BULLETIN OF MARINE SCIENCE, 62(3): 897–904, 1998 CORAL REEF PAPER

SEXUAL REPRODUCTION OF THE SCLERACTINIAN CORAL *MERULINA AMPLIATA* IN SOUTHERN TAIWAN

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ABSTRACT

Sexual reproduction of the scleractinian coral *Merulina ampliata* in Nanwan Bay, southern Taiwan was studied from 1990 to 1993. *M. ampliata* is a hermaphroditic broadcast spawner. Colony size at sexual maturity was 5.0–10.0 cm in diameter. Mature egg size and fecundity were 210 μm and 952 eggs cm^{-2} yr^{-1}, respectively. Monthly changes of mean oocyte diameters and frequencies of colonies containing different stages of gametes indicated a brief annual gametogenic cycle. Oogenesis began in June 1991 and May 1992. Spermatogenesis began 1 mo later than oogenesis. Spawning occurred in September 1990 and 1991, and August and September 1992 during late summer to early autumn. Spawning of *M. ampliata* took place about 1 to 2 mo later in southern Taiwan than in Okinawa. The delayed reproduction of *M. ampliata* at the lower latitude (southern Taiwan) suggests that sea temperature may not operate as a primary factor controlling the reproductive seasonality of this species.

Knowledge of coral sexual reproduction has increased greatly since the findings of the mass spawning on the Great Barrier Reef and other Indo-Pacific locations (Harrison et al., 1984; Willis et al., 1985; Babcock et al., 1986; 1994; Hayashibara et al., 1993) as well as the temporal separation of coral reproduction in the Red Sea and the Caribbean (Shlesinger and Loya, 1985; Szmant, 1986). The majority of scleractinian corals are hermaphroditic broadcast spawners with an annual cycle of gametogenesis that culminates in a brief period of spawning (Harrison and Wallace, 1990; Richmond and Hunter, 1990).

The synchronized sexual reproductive cycles of scleractinian corals have been related to various environmental factors (Harrison and Wallace, 1990). Environmental conditions may influence sexual reproduction as proximate factors which provide cues to synchronize reproductive cycles, and ultimate causes that exert selective pressure on the synchrony and timing of breeding within each species (Giese and Pearse, 1974; Oliver et al., 1988). Some studies suggest that seasonal variation in sea temperature or photoperiod may be the major proximate environmental factor controlling the annual cycle of reproduction (Babcock et al., 1986; Harrison and Wallace, 1990; Soong, 1991), while others indicate that sea temperature may not operate as a primary factor controlling the seasonality of reproduction (Babcock et al., 1994; Fan and Dai, 1995). The spawning period of some species often varies between localities (Harrison and Wallace, 1990; Richmond and Hunter, 1990). Regional comparison of the spawning period of the same coral species offers an approach of discerning species responses to various environmental conditions (Oliver et al., 1988; Babcock et al., 1994; Fan and Dai, 1995).

Merulina ampliata (Ellis and Solander, 1786), a potentially large (1 to 2 m in diameter) foliaceous species, is a widely distributed scleractinian on many Indo-Pacific coral reefs (Veron and Pichon, 1980) and is one of the most abundant species in some coral communities in southern Taiwan (Dai, 1993). It was suggested that *M. ampliata* is an efficient space competitor and often dominates the reef slopes (Dai, 1990). However, the only information available about its reproductive biology is that it is a hermaphroditic spawner and that it participates in the mass spawning event on the reefs of Okinawa, the Great

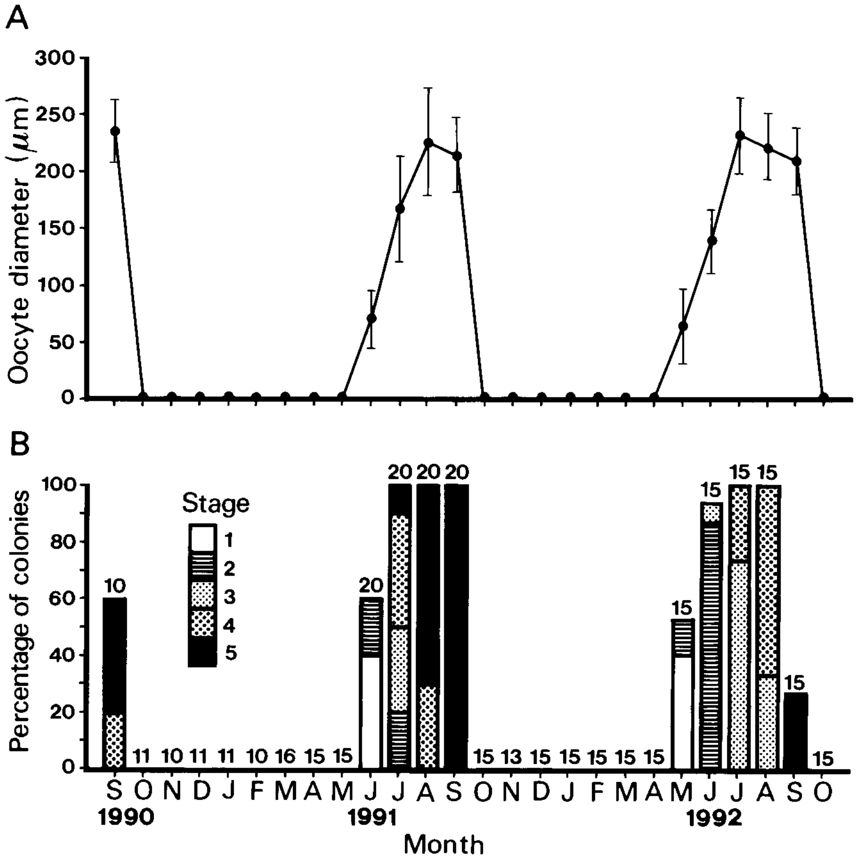

Figure 1. Seasonal cycle of mean oocyte diameters (A) and monthly changes in percentage of colonies containing gametes (B) for *Merulina ampliata* in Nanwan Bay, southern Taiwan. Numbers above bars indicate the number of colonies sampled.

Barrier Reef, and Western Australia (Willis et al., 1985; Babcock et al., 1986; 1994; Hayashibara et al., 1993).

Here we report the sexual reproductive characteristics and the gametogenesis of *M. ampliata* in southern Taiwan. The month of spawning of *M. ampliata* in southern Taiwan is compared with that in Okinawa, Japan (Hayashibara et al., 1993) and the environmental factors controlling the reproductive seasonality of *M. ampliata* is discussed.

Materials and Methods

Samples of 10 to 20 large coral colonies (>20 cm in diameter) were collected monthly from a population of *Merulina ampliata* in Nanwan Bay, southern Taiwan (21°55'N, 120°45'E) from September 1990 to October 1992. Samples were fixed with 10% formalin in seawater for at least 24 h, rinsed in freshwater, decalcified in 8% formic acid, and stored in 70% alcohol. Tissue samples were dehydrated with increasing concentrations of alcohol, cleared with xylene, and embedded in Paraplast. Serial sections 6 to 8 μm thick were prepared and stained with Mayer's hematoxylin and eosin. These tissue sections were examined for gamete development under a compound microscope at

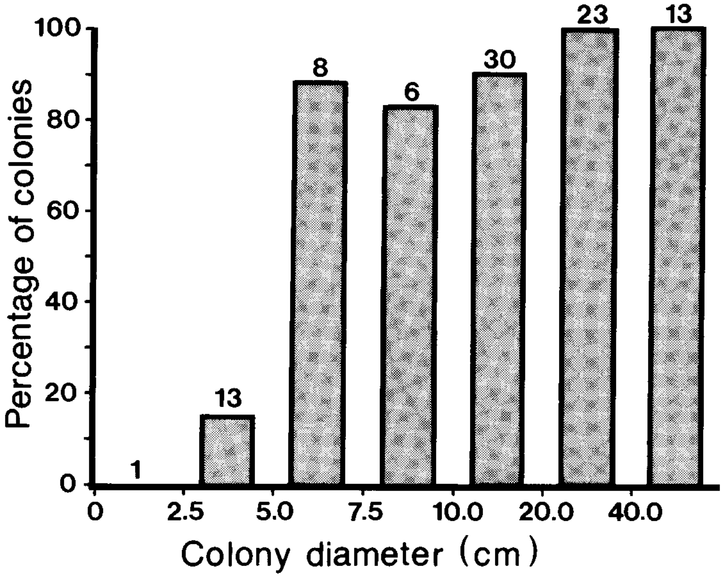

Figure 2. Percentage of colonies with oocytes per size class (mean diameter) for *Merulina ampliata* in Nanwan Bay, southern Taiwan. Numbers above bars indicate the number of colonies sampled.

magnifications up to 1000×. The length and width of at least six oocytes in nucleolar section were measured for each colony using a micrometer eyepiece. The monthly variation of oocyte size and percentages of colonies containing different developmental stages of gametes were used to determine the seasonal pattern of gametogenesis and spawning among colonies. The mature egg size was represented by the mean of the oocytes collected prior to gamete disappearance.

Fecundity was estimated from counts of eggs per mesentery and numbers of polyps cm^{-2}. Number of eggs per mesentery was calculated along the length of individual mesenteries from histological sections. Number of polyps cm^{-2} was calculated as the number of polyps in a circle of 2 cm in diameter from areas of colony skeleton 2 cm away from the edge.

In 1993, coral samples of various sizes were collected in July, 1 to 2 mo prior to the month predicted for spawning at Nanwan Bay. Two diameters perpendicular to one another across the colony center were measured and their average was taken as the diameter of the colony. Samples were fixed, decalcified and then examined at magnification 64× under a dissecting microscope. Colonies were considered to be sexually mature if oocytes were visible under a dissecting microscope.

Sea surface temperatures at the study site were measured by divers using a thermometer (±0.5°C) around noon on each sampling day.

RESULTS

GAMETOGENESIS.—*M. ampliata* is a simultaneous hermaphrodite. The oocytes and spermaries develop within each of the 12 mesenteries between the retractor muscles and the mesenterial filaments. Five development stages of gametes were classified according to the histological characteristics and relative sizes of oocytes and spermaries. The stages were: (1) oogonia, (2) developing oocytes, (3) developing oocytes and early spermaries,

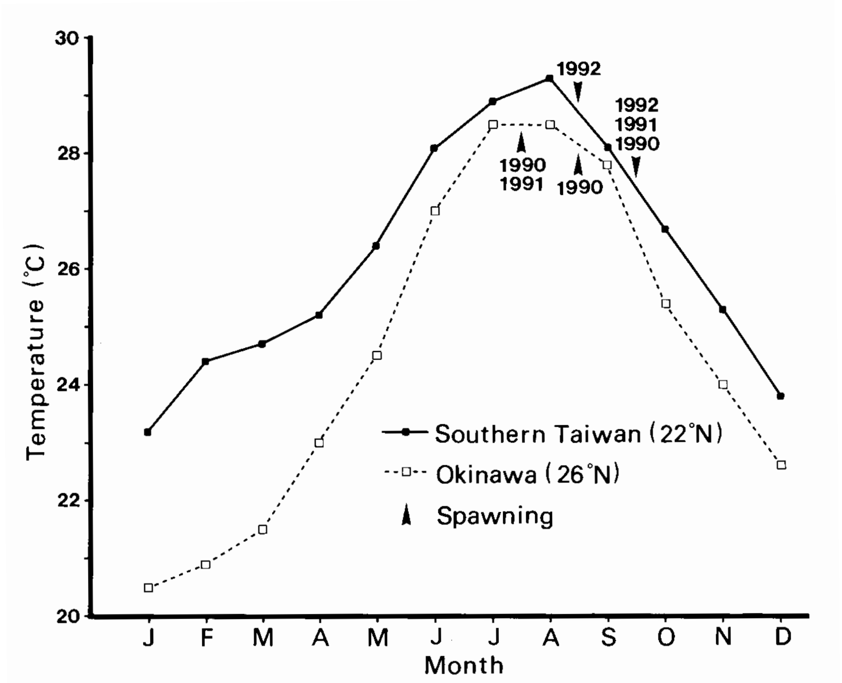

Figure 3. Spawning time of *Merulina ampliata* plotted against monthly mean of annual sea surface temperature in Nanwan Bay, southern Taiwan and Okinawa, Japan (from Hayashibara et al., 1993). The spawning periods in southern Taiwan were inferred from the histological data. Numbers above and below arrows indicate the year.

(4) developing oocytes and spermaries, and (5) mature oocytes and spermaries. In Stage 1, few oogonia were found in the mesoglea of the mesenteries and the oogonia were <75 μm in diameter. The oogonium had a nucleus with a prominent nucleolus and a thin layer of cytoplasm. In Stage 2, the oogonia underwent vitellogenesis and increased to 75–150 μm in diameter. In Stage 3, the oocytes were 150–225 μm and the spermaries appeared. The spermaries were composed of several discrete sacs which contain a few spermatogonia. In Stage 4, the oocytes were 175–250 μm in diameter. The spermaries increased in diameter and the spermatocytes became more numerous and smaller. In Stage 5, the mature oocytes reached a diameter of 200–275 μm. The sperm were arrayed in a bouquet with the heads located peripherally and the tails projecting toward the lumen.

MATURE EGG SIZE AND FECUNDITY.—Mean diameter of mature eggs was 214.2 ± 32.6 μm (± 1SD, n = 158) in 1991 and 211.1 ± 28.6 μm (± 1SD, n = 74) in 1992. Based on the combined data of 1991 and 1992, mean number of eggs per mesentery was 13.8 ± 2.6 (± 1SD, ranged from 10 to 21, n = 37), mean number of polyps cm^{-2} was 5.7 ± 0.3 (± 1SD, n = 20), and annual fecundity estimated was 952 eggs cm^{-2}.

REPRODUCTIVE SEASONALITY.—Changes of mean oocyte diameters and frequencies of colonies containing different stages of gametes in *M. ampliata* over each month of the 2 yrs indicated a clear annual gametogenic cycle (Fig. 1). Gametes were not found in samples taken monthly from October 1990 to May 1991 and from October 1991 to April 1992. Oocytes first appeared in June 1991 and May 1992, then increased in size from June to August in 1991 and from May to July in 1992 (Fig. 1A). Spermatogenesis started approximately 1 mo later than oogenesis (Fig. 1B). Most (>90%) or all colonies contained gametes from July to September in 1991 and from June to August in 1992. The sharp decline of colonies containing mature gametes occurred between September and October 1990 and 1991, and between August and October 1992. Since the coral samples were collected before the full moon during these months, the release of gametes most likely occurred in September 1990 and 1991, and in August and September 1992.

COLONY SIZE AT SEXUAL MATURITY.—Most colonies (>80%) of *M. ampliata* contain gametes when reaching a size of >5.0 cm in diameter (Fig. 2). The minimum colony size at sexual maturity was 4.5 cm in diameter. All colonies larger than 20.1 cm in diameter were mature.

SEA TEMPERATURE.—Sea surface temperature began to rise in February and reached its peak in August (Fig. 3). Spawning of *M. ampliata* occurred after the warmest period in Nanwan Bay.

DISCUSSION

Gonad structure of *M. ampliata* is similar to that of other hermaphroditic broadcasting corals in the Pectiniidae and Faviidae from the Indo-Pacific reefs (Kojis and Quinn, 1981; 1982; Harriott, 1983; Babcock, 1984; Harrison and Wallace, 1990; Fan and Dai, 1995). In these families, oocytes and spermaries occur within the same mesentery, with oocytes developing early in the gametogenic cycle.

Colony size at sexual maturity of *M. ampliata* in southern Taiwan was >5.0 cm in diameter. Studies on recruitment and growth of *M. ampliata* colonies indicated that the minimum age at first reproduction was 4–5 yrs (Fan and Dai, unpubl. data). It is similar to that of *Echinopora lamellosa*, another common foliaceous coral in southern Taiwan (Dai, 1993; Fan and Dai, 1995) and other gamete-releasing species. They usually became reproductive mature at 4 yrs or older (Harrison and Wallace, 1990).

Mature egg size and annual egg volume production of *M. ampliata* (210 µm and 4.6 $mm^3\ cm^{-2}$, respectively) were smaller than those of other gamete-releasing species except *Porites lutea* and *P. australiensis* (Harriott, 1983; Harrison and Wallace, 1990). However, *E. lamellosa* produced comparable size and volume of eggs (215 µm and 3.7 $mm^3\ cm^{-2}$, respectively) in southern Taiwan (Fan and Dai, 1995; unpubl. data). Thus, these two species allocate similar energy to reproduction.

M. ampliata has a brief annual reproductive cycle. Gametogenesis begins in May or June (late spring to early summer) and is completed within 4 to 5 mo. The length of the gametogenic cycle of *M. ampliata* resembles that of *E. lamellosa* (see Fan and Dai, 1995), but is shorter than that of most other Indo-Pacific scleractinian corals (Harrison and Wallace, 1990). *M. ampliata* also undergoes gametogenesis and spawning at a time similar to that of *E. lamellosa* (see Fan and Dai, 1995), but different from most other scleractinian corals in Nanwan Bay, southern Taiwan. Most spawning in Nanwan Bay occurs in late April or early May (Dai et al., 1992).

M. ampliata spawned during the full and the last quarter moon phases in Okinawa, the Great Barrier Reef, and Western Australia (Willis et al., 1995; Babcock et al. 1986, 1994; Hayashibara et al., 1993). Spawning of *M. ampliata* in southern Taiwan also took place during this period. The consistence of timing of spawning suggests that spawning of *M. ampliata* is likely controlled by lunar cycles (Babcock et al., 1994).

Spawning of *M. ampliata* in southern Taiwan occurred in late summer to early autumn (August to September) when the sea temperatures begin to decrease (Fig. 3). *M. ampliata* in Okinawa spawned in July and August 1990 and in July 1991 during the warmest period of the year (Hayashibara et al., 1993). Thus, spawning of *M. ampliata* in southern Taiwan (22°N) lagged 1 to 2 mo behind that in Okinawa (26°N).

The spawning pattern of *M. ampliata* is similar to that of *E. lamellosa* in northern and southern Taiwan (Fan and Dai, 1995) and the Caribbean coral *Montastrea annularis* (Van Veghel, 1994). The gametogenic initiation and spawning of *E. lamellosa* and *M. annularis* took place about 1 to 2 mo later at warmer localities than at colder localities in Taiwan and the Caribbean, respectively. The earlier reproductive seasons of *M. ampliata, E. lamellosa*, and *M. annularis* on higher latitude reefs contradicts the hypothesis concerning the role of sea temperature in the seasonality of reproduction (Orton, 1920; Giese and Pearse, 1974). Seasonal variation in photoperiod may operate as a possible proximate factor controlling the reproductive seasonality (Babcock et al., 1994) since latitudinal variation in reproductive seasonality of these species correlated with that in photoperiod.

The timing of reproduction may reflect environmental conditions favorable for the survival of larvae (Giese and Pearse, 1974). Perhaps the advantage for *M. ampliata* and *E. lamellosa* to breed near the end of seasonal disturbances (typhoons and heavy rainfalls) is to increase the substrate availability to larvae, to avoid the high mortality caused by disturbances and then to increase reproductive success (Fan and Dai, 1995). Environmental conditions during these months may be favorable for the survival of coral larvae is indicated by the fact that other sympatric foliaceous corals, including *Echinophyllia aspera* (Ellis and Solander, 1786) and *Mycedium elephantotus* (Pallas, 1766), also spawned in August and September (Fan and Dai, unpubl. data).

The life history of *M. ampliata* with a brief period of intense gametogenic activity may help to maintain its abundant population in southern Taiwan. In Nanwan Bay, algal coverage showed a remarkable seasonal variation which was high in February to April and low in summer (Dai, 1991). These algae, mainly *Codium* sp., often cause damage to corals by shading, smothering, or sediment entrapping. Interspecific competition and repair of damaged tissue involve great investment of energy which may reduce growth rate and fecundity of corals (Rinkevich and Loya, 1985; Van Veghel and Bak, 1994; Ward, 1995). The gametogenesis of *M. ampliata* begins after the seasonal algal bloom could not only favor the growth of adults but also increase the reproductive output.

In conclusion, aspects of sexual reproductive characteristics of *M. ampliata*, such as the age at first reproduction, mature egg size, reproductive effort, timing and period of gametogenesis, and the latitudinal variation of spawning are similar to those of *E. lamellosa*. The delayed reproduction of *M. ampliata* in southern Taiwan, compared to that in Okinawa, suggests that sea temperature may not be a primary factor controlling the reproductive seasonality of this species.

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