

## Spawning behavior of brooders

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Many corals spawn their eggs and sperm (i.e., their gametes) simultaneously in the water column at night at almost predictable times of the year. This type of reproductive mode is classified as broadcast spawning. Brooders, on the other hand, release their planula larvae directly into the water column after fertilization and growth in the coral polyps. All corals were previously regarded as brooders until it was discovered that the majority of corals were actually spawners (Harrison *et al.* 1984). More recently, some corals, such as *Goniastrea aspera*, appear to possess both reproductive modes (Sakai 1997).

Reproductive studies on brooding corals undertaken at the Palau Tropical Research Station in the 1940s revealed that Pocilloporidae and *Acropora brueggemanni* (*Isopora*) released their planulae into the water column (Atoda 1947a,b; 1951a,b). Pocilloporidae released planulae almost every month, throughout the year, in synchrony with the lunar cycle. This is in contrast to broadcast spawning corals which release gametes only once a year. In the other regions of the world, many brooders have also been observed to release planulae almost every month - for example in Hawaii, Guam, Australia (Great Barrier Reef), Red Sea, and Caribbean Sea (Richmond and Hunter 1990). In the vicinity of Ishigaki and Iriomote Islands, southwestern Ryukyu Islands, Japan, there is no data on the reproductive schedules of brooding corals, but if we extrapolate from data collected in (nearby) Taiwan (Dai *et al.* 1993), corals may also release planulae every month.

In Okinawa Island, which is located at a slightly higher latitude than Ishigaki and Iriomote Islands, reproductive schedules differ among Pocilloporidae: *Pocillopora damicornis* release their planulae for 8 months a year (May to December), while *Stylophora pistillata* and *Seriatopora hystrix* release for 3 months a year (May to July or June to August) (Yamazato 1991; Yamazato *et al.* 2000a, b; Permata *et al.* 2000).

While broadcast spawners release a great number of (tiny) eggs and sperm into the water column, where fertilization takes place, and the larvae require a few days to settle, brooders on the other hand release few planulae, more than 1 mm in length, and are well developed and ready for immediate settlement. But they don't always necessarily do so, yet the literature suggests that brooders have a narrower dispersal range than broadcasters because they usually recruit within the source area (Harrison and Wallace 1990). Yet, brooded planulae vary considerably in settlement-competency periods. *Pocillopora damicornis*, *Stylophora pistillata* and *Seriatopora hystrix* (Photo. 1a) planulae have zooxanthellae and can swim actively. While *P. damicornis* planulae can settle within a few hours after release, they can also settle after 100 days after release (Richmond 1987; Harii *et al.* 2002). Therefore, if these planulae do not find suitable habitats for settlement within a short time frame, they appear to have the potential to continue their planktonic life, disperse, and settle on distant reefs. However, genetic analyses of *P. damicornis* and *P. pistillata* populations in the Ryukyu Islands

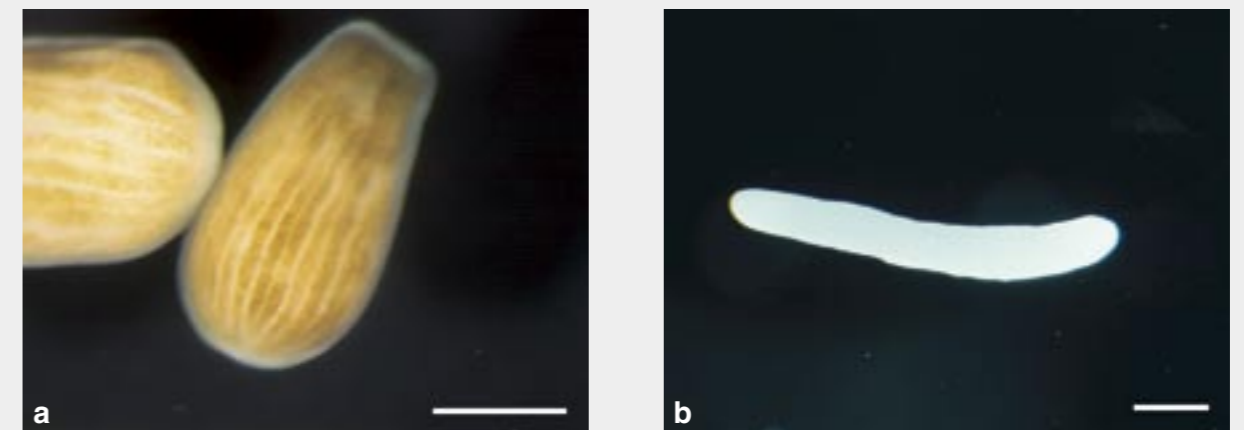


Photo. 1. Planulae of brooders: *Pocillopora damicornis* (a) and *Heliopora coerulea* (b). The scales are 0.5mm.

showed significant genetic differentiation among some populations which indicates that gene flow is not as high as expected (Adjeroud and Tsuchiya 1999; Nishikawa *et al.* 2003). Other brooding corals, such as *Acropora palifera*, *A. brueggemanni* and *Heliopora coerulea* (Octocorallia, Photo. 1b) do not have zooxanthellae. The less buoyant planulae of *H. coerulea* (blue coral) are usually found in the vicinity of substrate, and have the potential to immediately settle after release. They have been observed settling near parent colonies *in situ* (Harii *et al.* 2002; Harii and Kayanne 2003). These planulae appear to have a low dispersal potential because of their azooxanthellate nature, the low lipid concentrations, and short larval competency periods recorded (Harii *et*

*al.* 2002). *Alveopora japonica*, once a year releases both 'positively buoyant type' and 'benthic type' planulae, which are clearly at different stages of development (Igarashi *et al.* 1992; Harii *et al.* 2001). Benthic type planulae can settle immediately after release, but it generally takes positively buoyant type planulae a few days to settle. The latter have competency periods exceeding 100 days, suggesting that they have a different dispersal ranges compared with benthic type planulae. Although many studies suggest that the dispersal range of brooders is generally narrower than broadcast spawners, larval dispersal patterns are also dependent on the 'mother' colony's locality on the reef, settlement-competency periods, and local and regional currents patterns.