

REPRODUCTIVE BIOLOGY OF *MADRACIS DECACTIS* (LYMAN, 1859) (CNIDARIA, SCLERACTINIA) FROM SOUTHERN BAHIA REEFS, BRAZIL ¹

(With 4 figures)

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ABSTRACT: The reproductive biology of the scleractinian coral *Madracis decactis* (Lyman, 1859) was studied in southern Bahia reefs, the most extensive and richest reef areas of the South Atlantic. *Madracis decactis* is one of the most widespread zooxanthellate corals in Brazil and can be found at the edges of the reefs on exposed or cryptic areas. The objective of this study was to investigate patterns of the sexual reproduction of *M. decactis*. Information about sexuality, gonad arrangement, mode of development, gametogenesis and temporal patterns of the reproductive cycle were obtained using histological procedures. The results showed that *M. decactis* is a hermaphroditic species and probably presents a brooding mode of development in southern Bahia reefs. Reproductive cycle is annual and lasts about four months. Female and male gametes started to develop at different times, with spermaries appearing in approximately the second month of oogenesis and lasting about two months. Gametogenesis started on the summer onset (December) and was complete at early autumn (April). Mature gametes were not present in samples collected between the end of March and April. Evidences suggested that fecundation, embryogenesis and the possible planulae release occurred within this period, of approximately one month.

Key words: *Madracis decactis*. Coral reef. Reproduction. Southern Bahia. Brazil.

RESUMO: Biologia reprodutiva de *Madracis decactis* (Lyman, 1859) (Cnidaria, Scleractinia) de recifes do sul da Bahia, Brasil.

A biologia reprodutiva do coral escleractíneo *Madracis decactis* (Lyman, 1859) foi estudada nos recifes do sul da Bahia, a mais extensa e rica área recifal do Atlântico Sul. *Madracis decactis* é um dos corais zooxantelados mais amplamente distribuídos do Brasil, podendo ser encontrado nas bordas dos recifes em locais expostos ou abrigados. O objetivo deste estudo foi investigar padrões na reprodução sexual de *M. decactis*. Informações sobre sexualidade, arranjo das gônadas, modo de desenvolvimento, gametogênese e padrões temporais do ciclo reprodutivo foram obtidas através de procedimentos histológicos. Os resultados mostraram que *M. decactis* de recifes do sul da Bahia é uma espécie hermafrodita e provavelmente incubadora de larvas. O ciclo reprodutivo é anual e dura cerca de quatro meses. Gametas masculinos e femininos começaram seu desenvolvimento em momentos diferentes, com cistos espermáticos aparecendo aproximadamente no segundo mês da ovogênese e durando cerca de dois meses. A gametogênese se iniciou no começo do verão (dezembro) e completou-se no princípio do outono (abril). Não foram observados gametas maduros nas amostras coletadas entre o final de março e abril. Evidências sugeriram que a fecundação, a embriogênese e a possível liberação de plânulas ocorreram dentro desse período, com duração de cerca de um mês.

Palavras-chave: *Madracis decactis*. Recife de coral. Reprodução. Sul da Bahia. Brasil.

INTRODUCTION

The current contribution on the reproductive biology of *Madracis decactis* (Lyman, 1859) is part of a continuing project developed by the Laboratory of Cnidaria of the Museu Nacional, Universidade Federal do Rio de Janeiro, which focuses on the sexual reproductive patterns of species commonly found on Brazilian reefs (see PIRES, CASTRO & RATTO, 1999; CALDERON, CASTRO & PIRES, 2000;

PIRES, CASTRO & RATTO, 2002; NEVES & PIRES, 2002; PIRES & CAPARELLI, 2002; VENTURA & PIRES, 2002; LINS-DE-BARROS, PIRES & CASTRO, 2003). Data on corals reproduction are of great importance on studies about coral recruitment and distribution (FADLALLAH, 1983).

Southern Bahia stands out for the presence of coral reefs. This region, including the Abrolhos Reef Complex, is known as the most extensive and richest reef areas of the South Atlantic. In biological terms,

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its importance is showed by the fact that this region harbors all shallow-water species of stony corals found in Brazil (LABOREL, 1969, 1970; LEÃO, 1982; CASTRO, 1994).

There are still some knowledge gaps about the reproductive biology of few coral species from this area, including *M. decactis*. This is one of the most widespread zooxanthellate corals in Brazil, occurring from Parcel do Manuel Luiz, MA, to Arvoredo Island, SC, as well as in Fernando de Noronha (PIRES *et al.*, 1992) and Atol das Rocas (CASTRO & PIRES, 2001). It can also be found in southern Florida, the Bahamas and the Caribbean (LABOREL, 1969, 1970). On the reef its distribution is generally restricted to the edges where it can be found on exposed or cryptic areas (VERMEIJ & BAK, 2002). Colonies from the studied area usually occur at depths below two meters, at the edges and in vertical surfaces of the reefs. Nodular colonies are common, but massive globe and incrusting shapes are also observed. Adult colonies usually have a diameter of 15 cm, although they can easily reach twice that size (CASTRO, 1994).

Previous studies on the reproductive biology and variation in planulae release of *Madracis* species, including *M. decactis*, were conducted on the Caribbean by VERMEIJ *et al.* (2004 and 2003, respectively). Other studies with other species of the family Pocilloporidae, to which *Madracis* belongs, have already included some aspects of their reproductive biology (RINKEVICH & LOYA, 1979; HARRISON & WALLACE, 1990; GLYNN *et al.*, 1991; WARD, 1992; KRUGER & SCHLEYER, 1998).

The objective of this study was to investigate patterns in the sexual reproduction of *M. decactis* from the Southwestern Atlantic, providing information about sexuality, gonad arrangement, mode of development, gametogenesis, and temporal patterns of the reproductive cycle.

The present study gathered together original data concerning the reproductive patterns of *M. decactis* from the Southwestern Atlantic. These results will be useful on monitoring, management, and recovery programs of Brazilian reef environments.

MATERIAL AND METHODS

COLLECTION PROCEDURE

Colonies and central fragments of *Madracis decactis* were collected by SCUBA diving on reef areas of the southern coast of Bahia (Fig.1). Fragments and

colonies were obtained using a hammer and a chisel, at depths between 2 and 16 meters. Each fragment was taken from the center of different colonies haphazardly chosen. Histological procedures were made in 37 selected colonies (Tab.1). Logistical factors limited the collection of extra samples in some months. The studied material was deposited in the Cnidaria Collection of the Museu Nacional/ Universidade Federal do Rio de Janeiro (MNRJ).

HISTOLOGICAL PROCEDURES

Coral samples were fixed in a 10% solution of formaldehyde in seawater. Fragments were decalcified in a solution of 10% formic acid and 5% formaldehyde and then rinsed for 24 hours in running tap water. At least 10 polyps of each colony, selected with magnifying glass, were dehydrated in an alcohol series and cleaned in xylene for routine paraffin embedding. Tissue samples were oriented so that both longitudinal and cross sections were obtained. Serial sections 4 to 5µm thick were made from each block and stained with modified Mallory's triple stain. Each slide of cross sections had approximately 20 polyps. Gamete development was subdivided into three stages adapted from SZMANT-FROELICH, REUTTER & RIGGS (1985). Measurements of gametes were made with an Olympus BH-2 microscope supplied with a calibrated ocular micrometer. The largest axis was measured only when the nucleolus was visible in the histological section. Photomicrographs of selected sections containing gametes on different developmental stages were taken using a digital camera (Canon EOS Digital Rebel) connected to the microscope.

RESULTS AND DISCUSSION

SEXUALITY

All colonies of *M. decactis* observed within the same breeding cycle were found to be hermaphroditic. No gonochoric colonies were observed. These results corroborate the reproductive patterns previously reported for *Madracis decactis* and other species of *Madracis* genus and Pocilloporidae family (HARRISON & WALLACE, 1990; GLYNN *et al.*, 1991; VERMEIJ *et al.*, 2004). Hermaphroditism was described as the predominant pattern of sexuality within the families Acroporiidae, Faviidae, Merulinidae, Mussidae, Pectiniidae and Pocilloporidae (HARRISON & WALLACE, 1990).

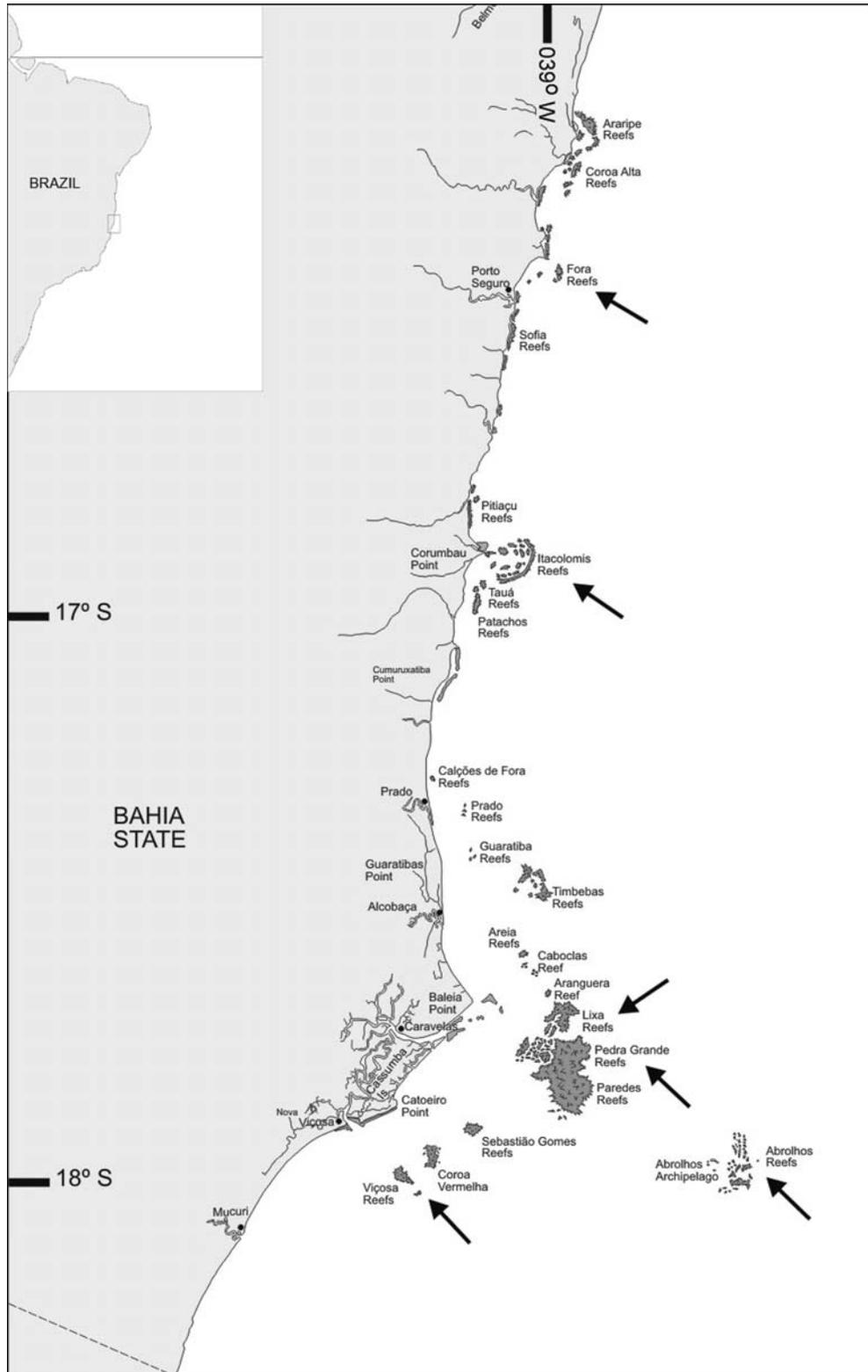


Fig.1- Map of studied area: southern Bahia reefs, Brazil. Arrows point the collection sites.

TABLE 1. Colonies of *Madracis decactis* selected for histological procedures with respective dates and sites from southern Bahia, Brazil.

DATE	COORDINATES	LOCALITY	NO. OF COLONIES	NO. OF BLOCKS	NO. OF MEASURED OOCYTES
07-Jan-04	16°54'S 039°04'W	IR	1	1	05
07-Jan-04	16°53'S 039°04'W	IR	1	1	10
24-Jan-91	17°47'S 038°53'W	PG	1	1	28
04-Feb-96	17°58'S 039°16'W	VR	1	1	29
19-Feb-00	17°47'S 038°53'W	PG	1	1	01
22-Feb-00	17°56'S 038°38'W	AR	1	1	10
01-Mar-94	16°24'S 038°59'W	FR	1	2	02
03-Mar-05	16°24'S 038°59'W	FR	6	8	71
25-Mar-05	16°24'S 038°59'W	FR	4	6	63
21-Apr-96	17°45'S 039°01'W	LR	1	1	-
08-May-05	16°24'S 038°59'W	FR	8	8	-
11-May-05	16°24'S 038°59'W	FR	1	1	-
10-Jun-04	16°24'S 038°59'W	FR	3	3	-
24-Aug-94	18°03'S 038°58'W	AR	1	1	-
02-Oct-92	18°47'S 039°14'W	VR	1	1	-
10-Nov-99	17°58'S 038°40'W	AR	3	3	-
14-Nov-99	16°54'S 039°04'W	IR	1	2	-
18-Nov-99	16°56'S 039°03'W	IR	1	1	-
TOTAL			37	43	219

(IR) Itacolomis Reefs; (FR) Fora Reef; (LR) Lixa Reef; (PG) Pedra Grande Reef; (AR) Abrolhos Reef; (VR) Viçosa Reef.

MODE OF DEVELOPMENT

The mode of development seems to be more variable than the sexuality at the family level (HARRISON & WALLACE, 1990). *Pocillopora verrucosa* and *P. damicornis* were reported to be facultative broadcast spawners (WARD, 1992; KRUGER & SCHLEYER, 1998) while most of pocilloporid corals brood and release planula larvae. *M. decactis* colonies are known to release larvae (VERMEIJ *et al.*, 2003),

however, embryos and planulae were not here observed in the histological slides. This result was also found by VERMEIJ *et al.* (2004), who related this fact with a short permanence of planulae in the polyp and suggested that the term "quick releaser" was more appropriate than "brooder".

A relation between mode of reproduction, polyp size and colony size were proposed in previous studies. RINKEVICH & LOYA (1979) suggested that coral species with small polyps produce small eggs and

brood planulae while large-polyped species spawn gametes for external fertilization. SZMANT (1986) observed that all the brooding species known in the Caribbean usually form small colonies. *M. decactis* present small size of polyps, around 1.5mm in diameter, and also relatively small colonies, approximately 15cm, and is a brooding species, supporting the relation between these features and the mode of reproduction.

GONAD ARRANGEMENT

Madracis decactis has 10 pairs of mesenteries per polyp (Fig.2), although it can eventually presents 12 pairs, all being capable to develop gonads. Most part of the gametes development takes place within the mesogleal layer, between the longitudinal retractor muscles and the mesenterial filament, as observed in other scleractinian corals (SZMANT-FROELICH, REUTER & RIGGS, 1985; GLYNN *et al.*, 1991, 1994; PIRES, CASTRO & RATTO, 1999; NEVES & PIRES, 2002; VERMEIJ *et al.*, 2004). Polyp cross sections showed a clear pattern in the disposition of male and female

gametes. These cells were present in the same polyp and each pair of mesenteries had one containing spermaries and the other one containing oocytes (Fig.2A-2B). Just a few polyps were seen developing gonads of only one sex in both mesenteries of the pair.

GAMETOGENESIS

The development of male and female gametes starts at different times and were classified into three different stages, according to their histological characteristics and sizes (Fig.3). The stages II and III of gametogenesis proposed by SZMANT *et al.* (1985) and VERMEIJ *et al.* (2004) were grouped in only one intermediate stage, here considered as stage II. These stages are arbitrary as they reflect a continuous process.

OOGENESIS

A round and bright red nucleolus was evident within the nucleus of all oocyte stages. None oocyte was observed to contain zooxanthellae.

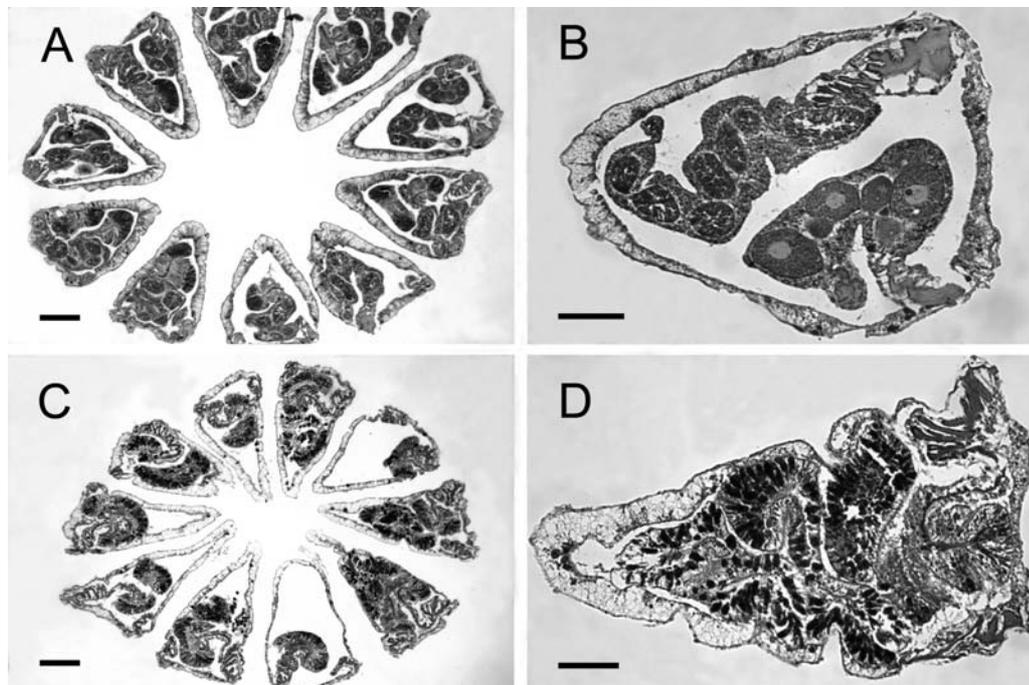


Fig.2- Cross sections of *Madracis decactis* fertile polyp and polyp after gamete/planulae release. (A) Polyp presenting 10 pairs of mesenteries filled with gametes (25 March/05). (B) Detail of one pair showing the disposition of female and male gonads. (C) Polyp with 10 pairs of mesenteries with no more gametes (8 May/05). (D) Detail of one pair presenting small granules: feature observed after gamete/planulae release period. Scale bars = 100 μ m (A and C), 200 μ m (B and D).

Stage I

The earliest detectable stage in oogenesis was represented by small cells with enlarged oval nuclei surrounded by a thin layer of cytoplasm (Fig.3A), as described for other coral species (SZMANT-FROELICH, REUTTER & RIGGS, 1985). Ranging from 8 to 23 μm in diameter, stage I oocytes stained light gray-blue to a bluish purple. They were frequently found within the mesoglea. The nucleus was granular and usually gray to colorless, but it did sometimes stain light pink. In some cases their boundaries were poorly defined.

Stage II

Stage II oocytes ranged from approximately 18 to 89 μm in diameter and differed slightly from the first stage (Fig.3B). Staining characteristics were similar to those of stage I, but a little more bluish. Frequently, refractive colorless vesicles were observed within the ooplasm. Stage II oocytes presented an increasing amount of grainy cytoplasm around nuclei, which were still found in the central portion of the cell and stained gray to light lilac. The cells commonly assumed a spherical form, but some of them exhibited an elongated shape.

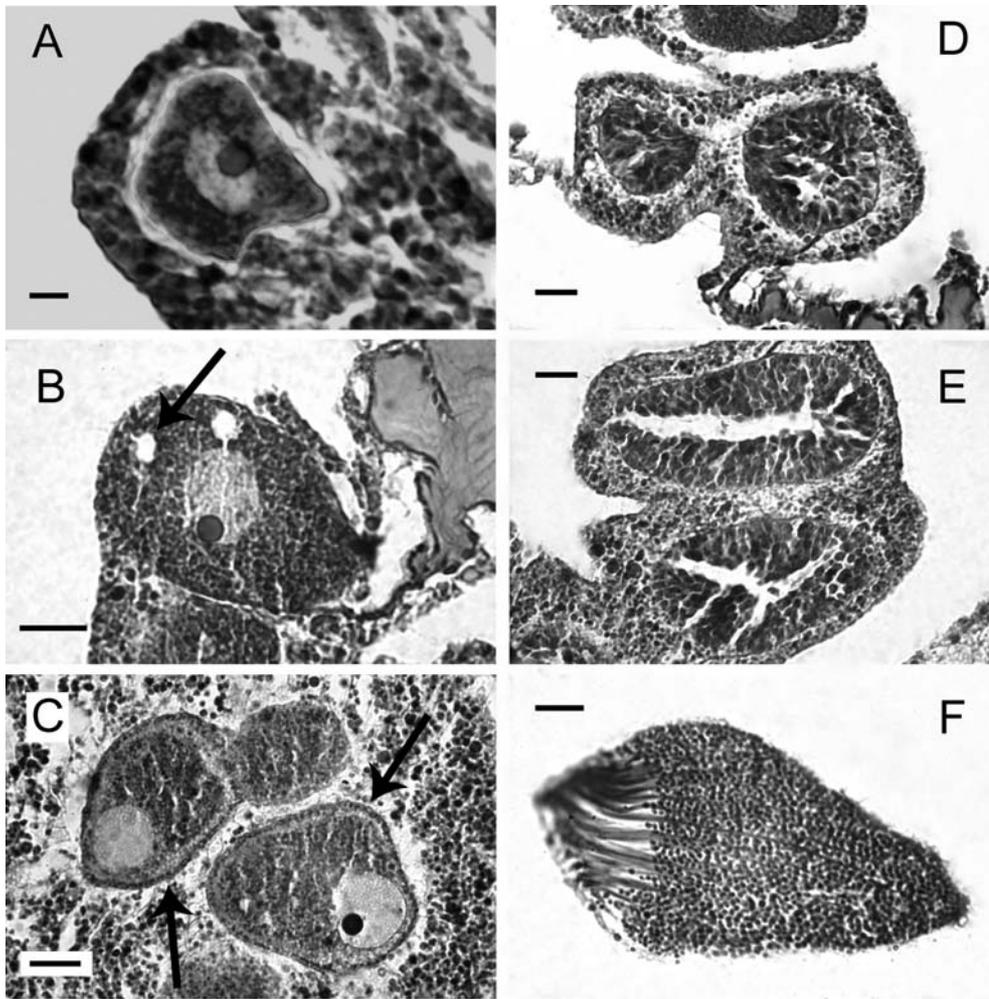


Fig.3- Gametogenic stages of *Madracis decactis* from southern Bahia reefs. (A) Late stage I oocyte (24 January/91). (B) Stage II oocyte (3 March/05). Arrow points to a colorless lipid vesicle within the ooplasm. (C) Stage III oocytes in the same mesentery (25 March/05); arrows pointing the halos that were present in some oocytes III. (D) Stage I spermaries (22 February/00). (E) Stage II spermaries with lumen present (3 March/05). (F) Stage III spermary forming a bouquet of mature spermatozoa (25 March/05). Scale bars = 10 μm (A), 20 μm (B-F).

Stage III

Stage III eggs were characterized by nucleus migration toward the periphery of the cell (Fig.3C). By this stage, nuclei stained light pink and had the same ovoid shape as in previous stages. The cytoplasm became denser and stained from a more homogeneous blue to a brownish-blue. Some stage III oocytes presented a light pink halo at their borders. Oocytes of this stage ranged from approximately 32 to 113µm.

SPERMATOGENESIS

Stage I

The first observed stage in spermatogenesis was characterized by clusters of cells surrounded by a blue-stained layer of mesogleal (Fig.3D). Early stage I spermaries often showed several irregular empty spaces and few cells only. Those generally stained lilac to purple with weakly marked outlines and presented large nuclei. Late stage I spermatic cysts started to increase in number of cells and had the same staining characteristics.

Stage II

Stage II cysts generally stained light brownish-green and cell proliferation continued to occur promoting spermaries enlargement (Fig.3E). A lumen was often present in stage II cysts, which were usually irregular in outline. The nuclei began their condensation and started to become smaller, as well as individual cells.

Stage III

Progressive nuclei condensation reduced even more spermatocyte size (Fig.3F). At this stage the cysts were packed with a large number of mature spermatozoa, which stained generally bright orange to dark pink and blue. Sperm tails become easily visible. Enlarged

stage III spermaries revealed many aggregates of sperm with their bluish tails gathered at the narrow end of the spermatic cysts forming large bouquets.

REPRODUCTIVE CYCLE

Colonies of *M. decactis* from southern Bahia presented annual reproductive cycle. Although the sampling was not the ideal, it enabled an overview of the annual reproductive characteristics of the species. Gametogenesis was probably positively related with seawater temperature, since it began on the summer onset. Female gametes were observed from January to March. However, primary oocytes size indicated that oogenesis may have started at December. Furthermore, since colonies from March 25th were seen filled with mature oocytes and no gametes were found in colonies from April 21st on, fecundation, embryogenesis and planulation were inferred to occur between these dates (Fig.4). Therefore, oocytes development lasted roughly four months. As oogenesis onset was prior to spermatogenesis within each breeding season, by the time spermaries began to develop oocytes were already at stage II. Spermatic cysts appeared in approximately the second month of oocyte development, lasting about two months (Fig.4). Gamete maturation occurred during the summer months and was complete at the beginning of autumn.

The mesenteries examined right after the reproductive peak presented an intact appearance. Though, these samples showed a striking feature: the presence of small red granules within the gametogenic areas of the mesenteries giving them a grainy aspect (Fig.2C-2D). These structures were observed in all histological slides of colonies collected in May but were not found in samples collected in subsequent periods. The presence of these granules was associated with a recent event of gamete release.

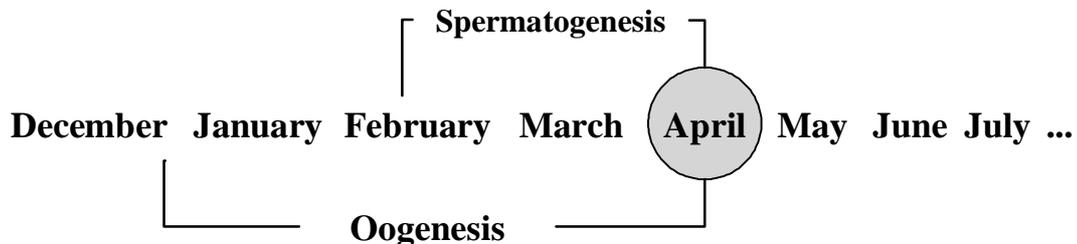


Fig.4- Timing of the gametogenic cycle of *Madracis decactis* from Southern Bahia reefs. Circle denotes the period of fecundation, embryogenesis, and the possible planulae release.

Female gametes development showed a slight asynchrony within and between colonies during the early stages of oogenesis, as expected for species with single annual gametogenic cycles (HARRISON & WALLACE, 1990). This initial asynchrony was a feature observed in all collected samples. Closer to the end of oogenesis all polyps and colonies presented a synchronous oocyte maturation.

Spermatic cysts in different stages of development were commonly found within the same mesentery, during the entire spermatogenesis. However, different colonies presented the same trend, establishing between them a synchrony in development for a given period. Conversely, more than one stage of spermatic cysts was found in some slides close to the reproductive peak (March). This fact suggested that male gametes release should have occurred in more than one event within a period of approximately one month. Fecundation, embryogenesis and the possible planulae release were inferred to occur within the same period, since no gametes were observed in samples from May to November.

These results seemed not to be in agreement with VERMEIJ *et al.* (2003, 2004), who observed an asynchronous gametogenesis and continuous release of planulae over an extended period (from April to December) in some *Madracis* species, including *M. decactis*. Previous data of *M. mirabilis* also showed asynchrony as a developmental feature for gametes (DELVOYE, 1988). However, in spite of the synchrony observed in the present study *M. decactis* did not show continuous breeding during the observation period.

It is important to point out that these previous studies were carried out in the Caribbean reefs, while the present report dealt with corals from the Southwestern Atlantic. Other studies show that some reproductive characteristics as broadcast spawning *versus* brooding can be variable between different populations of the same species (see SOONG, 1991). Additional studies would be required to evaluate if different environmental pressures could be acting on the reproductive strategies of geographically distinct populations and to explain the variations observed between *M. decactis* from the Caribbean and from the Southwestern Atlantic. Studies including the comparison of skeleton and genetic characters of *M. decactis* from both regions would be also important to determine if they represent the same species.

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REFERENCES

- CALDERON, E.N.; CASTRO, C.B. & PIRES, D.O., 2000. Natação, assentamento e metamorfose de plânulas do coral *Favia gravida* Verrill, 1868 (Cnidaria, Scleractinia). **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (429):1-12.
- CASTRO, C.B., 1994. Corais do Sul da Bahia. In: HETZEL, B. & CASTRO, C.B. (Eds.) **Corais do Sul da Bahia**, Rio de Janeiro: Nova Fronteira, p.160-176.
- CASTRO, C.B. & PIRES, D.O., 2001. Brazilian Coral reefs: what we already know and what is still missing. **Bulletin of Marine Science**, Coral Gables, **69**(2):357-371.
- DELVOYE, L., 1988. Gametogenesis and gametogenic cycles in *Agaricia agaricites* (L) and *Agaricia humilis* Verrill and notes on gametogenesis in *Madracis mirabilis* (Duchassaing & Michelotti) (Scleractinia). **Foundation for Scientific Research in Surinam and the Netherlands Antilles**, Amsterdam, **123**:101-134.
- FADLALLAH, Y.H., 1983. Sexual reproduction, development, and larval biology in scleractinian corals. A review. **Coral Reefs**, Berlin, **2**:129-150.
- GLYNN, P.W.; COLLEY, S.B.; EAKIN, C.M.; SMITH, D.B.; CORTÉS, J.; GASSMAN, N.J.; GUZMÁN, H.M.; DEL ROSARIO, J.B. & FEINGOLD, J.S., 1994. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). II. Poritidae. **Marine Biology**, Berlin, **118**:191-208.
- GLYNN, P.W.; GASSMAN, N.J.; EAKIN, C.M.; CORTÉS, J.; SMITH, D.B. & GUZMÁN, H.M., 1991. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). I. Pocilloporidae. **Marine Biology**, Berlin, **109**:355-368.
- HARRISON, P.L. & WALLACE, C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: DUBINSKY, Z. (Ed.) **Ecosystems of the World 25. Coral Reefs**. Amsterdam: Elsevier, p.133-207.

- KRUGER, A. & SCHLEYER, M.H., 1998. Sexual reproduction in the coral *Pocillopora verrucosa* (Cnidaria, Scleractinia) in KwaZulu-Natal, South Africa. **Marine Biology**, Berlin, **132**:703-710.
- LABOREL, J., 1969. Madreporaires et hydrocoralliaires récifaux des côtes Brésiennes. Systématique, écologie, répartition verticale et géographique. **Annales de L'Institut Océanographique**, Paris, **47**:171-229.
- LABOREL, J., 1970. Les peuplements des madreporaires des côtes tropicales du Brésil. **Annales de l'Université D'Abidjan**, Abidjan (serie E, Ecology), **2**(3):1-261.
- LEÃO, Z.M.A.N., 1982. **Morphology, geology, and developmental history of the southernmost coral reefs of western Atlantic, Abrolhos Bank, Brazil**. Miami. 218p. Ph.D. Thesis, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami.
- LINS-DE-BARROS, M.M.; PIRES, D.O. & CASTRO, C.B., 2003. Sexual reproduction of the Brazilian reef coral *Siderastrea stellata* Verrill, 1868 (Anthozoa, Scleractinia). **Bulletin of Marine Science**, Coral Gables, **73**(3):713-724.
- NEVES, E.G. & PIRES, D.O., 2002. Sexual reproduction of Brazilian coral *Mussismilia hispida* (Verrill, 1902). **Coral Reefs**, Berlin, **21**(2):161-168.
- PIRES, D.O. & CAPARELLI, A.C., 2002. Biologia reprodutiva de *Porites astreoides* Lamarck, 1816 (Cnidaria, Scleractinia) do Complexo Recifal de Abrolhos, BA, Brasil. **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (484):1-12.
- PIRES, D.O.; CASTRO, C.B.; MIGOTTO, A.E. & MARQUES, A.C., 1992. Cnidários bentônicos do Arquipélago de Fernando de Noronha, Brasil. **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (354):1-21.
- PIRES, D.O.; CASTRO, C.B. & RATTO, C.C., 1999. Reef coral reproduction in the Abrolhos Reef Complex, Brasil: the endemic genus *Mussismilia*. **Marine Biology**, Berlin, **135**(3):436-471.
- PIRES, D.O.; CASTRO, C.B. & RATTO, C.C., 2002. Sexual reproduction of the solitary coral *Scolymia wellsi* (Cnidaria, Scleractinia) from the Abrolhos Reefs Complex, Brazil. **Proceedings of the 9th International Coral Reef Symposium**, Bali, **1**:381-384.
- RINKEVICH, B. & LOYA, Y., 1979. The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. **Marine Ecology Progress Series**, Amelinghausen, **1**:133-144.
- SOONG, K., 1991. Sexual reproductive patterns of shallow-water reef corals in Panama. **Bulletin of Marine Science**, Coral Gables, **49**:832-846.
- SZMANT, A.M., 1986. Reproductive ecology of Caribbean reef corals. **Coral Reefs**, Berlin, **5**:43-53.
- SZMANT-FROELICH, A.; REUTER, M. & RIGGS, L., 1985. Sexual reproduction of *Favia fragum* (Esper): lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. **Bulletin of Marine Science**, Coral Gables, **37**:880-892.
- VENTURA, C.R.R. & PIRES, D.O., 2002. Ciclos de vida de invertebrados marinhos. In: PEREIRA, R.C. & SOARES-GOMES, A. (Orgs.) **Biologia Marinha**, Rio de Janeiro: Editora Interciência, p.49-67.
- VERMEIJ, M.J.A. & BAK, R.P.M., 2002. How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. **Marine Ecology Progress Series**, Amelinghausen, **233**:105-116.
- VERMEIJ, M.J.A.; SAMPAYO, E.; BRÖKER, K. & BAK, R.P.M., 2003. Variation in planulae release of closely related coral species. **Marine Ecology Progress Series**, Amelinghausen, **247**:75-84.
- VERMEIJ, M.J.A.; SAMPAYO, E.; BRÖKER, K. & BAK, R.P.M., 2004. The reproductive biology of closely related coral species: gametogenesis in *Madracis* from the southern Caribbean. **Coral Reefs**, Coral Gables, **23**:206-214.
- WARD, S., 1992. Evidence for broadcast spawning as well as brooding in the scleractinian coral *Pocillopora damicornis*. **Marine Biology**, Berlin, **112**:641-646.