

Sexual reproduction of the reef-building coral *Diploria labyrinthiformis* (Scleractinia: Faviidae), in the Colombian Caribbean

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Abstract: Sexual reproduction of the coral *Diploria labyrinthiformis* was studied for the first time. Monthly histological analyses at the Corales del Rosario National Park (Colombian Caribbean) from May 1997 to April 1998 show that *D. labyrinthiformis* is a hermaphroditic broadcasting species. It presents an annual gametogenic cycle with a 10-11 month period for gonad investment, in which oogenesis begins in August and ends in May-June. Spermiogenesis is short because sperm cysts were only observed in May tissue samples. In histological collected in May, an average of four mature eggs and six spermatid cysts per fertile mesentery were found. The mean diameter of mature eggs was 297 μm (\pm 97 SD) and 90 μm (\pm 33) for spermatid cysts. Rapid maturation of eggs from stage II to stage III coincides with increases in air temperature, high number of solar hours per month, decreases in wind velocity and absence of rainfall. Reproductive effort for *D. labyrinthiformis* (14.07 $\text{mm}^3/\text{cm}^2/\text{year}$) was similar to other Faviidae species. Although gamete release was not observed in the field, the absence of gonads in histological samples in June suggests spawning between May 25 (five days after full moon) and June 24. This event coincides with high air temperature, low number of solar hours per month, low wind velocity, and initiation of the rainy season. The earlier spawning time of this species differs from other species of the same family known for the Caribbean region. Rev. Biol. Trop. 52(4): 859-868. Epub 2005 Jun 24.

Key words: *Diploria labyrinthiformis*, coral reproduction, gametogenesis, Caribbean coral reefs, Colombia.

Studies on sexual reproduction of hermaphroditic corals have increased during the last two decades, with information of about 30% of the known species currently available. From 91 species of Faviidae within the Indo-Pacific region, information of only 40 species is known (Kojis and Quinn 1982, Harriot 1983, Harrison and Wallace 1990) and from 17 species of the Caribbean region, no more than eight species have been studied (Szmant 1986, Soong 1991, Acosta and Zea 1997).

Faviid species are mainly hermaphroditic and present gonads developing as local thickenings of the mesentery, in contrast with

those of Pocilloporidae, which are connected by a short stalk to the mesenteries and projected into the body cavity (Rinkevich and Loya 1979) or those of *Siderastrea siderea*, which are attached to the mesenterial filaments (Alvarado and Guzman unpublished). In the Colombian Caribbean, information on the reproductive biology of corals is available for the following species: *Porites porites* (Hernández and Manrique 1991), *Acropora palmata* (García 1994), *Acropora cervicornis* (Sanjuan 1995), *Tubastrea coccinea* (Uscategui 1996) and *Montastraea cavernosa* (Acosta 1992, Acosta and Zea 1997) as well as

on spawning season of *Montastraea annularis* and *M. faveolata* (Sánchez *et al.* 1999).

Diploria labyrinthiformis is a common species of the coral community in some areas of the Caribbean region and yet its reproductive biology is, so far, unknown. Previous studies on reproductive characteristics of *Diploria strigosa* (Wyers 1985, Szmant 1986, Wyers *et al.* 1991, Soong 1991) and *Diploria clivosa* (Soong 1991) document traits within the genus, such as reproductive patterns, gonadal arrangement, number of eggs per ovary, and size and shape of eggs. Gametogenic cycle of *D. strigosa* and spawning observations of *D. strigosa* and *D. clivosa* indicates a 9-10 month cycle with spawning occurring during the warmest season (July-September) synchronized with other faviid species. The only information we found in the literature is the release of traces of eggs from two colonies of *D. labyrinthiformis* in laboratory conditions, during late July (Wyers *et al.* 1991).

The present paper describes, for the first time, the reproductive pattern, mode of development, gametogenic cycle, gonadal arrangement, egg size, number of eggs per gonad, and reproductive effort of *D. labyrinthiformis*. These sexual characteristics were related to abiotic factors as well as compared with other species within the genus.

MATERIALS AND METHODS

The study was carried out at the Isla Grande coral reef (Caribbean coast of Colombia), between May 1997 and April 1998. This island forms part of the Parque Nacional Natural Corales del Rosario, which is located between 10°08' - 10°26' N and 75°30' - 75°48' W (Fig. 1). The area lies within the Intertropical Convergence Zone, under trade winds that alternate from northwest to southeast. Three climatic seasons have been described for the area, a dry season, occurring between December and April and dominated by the Alisios winds; an intermediate season (mild rainfall) between May and July; and a rainy

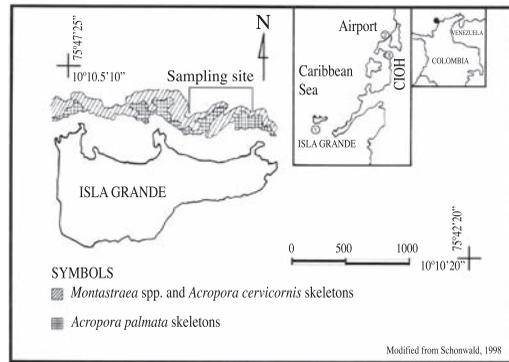


Fig. 1. Study area showing the sampling site. Isla Grande, Corales del Rosario National Park, Colombian Caribbean (1). Included also are the meteorological information centers: Airport (2) and the Centro de Investigaciones Oceanográficas e Hidrográficas-CIOH (3).

season (heavy rainfall), which occurs between August and November (Leble and Cuignon 1987). The annual average for seawater temperature is 27.5°C; precipitation is 1 013.1 mm and salinity 35 ‰ (Sánchez 1999).

Due to legal restrictions within the Protected Area, only three colonies per month were sampled. Each month, 5 days after full moon, two samples of 2.5 cm in diameter, per colony, were extracted from the center of three different colonies, located at depths of 7-12 m. These were fixed in Zenker solution for 24 hours, washed in running tap water for 24 hours and stored in 70% ethanol (Acosta and Zea 1997), until histological procedures. Tissue samples were dehydrated in alcohol and xylene series, embedded in Paraplast and serially sectioned at 6 µm. Sections, taken every 200-250 µm, were stained with Heidenhain's Azocarmine Aniline Blue (Luna 1968, Acosta and Zea 1997). Seven to nine slides with 4-8 sections each, and 20-56 mesenteries per section, were observed for each colony under light microscope. The slide containing the most reproductive material was used to estimate a) number of fertile mesenteries, b) total number of eggs and sperm cysts (Guzmán and Holts 1993), and c) size and stage of these gametes. Since there is not a clear polyp differentiation in this species, all information is referred to area, where 1 cm² contains 12 to 15 mesenteries.

A number of 220 complete eggs were observed in order to define different development stages based on descriptions for other species (Wyers 1985, Delvoeye 1988, Acosta 1992, Glynn *et al.* 1994, 1996). Three stages for oogenesis were defined using the following characteristics: 1) presence of single mesogleal layer surrounding the egg; 2) presence and thickness of basal membrane surrounding the egg; 3) presence of cytoplasmatic material inside the egg (scarce or abundant cytoplasmatic material); 4) presence of vesicular cytoplasmatic inclusions (few or high - giving the egg a bubbly appearance); 5) maximum length of eggs using an ocular micrometer (Olympus, OSM-4, 10 X).

Reproductive effort was calculated with a modification of the Gonadal Index used by Szmant (1986): number of mesenteries per cm² x number of gonads per mesentery x maximum number of eggs per gonad x volume of eggs per mm³ x number of cycles per year. The volume was calculated using the formula: $V = 4/3\pi r^3$.

Sunlight, air temperature, rainfall and wind velocity data for the study period (May 1997-April 1998) was provided by the Centro de Investigaciones Oceanográficas e Hidrográficas (CIOH) for two near-by sites (airport and Escuela Naval) (Fig. 1).

RESULTS

Diploria labyrinthiformis is a hermaphroditic broadcasting species with eggs and spermatocysts within each mesentery (Fig. 2A). Eggs and spermatocysts are located towards the aboral part of the mesentery (Fig. 2B). This species displays an annual gametogenic cycle in which oogenesis begins in August and ends between May and June (Fig. 3). Spermiogenesis is short, since sperm cysts were observed only in tissue samples from May. Nevertheless, our observations suggest synchronous maturation between eggs and sperm cysts during May.

Oogenesis: Stage I oocytes were small, ovoid or rounded and the main characteristic

was the presence of a thin, bluish-transparent mesogleal layer surrounding the egg (Fig. 2C). Cytoplasmatic material was absent (12%), scarce (86%), or abundant (2%). Mean diameter of oocytes was 116.1 μm (± 36.5 S.D.), and range from 53.9 to 213.0 μm ($n = 44$ oocytes). This stage was observed from August to April, with a peak in December (Fig. 3A).

Stage II oocytes were also small, ovoid or rounded (Fig. 2D), but with a basal membrane that thickened from November (11 μm) to April (33 μm). The majority had scarce cytoplasmatic material (67%), and the rest had either few vesicular cytoplasmatic inclusions or were empty. Mean oocyte diameter was 150.4 μm (± 32.6), and range from 57.7 to 209.6 μm ($n = 55$ oocytes). This stage was observed from November to April, with a peak in March (Fig. 3B).

Stage III oocytes were enlarged, ovoid or irregular, with a well-defined basal membrane and with high vesicular cytoplasmatic inclusions giving them a bubbly appearance (Fig. 2E). Mean diameter was 297.2 μm (± 96.9), and range from 73.5 to 584.3 μm ($n = 121$ oocytes). Mature eggs were only found in May (Fig. 3C).

In samples of June and July no eggs were found. This suggests that *D. labyrinthiformis* may have spawned between May 25 and June 24. Thus, this species has an annual reproductive cycle with a 10-11 months period for gonad investment.

Spermiogenesis: In May, spermatocysts were only present on 85% of the mesenteries. In no case they were observed without eggs in the same mesentery, which confirms a hermaphroditic pattern. An average of six cysts per fertile mesentery were found, with a mean diameter of 90.1 μm (± 32.9), and range from 27.5 to 220.5 μm , ($n = 160$ cysts). Cysts showed either dense (45%) or scarce (55%) cellular material (Fig. 2F).

Reproductive effort: On the total mesenteries observed ($n = 705$) for the one-year study period, 16% were fertile ($n = 114$), with 379 eggs and 208 spermatocysts (complete and incomplete). The highest percentage of

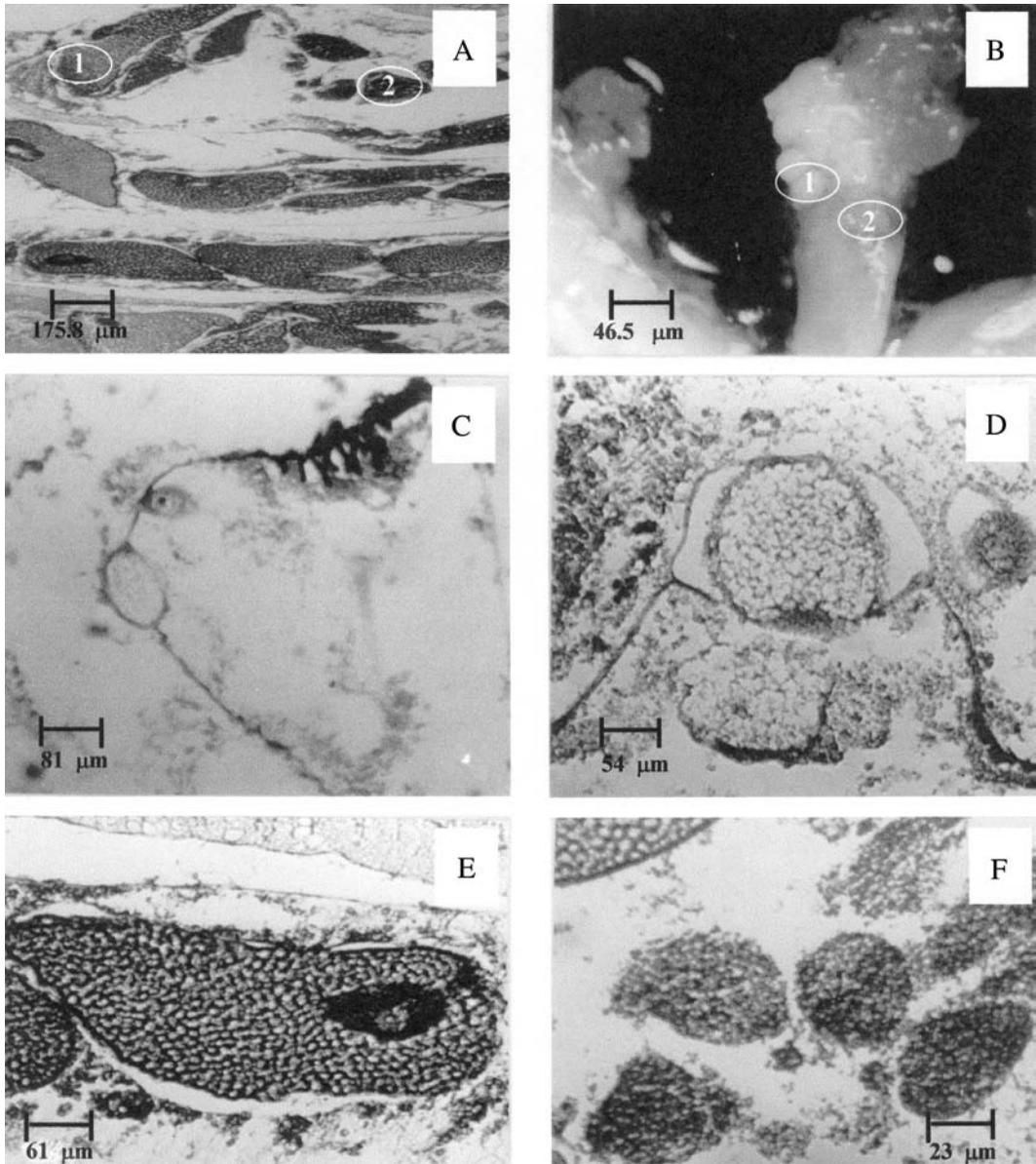


Fig. 2. Oogenesis. A) Stereoscopic view of a dissected decalcified mesentery showing mature eggs (1) and sperm cysts (2), located in the aboral part of the mesentery (upper-right in the photography). Photographs of histological preparations: B) hermaphroditic mesenteries showing mature eggs and sperm cysts . Note that mature eggs (1) develop towards the internal part of the mesentery meanwhile sperm cysts (2) are located close to the coelenteron. C) Stage I. Note two oocytes surrounded by the mesoglea, a nucleus in one of them. D) Stage II. Oocyte in the center of the picture is showing the thick basal membrane and the dense cytoplasmatic material. E) Stage III. Mature oocyte with vesicular cytoplasmatic inclusions, lateral nucleus and a nucleolus. F) Spermiogenesis. Several sperm cysts.

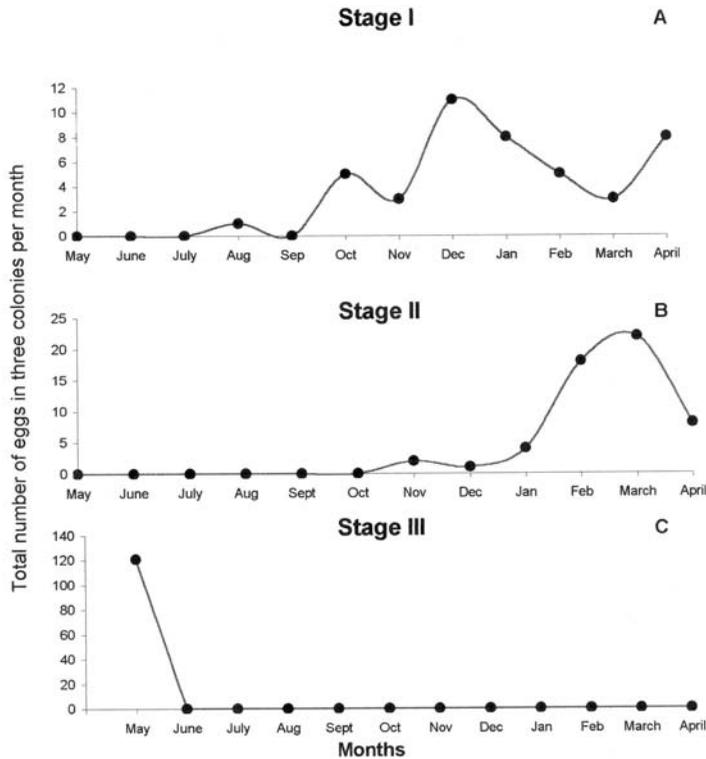


Fig. 3. Oogenic cycle. Three stages based on histological samples between May 1997 and April 1998. Data based on total number of eggs quantified in the slide containing the most reproductive material for each of the three colonies studied per month.

mature mesenteries was found in May (42%), bearing an average of four eggs per mesentery (range: 1-9; 21 per cm²) and six spermatid cysts per mesentery (range: 1-10; 21 cysts per cm²). The reproductive effort estimated by the gonad index obtained from mature eggs was 14.07 mm³/cm²/year (Table 1).

DISCUSSION

Reproductive type (hermaphroditic), mode of development (broadcaster), gonadal arrangement (oocytes and spermatid cysts in the same mesentery), oocyte mean size and shape, number of eggs per mesentery as well as duration of oogenesis seem to be conservative characteristics within any genus (Soong 1991) (Table 2). The similarity in the reproductive effort between the Faviidae species (Table 1)

and particularly for *D. labyrinthiformis* (this study) and *D. strigosa* (Wyers 1985) further supports Soong's hypothesis.

Although the length of the oogenic cycle (10 months) is similar between *D. labyrinthiformis* and *D. strigosa*, the initiation of oogenesis and spawning month differs between the two species. These events occur earlier for *D. labyrinthiformis* populations in Colombia than for its congeneric species in Bermuda (Wyers 1985) and Puerto Rico (Szmant 1986) (Table 2). Gametogenesis and spawning differences for the same species have been attributed to latitude (Szmant 1986, Soong 1991, Van Veghel 1994, Acosta and Zea 1997, Knowlton *et al.* 1997), temperature, day length or both (Babcock 1995, Fan and Dai 1995, Fadlallah 1996, Ben-David-Zaslow *et al.* 1999), solar energy (Van Veghel 1994), current and winds regimes (Babcock *et al.* 1986) and rainfall (Acosta and Zea 1997).

TABLE 1
Comparison of reproductive effort within corals of Faviidae in the Caribbean and Indo-Pacific

Region	Species	Reproductive Type	Mode of Development	Number of Cycles	Reproductive Effort (mm ³ /cm ² /year)	Reference
Caribbean	<i>Diploria labyrinthiformis</i>	H	BC	1	14.07	This study
	<i>Diploria strigosa</i>	H	BC	1	15.6-18.1	Wyers (1985)
	<i>Montastraea annularis</i>	H	BC	1	24.5	Szmant (1986)
	<i>Montastraea cavernosa</i>	G	BC	1	12.9	Szmant (1986)
	<i>Montastraea cavernosa</i>	G	BC	1	9.28	Acosta & Zea (1997)
	<i>Favia fragum</i>	H	BR	12	27.4	Szmant (1986)
Indo-Pacific	<i>Platygyra sinensis</i>	H	BC	1	12.2	Babcock <i>et al.</i> (1986)
	<i>Goniastrea favulus</i>	H	BC	1	15.3	Babcock <i>et al.</i> (1986)
	<i>Goniastrea aspera</i>	H	BC	1	22.8	Babcock <i>et al.</i> (1986)
	<i>Favia fava</i>	G	BC	1	50	Harriott (1983)

H: Hermaphroditic, G: Gonochoric, BC: Broadcasting, BR: Brooding.

TABLE 2
Comparison of reproductive characteristics between species of the genus *Diploria*

Species	Location	Latitude (°N)	Spawning	Gametogenesis	# Eggs/Mesentery	Egg Size (µm±SD)	Reference
<i>D. clivosa</i>	Curacao	12	October	-	-	-	Van Veghel 1993
<i>D. clivosa</i>	Panamá	9	August-Sept	-	6	600D	Soong 1991
<i>D. labyrinthiformis</i>	Bermuda	32	July	*	*	400 D	Wyers <i>et al.</i> 1991
<i>D. labyrinthiformis</i>	Colombia	11	May/June?	Aug-May	4 (H)	297±97 (H)	This Study
<i>D. strigosa</i>	Bermuda	32	August-Sept	Nov-August	10	320±40-370±60 (H)	Wyers 1985
<i>D. strigosa</i>	Pto. Rico	18	August	Dec-June	8-10	400 (H)	Szmant 1986
<i>D. strigosa</i>	Panamá	9	August	*	4-10	600 D	Soong 1991

H: from histological preparations, D: Disecting microscope, *No data available.

The first visible egg in *D. labyrinthiformis* was found during August; while most stage I oocytes were found during October and November, which in Colombia coincides with the highest temperature (Fig. 4A). Rapid maturation of eggs (Stage II to Stage III) coincides with highest number of solar hours per month (Fig 4B) and rising temperatures, which happens during the dry season. Spawning occurs during June when wind velocity is lowest (Fig. 4C), and temperature is high. Thus, initiation and maturation of oocytes coincides with environmental conditions reported for species of the same family, by other authors for the Caribbean region (Szmant 1986, Soong 1991, Wyers *et al.* 1991, Van Veghel 1994, Acosta and

Zea 1997, Sanchez *et al.* 1999). Nevertheless, gamete release does not occur during the months when most spawning events, known at low latitudes, take place (August-October) (Guzmán and Holts 1993, Van Veghel 1994, Acosta and Zea 1997, Sanchez *et al.* 1999).

It is worthwhile noting that temperature range for the Caribbean region is 3.2°C (Szmant 1986) and for Colombia, during the period studied, the temperature did not vary more than 1°C (27.8°C ± 0.4; 28.4°C ± 0.21). As has been noted by other authors, rising temperatures might cue the initiation of gametogenesis in broadcasters, but gamete release is controlled by other factors such as photoperiod (Soong 1991, Szmant 1991), low

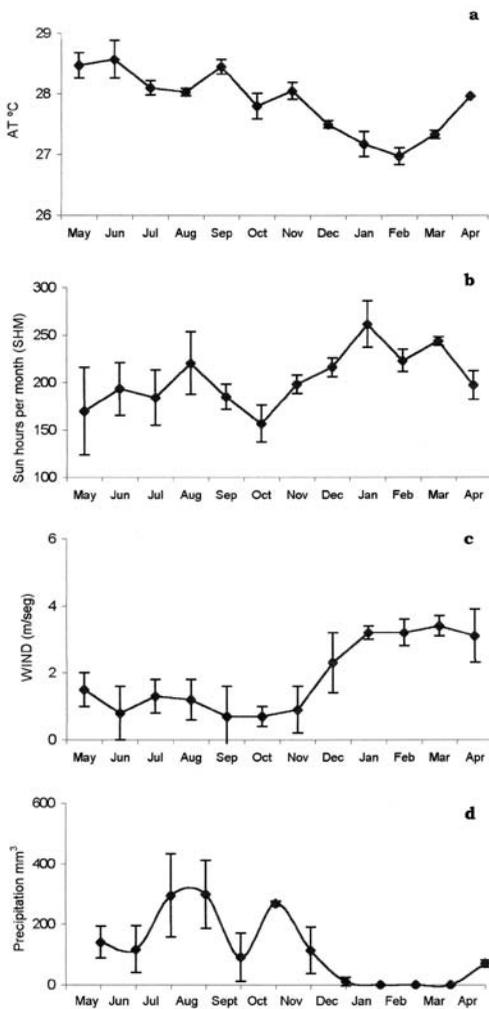


Fig. 4. Monthly averages and standard deviation of the environmental data from May 1997 to April 1998 in the study area. A) Air temperature (AT°C), B) Total solar hours month⁻¹ (TSH), C) Wind velocity (m/sec).

tides (Kojis and Quinn 1981), low current regimes (Babcock *et al.* 1986), low winds and scarce rainfall (Watson *et al.* 2000). In accordance, Bassim *et al.* (2002) states that the effects of high seawater temperature do not affect fertilization rates of *D. strigosa*; while embryonic development and larval viability decrease dramatically where abnormally high sea surface temperatures occur during the spawning season.

The adaptive value of spawning in late May and early June for *D. labyrinthiformis*, may be related to appropriate settling space (Fan and Dai 1995), associated with reduction in algae cover caused by local conditions (Soong 1991, pers. obs. in the studied area) or low current regimes and low winds which may ensure that egg clumps will not be carried out by currents and thus, favor high rates of fertilization (Kojis and Quinn 1981), which are the environmental conditions at the study site during these months. Timing of reproduction is of taxonomic significance and may reflect species recognition problems within a group (Johnson 1992). Therefore, the difference in timing of gametogenic cycle in *D. labyrinthiformis* may represent a mechanism of reproductive isolation to prevent hybridization and maintain species boundaries within the genus (Miller and Babcock 1997), or a strategy for self fertilization, as has been reported for *D. strigosa* (Hagman *et al.* 1998). Finally, but not least, it is possible that the effects of El Niño event, which was present during 1997, could have affected the cycle of gametogenesis and hence, spawning. But even then, it remains unclear why this event should have affected this species and not others in the same site as *M. annularis* and *M. faveolata* that spawned during September and October (Sánchez *et al.* 1999), as has been reported through out the Tropical Caribbean region.

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RESUMEN

La reproducción sexual del coral *Diploria labyrinthiformis* fue estudiada por primera vez. Análisis histológicos mensuales de muestras de *D. labyrinthiformis* extraídas en el Parque Nacional Natural Corales del Rosario (Caribe colombiano) entre mayo de 1997 a abril de 1998, muestran que es una especie hermafrodita, liberadora de gametos. Presenta un ciclo gametogénico anual de 10-11 meses para inversión en gónadas, en el cual la oogénesis comienza en agosto y termina en mayo-junio. La espermatogénesis es corta, ya que los paquetes espermáticos solo fueron observados en muestras de tejido del mes de mayo. En las muestras histológicas de mayo, un promedio de cuatro huevos maduros y seis paquetes espermáticos por mesenterio fértil fueron encontrados. El diámetro promedio de los huevos fue de 297 μm (\pm 97 DS) y de 90 μm (\pm 33) para los paquetes espermáticos. La rápida maduración de los huevos del estadio II al III coincidió con aumentos en la temperatura del aire, mayor número de horas de sol por mes, disminución en la velocidad del viento y ausencia de lluvias. El esfuerzo reproductivo de esta especie (14.07 $\text{mm}^3/\text{cm}^2/\text{año}$) fue similar al de otras especies de Faviidae. Aunque la liberación de gametos no fue observada en el campo, la ausencia de gónadas en las muestras histológicas del mes de junio sugieren que la liberación ocurrió entre el 25 de mayo (cinco días después de luna llena) y el 24 de junio. Este evento coincidió con altas temperaturas del aire, bajas velocidades del viento y la iniciación de la época lluviosa. El tiempo de liberación de gametos en esta especie difiere de otras de la misma familia, conocidas para la región del Caribe.

Palabras clave: *Diploria labyrinthiformis*, reproducción, gametogénesis, arrecifes coralinos, Caribe, Colombia.

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