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Reproductive Biology of the Temperate Soft Coral *Dendronephthya suensoni* (Alcyonacea: Nephtheidae)

Eun-Ji Choi[1] and Jun-Im Song[2,*]

[1]*Marine Resources Research Department, Korea Ocean Research & Development Institute, Ansan 426-744, Korea;* [2]*Division of EcoScience, Ewha Womans University, Seoul 120-750, Korea*

Abstract: The azooxanthellate soft coral *Dendronephthya suensoni* (Holem, 1895) is distributed mainly around Jejudo Island, Korea. This species was determined as gonochoric with a sex ratio of 2:1 (female:male). Both female and male colonies have one gametogenic cycle a year. The annual reproductive cycle of *D. suensoni* is dependent on the seawater temperature. In particular, reproduction of the male colony showed a higher positive correlation between seawater temperature and the mean diameter of the spermaries. Gametogenesis in females and males took 6 months and 12 months, respectively. The mean diameter of a mature oocyte was 249.29 ± 36.24 μm, with a maximum size of 354.45 μm. Spawning could have occurred in the fall after the seawater temperature began to decrease.

Key words: sexual reproductive cycle, *Dendronephthya suensoni*, azooxanthellate soft coral, Anthozoa, Cnidaria

Alcyonaceans (soft corals) are ecologically important, sessile members of coral reef communities. They are distributed from warm temperate to tropical areas, but some types are found in cold temperate regions such as the Antarctic (Slattery & McClintock, 1995). They are mainly distributed throughout the shallow waters of the Indo-West Pacific (Benayahu at al., 2002, 2004; Tursch & Tursch, 1982), the warm temperate Red Sea area (Ben-David-Zaslow et al., 1999; Benayahu,1990), the Great Barrier Reef (Dinesen, 1983) and southern Taiwan (Benayahu et al., 2004).

The peculiar soft coral community at the southern part of Jejudo Island was reported to the ICRI (International Coral Reef Initiative) of the UNEP (United Nations Environment Programme) (Choa & Lee, 2000; Song, 2000). In particular, the community including Munseom was designated as a Natural Monument No. 442, although there were no typical reef-building corals. Munseom (33°13'25"N, 126°33'58"E) is a desert islet, about 1 km away from the Seogwipo coast, and is affected by the warm Tsuchima Current, a branch of the Kurosio Current that creates tropical and subtropical elements and enriches the biodiversity (Kang et al., 2005; Pae & Je, 2004). This aspect of soft coral distribution at Munseom is similar to the alcyonacean distribution in southwestern Australia where the warm to cool waters of the Leeuwin Current contrast with the cold temperate waters off the southeastern Australian mainland. The Leeuwin Current's characteristic water temperature is responsible for the high level of biodiversity and endemism of marine organisms (Alderslade, 2003).

The reproductive biology of anthozoans is well documented with respect to gonadal morphology, general features of gametogenesis, and reproductive cycles (Larkman, 1983), especially for stony corals, sea anemones and zoantharians (Hexacorallia) (Eckelbarger et al., 1998). In the Alcyonacea, the sexual reproduction of the temperate species *Alcyonium digitatum* has been well-known for many years (Ben-David-Zaslow et al., 1999). More recently, three modes of sexual reproduction have been reported in alcyonaceans: internal brooding, external surface brooding of planulae and broadcast spawning (Benayahu et al., 1990). The first recorded internal brooding species was *Litophyton arboretum* of the Nephthydae, and species of the Xeniidae were also recorded as internal brooders (Benayahu & Loya, 1984; Benayahu et al., 1990). External brooding species were described for the first time in the Red Sea, namely *Parerythropodium fulvum fulvum* (Benayahu & Loya, 1983). This sexual reproductive strategy was later found in *Efflatounaria* spp. of the Xeniidae (Dinesen, 1985). A large variety of species of the Alcyoniidae and members of the Nephtheidae, such as *Dendronephthya hemprich*, are broadcast spawners (Benayahu et al., 1990; Dahan &

*To whom correspondence should be addressed.
Tel: 82-2-3277-2364; Fax: 82-2-3277-2385
E-mail: jisong@ewha.ac.kr

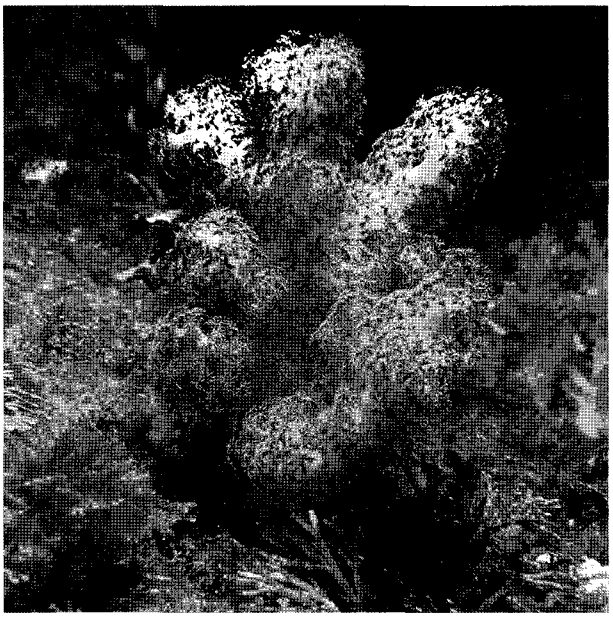

Fig. 1. Colony of *Dendronephthya suensoni* on the rock floor(20-30 m deep) at Seogwipo, Jejudo island, Korea.

Benayahu, 1997). Most of these studies and conclusions about the life cycle and reproduction of alcyonaceans apply to the Xeniidae or Alcyoniidae, but only a few studies have been reported about the Nephtheidae.

The azooxanthellate soft coral *Dendronephthya suensoni* (Holm, 1895) (Fig. 1) is a constitution species of the soft coral community at Munseom (Song, 2000). This species is not a main component of the coral community, but is spreading fast in the soft coral community of Munseom and around other islets by sexual and asexual reproduction methods similar to *D. hemprichi* (Barneah et al., 2002; Dahan & Benayahu, 1997). This is affected by the warm current and temporal changes. In this study, we examined in detail the annual reproductive cycle of *D. suensoni* and its relationship to environment factors.

MATERIALS AND METHODS

Sample collection

The study area for *D. suensoni* was Munseom (33°22'N, 126°33'E), located at Seogwipo on the coast of Jejudo Island, the southernmost part of Korea (Fig. 2). Five or six samples were collected monthly at depths of 5 m to 25 m by SCUBA from August 2003 to August 2005, except in January 2004, May 2005 and July 2005. About 5~6 cm long fragments were sampled from randomly selected colonies >15 cm in height. Samples were fixed in 4% formalin and transferred to 70% ethanol for preservation. The seawater temperature was measured when the monthly samples were collected.

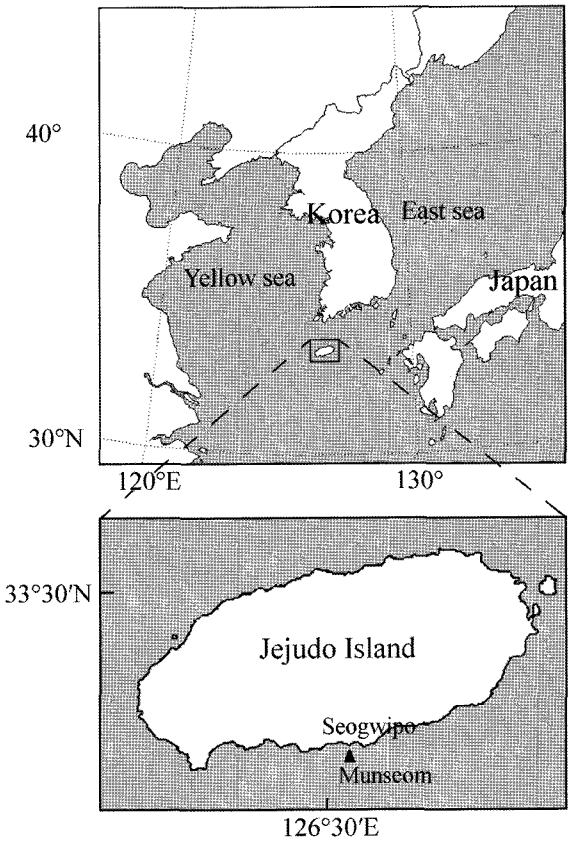

Fig. 2. Location of study site, Munseom, Jejudo Island, Korea.

Histology

The fixed samples were cut into 0.5 cm fragments for histological section. They were put in a 10% EDTA solution for 5 days for decalcification and dehydrated in increasing concentrations of ethanol and then cleared in a mixture of ethanol and xylene. The tissues were embedded in a series of mixtures of paraffin and xylene solution and were cut into 10 μm thick serial sections. The sections were stained with Harris hematoxylin and eosin Y and mounted.

Sexuality and sex ratio

For each collected sample, sexuality and sex ratio were determined after dissection under a stereomicroscope (ZEISS Stemi SV-6). In particular, the fresh gonads at maturation were examined to compare the color difference between mature and immature gonads. The χ^2 goodness-of-fit was used to test for deviation from a 1 : 1 sex ratio with SPSS (version 12.0K).

Gonadal development cycle and fecundity

Gametogenic stages were classified according to the diameter of the gametes and morphology criteria, which were obtained by examining histological sections. The mean diameters of gametes were measured from at least 30

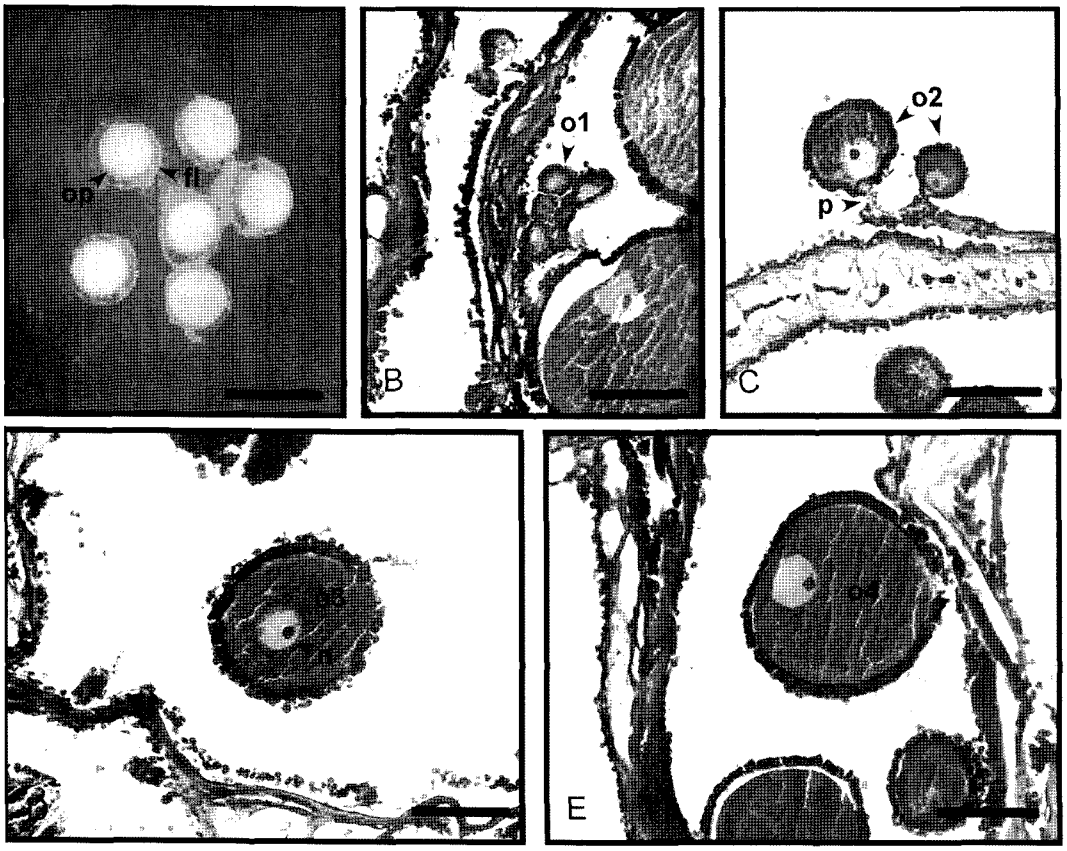

Fig. 3. Oogenesis of *Dendronephthya suensoni*. A. External shape of mature oocytes with follicular membranes. B-E. Histological sections of oocytes. B. Stage 1 oocytes enveloped in the mesoglea, showing the nucleus and nucleolus. C. Stage 2 oocyte attached to the mesentery by a pedicle. D. Stage 3 oocyte with the cytoplasm accumulatied around the nucleus. E. Full-sized stage 4 oocyte with a sharp edge. (*op,* ooplasm; *fl,* follicular layer; *o1,* stage 1 oocyte; *o2,* stage 2 oocyte; *p,* pedicle; *o3,* stage 3 oocyte; *n,* nucleous; *o4,* stage 4 oocyte) Scale bars = 300 μm (A) and 200 μm (B-E).

random gametes within each colony sample. Gametes were collected under a stereomicroscope, and gamete images obtained by a digital camera (Olympus 5060-WZ) attached to the stereomicroscope and light microscopy (Olympus BH-2). The longest and shortest axes of the gametes were measured by using an image analyzer (Motic images plus 2.0) and the average axis length was calculated. The relationship between the diameter of gametes and the seawater temperature was analyzed by linear regression. About 2-3 polyp masses were selected randomly from each colony, and all of the contained gametes were counted. The number of counted gametes was divided by the polyp number to derive fecundity. The change of fecundity values was then compared with the monthly changes in seawater temperature.

Spawning timing

During the various lunar phases, spawning was not observed in the field and laboratory. The releasing time of gametes from mother colonies was determined by measuring the decrease in the number of gametes contained within the gastrovascular cavity of polyps. Additionally, the releasing time was reconfirmed and narrowed by sampling and monitoring during the spawning season in 2006.

RESULTS

Sexuality and sex ratio

Dendronephthya suensoni was determined as gonochoric by microscopy and histological studies. Among 104 colonies analyzed, 47 female and 23 male colonies were defined, and 34 were reproductively inactive colonies which contained too small or no gametes. Females were significantly more abundant than males, with a sex ratio of 2 : 1. The ratio did not deviate from 2 : 1 (including the inactive colonies, $\chi^2 = 8.327$, df = 2, $p = 0.016$; excluding, $\chi^2 = 8.229$, df = 1, $p = 0.004$).

Gametogenesis (gonadal development)

Oogenesis: Living female gonads tended to change color from cream to orange as they matured and were covered with a transparent follicular layer (Fig. 3A). The color of oocytes changed to cream after preservation in alcohol.

Oogenesis was classified into four stages by size and

Table 1. Mean gamete diameter of each stage

Stage	Size (mm; mean ± SD, n)	
	Oocyte	Spermary
Stage I	30.34 (±6.46, 62)	23.36 (±5.05, 7)
Stage II	72.01 (±16.76, 571)	59.07 (±15.22, 215)
Stage III	130.73 (±26.58, 325)	120.85 (±21.50, 107)
Stage IV	249.49 (±36.24, 247)	226.04 (±52.07, 179)

character as follows (Table 1). During stage 1, oocytes were smaller than 40 μm in diameter and were in the mesoglea of the mesenteries (Fig. 3B). They had large nuclei and were of ellipsoidal or irregular shapes to fit into narrow spaces. The boundaries of nuclei, cytoplasm and cell membranes were not clear.

When the oocytes developed into stage 2, they migrated from the mesenteries to the gastrovascular cavity and attached to the mesenteries by pedicles with diameters ranging from 40 to 100 μm. At this stage, the ooplasm started to accumulate (Fig. 3C). Nuclei and nucleoli were obvious, and the boundary between the ooplasm and follicular layer became clearer.

Stage 3 oocytes, which had rough edges and diameters ranging from 100 to 190 μm, were detached from the mesenteries (Fig. 3D). The size of oocytes increased by the continuous accumulation of ooplasm around the nucleus, located at the center of the oocytes.

Stage 4 oocytes reached the full size, more than 190 μm in diameter, and had sharp edges (Fig. 3E). The nucleus was located at the periphery of the mature oocyte. Some oocytes were of an ellipsoidal shape to enable their large size to fit into the narrow cavity. At this stage, there were no embryos or planulae in the cavity.

Spermatogenesis: Spermaries were light cream in color and had no follicular layer (Fig. 4A).

Spermatogenesis was also classified into four stages (Table 1). Spermaries in stage 1 were embedded in the mesoglea of mesenteries, but they did not have obvious shapes (Fig. 4B). Diameters were shorter than 30 μm, and the spermaries were observed only through histological section.

In stage 2, the spermaries ranged between 30 and 90 μm. Pouches with spermatocytes were formed and connected to the mesenteries by pedicles (Fig. 4C). The spermatocytes were relatively more abundant at the periphery of the spermary than at the center, therefore irregular holes that lacked spermatocytes were sometimes present.

In stage 3, the spermaries ranged from 90 to 16 μm in diameter and were detached from the mesenteries. The spermatids were arranged at the periphery and clear lacunae were formed at the center (Fig. 4D).

During stage 4, the number of spermatozoa in the spermaries increased, and the spermaries reached their full

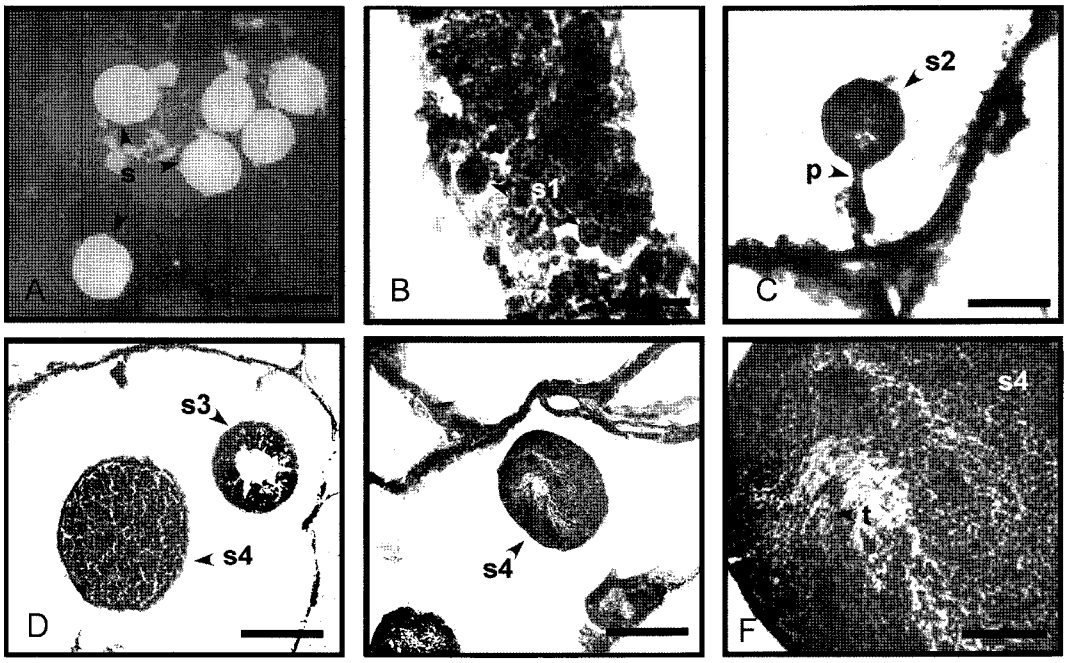

Fig. 4. Spermatogenesis of *Dendronephthya suensoni* A. External shape of mature spermaries. B-E. Histological sections of spermaries. B. Small spherical aggregations of stage 1 spermaries with spermatogonia in the mesentery. C. Stage 2 spermary attached to the mesentery by a pedicle. D. Spermatids arranged at the periphery of a Stage 3 spermary. Early stage 4 spermary was filled with a large number of spermatids. E. Mature stage 4 spermaries contained a large number of spermatozoa. F. Magnified stage 4 spermaries. Each spermary was filled with spermatozoa with tails in parallel array. (*s*, spermaries; *s1*, stage 1 spermary; *s2*, stage 2 spermary; *p*, pedicle; *s3*, stage 3 spermary; *s4*, stage 4 spermary; *t*, tail of spermatozoa). Scale bars = 25 μm (B), 50 μm (C,F), 100 μm (D), 150 μm (E) and 200 μm (A)

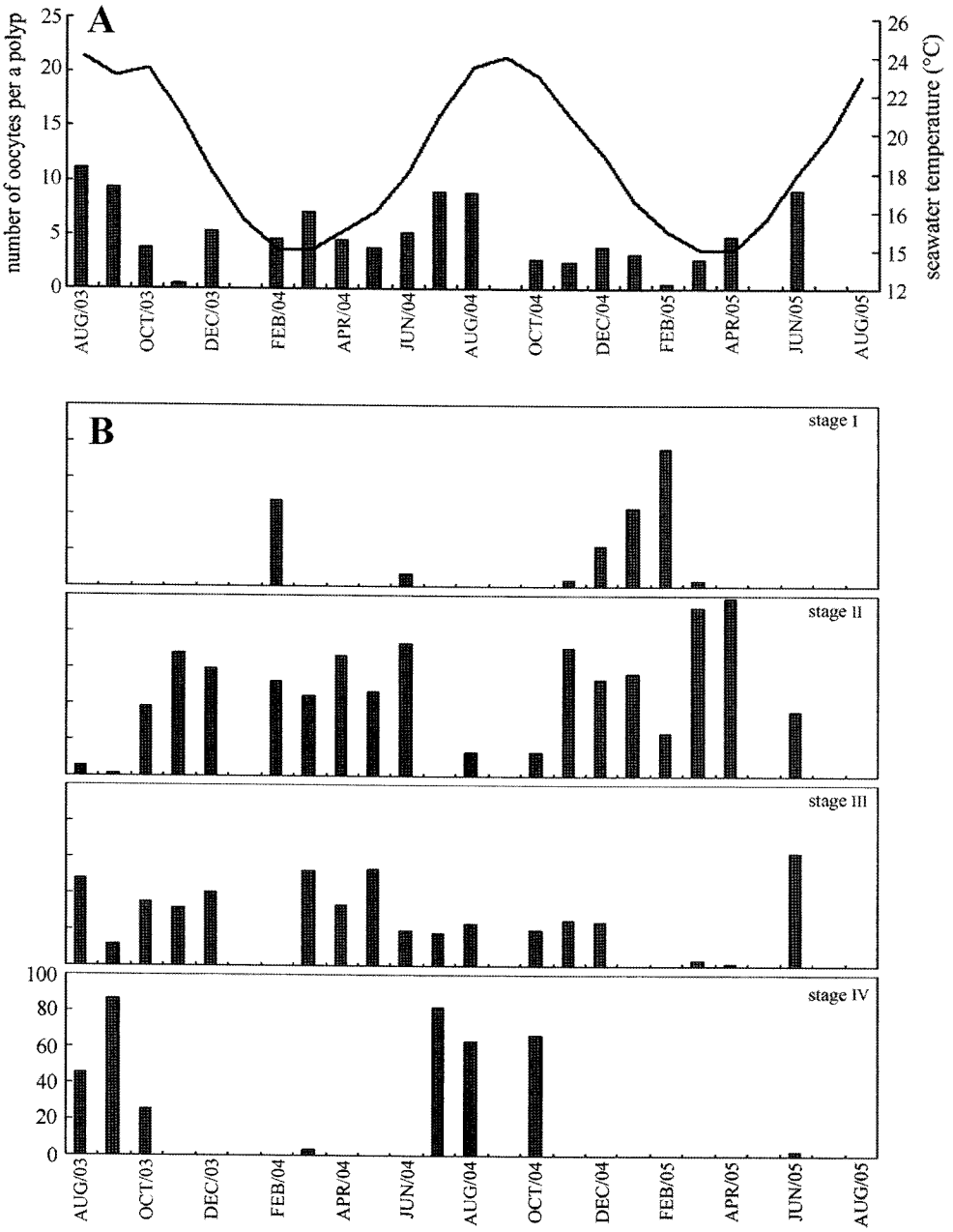

Fig. 5. *D. suensoni.* Annual pattern of oogenesis. A. Temporal density of oocyte. Monthly mean number of oocyte in a polyp from August 2003 to August 2005. B. Monthly frequency of each oogenic stage between August 2003 and August 2005 (n = 1205). Oocytes were observed in all year round except months that female colony not being collected.

size of greater than 160 μm in diameter. In the beginning of stage 4, spermatids evenly filled the full-sized spermaries (Fig. 4D). In the later part of stage 4, the mature spermaries were filled with spermatozoa with tails in parallel array (Fig. 4E, F).

Annual reproductive cycle and fecundity

The annual reproductive cycle of *D. suensoni* exhibited a distinct correlation with seasonal changes related to the temperature of seawater.

In females, oocytes were observed all year round except when female colonies were not collected (Fig. 5A). The number of oocytes per fixed polyp increased each month until the temperature of seawater reached its peak. Subsequently, the number of oocytes decreased until the seawater temperature was at its lowest. Stage 1 oocyte development began in winter with low seawater temperatures, when the frequency of mature oocytes dropped drastically (Fig. 5B). Mature oocytes were observed mainly between November and February, with an average frequency of 38.67% and a peak value of 76.19% in February 2004. Stage 2 ooctyes showed a relatively high frequency during

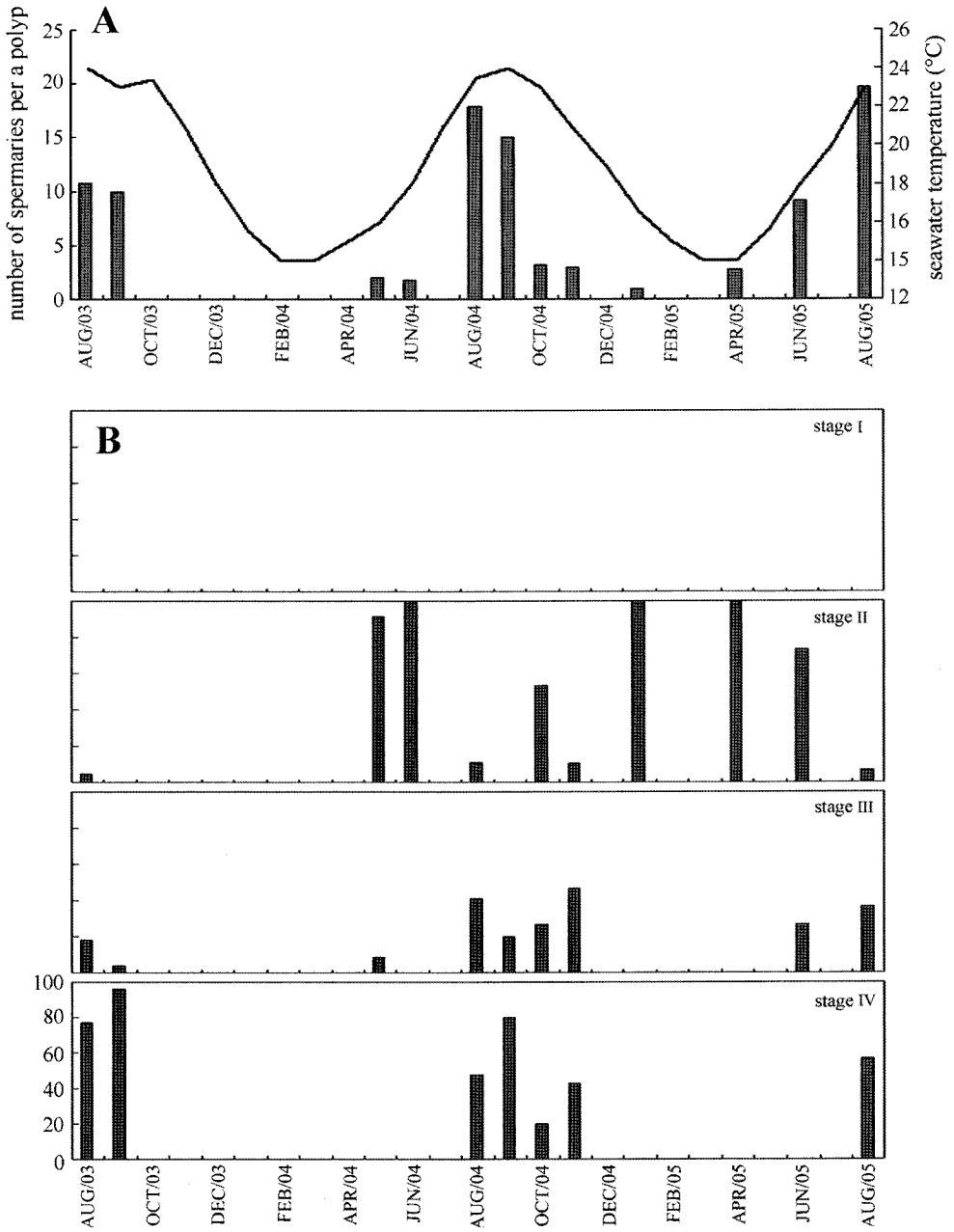

Fig. 6. *D. suensoni.* Annual pattern of spermatogenesis. A. Temporal density of spermary. Monthly mean number of spermary in a polyp from August 2003 to August 2005. Density change is relatively more remarkable than female. B. Monthly frequency of spermatogenic stage between August 2003 and August 2005 (n = 508). Spermary was mainly observed between April and January.

nearly the whole collecting period, with an average ratio of 48.21%. Their frequency increased until April, with a marked peak in April 2005 of 98.75%. At stage 3, oocytes were numerous from March 2004 to May 2004 and in June 2005. Their average ratio was 28.02%, and the peak value was 62.22% in June 2005. Mature stage 4 oocytes were observed mainly in summer and early fall except for low values in March 2004 and June 2005. The frequency of stage 4 had a high average ratio of 61.71% and a marked peak value of 86.84% in September 2003.

In males, spermatogenesis was more dependent on the temperature of seawater than oogenesis in female colonies. Production of spermaries rapidly increased for a short period, and the frequency was relatively high compared to the females. Their density was increased in late summer and early fall when the temperature of seawater was the highest (Fig. 6A) and dramatically dropped once the temperature began to decrease. In stage 1, spermaries could not be observed because of their obscure shape (Fig. 6B). The frequency of stage 2 was highest through winter, spring

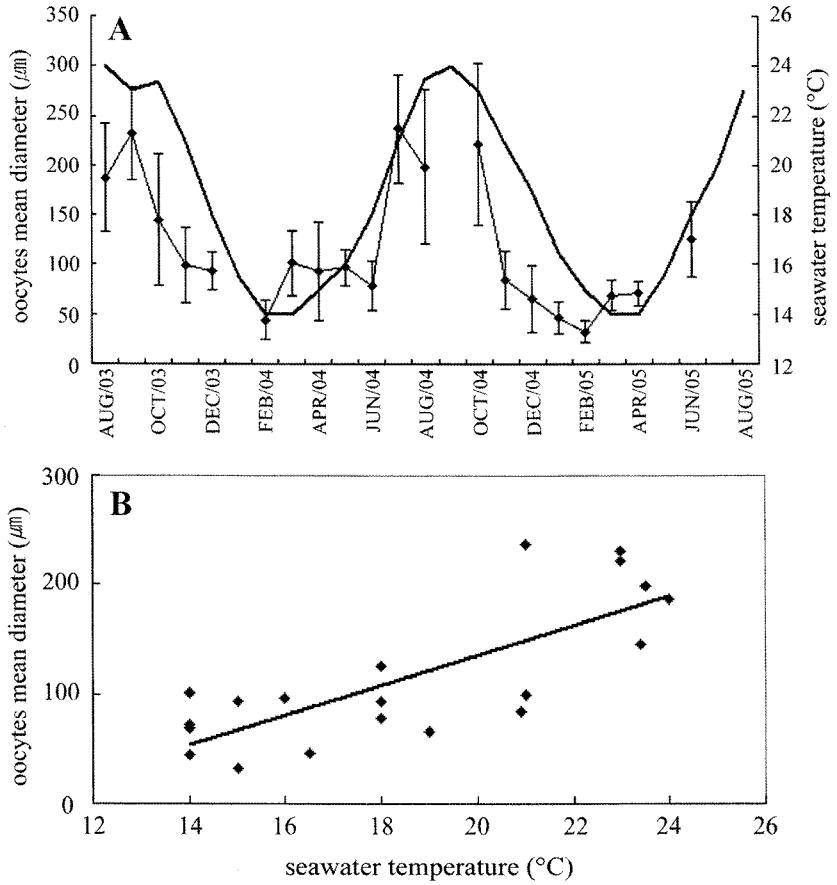

Fig. 7. *D. suensoni.* Oogenesis and seawater temperature. A. Temporal change in mean diameter of oocyte according to the seawater temperature (n = 1205, ±SD). B. Correlation between oocyte mean diameter and seawater temperature (r = 0.771, $P < 0.001$, n = 20). Trend-line formula is y = 13.514x – 137.8 .

and early summer, but was rapidly reduced in summer. The average frequency of stage 2 spermaries was 55.10% with a marked peak value of 100% in June 2004, January 2005 and April 2005, but their actual number was very low. In stage 3, spermaries were detected mainly through summer and early fall. They had an average ratio of 25.47% and a peak value of 46.43% in November 2004. The number of stage 3 spermaries, however, was higher in August 2004. The pattern of stage 4 frequency was similar to stage 3, but these mature spermaries had a higher average ratio of 60.10% and a higher peak value of 96.15% in September 2003.

The annual reproductive cycle could be confirmed by the changes in the monthly mean diameter of oocytes. In female colonies, the oocytes showed a relatively high mean diameter in August and September 2003 (Fig. 7A). The mean diameter and the quantity of oocytes decreased through October and November. The number of oocytes then increased in December, but there was little change in the number and diameter of oocytes until June, when the seawater temperature was below 20°C. The oocytes doubled in size and number between June and August, and a similar pattern was repeated. The correlation between the mean oocyte diameter and the seawater temperature was examined by linear regression (Fig. 7B). This showed a positive correlation; with the mean diameter of oocytes directly proportional to the seawater temperature (y = 13.514x – 137.8, r = 0.771, $P < 0.001$).

The number of spermaries reached a marked high value in August and September when the seawater temperature reached its peak (Fig. 8A). Furthermore, the number of spermaries decreased in October when the seawater temperature started to drop rapidly. Male colonies were especially dependent on the temperature, which affected the number of spermaries and the mean diameter. A higher slope of regression line between the mean diameter of spermaries and the seawater temperature (y = 14.389x – 214.58, r = 0.755, $P < 0.001$) proved male colonies to be more influenced by the temperature than female colonies (Fig. 8B).

Spawning time

During the study period, a release event was not observed in the field or in the laboratory. An increase in the number

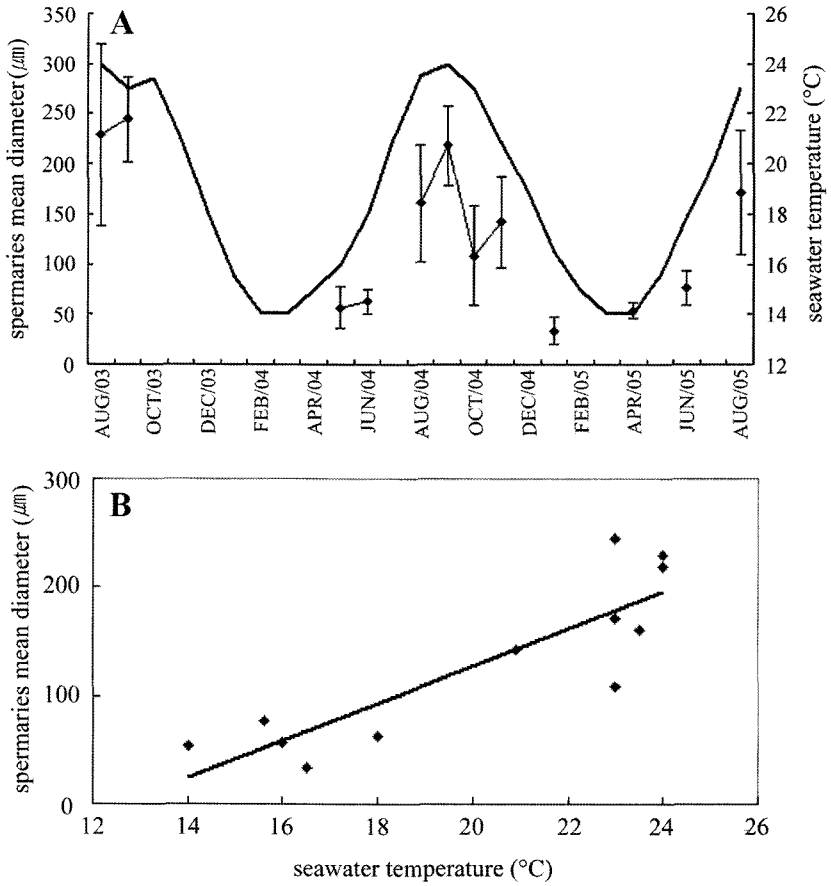

Fig. 8. *D. suensoni.* Spermatogenesis and seawater temperature. A. Temporal change in mean diameter of spermary according to seawater temperature (n = 508, ±SD). B. Correlation between spermary mean diameter and seawater temperature. (r = 0.755, $P < 0.001$, n = 12) Trend-line formula is y = 14.389x – 214.58.

of gametes, followed by a dramatic decrease, was confirmed during periods which contained the potential spawning time. In the sampling period from August 2003 to August 2005 and two additional collections in September 2006, potential release events related to lunar phases could have occurred at some points between September 25, 2003 and October 11, 2003 (between new and full moon in the lunar calendar), between September 11, 2004 and October 24, 2004 (between full and new moon in the lunar calendar), and between September 7, 2006 and September 22, 2006 (July 15, 2006 and August 1, 2006 in the lunar calendar) based on the disappearance of gametes within colonies.

DISCUSSION

Sexuality, sex ratio, and fecundity

Dendronephthya suensoni are known to have a gonochoric sexuality, but their reproductive mode was not directly observed in this study. Gonochorism is the predominant sexuality among alcyonaceans, while a few hermaphroditic alcyonaceans, such as *Heteroxenia coheni* and *Heteroxenia fuscescens*, have been observed (Benayahu et al., 1990). In *Heteroxenia elizabethae*, a mixed sexuality was reported according to location (Ben-David-Zaslow et al., 1999) and some gonochoric species had very low ratio of hermaphroditic colonies with a very low ratio, e.g. *Xenia macrospiculata* and *Capnella gaboensis* (Benayahu & Loya, 1984; Farrent, 1985). Alcyoniidae species are reported as broadcast spawners (Benayahu et al., 1990; McFadden, 1997; Schleyer, 2004; Yamazato et al., 1981), except for one surface brooder *Parerythropodium fulvum fulvum* (Benayahu & Loya, 1983) and the internal brooders *Alcyonium rudyi* (McFadden, 1997) and *Anthomastus ritteri* (Cordes, 2001). On the other hand, all reported Xeniidae reproduce by the internal brooding mode (Ben-David-Zaslow et al., 1999; Benayahu, 1991; Benayahu and Loya, 1984; Benayahu et al., 1990; Kruger et al., 1998), except for the surface-brooding *Efflatounaria* spp. and *Anthelia glauca* (Dinesen, 1985; Kruger, 1998). In the Nephtheidea, few studies about reproduction are available, except for the studies performed on the internal brooding species *Litophyton arboreum* (Benayahu et al., 1990), the broadcasting species *D. hemprichi* (Dahan & Benayahu, 1997), and the surface brooding *C. gaboensis* (Farrant, 1986). In the case of *D.*

suensoni, an embryo was not found in the polyp cavities by histological section and dissection, or on the surface of live colonies in the field or in collected samples. Based on the phenomenon that the quantity of gametes in the polyp cavity decreased drastically after the peak in seawater temperature, *D. suensoni* is possibly a broadcast-spawning species. On the other hand, its reproductive strategy could possibly be a quick-releasing mode. The scleractinian coral *Madricis* spp. is thought to a have 'quick planulae release' strategy because planulae were not found in histological slides and polyp cavities (Vermeij et al., 2004).

The sex ratio for *D. suensoni* has a female : male bias of 2 : 1. Both in the broadcast spawner *D. hemprich* and *Sarcophyton glaucum* (Alcyoniidae), females were significantly more abundant than males (Dahan & Benayahu, 1997; Schleyer et al., 2004). However, a 1:1 population sex ratio was also reported in the gonochoric broadcast-spawning alcyonacean, *Lobophytum pauciflorum* (Fan et al., 2005). In previous studies of external and internal brooding alcyoneans, the sex ratio of *A. gluca* did not differ from 1:1 (Kruger et al., 1998), and male colonies were significantly more abundant than females in *X. macrospiculata* of the Xeniidae (Benayahu & Loya, 1984). The sex ratio, however, was often reported to be different according to the depth or locality. In *P. f. fulvum*, the female ratio was 60% in the shallow water population, while the male ratio was 54% at a depth of 30 m (Benayahu & Loya, 1983). Also, a geographic variation was reported in gorgonians of the Western Mediterranean Sea. The sex ratio for both *Paramuricea clavata* and *Eunicella singularis* was 1 : 1 in the Medes Islands, while it is male-biased at 7 : 1 in *P. clavata* and female-biased at 1.7 : 1 in *E. singularis* at the Cape of Palos (Gori et al., 2007). These studies suggest that a male-biased sex ratio may increase fertilization success for a sessile gonochoric coral with internal or surface fertilization (Benayahu and Loya, 1984; Gori et al., 2007). Therefore, it is difficult to draw conclusions about the correlation between the sex ratio and reproductive mode due to variations in sex ratio and insufficient information available on reproduction of alcyonaceans.

The mean diameter of a mature oocyte was 249.29 ± 36.24 μm, and the maximum size was 354.45 μm. This was smaller than in other alcyonaceans. Mature oocytes of most known alcyonaceans are around 500 μm in mean diameter, while each has its own reproductive strategy (Benayahu, 1991; Benayahu and Loya, 1983, 1984, 1986; Dahan and Benayahu, 1997; Fan et al., 2005; Farrant, 1986; Kruger et al., 1998; Schleyer et al., 2004). Most species with a mature oocyte diameter around 500 μm are distributed in tropical regions, but *C. gaboensis* is distributed in the temperate region of Sydney Harbour, Australia (Farrant, 1986). Therefore, the size variation of oocytes does not depend on the reproductive mode or seawater temperature but is related to the characteristics of each species, such as the size of the gastrovascular cavity or siphonoglyph.

Fecundity

The mean number of gametes in polyps of *D. suensoni* was relatively small when compared with other alcyonaceans. *S. glaucum* and *A. glauca* have more oocytes or spermaries per polyp, and *Lobophytum crassum* has a higher fecundity (Benayahu & Loya, 1986; Kruger et al., 1998; Schleyer, 2004; Yamazato et al., 1981). On the other hand, in *P. f. fulvum*, each polyp produces 18-24 genital products, which is similar to the gamete number of *D. suensoni*. However, some colonies of *P. f. fulvum*, which contain parts with a thick coenenchyme, produce up to 100 gametes (Benayahu & Loya, 1983). In the previous studies on gamete number in alcyonaceans, male colonies contained more spermaries in polyps than the number of oocytes in female colonies (Farrant, 1986; Kruger, 1998; Schleyer, 2004). These differences in gamete numbers between species or sexes seem to depend on the size of the polyp cavity and the size of the gamete. For example, gorgonians with a short gastrovascular cavity have fewer oocytes per polyp; in the Antarctic gorgonian, *Thoaurella* sp., the number of oocytes per polyp ranges from 1.1 ± 0.10 to 1.5 ± 0.06. The species with low gamete number per polyp overcome their low fecundity rate by producing a high number of polyps in the colony (Orehas et al., 2006).

Gonadal development

The development of gametes in *D. suensoni* is seasonal with an annual cycle. Both female and male colonies have one gametogenic cycle each year. The temperature of seawater, which is affected by seasonal currents, is considered to be one of the most influential factors in this cycle. A few immature oocytes were observed after September, but they started to increase in number and to develop, especially when the seawater temperature rose over 20°C. In *C. gaboebsis* (Nephtheidae) in temperate Australian waters, gamete maturation begins soon after spawning (June) and continues to the following May, but the main period of maturation takes 6-7 months, depending on the seawater temperature (Farrant, 1985). On the other hand, in the broadcast spawning *L. pauciflofum* in southern Taiwan, it takes about 5 months to produce mature gametes (Fan et al., 2005). Also, *C. gaboensis* has an annual cycle with gametes developing in less than one year (Farrant, 1986). There are some octocorals in which oocyte development takes more than one year: e.g. the Antarctic gorgonian *Thouarella* sp. (Orejas, 2007), *Corallium rubrum* (Tsounis et al., 2006) *L. crassum* (Yamazato et al., 1981) and *S. glaucum* (Benayahu and Loya, 1986) have discrete size classes of oocytes in their polyps due to the long oogenic cycle. The variation in the gametogenesis period is affected

by geographic environmental factors. The oogenesis period of *S. glaucum* is as short as 16-18 months in KwaZulu-Natal, whereas it is 22-23 months in the Red Sea (Schleyer et al., 2004).

The annual cycle of plankton abundance may also be one of the contributing factors that influence the reproductive cycle. At the study site, there are two phytoplankton blooms, in May and September (Choa and Lee, 2000). The major bloom in May is believed to have contributed to the development of gametes in the azooxanthellate *D. suensoni* by providing a rich source of energy and nutrients. In the Red Sea, there are two algal blooms which are similar to the study site, and this suggests that the reproductive success of *H. fuscescens* is related to the changes in nutrients (Ben-David-Zaslow et al., 1999). Furthermore, the reproductive cycle of the sea anemone *Rhodactis rhodostoma*, which contains endosymbiotic zooxanthellae, is affected by annual cycles of food abundance for zooplankton (Chadwick-Furman et al., 2000).

The longer cycle of oogenesis compared with spermatogenesis is a common phenomenon not only in alcyonaceans but also in other coral species. Spermatogenesis of *L. crassum* is completed within a year, while a two-year period is required for oogenesis (Yamazato et al., 1981). In the gorgonian *Pseudopterogorgia elisabethae*, which has a relatively short oogenesis period (about 10 months), spermatogenesis requires only 2 months (Gutiérrez-Rodríguez and Lasker, 2004). The shorter period of spermary development is also confirmed in scleractinians. In *Acropora cervicornis*, spermatogenesis takes two months, while oogenesis occurs between September and April. The spermatogenesis period of most coral species is shorter than oogenesis, regardless of the duration of oocyte development.

Although the spawning event of gametes was not observed in the field and in the laboratory, the colonies were full of gametes on September 25, 2003 (new moon) and September 7, 2006 (full moon). They emptied on October 11, 2003 (full moon) and September 22, 2006 (new moon). Many spawning events occur between the full moon and the new moon not only in alcyonaceans (Benayahu and Loya, 1986; Schleyer et al., 2004) but also in gorgonians and stony corals (Bastidas et al., 2005; Vargas-Ángel et al., 2006). The spawning event of *Scleronephthya gracillimum*, which is in same order with *D. suensoni*, was observed between the new moon and the full moon in 2006, at Munseom. The event of *D. suensoni* did not occur on the full moon or the new moon, but the spawning at the near full or new moon was implied based on observations and several case of other anthozoan species. The spawning timing of *D. suensoni* may be related to the minor algae bloom that occurred between September and October (Choa & Lee, 2000). The algae bloom could offer nutrients for nearly released offspring, which can increase the survival rate of the planulae.

This study is a report on the reproductive pattern of *D. suensoni* that described the developmental stages of the gametes and determined the relationship between the reproductive cycle and environmental factors. The data from this study also suggests the time of spawning. Hereafter, concentrated monitering will be needed during September and October to confirm the exact timing.

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