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Reproductive cycle of *Strombus gigas* Linnaeus 1758 (Caenogastropoda: Strombidae) from Archipelago of San Andres, Providencia and Santa Catalina, Colombia

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**Summary**

The reproductive cycle of the Queen Conch, *S. gigas*, in the Archipelago of San Andres, Providencia and Santa Catalina, Colombia, was estimated during a 1-year period (February 2003–January 2004) from monthly observations on histological sections of gonads collected from sexually mature individuals. The resting, gametogenic, mature, and post-spawning stages were present almost all year long, while spawners (or “gamete producers” as *S. gigas* does not spawn into the water but copulates) appeared only twice, from March to April (6% males and 20% females) and in September (6% males, 43% females). The results of our histological analyses are congruent with those of previous works on *S. gigas* in San Andres Archipelago based only in mating and egg-laying behaviors, and in the presence of egg-masses as proxies for spawning. The current fishing season of Queen Conch in San Andres Archipelago extends from November 1 to May 31, according to Resolution No. 179 of May 5, 1995, and overlaps with the first reproductive event of this species. As harvesting egg-laying females during March–April could place the recovery of the population at risk, we suggest two possible scenarios to modify the current fishing regulation: a) reducing the fishing season from November 1 to March 1, and b) opening two fishing seasons per year, one from November 1 to March 1 and the other from June 1 to July 31. The success of any of these management options can only be evaluated by implementing a monitoring plan in San Andres Archipelago. This simple procedure will help protect this species, improve its sustainability through time, and guarantee the availability of the resource to local fishermen.

**Key words:** Colombia, Gonadic development stages, histology, Queen Conch, reproductive season, Seaflower Biosphere Reserve

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Introduction

The Queen Conch, *Strombus gigas* Linnaeus, 1758 (Caenogastropoda, Strombidae) is widely distributed in the territorial waters of 36 countries and dependent territories in the Caribbean Sea (CITES, 2003) and represents a commercially important item to a number of local economies in the region (Catarci, 2004; Medley, 2005). In Colombia, *S. gigas* is second in importance of all commercially harvested marine invertebrates, due to its size, attractive shell, and flavorful meat (Reyes and Santodomingo, 2002). Conch harvesting takes place mainly in the Archipelago of San Andres, Providencia and Santa Catalina, on a smaller scale in San Bernardo Archipelago and Rosario islands (Ospina-Arango et al., 1996; Pérez-Molina, 1997), and since the last decade in the Guajira (Castro-González, 2003).

Most laws and regulations promulgated to protect marine ecosystems use fishing seasons to improve the sustainability of resources by protecting stocks during critical periods, such as spawning. Establishing seasons allow individuals to gain growth by delaying recruitment to the fishery, reduce effective fishing mortality by limiting the number of days in which fishing occurs, and spread the fishing quota more evenly throughout the year (Theile, 2001; Medley, 2005; FAO, 2007).

Knowledge about the reproductive cycle of the target stock is essential for delimiting fishing seasons (Anonymous, 2001; Medley, 2005), and this cycle is best estimated by examining the anatomical features of gonads, gamete ducts, and gametes in sampled individuals through time. However, in contrast to other organisms such as fish, the external features of the Queen Conch glands can hardly be used to describe its reproductive dynamics. Instead, the description and categorization of the microscopic anatomy of its gonads and that of other reproductive tissues are the best suited means to achieve this end (e.g. Reed, 1993; Gordillo-Morales, 1996; Avila-Poveda, 2001; Aldana-Aranda et al., 2003a, b, c; Avila-Poveda et al., 2005a).

Declared a Seaflower Biosphere Reserve (SBR) by UNESCO’s Man and the Biosphere Program, in November 2000, the Archipelago of San Andres, Providencia and Santa Catalina, enjoys special protection from the Colombian government. It is in charge of enforcing the preservation of marine resources through sustainable development and fishery management and control (MAB, 2001).

The enforced fishing season of *S. gigas* in the San Andres Archipelago was established in 1995 (Resolution No. 179 of May 5) and extends from November 1 to May 31. The current knowledge about the reproduction of this species in the region, based solely on the observation of mating and egg-laying behaviors, and on the presence of egg-masses in the field, suggests the existence of a reproductive period extending approximately from April to October (García-Escobar et al., 1992; Márquez-Pretel et al., 1994). Apparently, the reproductive period of *S. gigas* in the San Andres Archipelago partially overlaps the fishing season.

In this paper, we compare the fishing season enforced in the San Andres Archipelago with the reproductive seasonality of the Queen Conch population, estimated from cycle in the microscopic anatomy of the reproductive tissue. This information is then used to discuss the current effects of the fishing season on the population, and to suggest modifications to its limits in order to improve the sustainability of the stock. Our results are compared to the reproductive cycles of other populations of *S. gigas* in the Caribbean region.

Materials and Methods

Sampling

Queen Conchs were obtained from the artisanal fishing fleet between February 2003 and January 2004. Gastropods were collected alive in three islands of the Archipelago of San Andres, Providencia and Santa Catalina (also known as San Andres Archipelago), Colombia (Avila-Poveda, 2004): San Andres Island (12°32’N, 81°42’W), Bolivar Cays (12°24’N, 81°28’W) and Alburquerque Cays (12°10’N, 81°51’W) (Fig. 1). Every month (except July 2003 during which sampling stopped due to Hurricane Claudette), 31 individuals with total shell length larger than or equal to 20 cm, with or without outer lip (age-groups locally known by fishermen as “Roundshell” and “Broadleaf”, respectively) were collected by free diving. In this species, sexes are separate, and the onset of sexual maturation occurs when the formation of the flared outer lip begins (Randall, 1964; Alcolado, 1976; Berg, 1976; Brownell, 1977; Coulston et al., 1987; Appeldoorn, 1988; Wicklund et al., 1991; Berg et al., 1992; Avila-Poveda and Baqueiro-Cárdenas, 2006).

Immediately after capture, we sampled approximately 1 cm$^3$ of visceral mass (gonad and digestive gland) from each individual (Fig. 2), and fixed it for 12–15 days in 10% neutral formalin saline solution in seawater. Once samples were fixed, they were preserved in 70% ethanol with 0.1% glycerin (Bondad-Reantaso et al., 2001) and air shipped to CINVESTAV-IPN, Merida, Mexico, for histological procedures.

Histological procedures

Preserved visceral masses were transferred to alcoholic Bouin’s fixative for 7 days and processed following standard histological routines: washing,
dehydration, clearing, and embedding (Avila-Poveda et al., 2005b, 2006). Sections 6 mm thick were stained using Harris’s hematoxylin–eosin regressive method (Howard and Smith, 1983). Slides were examined using a Carl Zeiss MC73A light microscope at low magnification (30×) to scan the entire gonad area and second, and at high magnification (100×, 400× and 1000×) to assess follicle stages. Sections were photographed using a high resolution Sony color video camera, model CCD-IRIS, mounted on the microscope.

The gonadic cycle was described by matching direct observations on the tissue with anatomical features corresponding to five ordered stages: resting, gametogenic, mature, spawning, and post-spawning (Egan, 1985; Gordillo-Morales, 1996; Pérez-Bouchez, 1996; Aldana-Aranda et al., 2003a, 2003b, 2003c; Delgado et al., 2004; Avila-Poveda et al., 2005b). These stages describe changes in the anatomy of gonads and other reproductive structures. They are recognized by differences in the relative surface area of distinct tissues in the gonad on histological sections, the presence and relative position of gametes, their developmental stage, the presence of amoebocytes (i.e., blood cells, following the descriptions by García-Cerruti, 1977; Sminia et al., 1983; van der Knaap et al., 1993), and the morphology and distribution of follicles. Notice that, strictly speaking, S. gigas does not spawn (i.e., production and deposition or releasing of gametes) but copulates. Here, spawning referred only to the period in which gametes were released from the gonad. The resulting sample size at each gonadic stage was reported using the uppercase letter N followed by the first letter of the corresponding stage name in lowercase.

**Reproductive cycle**

The reproductive season of Queen Conch from San Andres was considered to span from the moment in which their gonads were mature to that in which the spawning stage ended. The percentage of individuals at each gonadic stage within sexes was calculated from all the individuals of each sex collected that month. The reproductive cycle was compared to those reported from populations living in different Subregional Management Structures (SMS) in the Caribbean. The geographical range of S. gigas was divided into SMS to facilitate and promote the development of regionally-effective management plans and legislations (FAO, 2007). These structures are: the Northern Zone (NZ), including Bahamas, Cuba, Dominican Republic, Haiti, Turks and Caicos Islands, and Florida; the Eastern Zone (ESZ), including Lesser Antilles, Netherlands Antilles, Puerto Rico, and Venezuela, and the South Central Zone (SCZ), including Belize, Colombia (San Andres Archipelago), Guatemala, Honduras, Jamaica, Mexico (Yucatan), and Nicaragua.

**Results**

All gonadic stages were found in the 343 individuals examined throughout the year. At resting stages (Nr = 148), gonads had neither follicles producing germinal cells nor gametes. From 90–100% of the surface area of the gonadic tissue was filled by a distinctive reticular connective tissue, with few amoebocytes dispersed within it. Few broken or empty follicles were also present (Figs. 3A and 4A). The frequency of females
Fig. 3. Histological sections of the gonad of female *S. gigas* stained with Harris’s hematoxylin and eosin (400×). Stages: A, resting; B, gametogenic; C, mature; D, spawning; and E, post-spawning. Tissue labels: Ct, connective tissue; F, follicle; Ft, follicle tissue; O, oocyte; Og, oogonia; P, phagocytes; Vg, vitelline granules. Black scale bar = 50 µm.

(Fig. 5A) at this stage varied between 6–73% per month, while that of males (Fig. 5B), between 15 and 64%. Resting stages were found in monthly samples throughout the year. High frequencies of females at this stage occurred in May and December (>70%), in June and January (>63%), and in October (53%), while high frequencies of males occurred in January, May, and December (>62%), and in June (55%).

In gonads at the gametogenic stage (Ng = 78), follicles producing germinal cells were dispersed and filled 10% to 80% of their surface area. Few follicles were found close to the digestive gland. In females, oogonia formed groups of four to five cells located near the follicular wall, whereas oocytes were in the lumen (Fig. 3B). In males, the spermatogonia and spermatocytes of first and second order were found near the
follicular wall, while few isolated spermatozoa were found close to the lumen (Fig. 4B). The frequency of females (Fig. 5A) varied between 6 and 63% per month, and that of males between 5 and 33% (Fig. 5B). As in the previous stage, gametogenic gonads were found almost all year long. High frequencies of females at this stage were found in November (63%) and August (55%), while high frequencies of males were found in August (33%) only. No males with gametogenic gonads were found in March.

Almost all the surface area (>80%) of mature gonads (Nm = 31) was filled with bulging and anastomosed follicles, and most of them were located close to the digestive gland. In females (Fig. 3C), follicles contained...
Fig. 5. Tendency of the gonadic cycle of *S. gigas* in Archipelago of San Andres, Providencia and Santa Catalina, Colombia. Sexes: A, female; B, male.

eggs and vitelline granules. In males, follicles (Fig. 4C) were filled with spermatogonia, spermatocytes, and spermatozoa. The vas deferens (Fig. 4D) was filled or partially filled with spermatozoa and atypical spermatozoa, and had a distinguishable epithelial wall. Mature females were found only between February and March, at frequencies not larger than 6% per sample, and between August and September, at frequencies oscillating between 7 and 18% per month (Fig. 5A). In contrast, mature males were found all year long except in December, at frequencies varying between 5 and >30% per sample. The highest male frequencies occurred in March and August (Fig. 5B).

The follicular tissue found at the spawning stage (Ns = 11) filled 40–90% of the surface area of the gonad and had few amoebocytes. Follicles had distinguishable walls, were dispersed through the gonad, and their size was smaller than that of follicles in mature stages. In females, follicle walls were collapsing, few eggs were damaged, and vitelline granules were dispersed (Fig. 3D). In males, few spermatogonia and spermatocytes were close to the follicular walls and few spermatozoa were in the lumen (Fig. 4E). The vas deferens was empty or contained few atypical spermatozoa. Spawning females were found only in March (20%) and in September (43%) (Fig. 5A). Similarly, spawning males
were found only in April and in September at frequencies of 6% per month (Fig. 5B).

Post-spawning conchs (Np = 75) had 90% of the gonad surface area filled with reticular connective tissue. Phagocytes were abundant among follicular debris (Figs. 3E and 4F). The frequency of females varied between 6 and 60% per month, and that of males between 13 and 55%. Post-spawning females reached high frequencies in March (60%) and April (40%) (Fig. 5A). Maximum frequencies of males at this stage occurred in February (42%), March (55%), and September (33%). No post-spawning males were found in January and in August (Fig. 5B).

A non-exhaustive literature review on the reproductive cycle of *S. gigas* in different areas of the Caribbean Region is presented in Tables 1 and 2. Most contributions describe the reproductive cycle of the Queen Conch based on proxies such as mating, and egg-laying behaviors, and on the presence of egg-masses (Table 1). In contrast, few reports are supported by histological analyses (Table 2). For Queen Conchs in San Andres Archipelago, differences between these two approaches are compared in Fig. 6. The spawning stage found in this study perfectly matches the two reproductive seasons described by García-Escobar et al. (1992) and Márquez-Pretel et al. (1994), while the gametogenic and mature stages are present all year long in the archipelago. Months included in the current fishing season and two new suggested fishing seasons are presented in Fig. 6.

**Discussion**

The reproduction of Queen Conch in the Archipelago of San Andres, Providencia and Santa Catalina, Colombia, was seasonal, occurring two times per year. Female and male gonads were ready to release gametes synchronously between March and April and in September: around 6% of males matured and reached a spawning stage (in both seasons) together 20 to 43% of females (in March and September, respectively) (Fig. 5). These two peaks varied in intensity and duration. The high frequency of post-spawners during March suggests that a massive spawning event happened during this period; however, the number of spawners in September was larger than that in the previous event: less than 20% of females spawned in March, while 43% in September. Mature females were only found during the spawning season while mature males almost all year long (Fig. 5). Resting, gametogenic, and post-spawning stages occurred during almost all months in both sexes.

The extent and duration of spawning seasons might vary annually, and depend on exogenous factors such as climate and food availability, and on endogenous factors, such as genetics (e.g. Webber, 1977). Some authors suggest that, at least for certain Caenogastropoda, spawning seasons might not depend on climate but rather on the simultaneous reaction of all individuals in a population to a spawning stimulus. They also suggest that long spawning seasons may be the result of different age groups or individuals spawning at different times (Fretter, 1984). Other reasons why spawning season might look different even between populations of the same species may include more pragmatic aspects of these studies, such as differences in the methods used and the frequency and number of observations (Stoner et al., 1992).

Baqueiro-Cárdenas and Aldana-Aranda (2000) and Aldana-Aranda et al. (2003b), according to the intensity and duration of each gonadic stage, suggested that gonads of widely geographically distributed species of mollusks may be assigned to two types of strategies: (a) the gametogenic strategy is characterized by a continuous low intensity gametogenesis, one reproductive pulse per year, and slow gonad recovery, and (b) the spawning strategy, recognized by fast gametogenesis and gonadic recovery, mature stages present all or almost all year long, and two spawning pulses of low intensity and short duration. Queen Conchs from San Andres Archipelago follow the spawning strategy, which is also commonly found in most *S. gigas* populations from Mexico (Gordillo-Morales, 1996; Pérez-Bouchez, 1996; Aldana-Aranda et al., 2003a) and in Belize (Egan, 1985).

The reproductive cycles estimated from observations of mating and egg-laying behavior, and on the presence...
Table 1. Reproductive cycles of *S. gigas* in several Caribbean areas, from observations on mating, and egg-laying behaviors, and on the presence of egg-masses. Results are grouped according to Subregional Management Structures (SMS) (FAO, 2007)

<table>
<thead>
<tr>
<th>Reproductive cycle</th>
<th>Duration (months)</th>
<th>Geographical area</th>
<th>SMS</th>
<th>Locality</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>J F M A M J J</td>
<td>A S O N D</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.5</td>
<td>Florida</td>
<td>NZ</td>
<td>24°40' N, 82°00' W</td>
<td>Davis et al., 1984</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Turks and Caicos</td>
<td>NZ</td>
<td>21°30' N, 72°15' W</td>
<td>Davis et al., 1987</td>
<td></td>
</tr>
<tr>
<td>5.5</td>
<td>Bahamas</td>
<td>NZ</td>
<td>23°35' N, 76°05' W</td>
<td>Wicklund et al., 1991</td>
<td></td>
</tr>
<tr>
<td>4.5</td>
<td>Bermudas</td>
<td>NZ</td>
<td>32°20' N, 64°45' W</td>
<td>Berg et al., 1992</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Bahamas</td>
<td>NZ</td>
<td>23°35' N, 76°05' W</td>
<td>Stoner et al., 1992</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Virgin Islands</td>
<td>ESZ</td>
<td>18°15' N, 65°00' W</td>
<td>Randall, 1964</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Venezuela</td>
<td>ESZ</td>
<td>11°40' N, 66°30' W</td>
<td>Brownell, 1977</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Venezuela</td>
<td>ESZ</td>
<td>11°40' N, 66°30' W</td>
<td>Weil and Laughlin, 1984</td>
<td></td>
</tr>
<tr>
<td>5.5</td>
<td>St Kitts/Nevis</td>
<td>ESZ</td>
<td>17°05' N, 62°30' W</td>
<td>Wilkins et al., 1987</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Puerto Rico</td>
<td>ESZ</td>
<td>18°15' N, 66°30' W</td>
<td>Appeldoorn, 1988</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Santa Marta, Colombia</td>
<td>SCZ</td>
<td>11°30' N, 74°05' W</td>
<td>Botero, 1984</td>
<td></td>
</tr>
<tr>
<td>4.5</td>
<td>San Andres, Colombia</td>
<td>SCZ</td>
<td>13°00' N, 81°00' W</td>
<td>Garcia-Escobar et al., 1992</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>San Andres, Colombia</td>
<td>SCZ</td>
<td>13°00' N, 81°00' W</td>
<td>Martínez-Pretel et al., 1994.</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>San Bernardo, Colombia</td>
<td>SCZ</td>
<td>09°45' N, 75°50' W</td>
<td>Lagos-Bayona et al., 1996</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Alacranes Reef, México</td>
<td>SCZ</td>
<td>22°30' N, 89°40' W</td>
<td>Pérez-Pérez and Aldana-Aranda, 2002</td>
<td></td>
</tr>
</tbody>
</table>

NZ, Northern Zone; ESZ, Eastern Zone; and SCZ, South Central Zone. Uppercase letters under Locality: N, North and W, West. Authors within each SMS are ordered according to year of publication.
Table 2
Spawning season of *S. gigas* according histological analyses of gonads. Results are grouped according to Subregional Management Structures (SMS) (FAO, 2007)

<table>
<thead>
<tr>
<th>Spawning Duration (months)</th>
<th>Locality</th>
<th>Sampling period</th>
<th>Monthly sample size</th>
<th>SMS</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>St Kitts/Nevis 17°05' N, 62°30' W</td>
<td>June–December 1985</td>
<td>—</td>
<td>ESZ</td>
<td>Buckland, 1989</td>
</tr>
<tr>
<td>12</td>
<td>Boca Chica, Belize 17°45' N, 86°56' W</td>
<td>July–1981; May 1983, except few months June–September</td>
<td>34*</td>
<td>SCZ</td>
<td>Egan, 1985</td>
</tr>
<tr>
<td>3</td>
<td>Banco Chinchorro, Mexico 18°35' N, 87°23' W</td>
<td>June–September</td>
<td>10</td>
<td>SCZ</td>
<td>Gordillo-Morales, 1996</td>
</tr>
<tr>
<td>3</td>
<td>Alacranes Reef, Mexico 22°30' N, 89°40' W</td>
<td>March–November</td>
<td>20</td>
<td>SCZ</td>
<td>Aldana-Aranda et al., 2003a, 2003b</td>
</tr>
<tr>
<td>3</td>
<td>Banco Chinchorro, Mexico 18°46' N, 87°20' W</td>
<td>June–September</td>
<td>20</td>
<td>SCZ</td>
<td>Aldana-Aranda et al., 2003a, 2003b, 2003c</td>
</tr>
<tr>
<td>3</td>
<td>San Andres, Colombia 12°32' N, 81°28' W</td>
<td>February 2003–January 2004</td>
<td>31*</td>
<td>SCZ</td>
<td>This study</td>
</tr>
</tbody>
</table>

*Average of monthly samples.
ESZ, Eastern Zone and SCZ, South Central Zone. Uppercase letters under Locality mean: N, North and W, West. Authors within each SMS are ordered according to year of publication.
of egg-masses in the field, over all the Caribbean region are variable in length, during from 4 to 9 months per year, and frequently spanning from June to September. According to FAO (2007), there is a notorious change in duration of these cycles from high latitudes to the equator. In NZ, the reproductive seasonality extends over a stable and narrow time period of approximately five months, from May to September, while in the ESZ and SCZ, the reproductive cycle extends almost all year long (Table 1). Reproductive cycles based on microscopic analyses of the gonad of S. gigas are few and all are limited to the SCZ but one (Table 2). According to these studies, the spawning season occurs only once per year and last approximately three months, usually from June to August (Table 2), or occurs twice per year, from March to April and in September, as observed in this study (Fig. 5). The spawning season of Queen Conchs in St. Kitts/Nevis, locality belonging to the ESZ, occurs from April to September (Buckland, 1989) and is similar to that reported in this study (Table 2).

Our histological analyses demonstrate that spawning peaks (i.e., releasing of gametes from gonad) perfectly overlapped with the timing of mating, egg-laying behavior, and presence of egg-masses described by other authors working on S. gigas in the same archipelago (García-Escobar et al., 1992; Márquez-Pretel et al., 1994) (Fig. 6). Reproduction occurs between March and April, and in September. Hence, the current fishing season extending from November 1 to May 31 (Resolution 179, from May 5, 1995) does not completely reflect a reliable relationship with the reproductive ebiology of the Queen Conch in San Andres Archipelago as it includes all the first reproductive event of this species in the region (Fig. 6). Even if only 8% of males and 20% of females spawn between March and April, harvesting egg-laying females during the March–April period might hamper the recovery of the population. Considering the time that any individual of S. gigas requires to become an adult, we recommend two lines of action in order to modify the current fishing season: (a) to declare a continuous fishing season from November 1 to March 1 or (b) to declare two fishing seasons: the first one extending from November 1 to March 1, the second one from June 1 to July 31 (Fig. 6). Both strategies are congruent with the biology of the Queen Conch in the Archipelago, but the first one reduces the fishing season to 4 months per year. Despite of all the problems, with a double fishing season fishermen from San Andrés Archipelago should still be able to collect conchs 6 months per year, only one month less than the period established by current regulations, and the resource would be managed more adequately. As the reproductive cycle of the Queen Conch might vary year after year (Stoner et al., 1992), the only way to measure the success of any fishing control is by periodically monitoring the status of the resource. Then, we also recommend that a monitoring plan should be put into action in San Andres Archipelago in order to protect this species, to improve its sustainability through time, and to guarantee the availability of the resource to local fishermen.

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