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## Sexual Reproduction of *Millepora intricata* and *Millepora tenella* (Hydrozoa : Milleporidae)

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## 4. DISCUSSION

### 4 - 1 Development of ampullae

In both *Millepora* species, *M. intricata* and *M. tenella*, the medusae size increased steadily through the reproductive season (Figures 7 and 8). Each medusa fitted its ampulla independent of reproductive maturity (Figures 10, 11, 12 and 13) (Hickson 1891) and there was a significant correlation between medusae size and ampullae size (Figures 16 and 17). Therefore, it was found that *Millepora* increases the size of their ampullae relative to medusa development.

Medusae appear to break through the skeletal ampullae cover, judging by the irregular shaped fragmented openings following medusae release (Figure 24d). Lewis (1991c) also suggested that most of the skeletal cover is broken away prior to liberation of the medusae. However it is not clear whether physical or chemical factors might effect the disintegration of the trabeculae. In the juvenile mushroom coral *Fungia fungites* (Scleractinia, Fungiidae), it is known that chemical dissolution of the skeleton causes the separation of the disc from the stalk (Yamashiro & Yamazato 1987, 1996). A similar phenomenon could be occurring at the tissue-skeleton interface of the ampullae. Gradual degradation of the skeleton would allow easy

access through the thin covering once the skeleton has been disintegrated.

There were no medusae present in both species one week after "stage IV". Therefore, medusae seemed to be released approximately one week after "stage IV". Similarly no empty ampullae were observed in the same sections, and the ampullae tissue looked as if it had recovered completely in the surrounding tissue. Empty ampullae were rapidly covered with tissue immediately after medusae release. New skeleton also regenerated on the bottom of the empty ampullae (Lewis 1991c).

Medusae of both species were all located directly beneath the colony surface, with their umbrella mouths facing toward the colony surface (Figure 13). A small opening was pierced in the middle of each ampulla covering (Figures 22 and 24). This hole may effect medusae and ampullae development. Although speculative, this situation may be related to skeletal breakage by the medusae, where strong pulsations of the umbrella mouth break through the skeleton.

#### **4 - 2 Development of medusae**

*Millepora* species develop medusae with gonads in special ampullae structures in the colony, while scleractinian corals develop temporary

gonads in, or by, the mesenteries within their body cavities (Rinkevich & Loya 1979a; Fadlallah 1983; Veron 1995). In branching scleractinian corals, it is generally believed that most polyps are incapable of developing gametes at the branch tips (Rinkevich & Loya 1979b; Wallace 1985; Soong & Lang 1992). This study shows that the branch tips of *Millepora* also have a sterile zone since no ampullae were observed there (Figure 21b; Hickson 1891). Infertile polyps in fecund colonies were also found at the basal margin of some branching *Acropora* species (Soong & Lang 1992), however, *M. tenella* possessed many ampullae at the base of each colony. *M. intricata* colonies have numerous fine, crowded, branches where many adjacent branches ultimately shade each other (Figure 1b). There were few ampullae in shaded areas. This might indicate the relationship between ampullae development and light.

In this study, I could not obtain a mature medusae just prior to release. Hickson (1899), however, examined mature female medusae specimens, with 1 - 4 large oocytes, which were collected from *Millepora* sp. in Jamaica. The immature stage of that species had 30 - 50 oocytes of approximately equal size. He concluded that most of the oocytes are ultimately absorbed into the large oocytes. A similar phenomenon has been reported in some scleractinian species (Rinkevich & Loya 1979a;

Harriott 1983), and it is supposed that a number of oocytes are resorbed during oogenesis, which may provide nutrients for the remaining oocytes (Harrison & Wallace 1990)

There have been some detailed descriptions on gametogenesis in *Millepora* spp. (Hickson 1891, 1899; Mangan 1909), however, this study is the first attempt to investigate the period of gametogenesis. In both *M. intricata* and *M. tenella* it took approximately 18 days from "stage I" to "stage IV" (Figures 7 and 8). Gametogenic processes in scleractinian corals are generally cyclic and usually exhibit annual, or lunar rhythms (Harrison & Wallace 1990). In Figure 7, results from *M. intricata* "colony 4" seems to indicate monthly gametogenic cycles. The possibility of overlapping cycles is evident because "colony 4" possessed gametes at both "stage I" and "IV" on June 10 (Figure 7). However, this was the only sample which had different stages of development at the same time.

#### **4 - 3 Medusae release**

No medusae were observed in the samples collected from all the marked colonies on June 4. Therefore, the first medusae release, in 1997, appeared to have happened between May 27 and June 4 (Figures 7 and 8). The second medusae release for *M. intricata* seemed to have occurred between

June 26 and July 1 (Figure 7), while after first release *M. tenella* never again developed medusae in 1997. *M. intricata* released medusae in the last quarter of the lunar cycle. Lunar patterns of gametogenesis, spawning and planula release are present in many coral species, but in most cases it is not known whether these rhythms are regulated by moonlight, tidal cycles, or many related factors acting simultaneously (Harrison & Wallace 1990; Van Woesik 1995).

Medusae release was not observed directly in this study for either *Millepora* species. However, coincidental developmental stages among the colonies of each species may indicate that medusae could have been released synchronously. Synchronous release of medusae among colonies appears to be necessary in *Millepora* because male and female medusae are released from separate colonies. Moreover, the short life span of medusae, that was within 5 - 6 hours (Hickson 1899), and 24 - 48 hours (Lewis 1991c) for *M. complanata*, imply that male and female gametes must meet and fertilize in the water column within a limited period. Synchronous development and release of gametes among individuals in a population are important to maximize the probability of successful cross fertilization (Babcock & Heyward 1986; Richmond & Hunter 1990).

Medusae were released from *M. intricata* branches, in the evening of 20 August 1996, over a 4 hour period. This result, although preliminary, indicates that medusae may be released at night for this species. Similarly scleractinian coral spawning occurs at night, between dusk and midnight (Babcock & Heyward 1986; Veron 1995).

#### **4 - 4 Reproductive season**

Ampullae were observed in *M. intricata* from May to July in 1997 during a period when the water temperature was rapidly increasing (Figure 25). *M. tenella* developed medusae only in May in the same year. Most scleractinian corals have a similar annual reproductive period, and release gametes during a short period in early summer (Heyward et al 1987). At Mizugama, however, ampullae appeared on *M. intricata* colonies in August 1996. Differences in the reproductive seasonality of a coral can occur within a species over its distributional range (Richmond & Hunter 1990). This preliminary study suggests that *Millepora* reproduction occurs between May and August. Further long-term studies are necessary to clarify these results.

In other places, different reproductive periods have been reported: *M. complanata* in Barbados possessed ampullae from April to July (Lewis

1991c), and in Curaçao this species did so from June to March (de Weerd 1984). Synchronous reproductive behavior in each region appears critical to ensure reproductive success.

#### **4 - 5 Released medusae**

Medusae released from a *M. intricata* colony, at Mizugama, showed similar features to the medusae described by Lewis (1991c) for *M. complanata* rather than those described by Hickson (1899). These medusae were simple with neither tentacles nor marginal sense organs (Figure 26), and appear to be incapable of catching prey. Many nematocysts, scattered on the umbrella or aggregated at the umbrella margin (Figure 26a), may be used for protecting gametes from predators, but are unlikely used to capture prey given such a short life-span. Some differences between my observation and the previous studies by Lewis (1991c) show that medusa of *M. intricata* had an umbrella whose diameter was 1.0 - 1.2 mm, and an unclear velum and a ring around the umbrella mouth. Lewis's medusae (1991c), from *M. complanata*, were 0.5 - 0.7 mm in diameter and had an apparent ring or circular canal, around the umbrella mouth. It is still unknown whether medusae vary between species. Here, I could not find significant differences between *M. intricata* and *M. tenella* from histological sections of immature female medusae.



Unfertilized oocytes in released medusae of Dr. M Yamaguchi's sample collected in 1982 (personal communication) contained numerous zooxanthellae (Figure 27b). Zooxanthellae started to appear inside the medusa at "stage IV" (Figure 13) in the present study, but there were no zooxanthellae within the oocytes of *M. intricata* and *M. tenella* (Figures 13b and c). Mangan (1909) concluded that zooxanthellae pass from the manubrium into the ovum, and that this invasion may commence at a period just prior to the release of the medusae. In contrast, there is no evidence in the literature that symbionts are present in the testes.

Some species of scleractinian corals also have been observed to possess zooxanthellae in the oocytes (e.g. *Montipora digitata* and *M. tuberculosa*, Babcock & Heyward 1986). However, it is not well known how zooxanthellae participate in oogenesis.

#### **4 - 6 Reproduction and distribution**

Asexual reproduction is believed to be important for recruitment into a local area (Highsmith 1982; Richmond & Hunter 1990; Lewis 1991b). In this study, *M. tenella* was less abundant than *M. intricata*, and were aggregated in a limited area. All the marked colonies of this species

showed the same sexuality. Therefore, these colonies may have been produced by fragmentation. During the present study period, gametogenesis was observed twice in *M. intricata*, on the other hand, it was observed once in *M. tenella*. This sexual reproductive infrequency by *M. tenella* might also be related to the relatively lower abundance of this species at the study site and around Okinawa in general.

Generally hydrozoan medusae act as long-distance dispersal mechanisms. However, it is unlikely in *Millepora* medusae because of their short life span. From this preliminary study, medusae are expected to be released in a synchronized manner during the rising tide of the last quarter of the lunar cycle. During this period, eggs and sperms may be released and fertilization probably occurs in this short period, given the short life span of the medusae.

Previous studies (Hickson 1899, Lewis 1991c, Yamaguchi 1982 personal communication Figure 27) showed that *Millepora* had zooxanthellae within unfertilized oocytes, however, it is not clearly understood what role these zooxanthellae play in larval dispersal (Babcock 1990). Sexual reproduction, particularly for broadcast coral spawners, allows corals to distribute their offsprings across relatively large distances (Richmond &

Hunter 1990). In regard to *Millepora* species, further studies concerning the planktonic period of egg and planulae, and the survivorship of planulae are needed. It is also unknown whether the gametes are neutrally buoyant, and if so, is the formation of medusae merely a transport mechanism to the sea surface where fertilization takes place.

The principal objective of this study was to observe sexual reproduction of *M. intricata* and *M. tenella*, however, further studies should focus on the behavior, longevity and competence of the medusae, and subsequent formation and longevity of the *Millepora* larvae in order to more fully understand this ubiquitous genus.