

The Reproductive Cycle and Spawning in a Caribbean Gorgonian

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Abstract. The reproductive biology of *Plexuara* A, a common but undescribed Caribbean gorgonian, was studied in the San Blas Islands, Panama. Oocytes were present in the polyps throughout the year, though a seasonal developmental cycle is evident. Early stage oocytes appeared at the base of the polyps in November. In January total egg volume per polyp began to increase and reached a maximum in early May. Total egg volume per polyp then decreased through the summer as mature eggs were released. Spawning occurred over a period of 4–7 days following each full moon in May, June, and July. Egg release was synchronous, starting at approximately 18:30 and lasting 90 minutes. Larval development is initiated just prior to or at the time of release. Initiation of larval development at the time of release without brooding is unknown for any gorgonian or scleractinian. Of 265 colonies examined from 6 reefs near San Blas Point, all but 3 contained gonads and were female. No male or hermaphroditic colonies have been found in the San Blas Point population. The scarcity or possible absence of males suggests that the eggs may develop parthenogenetically. Both of these unusual characteristics point to the need to use caution whenever the reproductive biology of a coral is described without an exhaustive examination of the complete reproductive cycle.

Introduction

Gorgonians are an important component of many Caribbean reefs (Kinzie, 1970, 1973; Goldberg, 1973; Opresko, 1973; Muzik, 1982; Lasker and Coffroth, 1983). In some habitats they comprise the dominant coral cover, yet knowledge concerning the reproductive biology of these organisms is lacking. In contrast, sexual reproduction in scleractinians has become a topic of re-

newed interest (for review see Fadlallah, 1983; Harrison, 1985). This interest is due in part to the diverse assortment of reproductive strategies employed by scleractinians (Harrison, 1985; Szmant, 1986) and anthozoans in general (Chia, 1976). Compared to other anthozoan taxa, gorgonians exhibit a more limited range of reproductive strategies. Most gorgonians appear to be gonochoric brooders (Kinzie, 1970; Grigg, 1977; Weinberg and Weinberg, 1979; Brazeau, 1986). The combination of separate sexes and internal fertilization (or at best fertilization on the surface of the female colony) is an unusual strategy in other anthozoan taxa and is the rarest strategy displayed by the ecologically similar scleractinians (Szmant, 1986). The wide distribution and apparent success of gorgonians throughout the Caribbean and their reliance on a relatively unusual reproductive strategy suggests the need for more information on the basic reproductive biology of this group.

In this paper we report on reproduction in a Caribbean gorgonian. The species, a *Plexuara* sp. of uncertain affinity, is similar to *Plexuara homomalla* forma *küken-thali* and will be referred to as *Plexuara* A (after Lasker, 1984). *Plexuara* A is common in the San Blas Islands, Panama, and is locally abundant at sites throughout the Caribbean (Lasker, unpub. data). We present data on colony size at first reproduction, the annual cycle of gonad development, mode of reproduction, and timing of egg release.

Materials and Methods

Samples of *Plexuara* A colonies were collected from Korbiski reef, a small back reef and reef flat complex located near the Smithsonian Tropical Research Institute field station in the San Blas Islands, Panama (9° 33'N; 78° 52'W). To determine colony size at first reproduction, all *Plexuara* A colonies within a 10 × 10 m area were

examined *in situ* in July 1984. All colonies with visible gonadal material were scored positive for reproductive ability. To follow the yearly reproductive cycle, 10 colonies were tagged with aluminum tags nailed to the reef substrate and sampled monthly from July 1983 to July 1985. Multiple sampling of these colonies did not affect the results since there was no systematic change in reproductive state of the colonies over the two-year period. Samples were fixed in 10% formalin and later examined with a binocular stereomicroscope. Twenty polyps located between 5 and 15 cm from the branch tip were arbitrarily selected and the diameters of all oocytes were measured with an eyepiece micrometer. To follow oocyte development up to and during egg release, weekly samples of 5 tagged colonies were collected in May, June, and July of 1986 and 1987. During the spawning period in 1987, samples were taken twice daily from the same 5 colonies. The reproductive cycle of *P. homomalla*, a close congener of *Plexuara* A, was also followed on the same reef to determine if the two reproductive cycles were in synchrony. Samples from 5 tagged *P. homomalla* were collected monthly from July 1983 to July 1985 and weekly during May, June, and July of 1987.

Since none of the collections of *Plexuara* A from 1983, 1984, and 1985 included male colonies, 140 additional colonies were sampled from Korbiski reef in July of 1986 to determine the sex ratio of *Plexuara* A. Twenty colonies each were also collected from Macaroon, Sail Rock, Tiantupo, and T-Bar in 1987 to determine the sex ratio on these nearby reefs. Additionally, to determine if sex varied within colonies, 10 colonies were selected at Korbiski in July 1988. Sections of tissue from the outer, middle, and base of each colony were collected for sex determination.

To determine the sex and gonad developmental state of each sample, cross- and longitudinal-sections were decalcified, dehydrated, cleared, embedded in Paraplast, sectioned 7 μ m thick, and stained with Heidenhain's azocarmine-aniline blue (Yevich and Barszcz, 1977).

To observe egg release, a series of night dives were undertaken in May, June, and July of 1987 and 1988. During each dive in 1987, all colonies in 4 areas, approximately 100 m² each, were monitored. Colonies that released eggs were tagged each night and counted the following morning. In 1987 and 1988 eggs were collected with a large syringe as they emerged from the polyps. Eggs and larvae were fixed in 10% formalin and later embedded, sectioned, and stained as noted above.

Results

Colony size and gonad development

Figure 1 shows the percentage of colonies in 10 cm increment size classes which contained visible gonads in

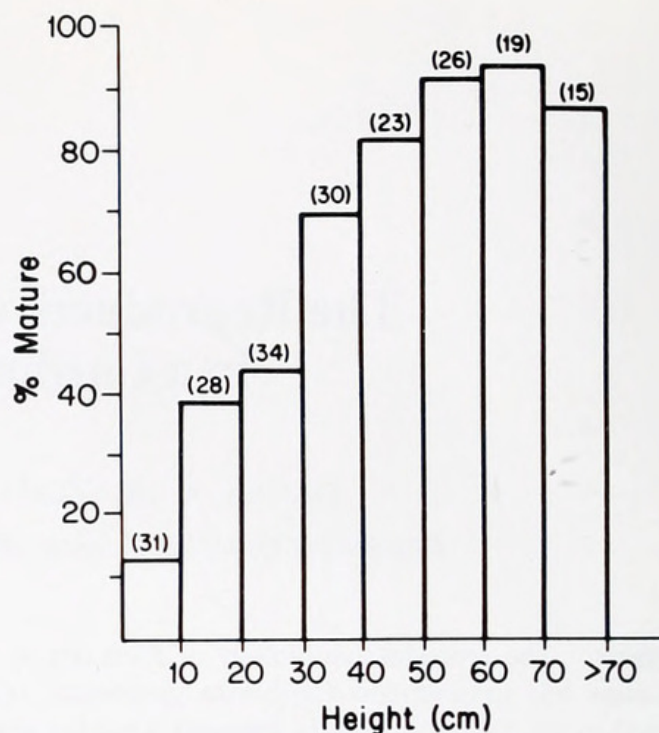


Figure 1. Proportion of *Plexuara* A colonies containing visible gonad. Colonies sampled in 1984 from a 10 \times 10 m site at Korbiski reef. Number sampled in each size class is noted in parenthesis.

July 1984. The presence of visible gonads is a good indicator of reproductive activity since only large mature gonads are visible to the naked eye. Of the 206 *Plexuara* A colonies, 58% had visible (mature) gonads. Small colonies, 30 cm or less in height, less frequently had mature gonads (32%), whereas 80% of the colonies greater than 30 cm in height had mature gonads. The smallest colony found to be reproductive was 10 cm in height.

Sexuality

No male or hermaphroditic polyps or colonies were found among the 265 colonies examined over 4 years from 6 reefs in the San Blas Point area. During the reproductive months of May, June, and July, all but three of the colonies examined histologically contained ovaries. There were no colonies in which the gender was ambiguous. From these data we conclude that male colonies are extremely rare or absent in this area.

Annual cycle of oocyte development

Plexuara A displays a yearly or multi-year cycle of oogenesis. Young oocytes appeared in the polyps each November (Fig. 2a). The oocytes were attached to the septa at the base of each polyp by a short mesogloea stalk. Larger oocytes, presumably from the previous year, were also present in November. The young oocytes increased in size and by January were indistinguishable from the older oocytes. From this pool of oocytes a portion began

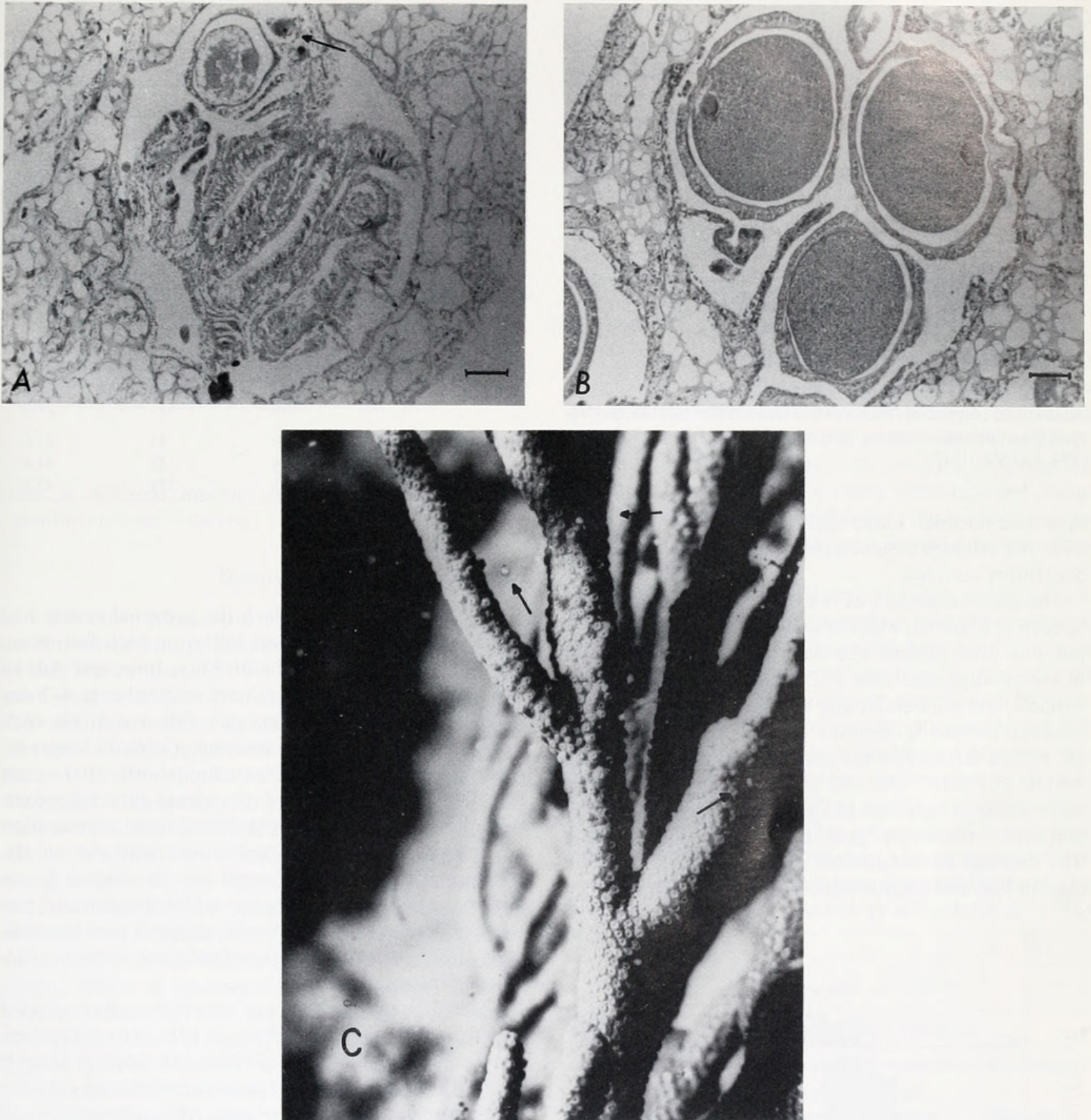


Figure 2. *Plexuara*. (A) Stages of oogenesis. (A) Young oocyte. Arrow indicates young oocyte. Note large, older oocyte also present. (B) Large oocytes at base of polyp. (C) Eggs at time of release. Arrows indicate eggs just released and eggs emerging from polyps. Scale bar = 125 μm .

to increase in size rapidly. An average of 1.9 oocytes/polyp ($SD = 0.99$) reached maturity each year. Maximum egg diameters ranged from 500 to 600 μm (Fig. 2b). The cycle of development can be seen in Figure 3, which shows mean total egg volume per polyp from June 1983 to July 1985. Since oocytes were present in the polyps

throughout the year, mean egg volume never decreased to zero. Total egg volume per polyp increased slightly in November of each year with the appearance of the new oocytes, and increased rapidly from January through May as a portion of the oocytes increased in size. In June, July, and August, total egg volume decreased as the large

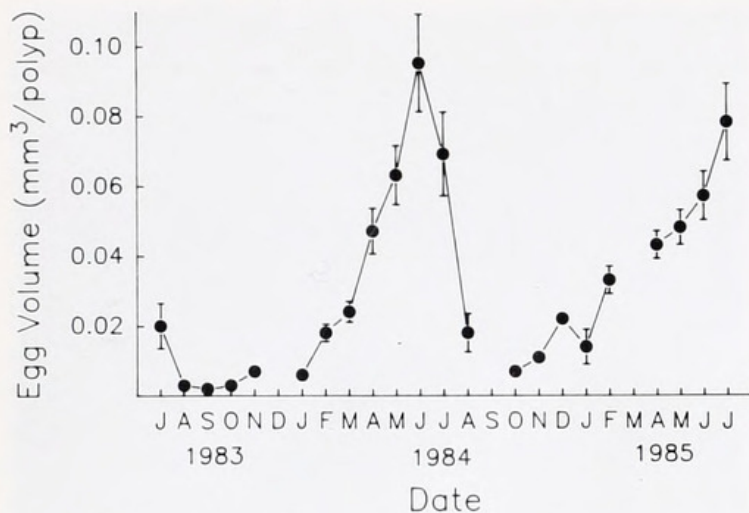


Figure 3. Total egg volume per polyp for *Plexuara A*. Based on means of 20 polyps from each of 10 colonies. Error bars denote 95% confidence intervals. Samples were not collected in Dec. 1983, Sept. 1984, and Mar. 1985.

eggs were released. Large eggs ($>400 \mu\text{m}$ diameter) that were not released degenerated and were not present in September samples.

The seasonal pattern of oocyte development can also be seen in Figure 4, which shows the number of eggs per polyp in three distinct size classes. The number of eggs in the smallest size class ($<200 \mu\text{m}$ diameter), though variable, did not exhibit any seasonal pattern. This size class represents the common pool of oocytes present in the polyps throughout the year. Numbers of eggs in the middle size class ($200\text{--}400 \mu\text{m}$ diameter) increased in early spring as eggs enlarged and then decreased in May and June as the oocytes grew into the $>400 \mu\text{m}$ size class. The decrease in the number of eggs in the largest size class in July and August was coincident with spawning.

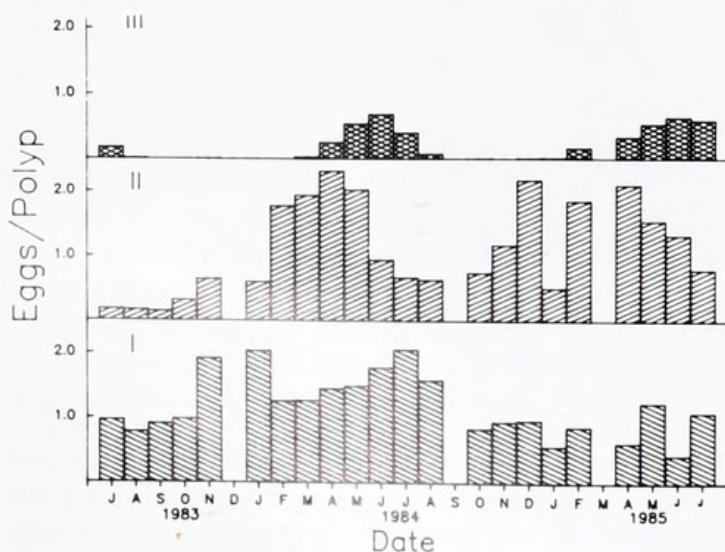


Figure 4. Monthly changes in mean number of eggs per polyp for *Plexuara A* in three size classes. I, $<200 \mu\text{m}$ diameter; II, $200\text{--}400 \mu\text{m}$ diameter; III, $>400 \mu\text{m}$ diameter.

Table I

Numbers of Plexuara A colonies observed to spawn in 1987 at Korbiski reef

Month	Site	Colonies spawning	Total number of colonies ($>20 \text{ cm}$)	Percent of colonies spawning
May	10 × 10	13	95	13.7
	I	11	84	13.1
	III	6	106	5.7
		30	285	10.5
June	10 × 10	40	95	42.0
	I	37	84	44.1
	II	52	144	36.1
	Wall	35	114	30.7
		164	437	37.5
July	10 × 10	39	95	41.0
	II	64	144	44.4
		103	239	43.1

Spawning

Mature eggs (eggs in which the germinal vesicle had broken down) were released following each full moon during the summer months. In May, June, and July of 1987 and 1988, mature eggs were released over 4–7 day periods, 1–2 days following each full moon (Fig. 2c). Spawning was highly synchronous. Colonies began releasing eggs at virtually the same time shortly after sunset (18:30–18:50). The period of release lasted approximately 90 minutes each night. Histological examination of branch samples collected twice daily during the spawning period did not reveal any developing larvae within the polyps nor any eggs in which the germinal vesicle had broken down. However, eggs collected immediately after release and held in polyethylene containers developed into planulae.

Table I shows the number of colonies that released eggs from four sites at Korbiski in 1987. These numbers are a minimum estimate of spawning colonies since it was not possible to simultaneously monitor all colonies during the periods of egg release. Although some small colonies contained oocytes, we never observed egg release in colonies less than 20 cm in height. The percentage of colonies releasing eggs was greatest in June and July and varied between sites. Many colonies spawned on more than one night in any given month (48% of the colonies in June and 32% in July) and in more than one month. This pattern is also evident in Figure 5, which shows the number of large ($>400 \mu\text{m}$) eggs per 20 polyps during 1984. The three colonies were chosen to demonstrate the variability in times of maximal development and release among colonies. Colonies had peak egg con-

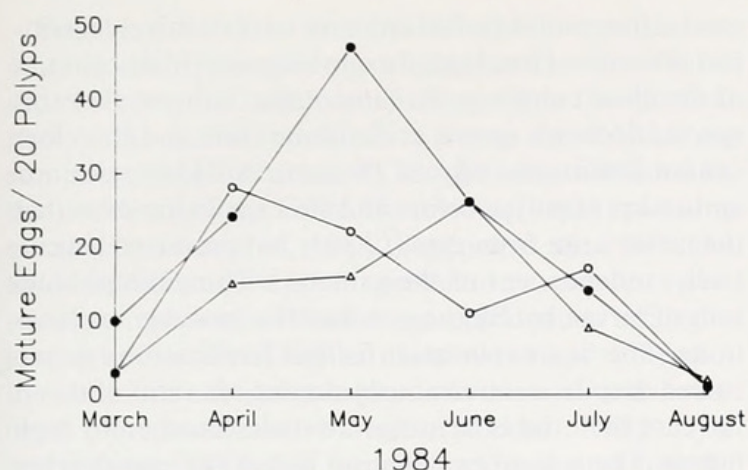


Figure 5. Total number of large eggs ($>400\ \mu\text{m}$) in 20 polyps of three *Plexaura A* colonies. Colonies were chosen to demonstrate the variability in times of maximum development and release.

tent in different months and also differed in which month(s) release occurred.

Discussion

As in other gorgonians, *Plexaura A* colony size was an important determinant of reproductive state. Wahle (1983) reports that only *Plexaura homomalla* colonies that are greater than 20 cm in height are reproductive. Our results are similar to Wahle's in that most colonies less than 20 cm in height were not reproductive. Furthermore, <20 cm tall colonies were never observed to release eggs. This indicates that either the eggs fail to mature or do so in very small numbers in small colonies. Unlike Wahle's observations, we did find reproductive tissue in some <20 cm colonies and even in some 10 cm colonies. The presence of gametogenesis among these colonies may indicate a smaller size of first reproduction among *Plexaura A* colonies, error introduced in using colony height to measure size of first reproduction, or effects of the age of the colony. First, *Plexaura A* may start reproduction at a smaller size than *P. homomalla*. Size of first reproduction varies among colonial coelenterates such as alcyonaceans (Benayahu and Loya, 1984) and scleractinians (Szmant, 1986). It is likely that gorgonians also will exhibit interspecific variation in this basic life history trait. Second, and perhaps most important is the fact that colony height is an approximate measure of overall colony size for organisms with arborescent growth forms like *Plexaura A*. Colonies of similar height often vary in the number of branches and thus in total biomass. More precise estimates of size may identify a less variable size of first reproduction. Finally, *Plexaura A* colonies of the same size vary in age. Growth of colonies monitored in the field in the San Blas indicate that 5 years may be the minimum time required for a colony

to reach 20 cm in height (Lasker, unpub. data), but the commonness of severe grazing among small colonies suggest that it may take many colonies substantially longer to reach 20 cm. Furthermore, many *Plexaura A* colonies develop from fragments broken off of large colonies (Lasker, 1984). Thus a small colony could come from a clone that is tens or hundreds of years old. Although we consider it unlikely that age alone has a significant effect on reproductive state, Hughes and Connell (1987) observed an age effect in the growth and mortality rates of some Great Barrier Reef scleractinians.

The mean diameter of mature oocytes in *Plexaura A* is large compared to many scleractinians, but similar to the large eggs seen in other octocorals (Benayahu and Loya, 1986). In addition, the number of mature eggs per polyp is low compared to most anthozoans, but similar to the values reported for other gorgonians (Table II). Alcyonaceans, like gorgonians, also produce large eggs but differ in that they produce many more eggs per polyp. The basis for the difference between the two alcyonarian orders is unknown but may be a simple function of the length of polyps.

One aspect of the reproductive biology of *Plexaura A* that differs from that of gorgonians and other corals is the pattern of oocyte development. Oocytes are present in *Plexaura A* colonies throughout the year. New oocytes are added to this standing pool of oocytes each November, and in January a portion of the oocytes initiate further development into large mature eggs. Large eggs that are not released degenerate and are resorbed by the polyps, however the small oocytes appear to persist through the reproductive season. This cycle suggests oocyte maturation time requires more than a single season. Two-year maturation times have been reported for the alcyonaceans, *Lobophytum crassum* (Yamazato *et al.*, 1981)

Table II

Mode of reproduction and number of mature eggs/polyp for gorgonian species

Gorgonian species	Mode of reproduction	Mature eggs/polyp	Reference
<i>Briareum asbestinum</i>	External Brooder	1.8	Kinzie, 1970; Brazeau, 1986
<i>Eunicella singularis</i>	Brooder	7	Weinberg and Weinberg, 1979
<i>Eunicella stricta</i>	Brooder	4	Theodor, 1967
<i>Muricea californica</i>	Brooder	1.6	Grigg, 1977
<i>Muricea fruticosa</i>	Brooder	3.8	Grigg, 1977
<i>Plexaura A</i>	Broadcast	1.9	
<i>Pseudopterogorgia elisabethae</i>	Unknown	7	Kinzie, 1970
<i>Pseudopterogorgia bipinnata</i>	Broadcast	7	Kinzie, 1970

and *Sarcophytum glaucum* (Benayahu and Loya, 1986) and the gorgonian *Corallium rubrum* (Vighi, 1972, in Yamazato *et al.*, 1981). However, two discrete size classes of oocytes could be identified in the polyps of these species. In *Plexuara A*, the primary oocytes that appear in November increase in size, and become indistinguishable from the older oocytes already present. Thus, the actual time for oocyte maturation is, at minimum, 7 to 9 months, but may be longer. To our knowledge, the maintenance of a pool of oocytes throughout the year is unknown for any coral. It may represent a mechanism by which mature egg production can be adjusted later in the developmental season (Jan.), rather than at the time of primary oocyte appearance (Nov.).

Spawning by *Plexuara A* colonies is extremely predictable. *Plexuara A* colonies release eggs at virtually the same time over 4 to 7 nights following the full moons of May, June, and July. The duration of egg release each night is also fairly constant (approximately 90 min). In addition, two other gorgonians release planulae and/or eggs on some of the same nights, *Briareum asbestinum* (planulae) and *Pseudoplexaura porosa* (eggs?) (pers. obs.). Although seven species of soft corals participate in the mass spawning events on the Great Barrier Reef (Babcock *et al.*, 1986), this is the first reported incidence of synchronous spawning in Caribbean gorgonians. A number of Caribbean scleractinians also spawn following summer full moons (Szmant, 1986), but it is not known whether these species spawn at the same time as *Plexuara A*. Like many of the Great Barrier Reef species, the time at which *Plexuara A* colonies began to release eggs each evening was fairly precise (18:34, ± 10 min.). The net result is one of a large number of eggs being released during the short period of time after sunset, but before moonrise. Such a strategy would be expected if visual predators are an important cause of larval mortality. Lasker (1985) reported that at least one predator, the butterflyfish *Chaetodon capistratus*, showed increased feeding activity on *Plexuara A* polyps on the days prior to egg release, and we observed *C. capistratus* feeding on released eggs immediately after sunset, at the start of spawning.

One of the most surprising aspects of *Plexuara A* reproduction in the study population was development of larvae from eggs released by the female colonies despite the extreme rarity or absence of males. In many gorgonians, spermaries develop rapidly within weeks prior to spawning. Among these species, samples taken at times other than during the peak reproductive period exhibit either skewed sex ratios or the total absence of males (Goldberg and Hamilton, 1974; pers. obs.). However, this does not explain our failure to locate male colonies in the San Blas Point population. Samples collected for sex determination were always collected during the re-

productive period and all colonies were positively identified as female. Histological examination of male colonies of the close congener, *P. homomalla*, indicate that this species does not spawn at the same time and therefore cannot fertilize the eggs of *Plexuara A*. Histological examination of polyps before and after spawning show that the larvae arise from eggs (*i.e.*, are not produced vegetatively, independent of the gametes). Thus, the production of larvae by *Plexuara A* has two possible explanations. The first explanation is that fertilization has occurred despite an enormously skewed sex ratio. If this is the case then the extremely rare males must enjoy high fitness. The second explanation is that the eggs develop parthenogenetically. Parthenogenesis has been reported for only one octocoral, *Alcyonium hibernicum* (Hartnoll, 1977) and is unknown in scleractinians. Asexual planulae have been reported in *Pocillopora damicornis* (Stoddart, 1983) and *Tubastrea diaphana* and *T. coccinea* (Ayre and Resing, 1986) but in all three the brooded asexual planulae appear to be derived independent of the gonads (Stoddart and Black, 1985; Ayre and Resing, 1986). The possibility of parthenogenesis is especially interesting given that *Plexuara A* also propagates via fragmentation (Lasker, 1984). Thus, *Plexuara A* clones may spread between reefs via the dispersal of parthenogenetic eggs as well as locally via fragmentation. Consequently, clones may exhibit wide geographic distributions.

Plexuara A also exhibits a unique developmental pattern among anthozoans. Eggs initiate development almost simultaneously with release from the polyps (with or without fertilization). The possibility that development is parthenogenetic confounds the interpretation of the reproductive strategy, but regardless of the genetics, the strategy is enigmatic. Like all octocorals examined to date, *Plexuara A* produces large eggs (Benayahu and Loya, 1986). However, most octocoral species, and all gorgonians, brood their eggs either within the polyp (Kinzie, 1970; Hartnoll, 1977; Weinberg and Weinberg, 1979; Sebens, 1983), or on the colony surface (Benayahu and Loya, 1983; Brazeau, 1986; Farrant, 1986). The production of a large and presumably costly egg, which is then cast into the water column, runs counter to the hypothesis that brooding has evolved as a mechanism of avoiding larval predation. Similarly, the initiation of development and the slow development of the embryos are unlike the known examples of broadcast spawners, where outcrossing, dispersal, and escape from water column predators are the presumptive selective agents. *Plexuara A*, like most octocorals, does not readily fit into reproductive strategies designed to explain scleractinian patterns. It is likely these models will require the inclusion of taxonomic/morphologic constraints and/or additional ecologic parameters in order to explain the reproductive patterns seen in octocorals.

Finally, it should be noted that from the examination of our monthly samples one might conclude that *Plexaura* A is a typical broadcast spawner. Only the observation of the actual reproductive event showed this assumption to be incorrect. As was first demonstrated by the discovery of the Great Barrier Reef mass spawning event (Harrison *et al.*, 1984; Babcock *et al.*, 1986), detailed field observations of reproductive events are a necessary component of discerning reproductive strategies among anthozoans. Detailed examinations of anthozoan life cycles have found exceptions to the traditional concepts of reproductive strategies (Stoddart, 1983; Ayre and Resing, 1986) and further work will undoubtedly discover additional exceptions.

Acknowledgments

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