REPRODUCTIVE PATTERNS OF THE CARIBBEAN CORAL *PORITES FURCATA* (ANTHOZOA, SCLERACTINIA, PORITIDAE) IN PANAMA

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ABSTRACT

The branched finger coral *Porites furcata* (Lamarck, 1816) is common throughout the Caribbean and is one of the dominant reef-builders of shallow habitats in Bocas del Toro, Panama. *Porites furcata* is a brooding species and we found male and hermaphroditic polyps in histological sections, suggesting a mixed brooding system. Planulation occurs monthly throughout the year during the new moon. Fertility varied among months, but trends were not significant. The reproduction of *P. furcata* appeared to be asynchronous; individuals released larvae over several days independently from each other. Mean size of larvae was 400 μm (SD ± 98) and the average number of larvae released by one colony (10 cm diameter) was 110 ± 65 and ranged from 62 to 224 larvae during the week of the new and first quarter moons.

Scleractinian corals are able to reproduce sexually by gametogenesis or asexually by fragmentation (Highsmith, 1982) and asexual larvae (Stoddart, 1983; Ayre and Resing, 1986). Early reproductive studies assumed that most scleractinian corals were brooders (Hyman, 1940), but more recently, studies have revealed that the majority are broadcasters (Kojis and Quinn, 1981; Harriott, 1983; Babcock et al., 1986; Szmant, 1986; Richmond and Hunter, 1990). Broadcasters have a short annual spawning period and usually a large colony size, and are likely to colonize habitats with stable conditions. In contrast, brooders are generally smaller, have multiple reproductive cycles per year, and usually an opportunistic life history that enables them to colonize unstable habitats such as shallow water reefs (Szmant, 1986). Brooding likely consumes a high amount of energy, as the larvae grow within the mother polyp and have to be nourished for a prolonged time. This can be disadvantageous with regard to resource allocation for growth, defense, and maintenance (Szmant, 1986). However, brooder species may have an advantage in isolated reef systems, as their larvae usually settle immediately after release without traveling over long distances (Harriott, 1992), thus avoiding high larval mortality and settlement on suboptimal substrates. Brooding is assumed to be a mechanism of increasing reproductive success and efficiency and according to Szmant (1986) is adaptive for situations that require high local recruitment rates.

Sixty-eight percent of scleractinians are hermaphroditic (Harrison and Wallace, 1990; Richmond and Hunter, 1990), whereby both sexes are present in the same polyp or colony. Hermaphroditism may increase fertilization and the ability to colonize remote areas and maintain small populations. Successful fertilization in hermaphrodites depends on a synchronous development of sperm and egg cells, while in gonochoric coral species it is only guaranteed at high densities. As out-crossing is an important selective force in some groups of corals, this could be the reason for the evolution of gonochorism (Szmant, 1986). However, variation in sexuality is known; changes from gonochorism to hermaphroditism may be induced by changes in the environment or can occur naturally (Chornesky and Peters, 1987; Tomascik and Sander, 1987; Richmond and Hunter, 1990).

The branched finger coral *Porites furcata* (Lamarck, 1816) is common throughout the Caribbean and forms large carpets in shallow reef areas. *Porites furcata* and its congeneric species *Porites porites* (Pallas, 1766) and *Porites divaricata* (Lesueur, 1821) were described for a long time as different forms of the same species, but are now recognized as different species (Veron and Stafford-Smith, 2000). *Porites furcata* is one of the most successful reef-builders in shallow habitats of Bocas del Toro, Panama (Glynn, 1973; Porter, 1974; Wulff, 1984; Guzman and Guevara, 1998a; Aronson et al., 2004; Kuntz et al., 2005). The living coral cover estimated for shallow reef habitats down to 2 m depth is 90% and a semi-continuous *P. furcata* reef of approximately 22 km in length was described by Guzman and Guevara (1998a) as unique for the region. However, there is little information about the reproductive cycle and strategy of *P. furcata*. Soong (1991) described the species as a gonochoric brooder, whereby sexes are separated and fully developed larvae are released during new moon. As his observations were made in an area which was affected by chronic oil pollution 3 yrs prior to the study (see Guzman et al., 1991; Guzman and Holst, 1993), we tested those observations in unaffected areas, where the species has shown a remarkable success out-competing other coral species and sessile organisms.

It is particularly important to understand the reproductive ecology of *P. furcata* in light of the increasing coastal development for tourism in Bocas del Toro, including deforestation of mangroves and increased erosion and runoff (Weber et al., 2006).

Materials and Methods

Study Area and Sample Collection.—The Bocas del Toro archipelago in northwestern Panama consists of seven main islands covered with mangroves and tropical forest, separated by two major water bodies, Chiriquí Lagoon and Almirante Bay (Fig. 1). The latter shows a major reef formation, whereas Chiriquí Lagoon is influenced by the run-off of several rivers and therefore has very poor reef development. High deforestation occurs in areas dominated by cattle farms, agriculture, and indigenous communities (Guzman and Guevara, 1998a).

Samples of *P. furcata* were collected on Cristóbal Island (9°17′20″N/82°15′24″W) (Fig. 1). Samples were obtained in 2 m depth by snorkeling on a weekly basis on the first day of each lunar quarter from February 2003 until January 2004, to determine the time of the planulating period and the time of larval release. An individual, sexually derived colony ("genet") is hard to define looking at the dense *P. furcata* carpets; therefore we referred to the collected samples as "ramets". Six adult, reproductive ramets with three or more branches were randomly selected in at least 5 m distance from each other.

Sample Processing.—Two branches were clipped off from each collected ramet, fixed in 5% formalin for 3 d and then transferred to 70% Ethanol until decalcification. The branches of *P. furcata* were decalcified with 5% nitric acid, while wrapped in a mosquito mesh to guarantee a homogenous decalcification. The acid was changed every 24 hrs until the skeleton was totally dissolved. This process usually took 2 d. After decalcification, the coral tissue was put into Histoprep tissue capsules, rinsed for 4 hrs under running water and then transferred into 5% sodium sulfate for 6 hrs. Finally, samples were rinsed under running water for 12 hrs and then stored in 70% ethanol. Tissue samples were stained with Methylene Blue for analysis. This colorant stains the mucus cells, while the gonads appear white and can be distinguished from other soft tissue (Soong, 1991). Samples were dissected under a stereo-microscope and the number of eggs was counted, their size measured, and their developmental stage evaluated in 200 polyps per sample, generating a total of 62400 polyps analyzed for the year 2003 (Table 1). Categories were established for the quantity of eggs in the tissues: category 0 for < 50 eggs in the analyzed tissue, category 1 for 51–200 eggs and category 2 for > 200 eggs in the tissue. Older tissue samples from 1999, collected on Colón Island, Bocas del Toro (Fig. 1),

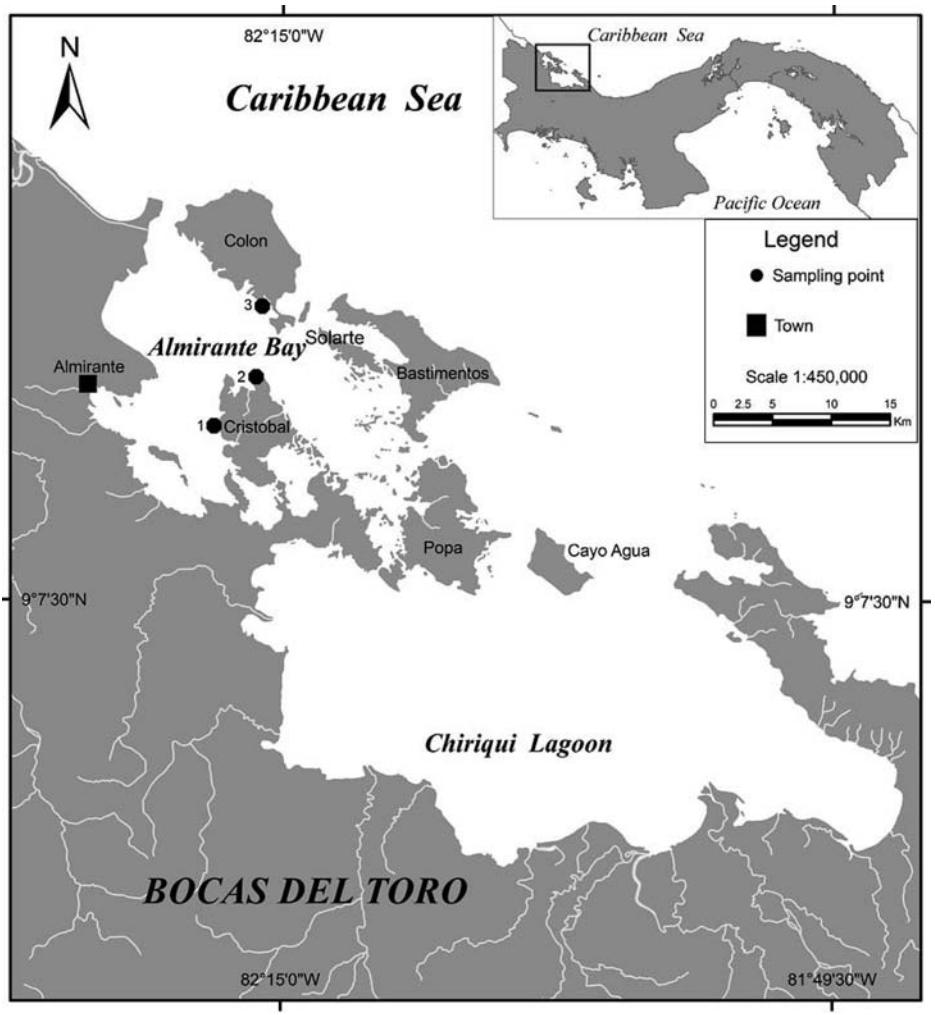

Figure 1. Map of the Bocas del Toro archipelago. The collection sites on Cristóbal and Colón Island are marked with black dots. 1 = Cristóbal-1; 2 = Cristóbal-2; 3 = Colón Island.

were analyzed as a comparison between two different years and sites. Samples from Colón Island (9°18′45″N/82°16′02″W) were collected monthly from March 1999 to January 2000 and preceded as described above for the samples from Cristóbal Island in 2003. We also dissected 200 polyps per sample, generating a total of 52800 polyps analyzed for the year 1999 (Table 1).

As spermaries cannot be easily identified under the stereo-microscope, histological sections were necessary to determine the sex of *P. furcata* individuals. Histological sections of 6 µm were obtained from a total of 131 samples using standard techniques (Guzman and Holst, 1993). One hundred samples were taken from a monthly collection of *P. furcata* on two sites on Cristóbal Island (64 from Cristóbal-1; 36 from Cristóbal-2; 9°17′32″N/82°16′16″W) from May 2004 until April 2005 (Fig. 1); another 31 samples were obtained from the monthly collection on Colón Island from March 1999 until January 2000 (Table 1).

Larval Behavior.—Individual *P. furcata* ramets of approximately 10 cm diameter were collected outside of the large carpets on Cristóbal Island (9°17′20″N/82°15′24″W). Ramets that did not form part of the carpet were easy to detach and their individual size could be defined. Individuals were immediately transported in insulated coolers to the Bocas del Toro

Table 1. Summary of sample collection and analyses.

Year	Collection site	No. of samples collected	No. of samples analyzed	No. of polyps analyzed	Analysis
Mar 1999–Jan 2000	Colón Island	528	264	52,800	Dissection
Mar 1999–Jan 2000	Colón Island	528	31		Histology
Feb 2003–Jan 2004	Cristóbal-1	624	312	62,400	Dissection
May 2004–April 2005	Cristóbal-1	144	64		Histology
May 2004–April 2005	Cristóbal-2	144	36		Histology

Field Station of the Smithsonian Tropical Research Institute on Colón Island. Upon arrival at the laboratory, corals were kept in large water tables, shaded from direct sunlight with translucent roofing panels and supplied with a continuous flow of filtered seawater. After acclimatization, 10 *P. furcata* ramets were placed individually in small 5 L plastic containers (15 cm height and 15 cm diameter) and independently supplied with running seawater. The larval traps were made from 0.7-L plastic beakers where the bottom was cut off and a 0.1 mm mesh glued to one opening; larval traps were placed at the outflow of the containers. The traps were emptied and rinsed twice a day to collect the larvae, over a month long period in each of November 2004 and March 2005. The number of larvae for each ramet was counted under a stereo-microscope and their size measured with a calibrated measuring lens. Larvae were transferred into petri dishes to observe metamorphosis and settlement. Ramets which released larvae were transferred into 2.5 L plastic jars in the night and left without running water to observe larval behavior right after release and to determine the exact time of release.

Results

Reproductive Patterns.—The monthly average number of eggs was calculated from weekly data. The number of eggs (i.e., the fertility of the adult ramets) varied among months (Kruskal-Wallis ANOVA: $P = 0.048$, $N = 24$) in the samples collected in 2003 (Fig. 2A). Significant differences were detected between March and August (Mann-Whitney: $P = 0.009$), May and August (Mann-Whitney: $P = 0.002$), and May and September (Mann-Whitney: $P = 0.03$). The lowest fertility was observed in March and May 2003 with 60 and 65%, respectively, while the highest fertility of 95% occurred during August and November 2003. The average number of eggs was high during the first lunar quarter as well as at full moon and had a tendency to be lower during the last quarter and new moons. However, average number of eggs during the different weeks of the year 2003 showed no clear pattern in relation to the lunar cycle (Fig. 3). The highest average egg number was 353 in 200 polyps, while the lowest egg number was 72 in 200 polyps analyzed from six individuals per week. No data were available for four non-consecutive weeks during 2003.

Only samples collected during the week of the full moon in 2003 were used to compare to monthly samples from 1999 to keep the timing and the number of samples equal for the 2 yrs. Egg numbers were significantly higher in samples collected during 2003 compared to the samples obtained for 1999 (Mann-Whitney; $P < 0.0001$; Fig. 2B). Highest fertility was observed from October to January and in the months of April in 2003. The samples from 1999 showed a similar trend, as fertility was highest from November until January. Lowest fertility in 2003 was documented for the month of June, while in 1999, the lowest fertility occurred in the months March and October. No data were available for the month of August in 2003.

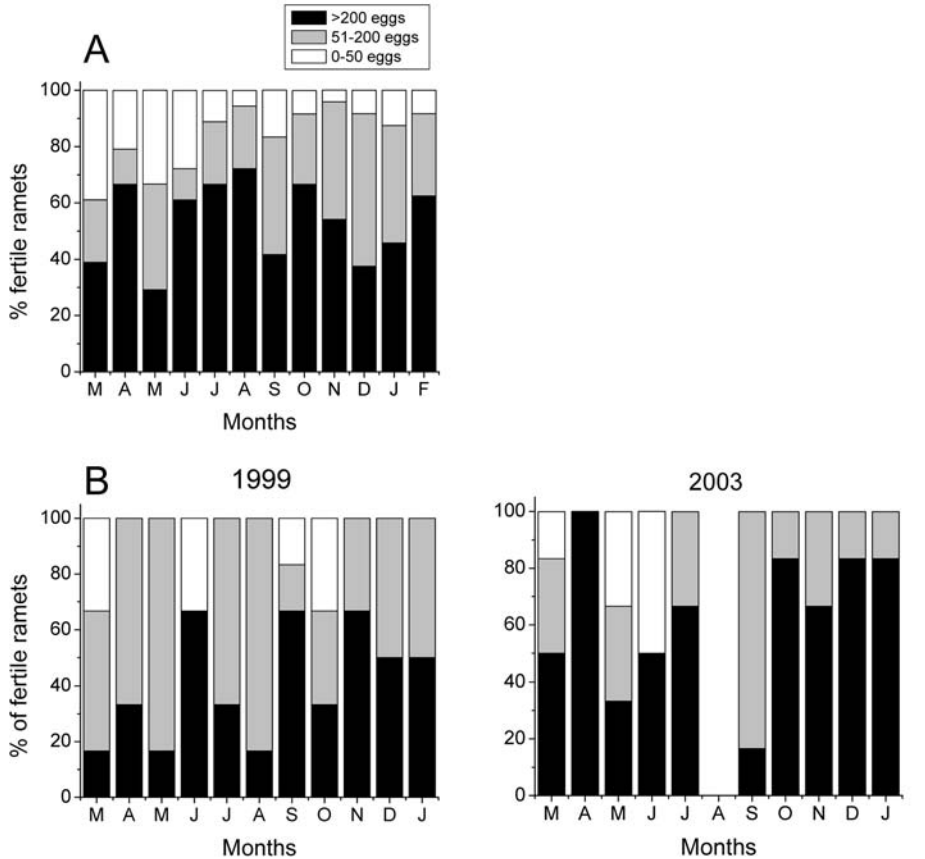

Figure 2. (A) Percentage of fertile *Porites furcata* ramets observed during the dissection of weekly tissue samples from February 2003 to January 2004. (B) Comparison of percentage of fertile colonies in samples of *P. furcata* from March 1999 to January 2000, and from March 2003 to January 2004 collected during the monthly full moon.

Four different developmental stages could be recognized in the dissected samples, based on the organization of eggs in the tissue and their size. During the first 2 wks, starting with new moon, eggs were mainly lined up like a chain connected to the mesenteries. During full moon and the last quarter, developed larvae were loose in the tissue rather than connected to the mesenteries. The smallest eggs were found during new moon, suggesting spawning during this period, while the largest eggs were found during the last quarter of the moon. A significant difference was detected between the mean egg size during new moon (159.7 µm) and the other lunar quarters (Kruskal-Wallis ANOVA; P = 0.001, N = 212), when egg size increased to 176.8 µm during the first quarter, decreasing slightly to an average size of 171.1 µm during the last quarter of the moon. However, there were different stages present simultaneously within individual polyps throughout the monthly oogenic period. Daily collections made in October and November 2003 during the week of the new moon revealed an uncoordinated release of larvae. Larvae appeared to be released over several days by different individuals and new, small eggs were immediately found in the tissues.

A mean ovary size of 84 µm ± 34 in histological samples was observed at new moon, whereas ovary sizes remained stable at 173 µm ± 36 during other lunar periods, in-

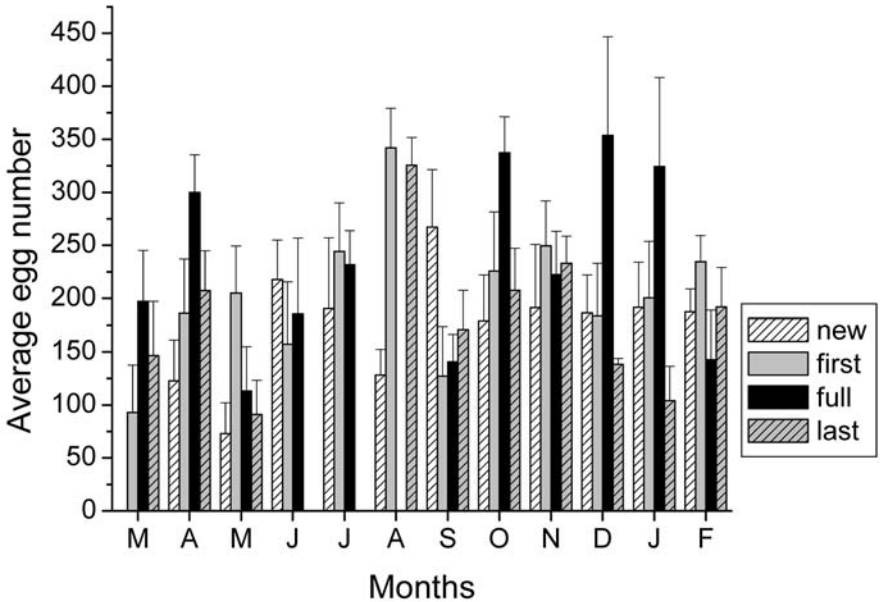

Figure 3. Average number of eggs in *Porites furcata* tissue per week from February 2003 until January 2004 in relation to lunar phase. Error bars represent the standard error (SE).

dicating larval release during the new moon. Our histological sections revealed that *P. furcata* can also be hermaphroditic, with ovaries and spermaries embedded in the same polyp (Fig. 4). Female and male gonads were located in different mesenteries of the polyp. From the 131 samples that were analyzed, 59 individuals were identified as hermaphrodites. We found 25 hermaphrodites, 38 males, and 1 sterile individual in the samples from Cristóbal-1 (2004); 15 hermaphrodites, 20 males, and 1 sterile individual in the samples from Cristóbal-2 (2004); 19 hermaphrodites and 12 males in the samples collected on Colón Island in 1999.

Larval Behavior.—Larvae were observed in the field during the weeks of the new and first quarter moons of September and November 2004 and of January and March 2005, between 0500–0600. After release, larvae moved up in the water column and were swimming on or close to the surface for several hours. No light sensitivity of the larvae was observed. Spawning began during the first day of the new moon and extended over nearly 2 wks. Individual ramets never released all larvae at once, but

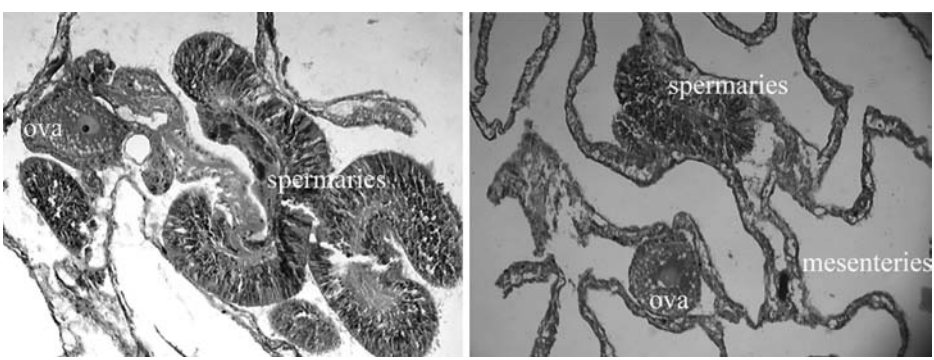

Figure 4. *Porites furcata* individual identified as a hermaphrodite due to the simultaneous presence of ovaries (left) and spermaries (middle and right) in the polyp.

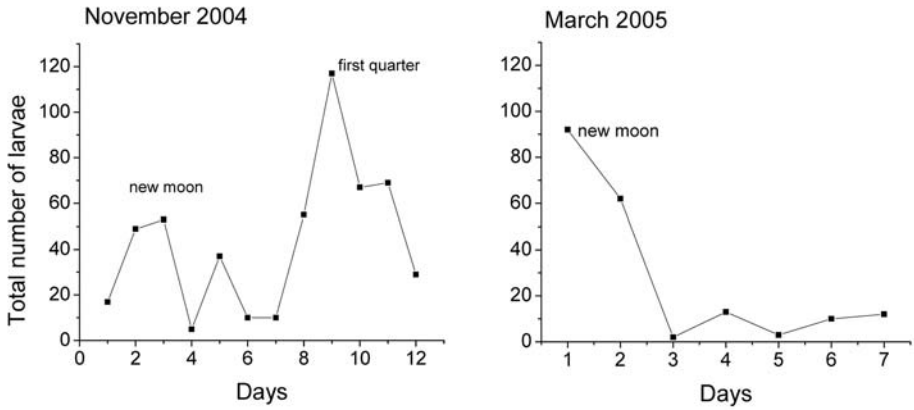

Figure 5. Daily larval release patterns of *Porites furcata* during November 2004 (12 d) and March 2005 (7 d), in relation to lunar phase.

spawned over several days, usually over four consecutive nights. The number of larvae released by 10 ramets observed in November 2004 and March 2005 varied greatly, ranging from 62 to 224 larvae with a mean of 110 ± 65 larvae per individual (10 cm diameter) during one spawning period (Fig. 5). The size of 100 *P. furcata* larvae was measured and an average size of 400 ± 98 µm calculated. Larvae kept in petri dishes metamorphosed in the water column after 6 d, showing a flat, umbrella like form. Larvae did not settle in the dishes and died within 10–30 d. Only two recruits were observed after 14 d and they survived for 60 d attached to the plastic surface.

Discussion

The extensive, carpet-like patch and fringing reefs formed by *P. furcata* in the Bocas del Toro region suggest an adaptation to different environmental conditions, but could also be a result of asexual reproduction (fragmentation) combined with fast growth and high competitive traits. High abundances of adult colonies are likely due to high recruitment rates, which require highly successful reproduction (Szmant, 1986). Brooder species usually spawn several times per year and are able to colonize unstable habitats (Szmant, 1986). *Porites furcata* exhibits those characteristics as it has a monthly planulating cycle and is able to colonize pristine as well as turbid waters influenced by run-off. *Porites furcata* spawned throughout the year in Bocas del Toro and elsewhere along the central coast of Panama (Soong, 1991; this study). The larvae of brooding species usually settle immediately after release (Harriott, 1992), increasing their fitness by avoiding the risk of larval predation (Isomura and Nishihira, 2001). Rapid settlement and metamorphosis may be beneficial in habitats with unusual environmental conditions or high predation, and may compensate for high adult mortality (Szmant, 1986; Shlesinger and Loya, 1991; Shlesinger et al., 1998). The larvae of *P. furcata* are approximately 400 µm long, which is relatively small in comparison to other Caribbean coral species, which range in size between 0.6 and 1.0 mm (Soong, 1991). Isomura and Nishihira (2001) pointed out that larger larvae may disperse over longer distances by using the photosynthetic energy transferred from the zooxanthellae. For example, larvae of *Pocillopora damicornis* (Linnaeus, 1758) are 900 µm long and have a dispersal potential of 103 d (Richmond, 1987). Prelimi-

nary molecular data on the population structure of *P. furcata* and larvae survivorship without settling for up to 30 d suggest larval dispersal over great distances and therefore a potentially high connectivity of the reef areas in Bocas del Toro. Further genetic analyses are required to assess the dispersal potential of *P. furcata*, which might be greater than expected.

Individual *P. furcata* ramets spawned independently over a 2 wk period beginning at the new moon, resulting in an unsynchronized release of larvae. Soong (1991) observed this pattern as well in *P. furcata*, *Porites astreoides* (Lamarck, 1816), and *Siderastrea radians* (Pallas, 1766), apparently a common feature among brooder species which typically show little evidence of lunar synchrony (Richmond and Hunter, 1990). According to Szmant (1986), brooder species tend to release a small number of larvae per planulating period because they have multiple reproductive cycles per year. The number of larvae released by a *P. furcata* ramet varies greatly: 62–224 larvae were released by different colonies during a single spawning period. Colony size is correlated to colony survival and fertility, with a larger colony expected to have a greater reproductive output than a smaller one (Hughes, 1984; Hughes and Jackson, 1985; Soong and Lang, 1992). The ramets collected for this study were of similar size, but the time when they fragmented and their size after fragmentation is unknown. A recently separated ramet might use its energy for growth and establishment and may therefore not be as fertile as an older one, which could explain the differences in the number of released larvae.

Larvae were released year-round in *P. furcata* collected in Bocas del Toro, whereas Soong (1991) did not observe larvae during February and March in samples from the central Caribbean coast of Panama. Reproductive tissue was not observed in the tips of the branches in our samples, as previously described (Soong, 1991; Szmant, 1986). Our histological data revealed that in local populations, *P. furcata* can be a hermaphrodite with ovaries and spermaries observed together in the same polyp, contrary to Soong (1991), who described the species as gonochoric. Pacific *Porites* spp. are known to be mainly gonochoric (Richmond and Hunter, 1990; Glynn et al., 1994). In the histological sections analyzed, we identified hermaphrodites, males, and sterile individuals. Mixed brooding systems are known from *P. astreoides*, where male and female polyps or colonies were observed in addition to hermaphrodites (Chornesky and Peters, 1987). Hermaphrodites, where eggs and sperm develop at different times in a colony, can lead to a misdiagnosis as gonochoric (Richmond and Hunter, 1990). This seems to be more likely for broadcasting species because their gamete development occurs over several months. Another feature known from plants could also explain the observed males and hermaphrodites: Androdioecy in plants describes the occurrence of males and hermaphrodites in sexually reproducing populations (Pannell, 2002) and might also exist as a strategy in corals. However, we assume that the males we found in our samples could be hermaphrodites, as (a) collected colonies might have been too young; (b) ovaries and spermaries might develop asynchronously at different times, or (c) the number of polyps cut to prepare a histological slide is much lower (15) than the number of polyps analyzed during dissection (200). Thus, gametes may not occur in some sections and therefore reproductive output may be underestimated (Harrison and Wallace, 1990).

High rates of inbreeding are expected from hermaphrodites, but it seems that outcrossing efforts are made by producing large numbers of sperm and by the separate locations of male and female gonads on the mesenteries (Szmant, 1986). Our his-

tological sections indicated that male and female gonads were located on different mesenteries in *P. furcata*. However, our observations suggest a lack of sperm. Generally, low numbers of larvae were released by a ramet, although high numbers of eggs were found in their tissues. Probably large numbers of eggs are produced to guarantee a successful fertilization, but only a small number of eggs are actually fertilized by the released sperm. It is possible that unfertilized eggs are fertilized during the next spawning cycle.

Monthly planulation cycles of *P. furcata*, release of fully developed larvae, and a modest dispersal potential seem to be the strategy for successful colonization of shallow water habitats in Bocas del Toro. In contrast to the expectations due to its branching morphology, the success of the species depends mainly on sexual reproduction rather than asexual propagation.

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