

Sexual Reproduction of *Anthoplexaura dimorpha* (Gorgonacea: Octocorallia) from Munseom, Jeju Islands, Korea

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Abstract: The gorgonian coral *Anthoplexaura dimorpha* Kükenthal, 1908 (Gorgonacea: Octocorallia) is abundant in Jeju Islands, Korea. To investigate the sexual reproduction of this species, we surveyed the morphology and cycle of gametogenesis. 5-6cm long fragments from 3-7 randomly chosen colonies were collected monthly at a depth of 12-24m in the water surrounding Munseom from August 2003 to August 2005. This species was gonochoric with sex ratio of 1.86:1 (female to male), and had one annual reproductive cycle affected by elevation of seawater temperature. Oogenesis was longer than spermatogenesis as 12 months in female and 6 months in male. The planulae were not observed from the field survey and histological sections, which suggested broadcast spawning for the reproductive mode in this species. The possible spawning events may occur after the seawater temperature attain to the annual peak in September.

Key words: sexual reproduction, gametogenesis, *Anthoplexaura dimorpha*, gorgonian coral, Anthozoa

Gorgonian corals belong to the subclass Octocorallia have three mode of reproduction: the broadcasting of gametes; the internal brooding; the external surface brooding of planulae (Kinzie, 1970; Grigg, 1977; Alino and Coll, 1989; Lasker et al., 1996). The sexual reproductive patterns of gorgonians are summarized Table 1. Generally, the brooding of planulae at inside or outside mother colonies is dominant, although some species of family Plexauridae have broadcasting mode (Kinzie, 1970; Goldberg and Hamilton, 1974; Brazaeu and Lasker, 1989). Gonochorism is dominant in the gorgonians such as in the soft corals (Hwang and Song, 2007). Hermaphroditism is not found in

the gorgonians until now.

In octocorals, the gonads of female and male develop within the gastrodermal mesenteries, especially ventral and lateral ones, and then detach from the mesenteries during the maturation (Benayahu 1991; Gutiérrez-Rodríguez and Lasker 2004).

In general, gametogenesis of cnidarians may be affected by environmental factors such as sea water temperature, lunar cycle, and energy resources (Campbell 1974; Ben-David-Zaslow et al. 1999; Zeevi Ben-Yosef and Benayahu 1999).

Most studies of the life history on gorgonians have been mainly conducted from the Great Barrier Reefs of Australia, Mediterranean Sea, Red Sea, California, Florida, Jamaica, Panama, and Caribben (Glodberg and Hamilton 1974; Grigg 1977; Alino and Coll 1989; Brazaeu and Lasker 1989; Allemand 1992; Zeevi Ben-Yosef and Benayahu 1999; Kruger et al. 1998; Kapela and Lasker 1999). To date, little information is known about the reproduction of gorgonians distributed in Pacific of North-East Asia. *Anthoplexaura dimorpha* Kükenthal, 1908 (Plexauridae: Holaxonia) as a fan-shaped gorgonian (Fig. 1) is abundant in the soft coral community on the southern coast of Jeju Islands, Korea. Of the same family, *Muricea californica* (Grigg 1977), *Muricea furticosa* (Grigg 1977), *Muriceopsis flavida* (Kinzie 1970), *Eunicella stricta* (Theodor 1967), *Paramuricea clavata* (Coma et al. 1995), *Eunicella clavigera* (Kinzie 1970), *Plexaura kuna* (Brazaeu and Lasker 1989; Lasker et al 1996), and *Plexaura homomalla* (Goldberg and Hamilton 1974) were surveyed on the reproductive pattern. However, reproductive studies on *A. dimorpha* have not been conducted in the world.

In this paper, we described morphological aspects of oogenesis and spermatogenesis, quantitative data regarding sex ratio, annual reproductive cycle of gametogenesis in *A.*

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Table 1. Reproductive patterns in various gorgonians studied so far

Species	Reproductive patterns	Localities	References
Suborder Scleraxonia			
Family Briareidae			
<i>Briareum asbestinum</i>	Gonochoric external surface brooding	Panama	Brazaeu and Lasker (1990)
<i>Briareum stechei</i>	Gonochoric external surface brooding	Australia	Alino and Coll (1989)
Family Coralliidae			
<i>Corallium rubrum</i>	Gonochoric internal brooding	Mediterranean	Allemand (1992)
Family Melithaeidae			
<i>Acabaria biserialis</i>	Gonochoric internal brooding	Red sea	Ben-Yosef and Benayahu (1999)
Suborder Holaxonia			
Family Gorgoniidae			
<i>Pseudoptergorgia bipinnata</i>	Gonochoric internal brooding	Jamaica	Kinzie (1970)
<i>Pseudoptergorgia elizabethae</i>	Gonochoric external surface brooding	Jamaica	Kinzie (1970)
Family Plexauridae			
<i>Muricea californica</i>	Gonochoric internal brooding	California	Grigg (1977)
<i>Muricea furticosa</i>	Gonochoric internal brooding	California	Grigg (1977)
<i>Muriceopsis flavida</i>	Gonochoric internal brooding	Jamaica	Kinzie (1970)
<i>Eunicella stricta</i>	Gonochoric internal brooding	Mediterranean	Theodor (1967)
<i>Paramuricea clavata</i>	Gonochoric external surface brooding	Mediterranean	Coma et al. (1995)
<i>Eunicea clavigera</i>	Gonochoric broadcasting	Jamaica	Kinzie (1970)
<i>Plexaura kuna</i>	Gonochoric broadcasting	Panama	Brazaeu and Lasker (1989); Lasker et al. (1996)
<i>Plexaura homomalla</i>	Gonochoric broadcasting	Florida	Goldberg and Hamilton (1974)
<i>Pseudoplexaura porosa</i>	Gonochoric broadcasting	Caribbean	Kapela and Lasker (1999)
Family Primnoidae			
<i>Fannyella rossii</i>	Gonochoric internal brooding	Antarctic	Orejas et al. (2007)
<i>Fannyella spinosa</i>	Gonochoric internal brooding	Antarctic	Orejas et al. (2007)
<i>Thouarella</i> sp.	Gonochoric internal brooding	Antarctic	Orejas et al. (2007)



Fig. 1. A colony of *Anthoplexaura dimorpha* from Munseom, Jejudo island, Korea.

dimorpha including the comparison of gonadal development with environmental factors

MATERIALS AND METHODS

Collection of specimens

Samples of *A. dimorpha* colonies were collected at Munseom of Jejudo Is. (33°22'N, 126°33'E, Fig. 2) locating at the temperate zone showing somewhat subtropical climate affected by the Taiwan branch stream of the Kuroshio warm current. The water temperatures of study area range from 14 to 26°C depending on season. Colonies are normally distributed on the horizontal and vertical rocky substrata from 10 to 30 m in depth (researcher's observation).

5-6 cm long fragments from 3-7 randomly chosen colonies (height > 30 cm) were sampled at a depth of 12-24 m using SCUBA, during the period from August 2003 to August 2005. These samples were fixed in 4% formaldehyde with sea water for 24 hours. In the laboratory, they were rinsed with tap water, and then preserved in 70% ethanol.

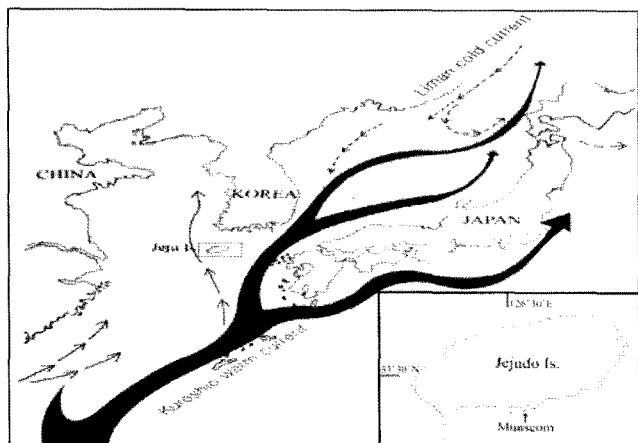


Fig. 2. Location of Jejuo islands with the sampling site, Munseom, on the south coast of Korea. The Kuroshio warm current flows around Jejuo Is. Solid and dot line indicate the warm and cold current, respectively.

Dissection and histology

Preserved 2-3 cm long fragments from each sample were dissected under a stereomicroscope (Zeiss SV6) for surveying about the sexuality of each colony and the external feature of the gonads. The sex ratio within the population was measured by calculating the number of female and male colonies from June to November through the study periods when the oocytes and spermaries were observed together.

To investigate the cycle of gametogenesis, about 100 gonads per a colony were taken out under a stereomicroscope (Zeiss 475002). The longest and shortest axes of oocytes and spermaries were measured with a micrometer under a light microscope (Olympus CX-40).

To examine the gametogenic stages and the reproductive mode, histological sections were prepared. For histological section, the 0.5-1.0 cm fragments from the samples fixed in 70% ethanol were decalcified in the 10% (w/v) EDTA solution for 7 days. They were dehydrated in a graded series of ethanol, cleared in ethanol-xylene mixtures and then infiltrated with a series of xylene-paraffin mixtures. After embedding the fragments into paraffin, were cut crossly and longitudinally into 8 μ m thick serial sections by using microtome. Sections were stained with Harris Hematoxylin and eosin Y, and then mounted in the canada balsam for the preparing the permanent slides.

Images of gonads were obtained by a digital camera (Olympus 5060-WZ) attached to a stereomicroscope and a light microscope (Olympus BH2). Data of sea water temperature around the collecting site were monthly measured by using a water checker (Horiba W-23XD) during the study periods.

RESULTS

Sexuality and sex ratio

A. dimorpha was turned out to be a gonochoric through the microscopic and histological studies. Oocytes developing in female colonies continuously were observed in the all samples during the study periods, while spermaries developing in male colonies were only surveyed during summer and fall seasons, from June to November (Fig. 3). Among the total 117 colonies examined, 96 colonies having either female or male gonads were consisted of 74 females and 22 males respectively. Especially, among 74 female colonies, 41 were observed from June to November when the spermaries were occurred. So, female colonies were

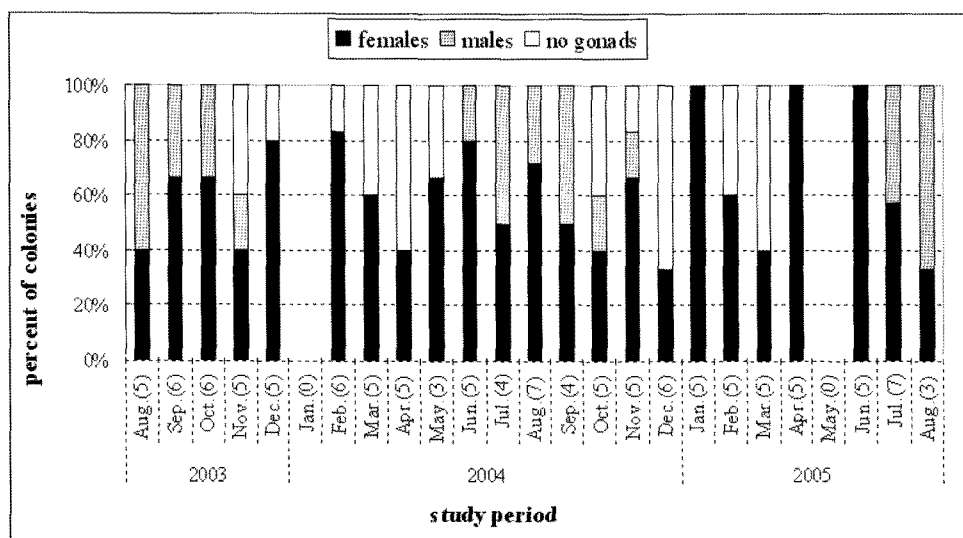


Fig. 3. Sex ratio of *A. dimorpha*. Percentage of colonies having oocytes, spermaries, and no gonads during the study period. Numbers of colonies are indicated at each column (N=117). Colonies were not collected in January 2004 and May 2005.

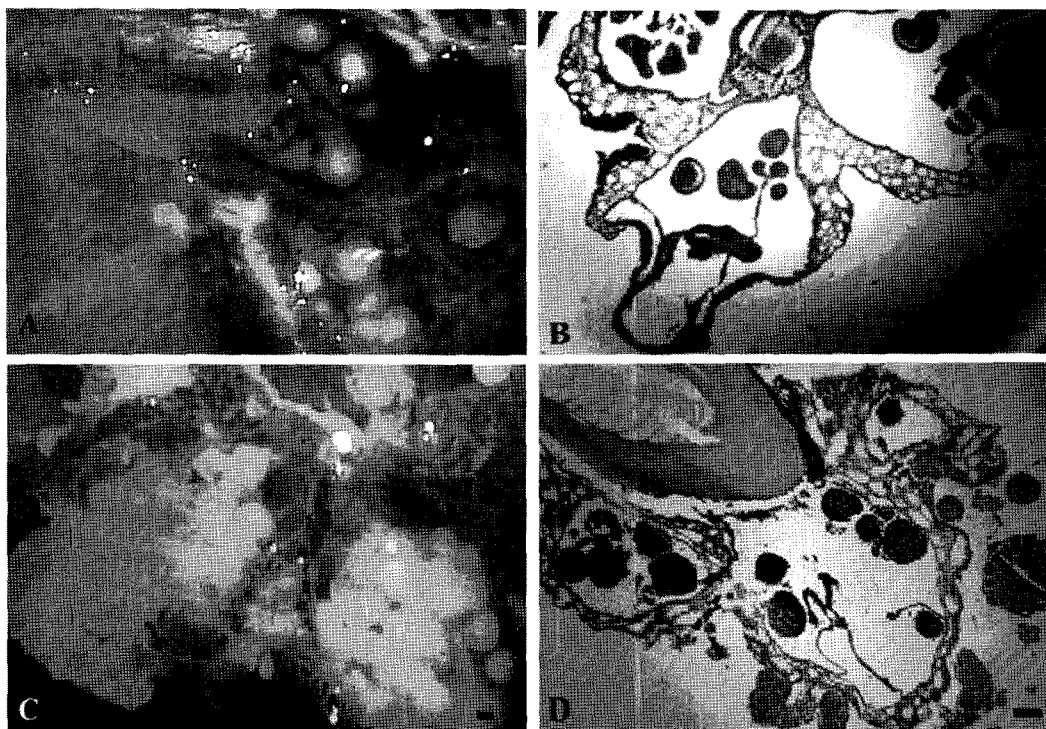


Fig. 4. Gonads of *A. dimorpha*. (A) Oocytes in female polyps. (B) General view of female polyps showing the arrangement of oocytes (C) Spermaries in male polyps. (D) General view of male polyps showing the arrangement of spermaries. Scale bars=100 μm .

Table 2. Mean diameter of gonads, which depends on gametogenic stages

Oocytes				Spermaries			
Stage	Range (μm)	Mean \pm SD (μm)	n	Stage	Range (μm)	Mean \pm SD (μm)	n
O1	<51	43 \pm 8	131	S1	<76	56 \pm 10	46
O2	51~175	114 \pm 34	1424	S2	76~175	136 \pm 99	325
O3	176~275	211 \pm 28	559	S3	176~275	214 \pm 27	294
O4	276>	359 \pm 62	252	S4	276>	315 \pm 36	75

significantly abundant in the population showing the sex ratio of 1.86:1.

Gametogenesis

The gonads of both sexes were developed from the gastrodermal mesenteries within the calyx of autozooid, and moved into the gastrovascular cavity (Fig. 4A and 4C). Immature gonads were attached to the mesenteries by pedicles, and gradually detached themselves from the mesenteries as they matured (Fig. 4B and 4D). Oogenic and spermatogonic development were divided into four stages depending on maturity (Table 2) based on Schleyer et al. (2004).

Oogenesis

Oocytes were covered with follicular layer and had prominent nucleus with a nucleolus, and the color of oocytes changed from cream to red as they matured. The earliest oocytes, stage 1, having the large nuclei were

embedded in the gastrodermal mesenteries and clustered together (Fig. 5A). These oocytes were transparent in color owing to a lack of cytoplasm. The diameter of these primordial oocytes was under 50 μm , with an average of 43 \pm 8 μm (mean \pm SD, n=131). As the oocytes developed into stage 2, the color of them changed to opaque owing to accumulation of cytoplasm around nuclei, and they were separately connected to mesenteries by pedicles (Fig. 5A). These stage 2 oocytes ranged from 51 to 175 μm in diameter having a mean diameter of 114 \pm 34 μm (n=1424). By the stage 3 oocytes, which were detached from the mesenteries and ranged in diameter from 176 to 275 μm (n=559) having an average of 211 \pm 28 μm (n=559), the accumulation of yolk had started having vacuoles patchily distributed in the ooplasm, so that these oocytes became orange in color (Fig. 5B). Nucleus moved towards one side of the oocyte, and nucleolus was always positioned on the periphery of the nucleus. The stage 4 oocytes that reached their full size changed to red in color and had sharp edges

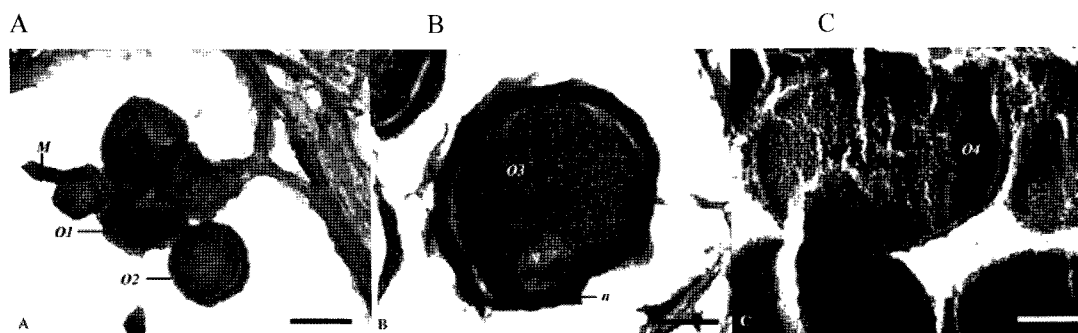


Fig. 5. Oogenesis of *A. dimorpha*. (A) Stage 1 oocyte (O1), Stage 2 (O2). (B) Stage 3 (O3). (C) Stage 4 (O4). M, mesentery; N, nucleus; n, nucleolus. Scale bars=100 μ m.

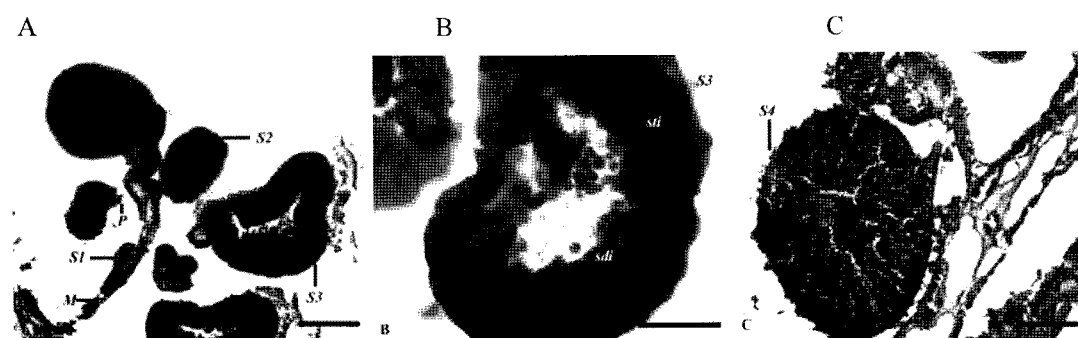


Fig. 6. Spermatogenesis of *A. dimorpha*. (A) Stage 1 sperm-sac (S1), Stage 2 (S2), Stage 3 (S3). (B) Stage 3 (S3). (C) Stage 4 (S4). M, mesentery; sdi, spermatid; sti, spermatocytes. Scale bars= 100 μ m.

and numerous granules containing yolk (Fig. 5C). The oocytes ranged in diameter over 276 μ m, with a maximum of 540 μ m and an average of 359 \pm 62 μ m (n=252).

Spermatogenesis

The stage 1 spermaries containing small clusters of spermatogonia were embedded in the mesenteries (Fig. 6A). The diameter of these transparent primordial spermaries was under 75 μ m, with a mean diameter of 56 \pm 10 μ m (n=46). By the stage 2, the opaque spermaries having spermatocytes moved into the gastrovascular cavity, and were attached to mesenteries by pedicles (Fig. 6A). At this stage, spermaries had distinct boundaries and an average of 136 \pm 99 μ m (n=325) ranging from 76 to 175 μ m. At the stage 3, spermatocytes were arranged in the periphery of spermaries, and the centripetal maturation gradient in that less mature and larger spermatocytes were located on the periphery of the spermaries, while more mature and smaller ones (spermatids) were located in the center were generated as they grew (Fig. 6B). The range of diameter in spermaries was from 176 to 275 μ m, with an average of 214 \pm 27 μ m (n=294). The stage 4 spermaries were fully matured and had spermatozoa with sperm tails arranged in arrays (Fig. 6C). At this stage, spermaries was dark opaque cream in color and ranged over 276 μ m having a maximum of 425 μ m and a mean diameter of 315 \pm 36 μ m (n = 75).

Annual reproductive cycle and spawning

Anthoplexaura dimorpha had one reproductive cycle per a year. While spermaries were only observed from June to November in 2003 through 2005, oocytes were detected at all times of the year except in January 2004 and May 2005 when the samplings were not conducted (Fig. 7 and 8). The annual cycle of *A. dimorpha* showed a distinct correlation with seawater temperature (Figs. 9 and 10).

In female, stage 1, stage 2, and stage 3 oocytes were almost found throughout the study periods, while stage 4 oocytes were detected only from August to December in 2004, from June to October in 2004, and from April and August in 2005 (Fig 9). Through the study, frequency of immature oocytes (stage 1 and 2) began to increase during the period from October 2003 when the seawater temperature started to decrease and marked high frequency ranging from 68 to 82 % until June 2004. The frequency of immature oocytes decreased from July 2004 having a fall with 43 %, and increased from October 2004 to April 2005 showing a distinct rise over 74%. And again, their frequency sharply dropped from June 2005. The stage 3 oocytes had a distinct rise and fall in frequency over the year. Their frequency decrease between September 2003 and April 2004, and increased between May 2004 and September 2004. And the frequency of these vitellogenic oocytes dropped from October 2004, and increased from May 2005.

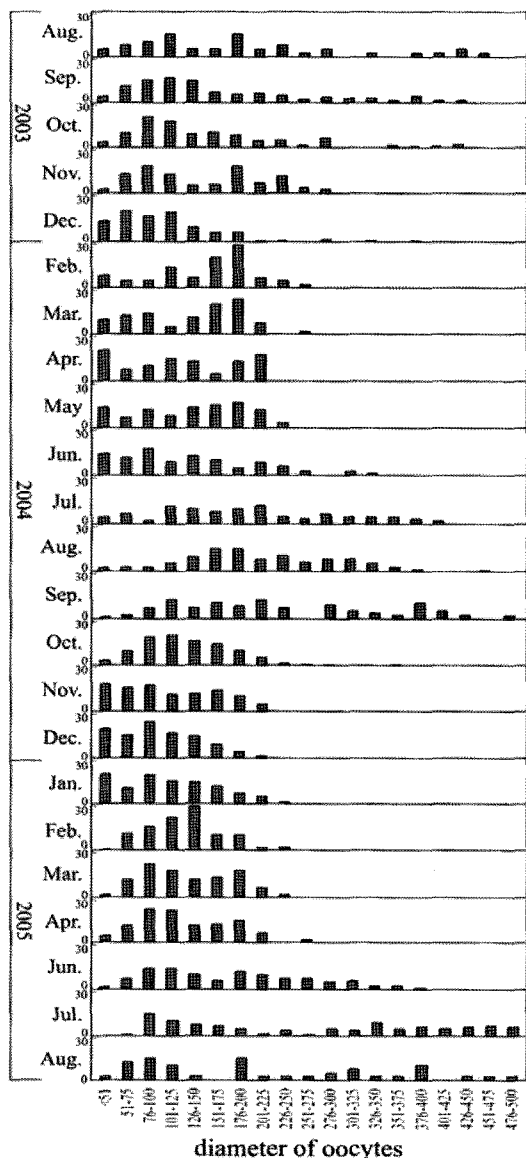


Fig. 7. Monthly size-frequency distributions of oocytes during the study period (n=2366). diameter unit: μm .

Mature oocytes, stage 4, were highly found from summer (July) to early fall (September) seasons when the seawater temperature reached at a peak.

Spermatogenesis occurred during a maximum period of 6 months when the seawater temperature was high over 18°C, which is short comparing with oogenesis (Fig. 10). Stage 1 spermaries were produced highly with first 2 months (from June to July 2004) showing a slightly high frequency, and their frequency sharply dropped from August 2004. The frequency of stage 2 spermaries was constantly high with ranging from 20 to 70 %, and these spermaries were observed through the study periods. Frequency of stage 3 and stage 4 spermaries increased from July 2004, and reached a peak at August 2004 when the seawater temperature was recorded at the highest value.

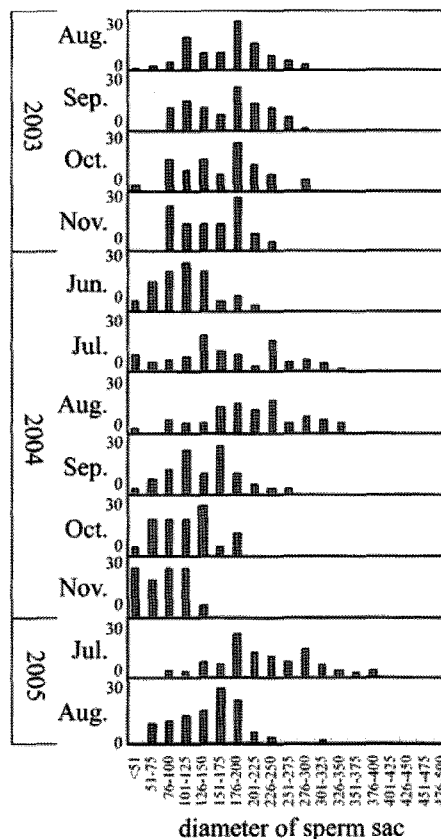


Fig. 8. Monthly size-frequency distributions of spermaries during the study period (n=740). diameter unit: μm .

And frequency of mature spermaries (stage 4) remarkably decreased in September 2004, and these spermaries were not observed from October 2004.

Brooding of embryos or larvae internal or external of polyps were not found from the histological sections and dissected mother colonies, which suggested broadcast spawning for the reproductive mode of *A. dimorpha* although the actual spawning events were not observed. The number of the mature oocytes and spermaries abruptly decreased in October 2003 and September 2004 (Figs. 7 and Fig. 8), presumably suggesting the spawning event at these times.

DISCUSSION

Sexuality, sex ratio, and gametogenesis

Anthoplexaura dimorpha shows sexual pattern of gonochorism found in the most of gorgonians investigated so far (Kinzie 1970; Goldberg and Hamilton 1974; Grigg 1977; Alino and Coll 1989; Gutiérrez-Rodríguez and Lasker et al. 2004). And also, gonochorism is known to be the dominant reproductive pattern in the soft corals belonging to octocorals together with gorgonians, although a few species have a hermaphroditic sexuality (Benayahu et

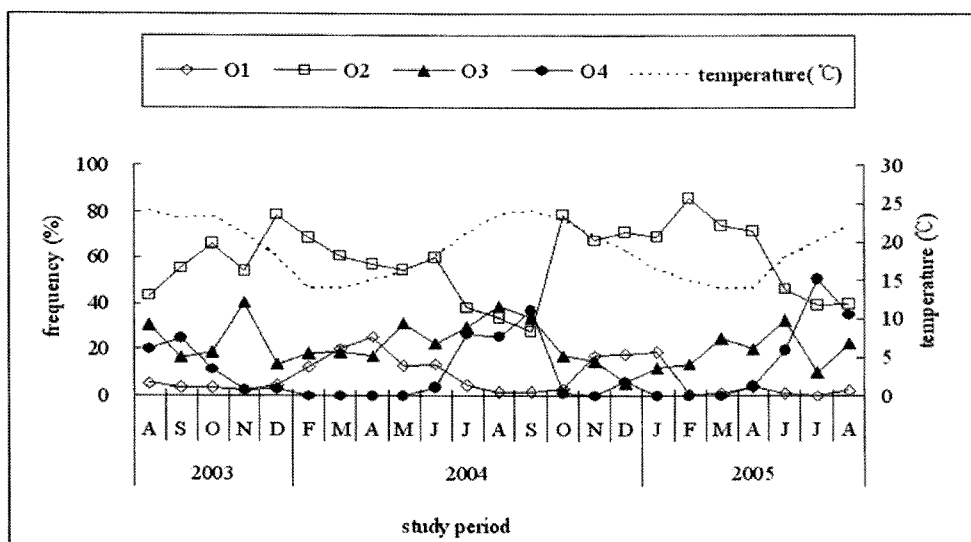


Fig. 9. Oogenic cycle in terms of sea temperature in the sampling site from August 2003 to August 2005.

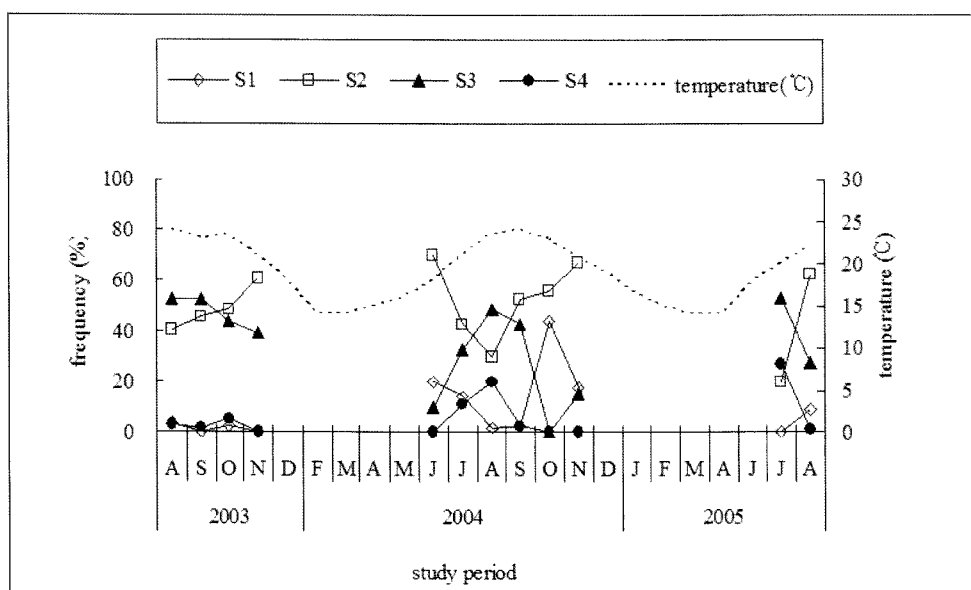


Fig. 10. Spermatogenic cycle in terms of sea temperature in the sampling site from August 2003 to August 2005.

al. 1990; Benayahu 1991; Achituv et al. 1992). In soft corals, the sexuality changes according to the geological regions; for example, *Heteroxenia elizabethae* is a gonochoric in the Great Barrier Reef, Australia, but hermaphroditic in the Red Sea (Benayahu et al. 1990). In respect of sexual evolution, gonochorism is more evolved pattern compared with hermaphroditism, so gorgonians have more developed sexual pattern than the soft corals.

The fertilization rates are mainly affected by sperm density, and so the timing of spawning, the level of synchronism, and number of male colonies in the population are extremely powerful factors to control the reproductive success (Coffroth and Lasker 1998; Zeevi Ben-Yosef and Benayahu, 1999). Spawning at the stand of tide minimizes

the sperm dilution, and consequently maximizes the fertilization (Neves and Pires, 2002; Penland et al., 2004). Synchrony of spawning which is crucial for the optimal reproductive success has been reported for other octocorals (Benayahu and Loya 1986; Kapeal and Lasker 1999; Schleyer et al., 2004). However, *Pseudopterogorgia elizabethae*, a Caribbean gorgonian, showed high levels of fertilization, despite of the asynchrony (Gutiérrez-Rodríguez and Lasker, 2004). *A. dimorpha* had gonads in different developmental stages within the same polyps during the reproductive periods, which show less synchronous spawning suggesting the continuous releasing of gametes like as *P. elizabethae*. To make up for the possible low level of fertilization in the asynchronous spawning, some species increase the number

of male colonies in the population compared with synchronous spawning species. For example, *Sarcophyton glaucum* and *Corallium rubrum*, synchronous broadcasting spawners, had a female to male ratio of 1:1, but the asynchronous spawners *Dendronephthya hemprichi*, *Calicogorgia granulosa*, and *A. dimorpha* exhibited sex ratios of 3:2, 1.5:1 and 1.8:1, respectively (Dahan and Benayahu, 1997; Tsounis et al., 2006; Schleyer et al., 2004; Cho, 2007).

The production and development of gonads in *A. dimorpha* are similar with those of other octocorals (Farrant, 1986; Benayahu, 1991; Kapela and Lasker, 1999; McFadden and Hochberg, 2003; Gutiérrez-Rodríguez and Lasker, 2004). As the result of histological studies, the gonads are generated in the mesenteries of autozooids, and then move into the polyp cavity connecting the mesenteries by pedicles. Similar to the other octocorals, the color of oocytes is changed throughout maturation by yolk synthesis, while spermaries don't exhibit a distinct color change (Dahan and Benayahu, 1997; Choi and Song, 2007; Hwang and Song, 2007). The fully matured red oocytes are visible through the external surface of polyps having transparent calyxes, which may be a good to infer the level of maturation in oocytes and consequently timing of spawning.

It is not clear if the oocyte size of *A. dimorpha* is related to the polyp size or reproductive mode. The large oocytes over 500 µm in *A. dimorpha*, *Briareum asbestinum*, and *C. granulosa* could be related to the larger size polyps (over 1.5 mm in diameter) compared with maximum oocyte diameter of 240 µm in *Acabaria biserialis* having smaller polyps (Zeevi Ben-Yosef and Benayahu, 1999; Gutiérrez-Rodríguez and Lasker, 2004; Cho, 2007). However, the study about stony corals from the Red Sea revealed no correlation between oocyte size and polyp size (Shlesinger et al., 1998). The diameter of mature oocytes in brooders, *Fannyella rossi* (200-250 µm) and *F. spinosa* (150 µm), are smaller than those of the broadcast spawners, *P. porosa* (560-800 µm) and *P. americana* (300-580 µm) (Kapela and Lasker, 1999; Gutiérrez-Rodríguez and Lasker, 2004; Orejas et al., 2007). And also, *A. dimorpha* has slightly large oocytes ranging from 276 to 540 µm, which is similar to other spawners. However, the surface brooders, *B. asbestinum* and *P. elisabethae* have large oocytes ranging from 600 to 900 µm and from 300 to 580 µm, respectively (Gutiérrez-Rodríguez and Lasker, 2004). It thus appears that oocytes size may be related to the storage of energy for dispersal and early development of planulae rather than reproductive mode, because non-feeding and azooxanthellate planulae are common among octocorals (Dahan and Benayahu, 1998; Cordes et al., 2001; Hwang and Song, 2007).

The fact that size of colony has a clear influence on reproduction in corals has been revealed by several studies. For example, only colonies over 50 cm had the gonads in

Pseudoplexaura porosa, and the colonies of *Plexaura kuna*, *P. homomalla*, and those of *P. elisabethae* smaller than 18 cm were not reproductive (Wahle, 1983; Brazeau and Lasker, 1989; Kapela and Lasker, 1999; Gutiérrez-Rodríguez and Lasker, 2004). According this rule of size-dependent reproduction, the colonies smaller than 30 cm didn't have gonads in *A. dimorpha*. Several studies indicated that colonies allocate energy resources to growth prior to reproduction to grow out of the size minimizing the mortality rates (Lasker, 1990; Babcock, 1991). So, colonies of gorgonians may not reproduce the gonads until certain size classes enhancing the survival rates.

A. dimorpha shows one seasonal gametogenic cycle from each female and male colony. While female colonies have gonad all the year round, male colonies have gonads only within a certain period of time, from summer to fall (June to November). Generally spermatogenesis is completed within a short period compared with oogenesis among octocorals (Goldberg and Hamilton, 1974; Benayahu and Loya, 1984; Brazeau and Lasker, 1990). Oogenic and spermatogenic development of *A. dimorpha* were required 12 and 6 months, respectively. The duration for the oogenic development varies among octocorals; for example, *Paramuricea clavata* (13 to 18 months), *P. kuna* (20 months), and *C. rubrum* (more than 12 months) (Kapela and Lasker, 1999; Tsounis et al., 2006). And also, the gametogenic period may differ from the geological regions in same species such as *S. glaucum* which has a shorter oogenic cycle in the Africa (16-18 months) than in Red Sea (22-23 months) (Schleyer et al., 2004).

The reproduction of corals including maturation and releasing of gametes was directly related seasonal factor such as elevating of seawater temperature (Harii et al., 2001; Neves and Pires, 2002; Vermeiji et al., 2004). In *A. dimorpha*, seawater temperature is clear trigger cue for the reproduction. The mature oocytes and spermaries were found from when the seawater temperature was over 18-21 in June to July. And possible spawning events may be occurred after the temperature reached the annual peak in September. Similarly, *D. gignatea* and *D. suenisoni*, sympatric soft corals, had reproductive cycles correlated with fluctuation of seawater temperature and released the planulae or gametes at the same periods (Choi and Song, 2007; Hwang and Song, 2007).

Several studies indicated that warm temperature could maximize the survivability of planulae by increasing the larval metamorphosis rate (Ben-Dvid-Zaslow and Benayahu, 1996; Nozawa and Harrison, 2000). In addition, food availability is crucial factor to produce the gonads for the azooxanthellate octocorals including *A. dimorpha*. Azooxanthellate corals take in directly phytoplanktons and zooplanktons in the water to get the energetic resources for growth and reproduction (Fabricius et al., 1995a and

1995b). In water of Munseom, there are two phytoplankton blooms in May (major) and September (minor) (Choa and Lee, 2000). The major algal bloom may contribute to rapid development of immature gonads into the mature ones, and minor one can offer the nutrient for the growth of colonies after sexual reproduction and early development of offspring. *A. biserialis*, the azooxanthellate gorgonian of the Red Sea, also released planulae after an algal bloom (Zeevi Ben-Yosef and Benayahu, 1999).

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