Reproductive Patterns of *Strombus gigas* from Alacranes Reef *Versus* Chinchorro Bank of Mexico

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ABSTRACT

The reproductive cycle of the herbivore gastropod *Strombus gigas* (Linnaeus, 1758) is analyzed from two different coral reefs, Chinchorro bank on the Caribbean sea and Alacranes reef from the Gulf of Mexico, to determine the variability and similarities of their reproductive cycle under diverse environmental conditions, mainly to understand the behavior of gonads during the spawning season of both sites by a direct method. Twenty organisms were sampled monthly and processed for histological section, from March to November at Alacranes reef and from June to September at Chinchorro. For *S. gigas* of Alacranes, gametogenesis was the dominant stage from March to November, with presence of mature organisms only from June to October. While at Chinchorros, during the reproductive season gametogenesis involved no more than 40 %, with mature organisms involving from 40 to 50 %. There was an increase of mature organisms during September at both localities, but at least at Alacranes, there was no evidence of an accumulation of mature organisms through the winter or of a later spawn. Spawn was detected from June to August with a peak in July but just in 10% of the samples from Alacranes and 40% from Chinchorros. Although 40% post spawners during July at Alacranes, suggest an important spawn from May to July.

This study showed two gametogenic strategies as a response to the environment:

i) Populations of fast gametogenesis during a short lapse of time (*S. gigas* from Chinchorro), and
ii) Population with a continuous gametogenesis throughout most of the year (*S. gigas* from Alacranes).

The variations on the reproductive cycle of a species among different localities can be associated to environmental levels of instability. Predation and competition induce massive spawning and reduction of the spawning periods.

The knowledge of their reproductive cycle of *S. gigas* is mandatory for proper management of their populations. The scope of this paper to present and compare the reproductive cycle of *S. gigas* populations from mainly fishing sites from

Mexico, their variations and similarities in relation to prevailing environmental characteristics of their habitats.

KEY WORDS: Queen conch, *Strombus gigas*, reproductive cycle

INTRODUCTION

Strombus gigas is an important fisheries resource in Mexico and Caribbean sea, and the knowledge of their reproductive cycle is mandatory for proper management of their populations. *S. gigas* has a wide distribution area and its reproductive cycle is under diverse environmental conditions. Mackie (1984), showed that reproductive cycles are a response to life strategies and habitat where populations live. Species are classified in two groups, given the duration of their reproductive cycle: taquitictic, with short reproductive periods and (2) braditictic, with extended reproductive periods. Species with a wide geographical distribution show an ample variation of reproductive strategies in both duration and intensity (Bricej and Malouf 1980, Kennedy and Kratz 1982, Knaub and Eversole 1988). This has been associated to latitude, but with more precision to temperature and food availability (Bayne 1978, Sastry 1979, Webber 1977, Fretter 1984, Mackie 1985), which conditioning in the laboratory of organisms of one specie from different populations has experimentally proven (Loosanoff and Davis 1963, Bayne 1978, Ino 1970, Lubet and Choquet 1971, Hines 1979, Castagna and Kraeuter 1981).

The scope of this paper is to present and compare the reproductive cycle during the spawning of *S. gigas* from two different reef systems in Mexico, by a direct method (histological method) in relation to prevailing environmental characteristics of their habitats.

MATERIAL AND METHODS

S. gigas (Linnaeus, 1758) was studied from two different coral reefs: Alacranes reef from the Gulf of Mexico and Banco Chinchorro on the Caribbean Sea.

Twenty individuals from each site were collected monthly, trying to cover the spawning season of both sites, from March to November at Alacranes reef and from June to September at Chinchorro. Collection was done by SCUBA diving. The shell length and width were measured for all animals, and the whole organism and soft parts were weighted after extraction in the laboratory. To extract the whole body whorl, the shell was broken with a hammer. A section of the visceral mass and gonad was fixed with Bouin solution for *S. gigas* from both localities. Samples fixed with Bouin were rinsed after 24 hours.

Sections of 1 cm^3 were dehydrated with alcohol, cleared with Xylen and included in 53° - 56° melting point paraffin. Sections were cut 7 µm and 12 µm for males and females, respectively with a rotation microtome. All species were stained with Hematoxiline–eosine (Luna 1968) and Masson tri-chromic (Gabe 1968).

Practical classification of Lucas (1965) was used to define the reproductive cycle, which considers five stages:

i) *Rest* — the sex may not be identified from the microscopic section.
ii) Gametogenesis — active cell division, mature gametes may or may not be present.
iii) *Mature* —dominance of mature gametes, although some gametogenesis may be present.
iv) Spawn — partially emptied follicles.
v) *Post spawn* —follicles are partially or totally emptied and broken, eggs and sperms are being reabsorbed, presence of phagocytes.

Sampling Sites

Banco Chinchorro — is a coral reef, it is a false atoll located 16 miles offshore from southern Quintana Roo, on the Caribbean coast of Yucatan peninsula, between 18°22'- 18°48' N and 87°16'- 87°32' W. (Figure 1). It forms an irregular oval of 46 km long, 19 km in the widest part, has an area of 561 km^2. With bordering emerging islands of sand, coral and mangrove that limit an inner lagoon that has a mean depth of 7 m with sandy bottom and patches of *Thallassia*. Depth inside the lagoon reef decreases from 12 m in the south region to 7 to 3 m in the central part to 2 m in the north Chinchorro has four keys, two small keys known as Cayo Norte, the largest Cayo Centro and Cayo Lobos, the smallest located on the southern end. The weather is hot, humid with summer and winter rains, with 10.2 % during winter, average temperature is 26.1° C; average rainfall is 1,249 mm (Garcia 1981).

Alacranes reef — is an oval-shaped bank reef formation, covering an area of 293 km^2 with a maximum length and width of 26.5 km and 14.8 km, respectively (Figure 2). It is located on the north coast of Yucatan, 80 miles off the coast, between 22° 21' and 22° 35' N and between 89° 38' and 89° 49' W (Kornicher and Boyd 1962). The windward zone of the reef system arises at sea level, while the leeward zone is between 1 and 10 m below the surface. These two extremes enclose a lagoon. Near the western and southern reef edges are five small islands: Pajaros, Chica, Perez, Desterrada, and Desterrada (Hilderbrand et al. 1964). The weather is hot, humid with summer and winter rains, with 10.2 % during winter; average temperature is 25.5° C; average rainfall is 444 mm (Garcia, 1981). *S. gigas* were sampled at western of Isla Perez.

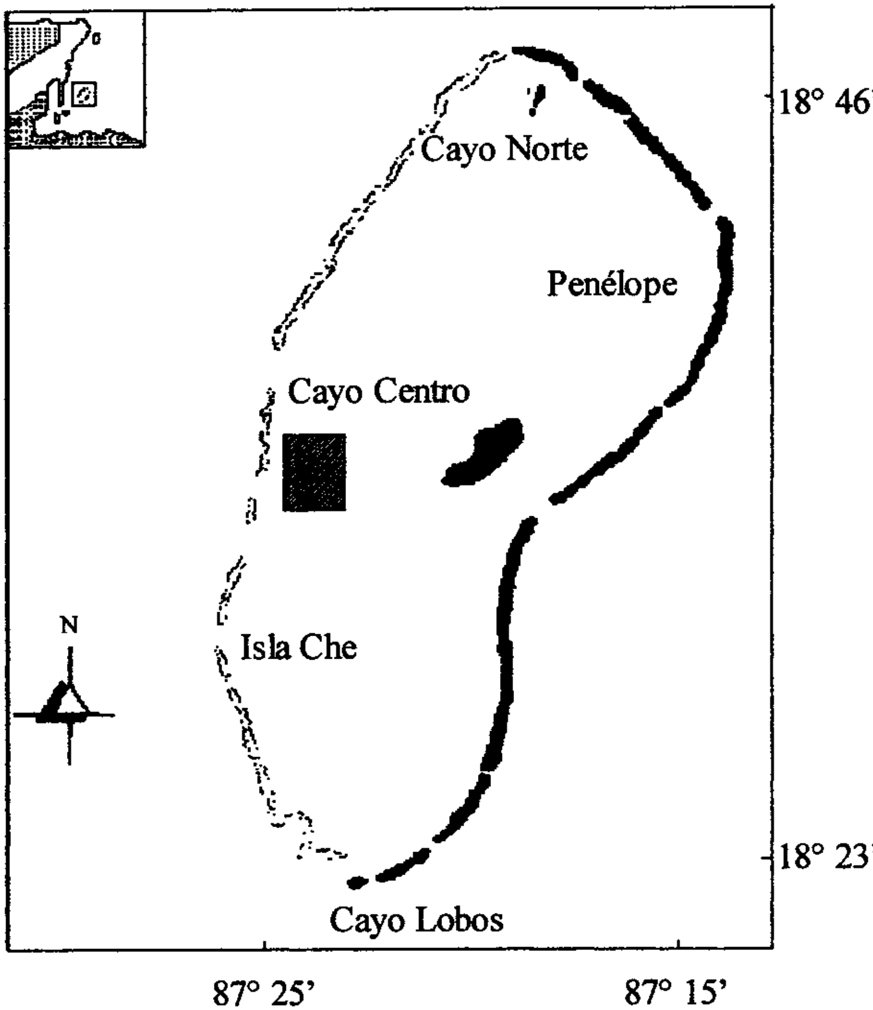

Figure 1. Location of *Strombus gigas* sampling site at Chinchorro reef, Quintana Roo, Mexico

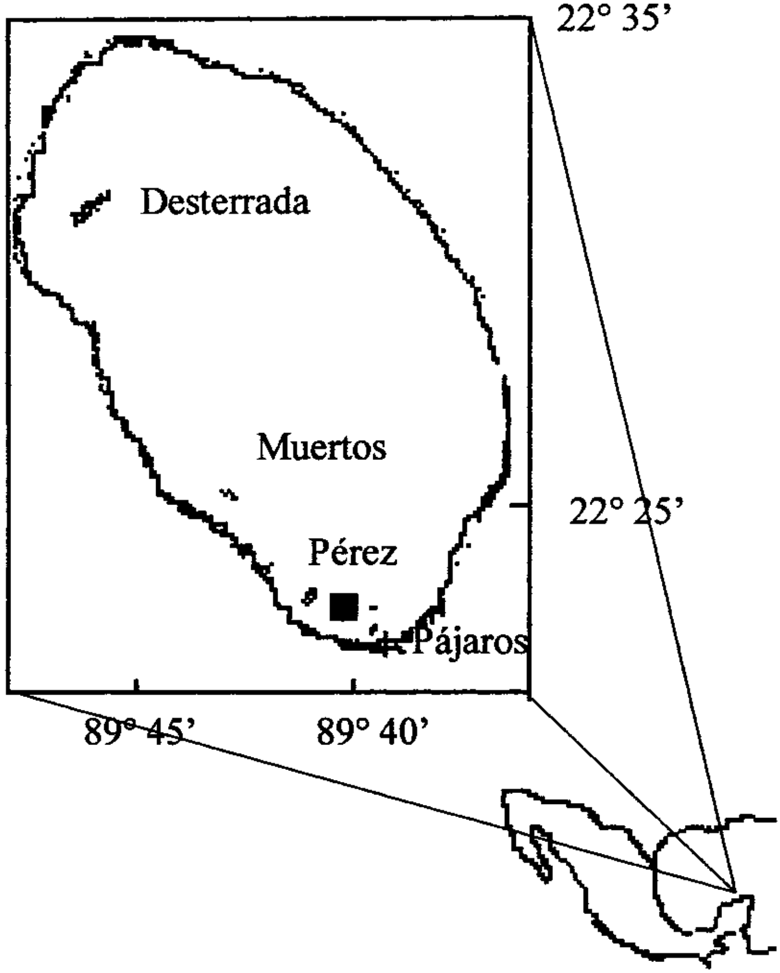

Figure 2. Location of *Strombus gigas* sampling site at Alacranes reef, Yucatan, Mexico

RESULTS

Gonad development

At microscopic levels, both the ovary and testis have a similar structure. From the exterior in, they are covered by a cylindrical and cubic epithelium, underlined by a thin layer of compact connective tissue with few muscular fibers. Under this cover of protective tissue is a layer of reticular connective tissue, in which is embedded the germinal tissue.

The germinal tissue can be identified by its acidophilus staining cells that stand out from the connective tissue as compact packets of cells. As maturation proceeds a follicle is formed, which gradually fuses with other follicles to form an oviduct or seminal duct.

Reproductive Stages

Rest — For both sexes, no signs of sexuality are evident in the connective tissue that forms the gonad. It is hardly differentiated from the digestive gland. The reticular connective tissue occupies 90 % of the gonad. Few follicles can be detected with a diameter of 39.50 ± 12.53 mm. The diameter of germinal cells is 6.05 ± 0.65 mm (Figure 3)

Gametogenesis — In females the gonad becomes thicker and occupies 30 % of the section. The follicles are well defined with diameters of 68.00 ± 18.73 mm. Ovogonias form groups of four to five cells. The nucleus is spherical, with a clear nucleolus. When vitellogenesis starts, cell diameter increases and is distinguished by basophilic cytoplasmic inclusions. Maturing oocytes are 14.25 ± 4.03 mm in diameter. As maturation proceeds the connective tissue is displaced by the follicles increasing in diameter to 153.00 ± 34.19 mm. At this stage, oocytes are 73.00 ± 38.94 mm. The nucleolus is clearly visible within the nucleus, with vacuolated cytoplasm (Figure 4).

For males the connective tissue forming over 80 % of the gonad. Follicles are very abundant with a diameter of 48.50 ± 1.29 mm. Spermatogonia have a diameter of 15.80 mm, as they grow, they separate from the wall of the follicle, occupying the lumen. First order spermatocytes have a diameter of 7mm, and second order spermatocytes of 3.60 mm. The connective tissue retracts to the inner and outer walls of the gonad as spermatogenesis advances, allowing for follicles to anastomose. Spermatids have a diameter of 5.50 mm. At this stage the follicles are 160.00 ± 1.29 mm in diameter and show maturing cells in all stages. Some spermatocytes become apyrene and oligopyrene spermatozoa, forming elongated nutritious cell of 9.35 mm long, with lateral projections that take an acidophilus stain (Figure 5).

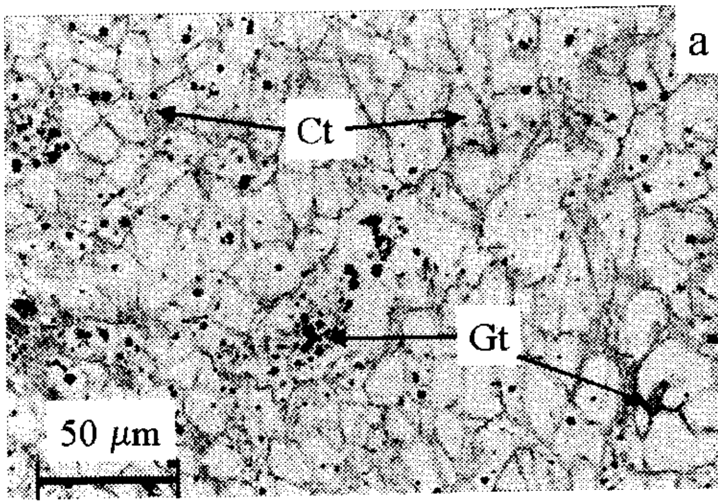

Figure 3. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico. Rest stage stained with Masson tri-chromic. No signs of sexuality are evident in the connective tissue that forms the gonad. Ct: connective tissue, Gt: Germinal tissue

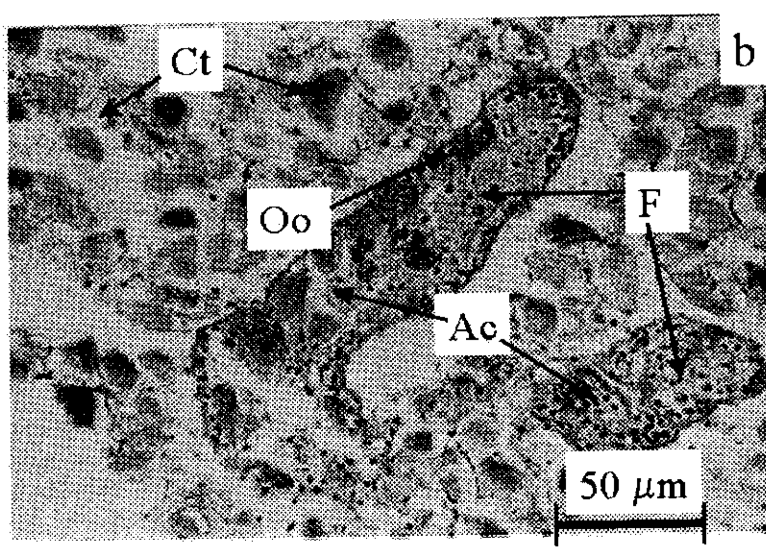

Figure 4. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico Gametogenesis stage in females stained with Masson tri-chromic. Ac: Accessory cells, Ct: connective tissue, F: Follicle.

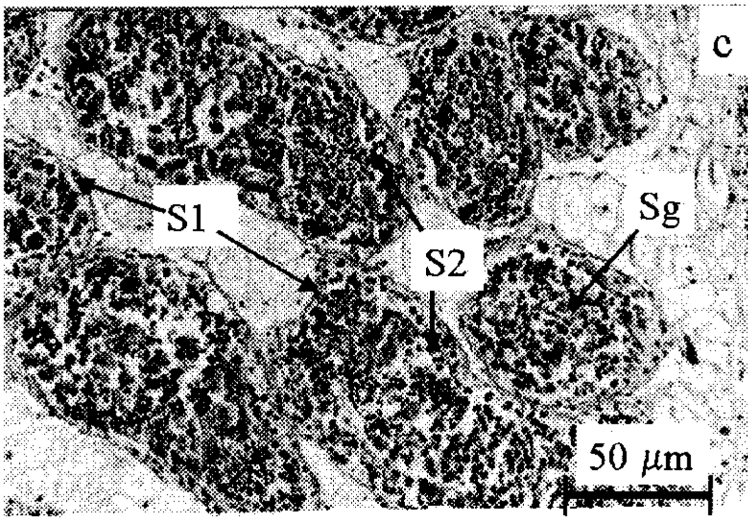

Figure 5. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico Gametogenesis stage in males stained with Masson tri-chromic. S1: first order spermatocytes, S2: second order spermatocytes, Sg Spermatogonias.

Mature — In females, the follicles are 266.50 ± 77.15 mm, they have anastomose, their walls are very thin and germinal cells are absent. Eggs are 168.50 ± 20.37 mm in diameter, they fill the follicles, with abundance of vitelline granules (Figure 6)

Follicles in males are anastomose and occupy the whole gonadic tissue; their diameter is 114.00 ± 24.51 mm with connective tissue around follicle walls and inner and outer walls of the gonad. Germinal tissue is present and active, but sperms are the dominant stage, forming a large mass in the center of the follicles of eupyrene, oligopyrene and apyrene sperms. The vases deferent are clearly formed and filled with sperm. In areas filled with sperm the walls have columnar epithelium, while in empty sections it is destroyed (Figure 7)

Spawn — In females, the follicles are emptied and their walls start to collapse. Connective tissue starts to form from the outer wall of the gonad and between the gonad and digestive gland. Sparse ovocytes can be detected with disperse vitellum, and residual oocytes in re-absorption (Figure 8)

In males the follicles continue to anastomose, with diameter of up to 334.00 ± 83.33 mm. Sperms are moved to the testis duct, leaving empty spaces in the follicles, but gametogenic activity continues keeping the production of the three types of sperms (Figure 9)

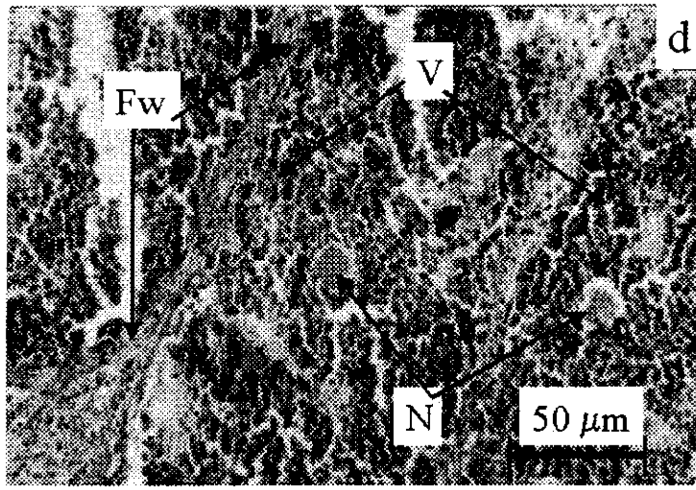

Figure 6. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico Mature stage in females stained with Masson tri-chromic. Fw: Follicle wall, N: Nucleus, V, vitellum

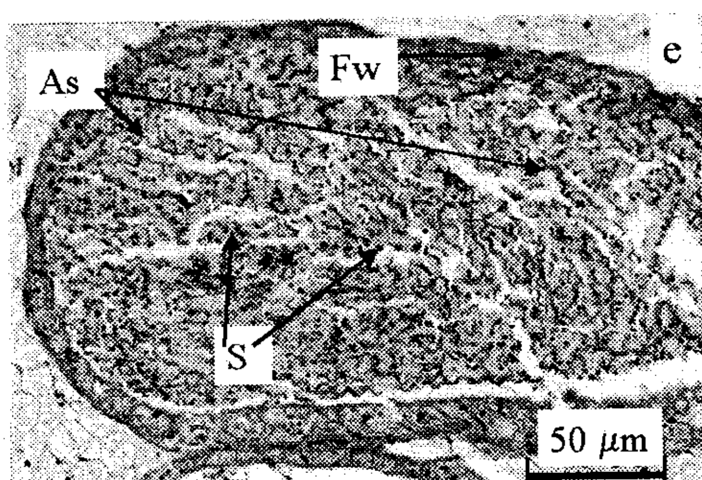

Figure 7. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico. Mature stage in males stained with Masson tri-chromic. Sperms are the dominant stage, forming a large mass in the center of the follicles of eupyrene, oligopyrene and apyrene sperms. As: Abnormal spermatocytes, Fw: Follicle wall, S: spermatozoids

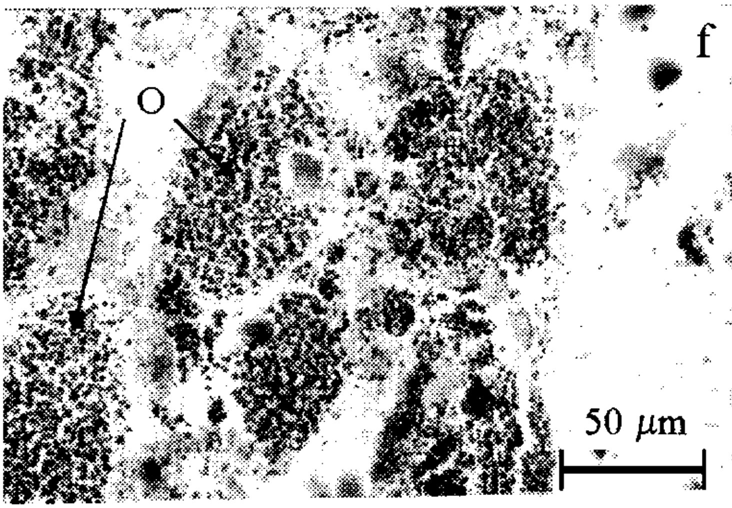

Figure 8. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico. Spawn stage in females stained with Masson tri-chromic. O: Ovums.

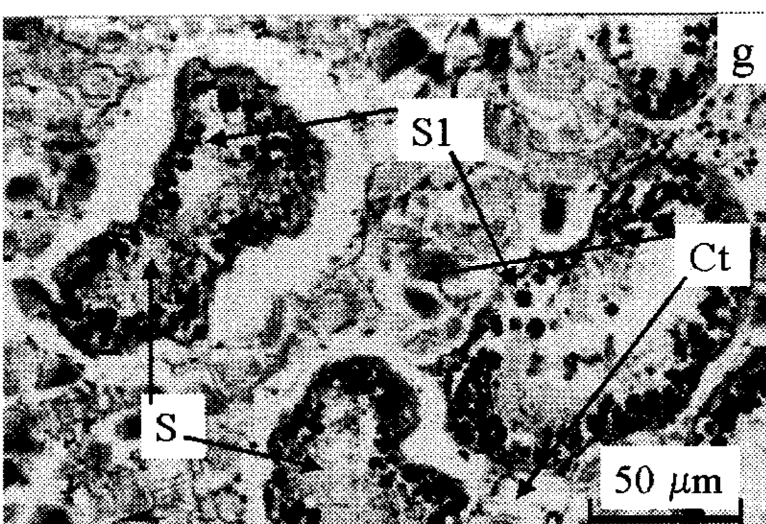

Figure 9. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico Spawn stage in males stained with Masson tri-chromic. Sperms leaving empty spaces in the follicles, that causes their collapse, but gametogenic activity continues keeping the production of the three types of sperms. Ct: Connective tissue, S: spermatozoids, S1: first order spermatocytes.

Post spawn — In both sexes the gonadic tissue is occupied by reticular connective tissue. Follicles are broken and some reproductive cells can be seen in different stages of development. Numerous phagocytes are among the rest of the follicles and gametes. Any remaining oocytes are broken or present wrinkles on their cell wall. The connective tissue close to the outer wall of the gonad has a packed appearance (Figure 10) shows post spawned male.

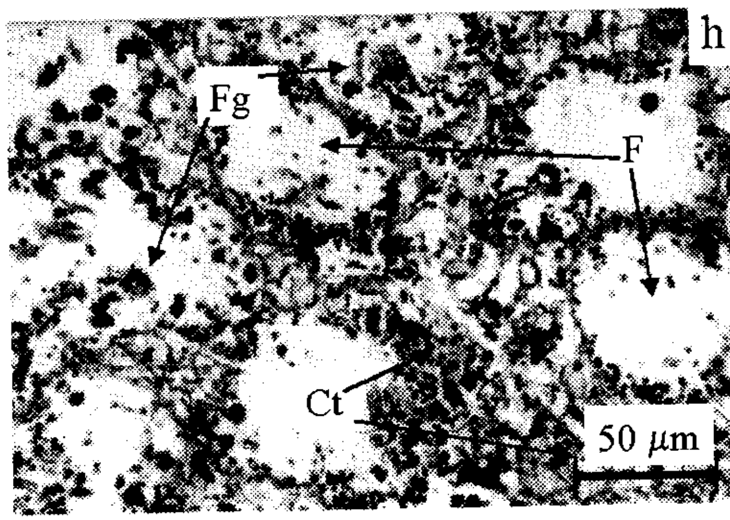

Figure 10. Microphotography of *Strombus gigas* gonad from Chinchorro, Mexico. Post spawn stage in males stained with Masson tri-chromic. Fg: Phagocytes, Ct: Connective tissue, F: Folicles

Reproductive Cycle

Reproductive cycle of S. gigas on Chinchorro reef — was established with organisms for this sample were collected from the central lagoon, from coral and sandy bottoms. The sampling period covers from June to September, as it was designed to cover season spawning period, mainly of higher presence of egg masses in the field.

i) *Females* — The rest stage was present during May (13 %) and September (33 %). Gametogenesis was present through the sampling period in average of 39 % of the female population, with slightly higher frequency during June (50 %). A similar behavior was detected for the mature stage with a mean of 36 % through the sampling period and a maximum of 40 % during May and July. The spawning period is limited to the months of July and August in 20 and 33 % of the population respectively (Figure 11)

ii) *Males* — A rest period in 30 % of the population was registered during September. Gametogenesis was present in two peaks, May (69 %) and

August (67 %), with a minimum of 14 % during September. Followed by a clear mature stage with peaks in June (50 %) and September (57 %), with a minimum during July (20 %). Giving place to a short spawning period during June and July, with a maximum of 60 % in July. Only minimum post spawn was detected during May in 8 % of the male population (Figure 12)

iii) *Both sexes* — For the whole population were detected two low frequency periods of rest during May and September in 13 and 33 % of the population respectively. Gametogenesis was present through the sampling period, with two peaks during May (54 %) and August (44 %). Maturity was constant during the sampling period with a mean of 37 % of the whole population, reaching a maximum (50 %) during September. Spawn was from June to August with a maximum during July (40 %). P ost spawn was only registered during May and June (Figure 13)

Through the five sampling months gametogenesis and mature organisms were present. Spawn was detected from June to August with a peak in July. The presence of a high percentage of mature organisms during September suggest that there might be a spawn later in the year or the accumulation of mature gametes for an early spawn during spring. Action that is supported by the presence of post spawners and organisms at rest during May and June.

Reproductive cycle of Strombus gigas, for Alacranes reef — was determined from organisms sampled along the west of Perez Island, on sandy bottom and *Thallasia*. The samples for this population were also designed to cover the spawning period, based on the presence of egg masses in the field during previous studies.

i) *Females* — The rest stage was present during March (30 %) until November (30 %), May and September do not show this stage. Gametogenesis was present through the sampling period in average of 35 % of the female population, with slightly higher frequency during May (75 %). Mature stage does not observed. The spawning and post spawning periods were limited of June and July with 10 and 20% of the population respectively (Figure 14).

ii) *Males* — A rest period in 20 % mean of the population was registered during March to November. Gametogenesis was present in two peaks, April (60 %) and September (50 %), with a minimum of 10 % during June and July. Followed by a not clear mature and spawn stages. Giving place to a minimum post spawning period during July to October, with 20 and 10% respectively (Figure 15).

iii) *Both sexes* — A discontinuous rest stage was detected in up to 30 % of the population, with only one peak correlated to the spawning period. Gametogenesis is constant through the sampling period, with a minimum of 30 % during July and a maximum in May, previous to the accumulation of mature gametes that is present from June to September. Period that cover the spawning season, although, only a very low percentage of the population was caught during spawn, the very large percentage of post spawners, clearly defines the spawning period from June to October (Figure 16).

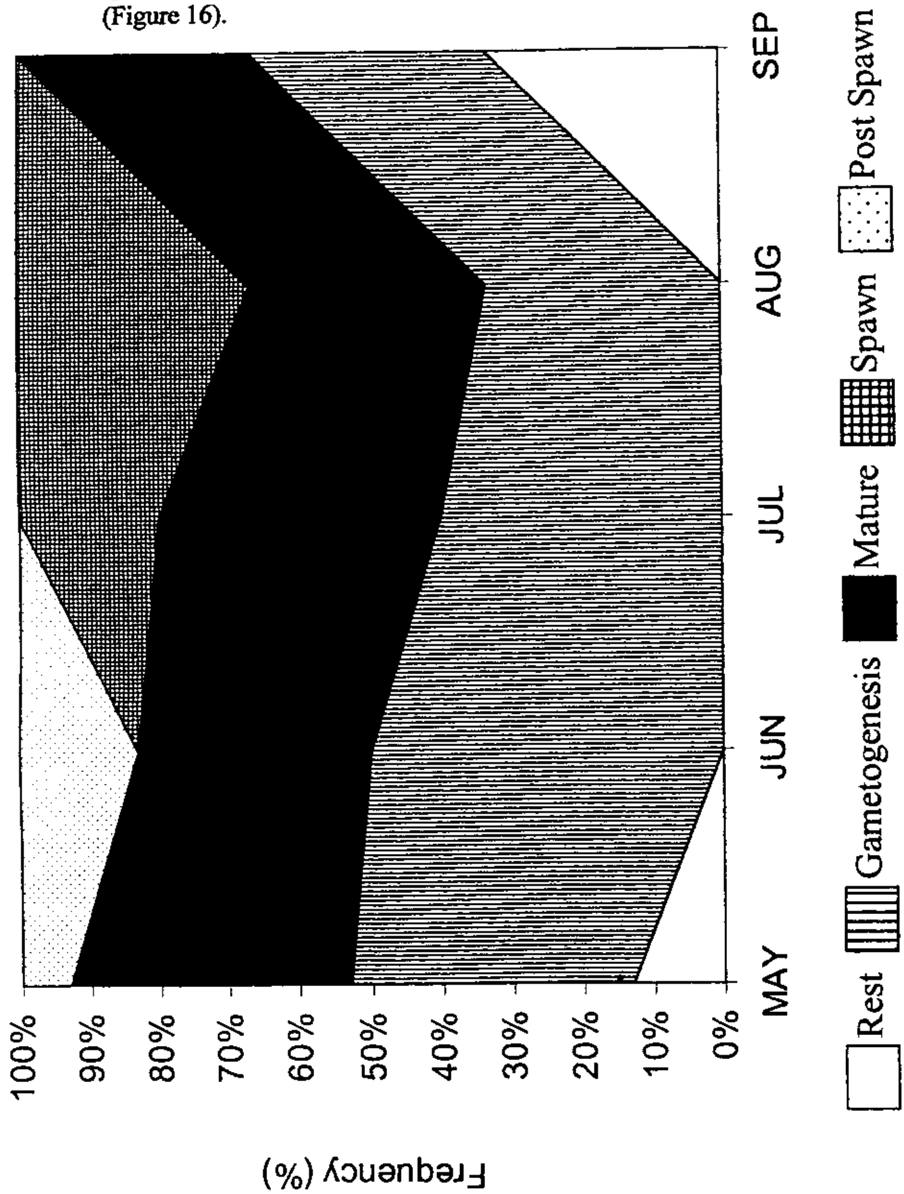

Figure 11. *Strombus gigas*. Percentage of females organism in the different reproductive stages from Chinchorro, Mexico in the Caribbean sea.

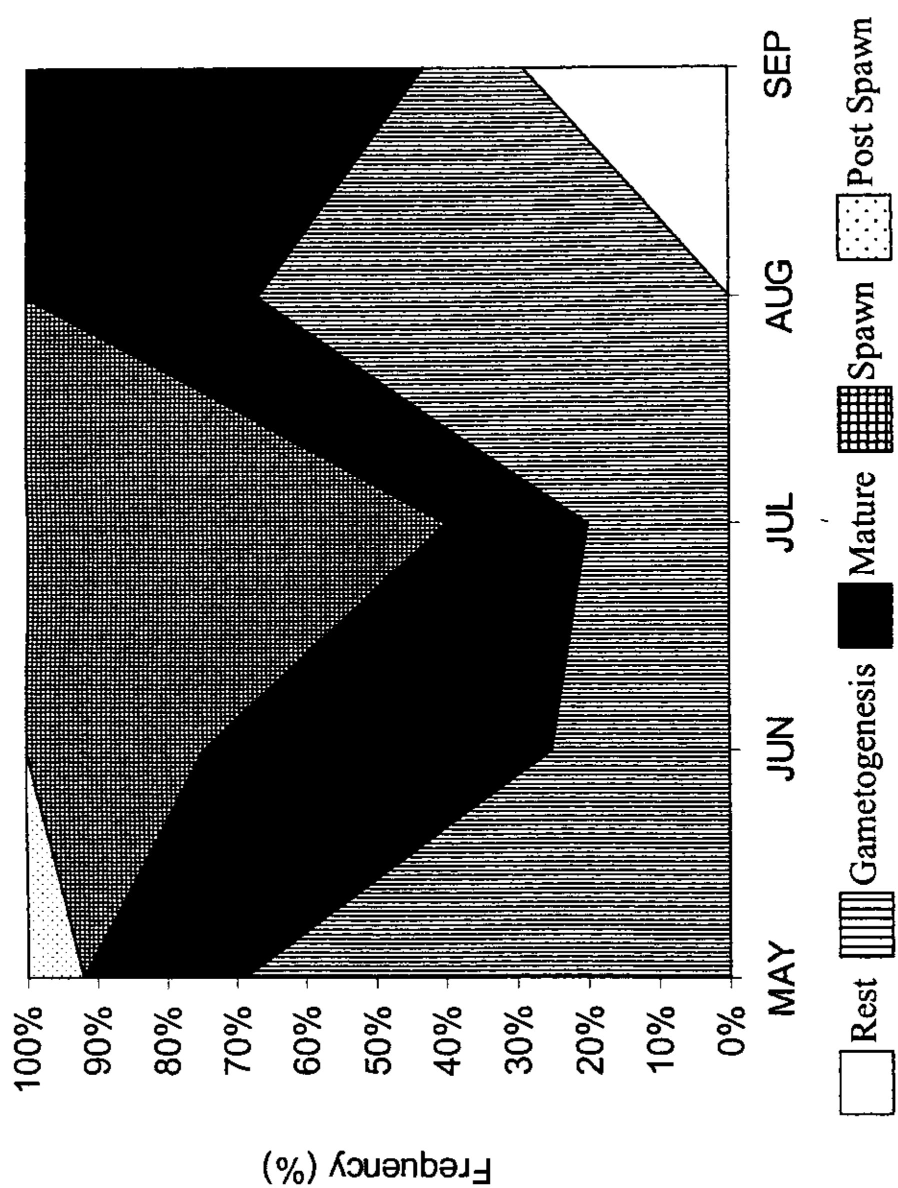

Figure 12. *Strombus gigas*. Percentage of males organisms in the different reproductive stages from Chinchorro, Mexico in the Caribbean sea.

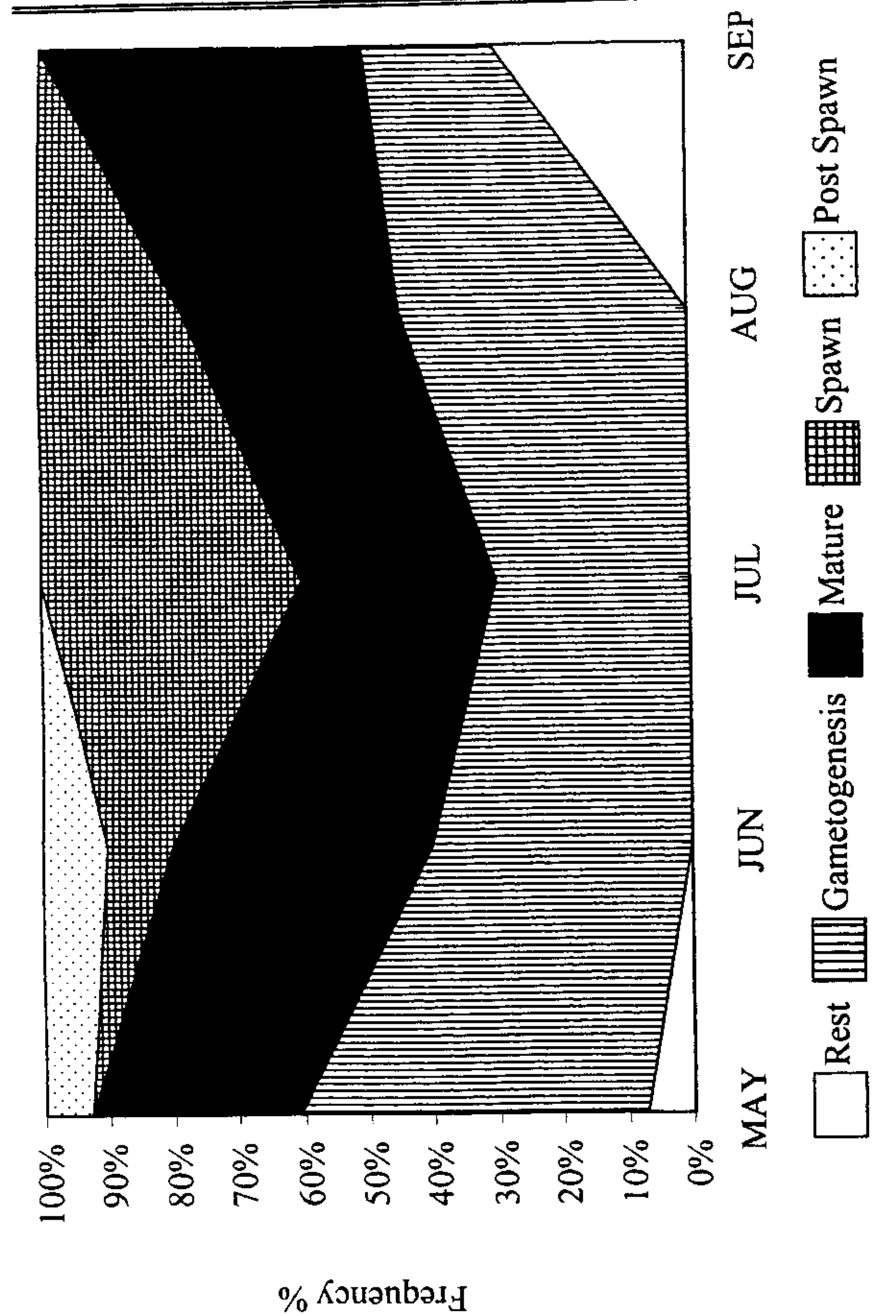

Figure 13. *Strombus gigas*. Percentage of males and female organisms in the different reproductive stages from Chinchorro, Mexico in the Caribbean sea.

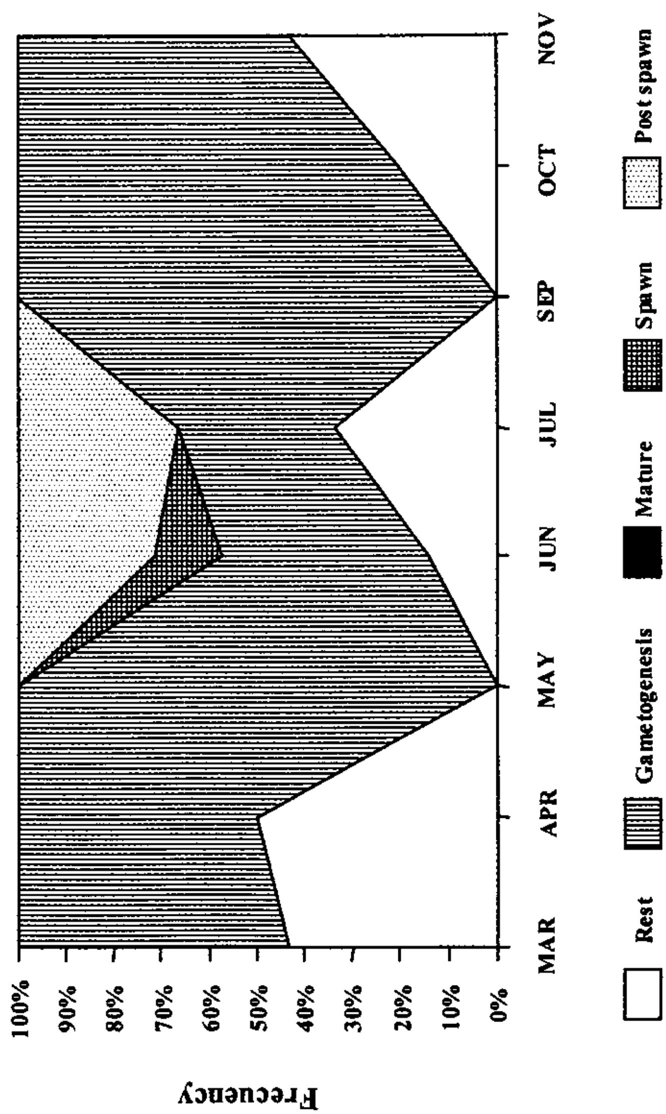

Figure 14. *Strombus gigas*. Percentage of females organism in the different reproductive stages from Alacranes reef, Mexico in the Gulf of Mexico.

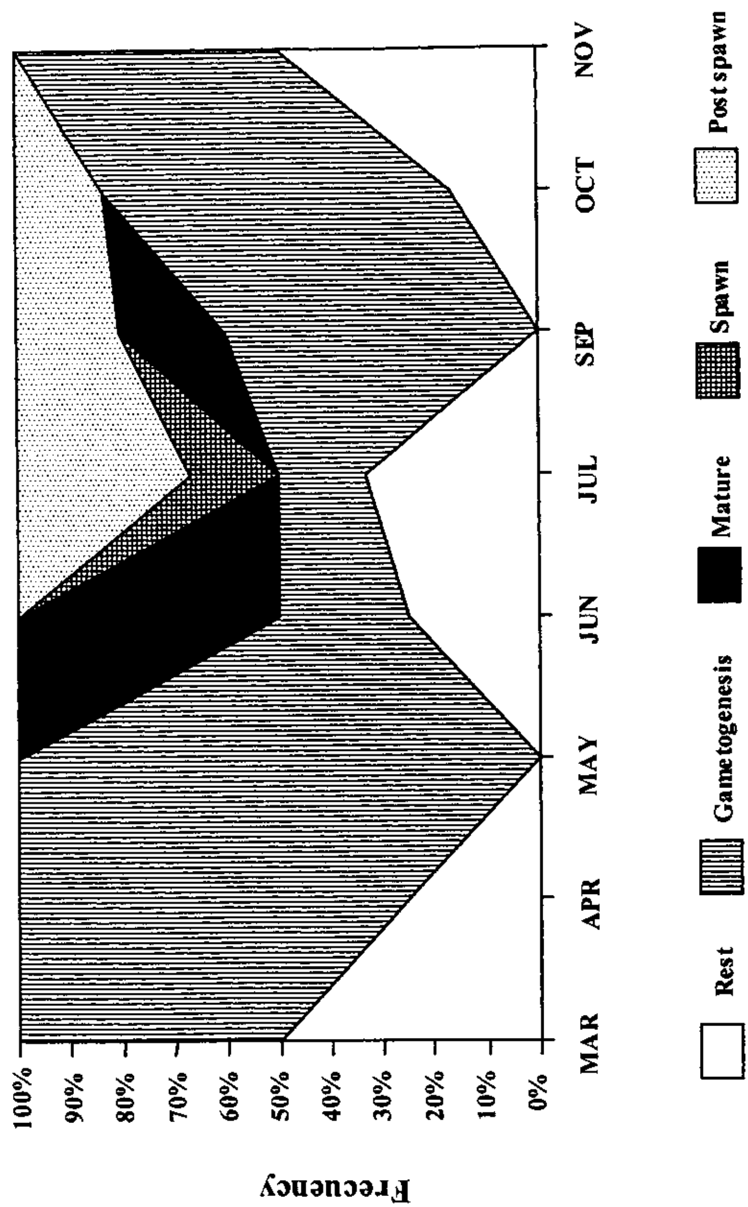

Figure 15. *Strombus gigas*. Percentage of male organisms in the different reproductive stages from Alacranes reef, Mexico in the Gulf of Mexico.

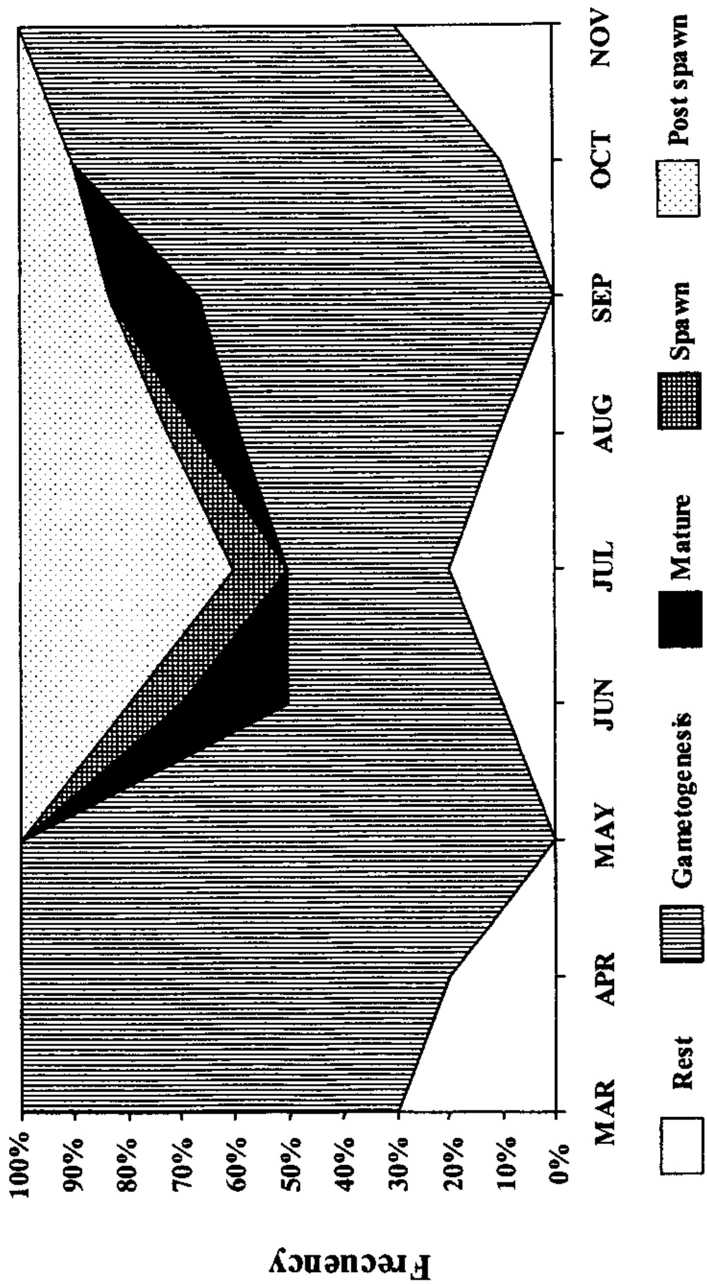

Figure 16. *Strombus gigas*. Percentage of male and female organisms in the different reproductive stages from Alacranes reef, Mexico in the Gulf of Mexico

DISCUSSION

For the two populations of *S. gigas* analyzed spawning occurs during the same months, July to August, although significant variations are evident. The population from Chinchorro reef showed a constant presence of organisms with mature gametes, with up to 40 % at the beginning of the spawning period, increasing up to 50 % at the end of the spawning season, and a maximum percentage of spawners of 40 %, and with no evident post spawning, except for 10 % of the population at the beginning of the season. Whilst the population from Alacranes reef presented a preparation for spawn in just 20 % of the population with the total participation of mature organisms at the peak of the spawning season, when up to 40 % of the population had spawned and 10 % were spawning. A similar increase in the percentage of mature organisms was detected at Alacranes at the end of the spawning season, but it had totally disappeared in October. This population presented a clear post spawn and fast gonad recovery, represented by the high percentage of organisms in gametogenesis during September. Apparently, in both populations a period of re-absorption started in autumn, exhibited by the increasing percentage of the rest stage after September.

Chinchorro Bank, being a more stable environment, more organisms exhibited a readiness for spawn but with fewer spawning. Reproductive seasons reported for *S. gigas* in the Caribbean region does not include histological results. The reproductive season of *S. gigas* has been obtained by observations of copulating or egg-laying periods. Stoner et al. (1992) compiled information on the reproductive seasons for queen conch based on behavior, taking data from different authors. At Bermuda (most northern locality), the reproductive season for *S. gigas* begins in May and ends in September. In the Florida Keys, the reproductive season is between middle January to middle September. At Venezuela (the most southern locality) the reproduction is from mid-March to mid-November. Corral and Ogawa (Stoner et al. 1992) showed that *S. gigas* at Chinchorro bank, Quintana Roo, Mexico produced eggmasses year-round. Pérez Pérez and Aldana Aranda (2000) reported a reproductive period for *S. gigas* from May to September in Alacranes reef. Stoner et al. (1992) said there was no apparent trend related to latitude for the beginning, end, or duration of the reproductive season for queen conch from Bermuda to Venezuela. Geographic comparisons of seasonality in reproduction must be interpreted cautiously due to different methods, frequency, number of observations, and different habitat types. In this study the gametogenic cycle for *S. gigas* presented differeces, even though the gonads samples were taken during the same period for Alacranes reef and Chinchorro bank. Therefore, it can be ascertained that the reproductive activity was controlled by environmental conditions.

Several authors have shown that duration and intensity of the gonadal stages are a function of temperature and food availability (Bayne 1978, Sastry 1979, Webber 1977, Fretter 1984, Mackie 1984), as well as other environmental factors (Bricelj y Malouf 1980, Syed-Shafe 1980, Jones 1981, Kennedy y Krantz 1982, Shephton

1987, Brevber 1980, Jaramillo et al. 1993).

In the reproductive cycle, the factors that induce gametogenesis and define the length and intensity of recovery periods are temperature and food availability (Lubet and Choquet 1971, Bayne 1978). While spawn may be induced by several factors as temperature (Galtsoff 1954, Holand and Chew 1973, Hines 1979), salinity fluctuations (Cain 1974, Stephner 1981), currents (Davis and Chanley 1955, Ino 1970), and the presence of some microalge (Brese and Robinson 1981) among others.

A higher frequency of mature and gametogenic organisms after the spawning peak of July is evidence of rapid gonadal recovery during the summer, which is not the case during fall and winter – spring. Slow gonad recovery is evidenced by increasing frequency of organisms at rest during September, and reminiscent of post spawners and rest organisms observed during May and June. *S. gigas* at Chinchorro has a reproductive strategy of fast gametogenesis. From the results presented herein, the need for a full cycle including several years is recommended, emphasizing environmental factors, such as temperature, food availability, and currents to better understand which might influence the gonad development and spawning periods.

For *S. gigas* at Chinchorro, one or several of these factors may be necessary to induce a massive spawn, as only a fraction of the mature population spawned, with an increasing number of mature organisms towards fall. Spawning may be induced by several factors as temperature (Hines 1979, Stoner et al 1992). Spawning has been reported from March to October at different localities on the Caribbean being more intense during May to August (Hesse 1972, Berg 1981, Orr and Berg 1987). The increasing number of mature organisms in September suggest there might be spawning in late fall or early winter, or that mature gametes are stored through the winter to spawn in early spring, as evidenced by the presence of post spawners and organisms at rest in May.

CONCLUSIONS

The gonadic cycle of any one species may vary in its seasonality, duration, and intensity of the rest and post spawn, as well as the duration and intensity of the gametogenic, maturation, and spawning periods.

Two gametogenic strategies were identified as a response to the environment:

i) Populations with a short gametognic stage or a small percentage of gametogenic organisms, which represents fast gametogenesis (*S. gigas* from Chinchorro), and
ii) Populations with a continuous gametogenesis in a very large number of organisms (*S. gigas* from Alacranes) with a very low percentage of mature organisms previous to a massive spawn in a very short time, with a very fast gonadal recovery, resuming gametogenesis.

With regards to spawning intensity and duration, one variant was identified: (1) Populations with one short defined pulse (*Strombus gigas* from both localities).

The capacity of gonad regeneration is another factor that expresses it self in the duration and intensity of the post spawning and rest periods, and on the gametogenic and maturity periods. For this, two variants were identified:

i) Populations without or with a very short and of low intensity post spawning and rest periods (*S. gigas* from Chinchorro reef), and
ii) Populations with limited or no mature stage that can support a constant or intense spawn. The characteristics presented are summarized in Table 1.

Table 1. Reproductive patterns presented by Strombus gigas at two different sites: Chinchorro bank, Quintano Roo Mexico in the Caribbean sea and Alacranes reef, Yucatan Mexico, in the Gulf of Mexico.

Patterns of S. gigas reproductive cycle	Locality	Locality
	Chinchorro bank in the Caribbean sea	Alacranes reef in the Gulf of Mexico
Gametogenesis		
Intense gametogenesis	+	-
Low intensity gametogenesis	-	+
Spawning		
One short spawning pulses	+	+
Gonad recovery		
Minimum or no post spawn and rest stages	+	-
Limited or no mature stages	-	0

From the results presented herein, knowledge of the reproductive cycle, over several years and different localities, with an emphasis on environmental factors such as temperature, food availability, and currents, as they influence gonadal development and spawning periodicity, are necessary to manage *S. gigas* populations based on reproduction activity.

LITERATURE CITED

Bayne, B. 1978. Reproduction of bivalve molluscs under environmental stress. Pages 259-278 in: J. F. Vernberg (ed.) *Physiological Ecology of Estuarine Organisms*. The Belle W. Baruch Library in Marine Science, Charleston, South Carolina USA.

Berg, J.C. 1976. Growth of the queen conch Strombus gigas, with a discussion of the practicality of its mariculture. *Marine Biology* **34**:191-199

Berg, J.C. 1981. Conch Biology. Pages 9-26 in: C. Berg (ed.) *Proceedings of the Queen Conch Fisheries and Mariculture Meeting.* The Wallace Grove Aquaculture Foundation. Freeport, Bahamas.

Berg, J.C. and N.L. Adams. 1984. Microwave fixation of marine invertebrates. *Journal of Experimental Marine Biology and Ecology* **74**:195-199.

Breese, W.P. and A. Robinson. 1981. Razor clams, *Siliqua patula* (Dixon): gonadal development, induced spawning and larval rearing. *Aquaculture* **22**:27-33.

Brevber, P. 1980. Annual gonadal cycle in the carpet shell clam Venerupis decussata in Venice lagoon, Italy. *Proceedings of the National Shellfisheries Association* **70**(1):39-85.

Bricelj, M.V. and R.E. Malouf. 1980. Aspects of reproduction of hard clams (*Mercenaria mercenaria*) in Great South bay, New York.*Proceedings of the National Shellfisheries Association* 70: 216-229.

Cain, T.M. 1974. Reproduction and recruitment of the brackish water clam *Rangia cuneata. Fisheries Bulletin* **73**(2):412-430.

Castagna, M. and J.N. Kaeuter. 1981. Manual for growing the hard clam *Mercenaria* sp. Virginia Institue of Marine Science Reports o Applied Marine Science and Ocean Engineering. **249**. Gloucester Point, Virginia USA. 110 pp.

Davis, H.C. and P.E. Chanlely. 1955. Spawning and egg production of oysters and clams. *Proceedings of the National Shellfisheries Association* **46**:40-51.

Fretter, V. 1984. Prosobranchs. Pages 1-45 in: Wilburn, M K. (ed.) *The Mollusca*, Vol 7. Reproduction, Tompa, A. S., N. H. Verdonk y J. A. M. den Biggelaar (eds.). Academic Press. Orlando, Florida, USA.

Gabe, M. 1968. *Techniques Histologiques*. Edit. Masson and Cie. 1136 pp.

Galtsoff, P.S. 1964. The American oyster *Crassostrea virginica* Gmelin. *Fisheries Bulletin* **64**:1-480.

García, E. 1981. Modificaciones al sistema de clasificación climática de Köppen. Ed. Larios, México, segunda ed. D.F. : 252 pp.

Graffé, F.S., 1990. Tablas de Predicción de Mareas. Puertos del Golfo de México y mar Caribe. Datos Geofísicos serie A Oceanografía. Inst. Geof. U.N.A.M.: 113 - 144.

Hesse, K.O. 1976. An ecological study of the queen conch, *Strombus gigas*. M. Sc. Thesis Univ. Connecticut. 107 pp.

Hilderbrand, H.H., H. Chávez, and H. Compton. 1964. Aporte al conocimiento de los peces del arrecife Alacranes, Yucatán (México). *Ciencia* **23**(3):107-134.

Hines, A.H. 1979. Effects of a thermal discharge on reproductive cycles in *Mytilus edulis* and *Mytilus californianus* (Mollusca, bivalvia). *Fisheries Bulletin* **77**(2): 125-132.

Holland, D.A. and K.K. Chew. 1973. Reproductive cycle of the manila clam (Venerupis japonica) from hood canal, Washington. *Proceedings of the National Shellfisheries Association* **64**:65-72.

Ino, T. 1970. Controlled breeding of molluscs. Indo Pacific Fishr. Coun. F. A. O. IPFC/070/SYM 35. 24 pp.

Jaramillo, R., J. Winter, J. Valencia, and A. Rivera. 1993. Gametogenic cycle of the Chiloe scallop (*Chlamys amandi*). *Journal of Shellfish Research* **12**:59-70

Jones, S. D. 1981. Reproductive cycle of the Atlantic surf clam *Spisula solidissima*, and the ocean quahog *Arctica islandica* off New Jersey. *Journal of Shellfish Research* **1**:23-32.

Jungers, W.L., A.B. Falsetti, and C.E. Wall. 1995. Shape, Relative sise, and Size Adjustments in Morphometrics. *Yearbook of the American Journal of Physical Anthropology* **38**:137-161.

Kennedy , V.S. and. L.B. Krantz. 1982. Comparative gametogenic and spawning patterns of the oyster *Crassostrea virginica* (Gmelin) in central Chesapeake bay. *Journal of Shellfish Research* **2**(2):133-140.

Knaub, R.S. and A.G. Eversole. 1988. Reproduction of different stocks of *Mercenaria mercenaria*. *Journal of Shellfish Research* **7**(3):371-376.

Kornicher and Boyd, D. 1962. Shallow-water Geology and environments of Alacran reef Complex, Campeche Bank, México. *Bulletin of the American Association of Physical Geologist* **46**:640-673.

Lankford, R.R. 1974. Coastal lagoons of Mexico, their origin and classification. Pages 182-215 in: Cronnin, L. E. (ed.) *Estuarine Processes. Circulation, Sediments and Transfer of Material, in the Estuary*. Academic Press Inc. New York, New York USA.

Loosanoff, V.L. and H.C. Davis. 1963. Rearing of bivalve mollusks. Pages 2-36 in: F.S. Russell (ed.) Advances in Marine Biology. Academic Press. New York, New York USA.

Lubet, P. et C. Choquet, 1971. Cycles et rythmes sexuales chez les mollusques bivalves et gastropods. *Haliotis* **1**(2):129-149.

Lucas, A. 1965. Recherche sur la sexualité des mollusques bivalves. Tesis doctoral Fac. Sci. Univ. Rennes, Francia. 136 pp.

Luna, G.L. 1968. *Manual of Histologic Staining Methods of the Armed Forces* Institute of Pathology. Tercera Ed. McGraw-Hill Book Co. New York, New York USA. 258 pp.

Mackie, G.L. 1984. Bivalves. Pages 305-418 in: K.M. Wilbur (ed.). *The Mollusca*. Vol. 7. Reproduction Tompa, S. A., N. H. Verdonk y J. A. M van den Biggelaar, Academic Press. Londres, U. K.

Orr, K.S. and C.J. Berg, 1987. *The Queen Conch*. Winward Publishing, Inc. Miami, Florida USA. 32 pp.

Pérez Pérez, M. and D. Aldana Aranda. 2000. Distribución, abundancia, densidad y morfometría de Strombus gigas (Mesogasteropoda:Strombidae) en el arrecife Alacranes, Yucatán, México. *Revista Biologo Tropical* **48**(1):51-57.

Sastry, N.A. 1979. Pelecypoda (Excluding Ostreidae). Pages 113-192 in: A.C. Giese and J.S. Pearse (eds.) *Reproduction of Marine Invertebrates, Volume 5*. Academic Press. Orlando, Florida USA.

Shephton, T.W. 1987. The reproductive strategy of the Atlantic surf clam, *Spisula solidissima*, in Prince Edwards island, Canada. *Journal of Shellfish Research* 6(2):97-102.

Siddall, S. 1984. Synosis of recent research on the queen conch *Strombus gigas* Linné. *Journal of Shellfish Research* 4(1):1-4.

Stephner, D. 1981. Induction of Spawning four species of Bivalves of the Indian coastal waters. *Aquaculture* **25**:153-159.

Stoner, A.W., J.S. Veronique, and I.F. Boidron-Metairon. 1992. Seasonality in reproductive activity and larval abundance of queen conch *Strombus gigas* . *Fishery Bulletin* **90**(1):161-170.

Syed-Shafe, M. 1980. Quantitative studies on the reproduction of black scallop, Chlamys varia (L.) form Lanveoc area (Bay of Brest). *Journal of Experimental Marine Biology and Ecology* **42**:171-186.

Webber, H.H. 1977. Gastropoda: Prosobranchia. Pages 1-98 in: C.G. Giese and J.S. Pearse (eds.) *Reproduction of Marine Invertebrates. Vol. IV. Molluscs: Gastropods and Cephalopods*. Academic Press. Londres, UK.