insitu* method from coral branches breakage. Visible indications of gonad maturity showed colour of yellowish or orange or redish on coral breakage (Harrison *et al.*, 1984). At the same time, coral spawning observed in the laboratory (*ex situ*) of Marine Station in Barrang Lompo Island. The mature coral were took from reef habitat then placed in nubin container with volum of seawater. We were waiting the coral spawning till night of full moon.

Variables of coral spawning were consisted of spawning models (whether the broadcaster or brooder corals) and sex: hermaphrodites or gonochoric (Richmond and Hunter, 1990; Wallace, 1999; Thamrin, 2006) and spawning time are include month, date and hour of spawning (after sunset) (Willis *et al.*, 1985).

Environmental factors have a major impact on coral reproduction, these are sea surface temperature (SST) and tides (Oliver *et al.*, 1988; Mendes and Woodley, 2002), lunar phase (Baird *et al.*, 2009b) and precipitation (Mendes and Woodley, 2002). Sea surface temperature was measured

manually using digital thermometer, during morning (06:00-7:00am), midday (12:00-13:00) and afternoon (17:00-18.00pm). The sampling was done in the period of September 1, 2009 to 30 April 2011 in Badi Island, Spermonde Islands. Anomaly data analysis for SST was based on the normal average temperature of 29.08°C in 2004-2006. Rainfall data set (2004-2011) in Spermonde Islands were obtained from Maritime Meteorology Station (BMKG) of Paotere Makassar.

Results and Discussion

Coral reproduction pattern

Seven species from genus *Acropora* corals that have been known their gonad maturation and spawning time, namely: *A. loripes*, *A. digitifera*, *A. cerealis*, *A. nasuta*, *A. aculeus*, *A. nobilis* and *Acropora sp* in Spermonde Islands (Tables 2 and 3). This study was also recorded date and month that determined within the moon cycle days. On March 19, 2011 to coincide with the full moon on one night before full moon. Recorded spawning event in the same date and night time (hour) of four species of *Acropora*: *Acropora nasuta*, *A. aculeus*, *A. digitifera* and *A. cerealis*. Likewise in the previous year, the *Acropora loripes* spawned on March 4, 2010 to

coincide with two days before full moon. The last *Acropora sp* was recorded on March 8, 2012 that looked visually mature gonads in Badi Island. All species of *Acroporoid* spawned in March for three years while around the full moon phase. These phenomenon of many species of *Acroporoid* which is not suggest 'mass spawning', but this is namely 'the multispecific synchronous spawning' indicator. So Rani and Jompa (2005) found that *A. nobilis* had the mature gonad and spawned in February 2002 (Table 2). All of the time of gonads mature from small polyps of *Acropora* had been seing on the raining or end of raining seasons (February and March).

The studies of *Acropora* reproduction have been done in three Gili in Lombok Strait observing *A. nobilis* and *A. cytherea* gonads (Bahtiar, 2002) and in Panjang Island of Jepara was the *Acropora aspera* (Munasik and Widjtmoko, 2004). Multi-species coral spawning accoured in the tropic water in Singapore (Guest et al., 2002) and 12 species in Karimunjawa Islands in Java Sea in 1995 (Tomascik et al., 1997), and in the Sambangan Island Karimunjawa 2009 (Permata et al., 2012). In addition, as many as 17 species of the genus *Acropora* are ripen gonads simultaneously around the coral reefs of the Red Sea Hurgada (Hanafy et al., 2010) indicated of synchronous spawning in tropics.

Table 1. Spawning time of *Acroporoid* in Spermonde Islands

Species	Location	General dates	Moon phase	Time
<i>Acropora loripes</i>	Langkai Island	March 14, 2010	+1 FM	18.15 H
<i>Acropora digitifera</i>	Bone Tambu Island	March 19, 2011	0 FM	18.10 L
<i>Acropora cerealis</i>	Bone Tambu Island	March 19, 2011	0 FM	18.20 L
<i>Acropora nasuta</i>	Bone Tambu Island	March 19, 2011	0 FM	18.22 L
<i>Acropora aculeus</i>	Bone Tambu Island	March 19, 2011	0 FM	18.22 L
<i>Acropora sp</i>	Badi Island	March 8, 2012	-1 FM	

Note: L= in the laboratory, H= habitat, FM= full moon (+) after (-) before

Table 2. Timing of Gonad Maturation and Spawning Reefs in Spermonde Islands.

Seasons	Seasons (month)	Spawning on	Species
Rain	December	February	<i>A.nobilis</i>
	January February March	March	<i>A. loripes</i> , <i>A. digitifera</i> <i>A. cerealis</i> , <i>A. nasuta</i> , <i>A. aculeus</i> <i>Acropora sp</i>
First Transition	April, May, June	No data	
Summer	July August September	August September	Bigger polyp coral (<i>Euphyllia</i> , <i>Galaxea</i>) Mustafa (2011); Patiung (2011)
Second Transition	October November	No data	

Table 3. Model of Coral Spawning and Sex in Spermonde Islands

No	Type of Coral Spawning	Spawning Mode	Sex
1	<i>Acropora loripes</i>	-	hermaprodite
2	<i>Acropora digitifera</i>	Broadcaster	hermaprodite
3	<i>Acropora cerealis</i>	Broadcaster	hermaprodite
4	<i>Acropora nasuta</i>	Broadcaster	hermaprodite
5	<i>Acropora aculeus</i>	Broadcaster	hermaprodite
6	<i>Acropora nobilis</i>	Broadcaster	hermaprodite
7	<i>Acropora spp</i>	-	hermaprodite

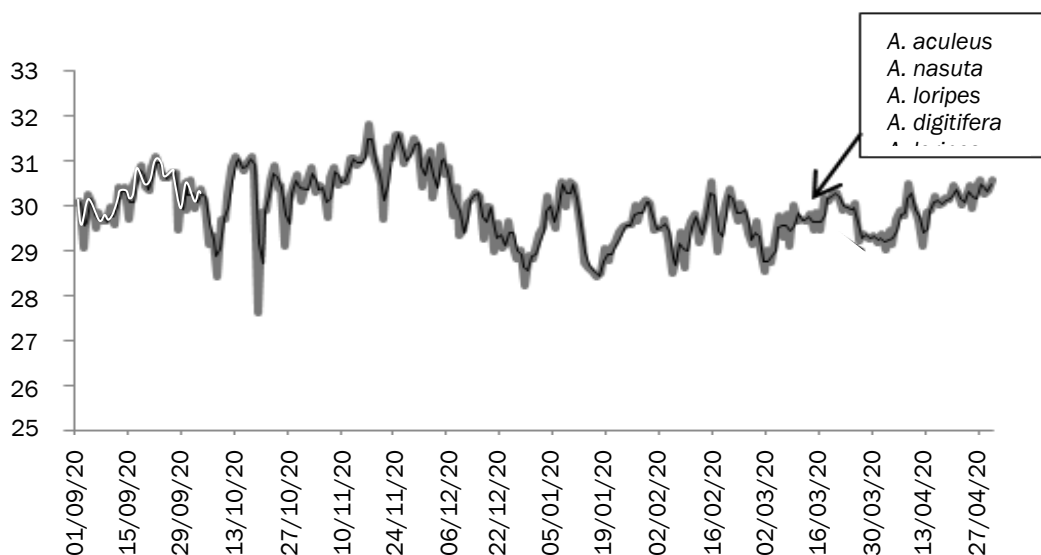


Figure 1. Sea water temperature (SST) in Spermonde Islands, Makassar (September 2010–April 2011)

Four species *A. digitifera*, *A. nasuta*, *A. cerealis* and *A. aculeus* from Bone Tambung island took place multispecific synchronous spawning at the same hour (18:10 to 18:22). While *A. loripes* spawned in Langkai Island reef by insitu breakage coral branch. Rani and Jompa (1996) reported *A. nobilis* in Barrang Lompo spawned in 2004 different years with the four species of *Acropora* from the othes site of Spermonde Islands. Fukami *et al.* (2003) studied for the *A. digitifera* and *A. gemmifera* spawned between the hours of 21:00 to 22:00 in off southern Japan reefs, while *A. tenuis* spawned hours of 19:00 to 20:00 on the GBR. Synchrony of coral spawning time depends on the time of sunset, which differ according to the latitude of the earth due to coral spawning usually begin just after sunset (Brady *et al.*, 2009).

Coral reproduction patterns

In Tables 2 and 3 could be seen that in Spermonde Islands, coral *Acropora nobilis* spawned in February, while *A. loripes*, *A. digitifera*, *A. cerealis*, *A. nasuta*, *A. aculeus* and *Acropora sp* matured gonads and spawned in March (2010, 2011 and 2012). Another studied in Karimunjawa reef that

Acroporoid took place spawning on March 2009 (Permata *et al.*, 2012). From these studies, we can say that Acroporoid corals had have mature gonad and spawning on March all the year when the end of rainy season (Table 3). While some bigger polip corals such as *Heliofungia actiniformis* (Romawanti, 2006), *Euphyllia glabrescen* (Patiung, 2011) and *Galaxea* (Mustafa, 2011) had gonad mature in the dry season.

In normally, the rainy season accour during October to April, while the dry season during April to October (Nontji, 2006). We had not found the mature gonads and spawning of any scleractinian corals. coral reproduction occur along the year (Munasik, 2002), bianual multispecific spawning (Permata *et al.*, 2012) in Indonesia (Java Sea case study). Munasik (2002) divided in three periods of coral reproduction pattern, namely: 1) spawning before the rainy season (October-November), 2) spawning in time and after the rainy season (January to April), 3) Spawning along the year or do not influenced by season, such as brooding coral. Based on these seasons, Acroporoid corals were placed on the second category is spawning in time and after rainy season on January to April. In Magnetic island

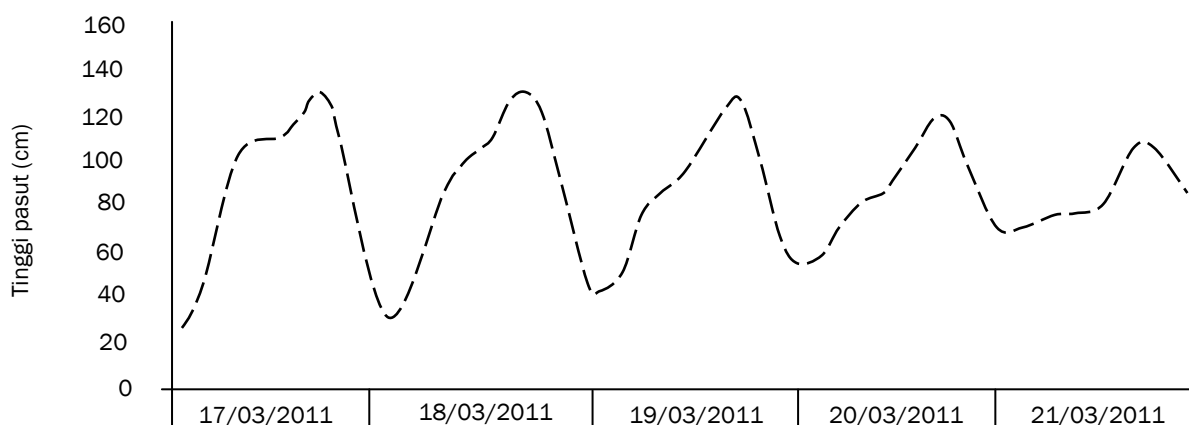


Figure 2. High and low tides in March 17 - 21 th , 2011 of Spermonde Islands, Makassar and its position of the high tide while spawning time of Acroporids

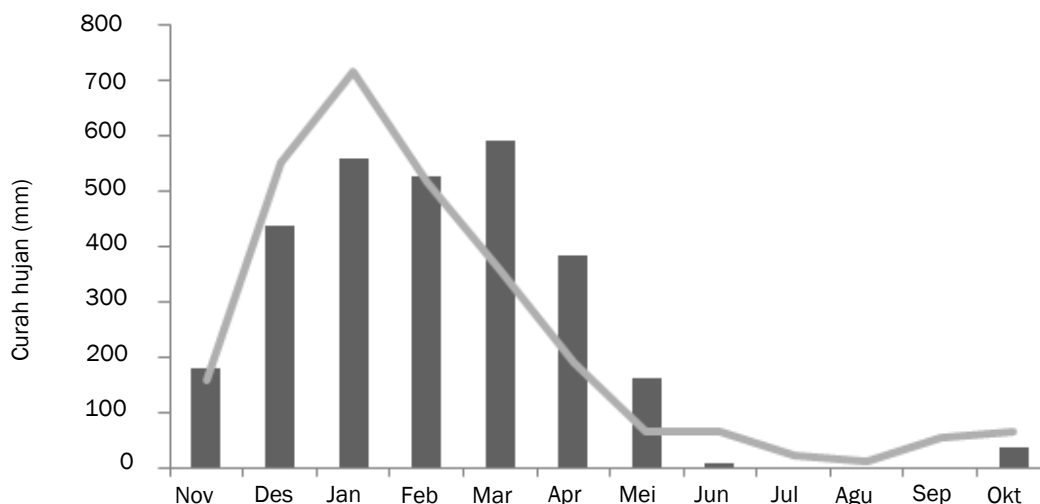


Figure 3. Average of rainfall allthe year in 2011 and average of (2004-2011) in Spermonde Island, Makassar
Keterangan : — = T.2004-2011, █ = T.2011

Acropora tenuis spawned in November and October, and in the GBR the *A. tenuis* took place in December (Wallace, 1999; Willis et al., 1985). While *A. millepora* was commonly spawning in November, December in Central GBR (Wallace, 1999), Richmond and Hunter (1990). In the Gulf of Eilat, six species of *Acropora* have a wide spawning time during May-June and June to July depending on the year (Shlesinger et al., 1998)

Spawning model and colony sex of Acropora

Coral spawning models and sex that directly observed on the specimen. All species of observed released sperm and eggs into the water column and fertilization took place outside of the polyps, namely broadcasting spawning. They were also had hermaphrodite type of sex which had eggs and sperms from same parent and polyps (Table 3). Almost all of *Acropora* genus showed synchronous

spawning mode (broadcaster) and hermaphrodites sex (Richmond and Hunter, 1990; Wallace, 1999; Baird et al., 2009a), except of *Acropora palifera*, *A. bruegemmani* and *A. togianensis* which released planulae larvae or brooder (Wallace, 1999). Richmond and Hunter (1990) determined that approximately 68% of all coral species in the world are hermaphrodites.

Environmental cues of coral reproduction

Sea surface temperature (SST) recorded during four months (January-April 2011) in Spermonde island ranged between 26.5-32.5°C with an average of 29.7±0.8°C. The average SST was higher than the annual average temperature of 29.08°C (Figure 1). At the time of coral spawning took place on March 19th 2011, SST recorded 30.3°C, it was 1 degree higher than recent and the annual average temperature. However, in the seven

days before and after spawning, water temperature ranged from 29.0 to 30.8°C. According to Baird *et al.* (2009b), SST was environmental factors that affect to the reproductive process of gametogenesis and scheduling the annual cycle of spawning. Although spawning occurs at water surface temperature (SST) in particular, but the temperature is not the only factor that could determine the time of spawning in the Australian east coast and west coast with the same SST pattern (Baird *et al.*, 2009b). On the other hand, changes in solar radiation are good predictor or marker that empirically determine the spawning time of *Montastrea annularis* in the Caribbean Sea (van Woessik *et al.*, 2006).

While *Acropora* spp coral spawning event in Spermonde Islands (Figure 2) were around the peak of high tide with a 0.9 meter of tidal range, the tidal type was semidiurnal (Nontji, 2006). The study revealed a relationship between time of spawning with tidal position. Coinciding with that, the position of the full moon is called 'supermoon' which were momentary calm ocean water masses signed water current almost to zero velocity, it was an opportunity to conduct coral spawning and fertilization. Annual rainfall variability in different areas affect the time of gonad maturity and spawning of corals. Coral spawned on March were observed in tree years namely 2010-2011-2012 (Figure 4). The highest peak of rainfall during 2004-2011 were occurred in January of about 714.83 mm. While in 2011 the rainfall almost evenly distributed in January-March with the highest peak on March of 592.5 mm lower than the annual average.

Conclusion

Reproduction of corals *Acropora* spp in Spermonde islands occurred during the rainy season between February and March. All of the Acroporidae were hermaphrodites and spawned in the same time as an indicator of synchronous spawning. The broadcasting event took place at night time for several minutes after sunset (18:10 to 19:00) during full moon and after full moon (0-2 AFM). The corals were spawned around the peak of high tide with an average daily temperature of 30.3°C and the waters are still in dense of rainfall during March.

References

Bahtiar, I. 2002. Promoting recruitment of Scleractinian corals using artificial substrate in the Gili Indah, Lombok Barat Indonesia. *Proc 9th International Coral Reef Symposium*. Bali Indonesia, October 23-27, 2000. p 425-430.

- Baird, A.H., S.J. Campbell, A.W. Anggoro, R.L. Ardiwijaya, N. Fadli, Y. Herdiana, T. Kartawijaya, D. Mahyidin, A. Mukminin, S.T. Pardede, M.S. Pratchett, E. Rudi & A.M. Siregar. 2005. Acehese reefs in the wake of the Asian tsunami. *Curr. Biol.* 15:1926-1930.
- Baird, A.H., T.P. Hughes, S. Nojima, M.S. Pratchett, R. van Woessik & H. Yamasaki. 2009a. Latitudinal pattern in spawning synchrony in the Acropora. Japan vs Great Barrier Reef. *Galaxea*. 11:37
- Baird, A.H., J.R. Guest & B.L. Willis. 2009b. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annu. Rev. Evol. Syst.* 40:551-571.
- Brady, A.K., J.D. Hilton & P.D. Vize. 2009. Coral spawn timing is a direct response to solar light cycles and is not an entrained circadian response. *Coral Reefs*. 28:677-680.
- Fukami, H., M. Omori, K. Shimoike, T. Hayashibara & M. Hatta. 2003. Ecological and genetic aspects of reproductive isolation by different spawning times in Acropora corals. *Mar. Biol.* 142:679-684.
- Guest, J.R., L.M. Chou, A.H. Baird & B.P.L. Goh. 2002. Multispecific synchronous coral spawning in Singapore. *Coral Reefs*. 21:422-423.
- Hanafy, M.H., M.A. Aamer, M. Habib, A.B. Roupheal, & A.H. Baird. 2010. Synchronous reproduction of corals in the Red Sea. *Coral Reefs*. 29:119-124.
- Harrison, G.D., J.K. Oliver, C.C. Wallace & B.L. Willis. 1984. Mass spawning in tropical reef corals. *Science*. 223:1186-1189.
- Loya, Y., K. Sakai & A. Heyward. 2009. Reproductive pattern of fungiid corals in Okinawa, Japan. *Galaxea*. 11:119-129.
- Mendes, J.M. & J.D. Woodley. 2002. Timing of reproduction in *Montastrea anularis*: relationship to environmental variables. *Mar. Ecol. Prog. Ser.* 227:245-251.
- Munasik. 2002. Reproduksi seksual karang di Indonesia: Suatu kajian. Konferensi Nasional III Wilayah Pesisir dan Laut. Pengelolaan Sumberdaya Pesisir dan Lautan Indonesia; Bali 21-24 Mei 2002:157-165.
- Munasik & W. Widjatmoko. 2004. Sexual reproduction of coral *Acropora aspera* from

- Panjang Island: (I. Gametogenesis). *Ilmu Kelautan*. 9(4):211-216.
- Nontji, A. 2006. Laut Nusantara. PT. Djambatan. Jakarta.
- Oliver, J.K, R.C.Babcock, P.L. Harrison, & B.L. Willis. 1988. Geographic extent of mass spawning: clues to ultimate causal factors. *Coral Reefs*. 27:123-132.
- Patiung, R. 2011. Keterkaitan Sinyal Reproduksi Alam dalam Proses Reproduksi dan Perkembangan Sel Telur Karang Keras (*Scleractinia*) Polip Besar Di Pulau Badi Makassar. *Tesis*. Sekolah Pascasarjana Institut Pertanian Bogor.
- Poinski, M. 2004. Underwater sex: Virgin Islands coral expected to spawn soon. Cyber Diver News Network (CDNN) Eco News Science - Underwater Sex Virgin Islands Corals Spawn Soon.mht. <http://WWW.CDNN>. (10 April 2008).
- Mustafa, R. 2011. Studi perkembangan gonad karang keras *Galaxea fascicularis* (Linnaeus 1767) di Pulau Badi Kabupaten Pangkep, Sulawesi Selatan. [Thesis]. Sekolah Pascasarjana Institut Pertanian Bogor.
- Permata D, E Indrayanti, D Haryanti, L Fika, A Arfiyan & A. Ahmad 2012. Bilingual Multispecific Spawning in Karimunjawa Archipelago, Indonesia. *Coral Reefs*, 31:907. DOI 10.1007/s00338-012-0909-9.
- Rani, C. & J. Jompa. 2005 Tingkahlaku memijah karang *Acropora nobilis* dan *Pocillopora verrucosa* di terumbu karang tropik Pulau Barrang Lompo, Makassar. *Torani*. 15:221-228.
- Richmond, R.H. & C.L. Hunter. 1990. Reproduction and recruitment of corals: comparisons among the caribbean, the Tropical Pacific and the Red Sea. *Mar. Ecol. Prog. Ser.* 60:185-203.
- Romawanti, S.A. 2006. Studi perkembangan gonad karang *Heliofungia actiniformis* (Fungiidae) di Pulau Barrang Lompo Makassar Sulawesi Selatan [Bachelor Degree]. Makassar: Jurusan Biologi FMIPA, Universitas Hasanuddin.
- Shlesinger, Y. & Y. Loya. 1985. Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. *Science Magazine*. <http://www.sciencemag.org.html> [3 April 2008].
- Shlesinger Y, T.L. Goulet & Y. Loya. 1998. Reproductive pattern of scleractinian corals in the northern Red Sea. *Mar. Biol.* 132:691-701.
- Szmant, A.M. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs*. 5:43-54.
- Thamrin. 2006. Karang: Biologi reproduksi dan ekologi. Pekanbaru: Minamandiri Press.
- Tomascik, T., A.J. Mah, A. Nontji & M.K. Moosa. 1997. The Ecology of the Indonesian Seas Part One. Periplus Hongkong.
- Woesik, R., F. Lacharmonise & S. Koksai. 2006. Annual cycles of solar isolation predict spawning times of caribbean corals. *Ecol. Lett.* 9:390-398.
- Wallace, C.C. 1999. Staghorn Corals of the World: A Revision of the Genus *Acropora*. Australia. CSIRO.
- Wallace, C.C. & J. Walstenholme. 1998. Revision of genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) in Indonesia. *Zoo. J. Linnean Soc.* 123:199-384.
- Willis, B.L., R.C. Babcock, P.L.Harrison, J.K. Oliver & C.C. Wallace. 1985. Pattern in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. *Proc. 5th Int. Coral Reef Symp. Tahiti*. 4:343-348.