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## INFLUENCE OF ENVIRONMENTAL FACTORS ON THE REPRODUCTIVE CYCLE OF THE EARED ARK *ANADARA NOTABILIS* (RÖDING, 1798) IN NORTHEASTERN VENEZUELA

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**ABSTRACT** The reproductive cycle of the eared ark *Anadara notabilis* and its relationship with environmental factors was evaluated every 15 days between March 2004 and February 2005 at the northern part of the Peninsula de Araya, Venezuela. Environmental factors measured included temperature, salinity, chlorophyll *a*, and total seston, including the particulate organic matter and particulate inorganic matter fractions. Adult specimens were collected using a net drag and then randomly selected to estimate wet live biomass and dry biomass of soft body tissues. Gonad samples were processed with histological analysis to determine sex ratio, developmental stages, and variations of follicle size. Reproduction in *A. notabilis* was continuous throughout the year, with spawning peaks occurring in June and October, coinciding with the lowest water temperatures. In March, September, and November 2004, specimens attained the highest dry biomass values, whereas lowest dry biomass occurred in June and October 2004. Stepwise regression analyses demonstrated that temperature and particulate organic matter values are the main modulators of reproductive events. When temperature decreased, dribble spawning was detected in this species, possibly inducing a survival strategy whereby the spawning period is extended to increase reproductive success.

**KEY WORDS:** eared ark, *Anadara notabilis*, environmental factors, gametogenesis, Venezuela

### INTRODUCTION

The eared ark *Anadara notabilis* (Röding, 1798) is a bivalve of the Arcidae family inhabiting the occidental Atlantic Ocean, from North Carolina and the Bermudas to northern Uruguay (Lodeiros et al. 1999). The genus *Anadara* is also found distributed in the tropical Pacific Ocean from Mexico to Peru (MacKenzie 2001). In the Caribbean, *A. notabilis* economic importance has grown, which has resulted in an urgent need in improving culture protocols (Gáldamez et al. 2007). In Venezuela in particular, *A. notabilis* has been reported to be abundant in shallow waters, thus representing an important regional fishery resource that includes other bivalve species such as *Arca zebra* and *Pinctada imbricata* (Prieto et al. 1999, Jiménez et al. 2004).

Preliminary surveys of the reproductive biology of the genus *Anadara* were conducted in Malaysia (Pathansali 1966) and Indonesia (Kastoro 1978). From these studies, it is known that *A. granosa* exhibits maximum spawning activity from June through October (Pathansali 1960), whereas *A. antiqua* spawns multiple times throughout the year, with ripe and spent gonads occurring regularly every month (~50%) (Kastoro 1978). In contrast, studies of reproductive biology of *A. notabilis* in the Caribbean and Venezuela are rather scarce and report 2 spawning peaks—one in June through July and the other from October through December (Giles 1984). However, Giles (1984) did not establish the influence of environmental factors on reproductive cycle of the species.

Regardless of the geographical area and species under study, growth and reproduction in marine bivalves is grossly regulated by similar environmental factors, particularly temperature and food availability (MacDonald & Thompson 1985, Baqueiro-

Cardenas & Aldana-Aranda 2000). Temperature, for instance, triggers the start of gametogenesis (Bayne 1985), regulates the differentiation of stem cells into male and female gametes (Bayne et al. 1976), and controls the rate of gamete development and release, as well as resorption of nutrients as a generalized energy budget strategy (Newell et al. 1982, Shpigel et al. 1992). In addition, changes in quantity and quality of phytoplankton species affect growth and reproductive physiology of the animals (Lodeiros & Himmelman 1999, Barber & Blake 1991). In general, the interaction between environmental factors and reproduction of tropical marine bivalves is well documented for species living under different environmental conditions. In contrast, there is a paucity of information concerning the regulation of gametogenesis by the environment in the Arcidae.

This study evaluated the influence of environmental factors on the reproductive cycle of *A. notabilis*, determining temporal changes in the gross condition of animals, gonad developmental stages, sex ratio, and type of reproductive strategy used.

### MATERIALS AND METHODS

#### Collection of Gonad Samples

Adults of *A. notabilis* (76 ± 7 mm; range, 60.02–97.03 mm) were collected twice a month during March 2004 through February 2005 from natural grounds near the Chacopata Peninsula on the northeastern coast of Venezuela (10°43', 10°48' N; 63°49', 55°49' W). The study area is 12 km south of Isla Margarita and 4 km north of the Gulf de Cariaco (Fig. 1). After collecting the specimens with a bottom drag net, they were stored in isotherm containers at 20°C and immediately transported to the laboratory, where they were fully removed from biofouling and other adherences and measured for basic morphometric dimensions,

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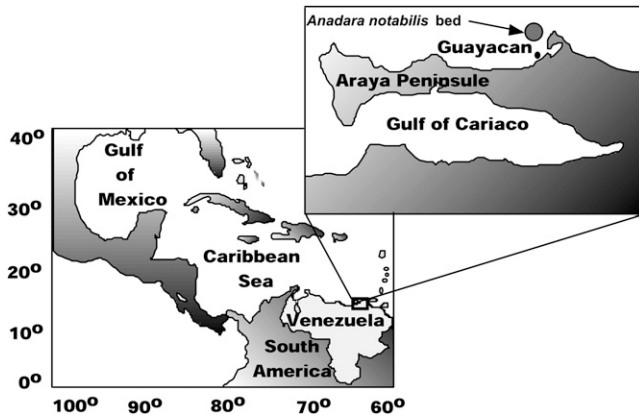


Figure 1. Sampling area of *Anadara notabilis* from the Chacopata Peninsula, north of the Araya Peninsula, Venezuela, 2004 through 2005.

including shell length to the nearest 0.1 mm and wet weight to the nearest gram. Afterward, they were separated into 2 groups of 18 individuals destined for estimating wet and dry tissue biomass and a condition index, and 12 were used for dissection and histological examination of the gonads.

#### Collection of Seawater Samples (Environmental Study)

Every 15 days at the collection site, water temperature ( $\pm 1^\circ\text{C}$ ) and salinity ( $\pm 1$  psu) data were recorded with a YSI-30 device and a hand refractometer (ATAGO Inc, Bellevue, WA). Seawater samples were collected routinely at a 5-m depth using Niskin bottles, the contents of which were transferred to plastic dark containers and transported to the laboratory for determining changes in chlorophyll *a* (Chl *a*) levels. Pigments were extracted using 90% acetone for 24 h, and quantification of Chl *a* was completed according to Strickland and Parsons (1972). Total particulate matter (TPM) was estimated using prewashed and weighed filters glass fiber cartridges (GFC) heated in the furnace for 4 h. Three seawater aliquots were filtered, washed with ammonium formate, and dried in an oven at  $60^\circ\text{C}$  for 24 h. Thereafter, filters were weighed to estimate TPM. Particulate organic matter (POM) and particulate inorganic matter (PIM) were determined by weight difference after heating at  $450^\circ\text{C}$  in a furnace for 4 h.

#### Condition Index

Throughout the study, the entire body tissue biomass (meat) was excised from each specimen, weighed to the nearest 0.01 g, dried in an oven at  $80^\circ\text{C}$  for 72 h, and weighed again. These data were used to calculate a condition index (CI), according to Le Cren (1951):

$$\text{CI} = [100 \times W_{\text{exp}}/W_{\text{st}}]$$

where  $W_{\text{exp}}$  is the total live weight biomass of the animal and  $W_{\text{st}}$  is the total weight of a "standard bivalve." Thereafter, regression analyses between weight versus shell length values of experimental specimens were done based on the formula ( $W = aL^b$ ), where  $W$  and  $L$  are the weight and length of the animals and  $a$  and  $b$  are constants of the length-weight relationship.

#### Histological Analysis

Gonad samples were fixed in buffered formalin solution for 48 h and then rinsed, dehydrated with ethanol, embedded in paraffin, cut at  $5\ \mu\text{m}$ , and stained with Harris hematoxylin and eosin stain (Howard & Smith 1983). Finished slides were observed under light microscopy to determine variations in the sex ratio and stages of female and male development of the gonad. The gonads were classified as either (1) active developing, (2) ripe, (3) partial spawned, (4) spent, and (5) inactive (Sahin et al. 2006). Variations in the diameter of male and female follicles and oocytes ( $0.1\ \mu\text{m}$ ) were determined throughout the annual cycle.

#### Statistical Analysis

The reproductive cycle was evaluated with stepwise multiple regression analyses using the percentage of each reproductive stage as the dependent variable and environmental factors the independent variable. When necessary, tissue biomass data were graphically represented in a logarithmic scale, and reproductive stage percentages were represented in an arcsine scale to obtain maximum regression coefficients ( $r^2$ ). Variations in sex ratios were analyzed by a chi-square test (Zar 1984). For all analyses, the significance level was set at  $P \leq 0.05$ .

## RESULTS

#### Environmental Factors and Their Relation to the Reproductive Cycle

Phytoplankton biomass (Chl *a*) indicated a higher variability throughout the year (Fig. 2A). Biomass values more than  $2.5\ \mu\text{g/L}$  occurred in April and October 2004, with a peak in January 2005 ( $5.45 \pm 1.16\ \mu\text{g/L}$ ). Minimum values occurred in August 2004 ( $0.16 \pm 1.10\ \mu\text{g/L}$ ), October 2004 ( $0.40 \pm 0.08\ \mu\text{g/L}$ ), and February 2005 ( $0.64 \pm 0.16\ \mu\text{g/L}$ ).

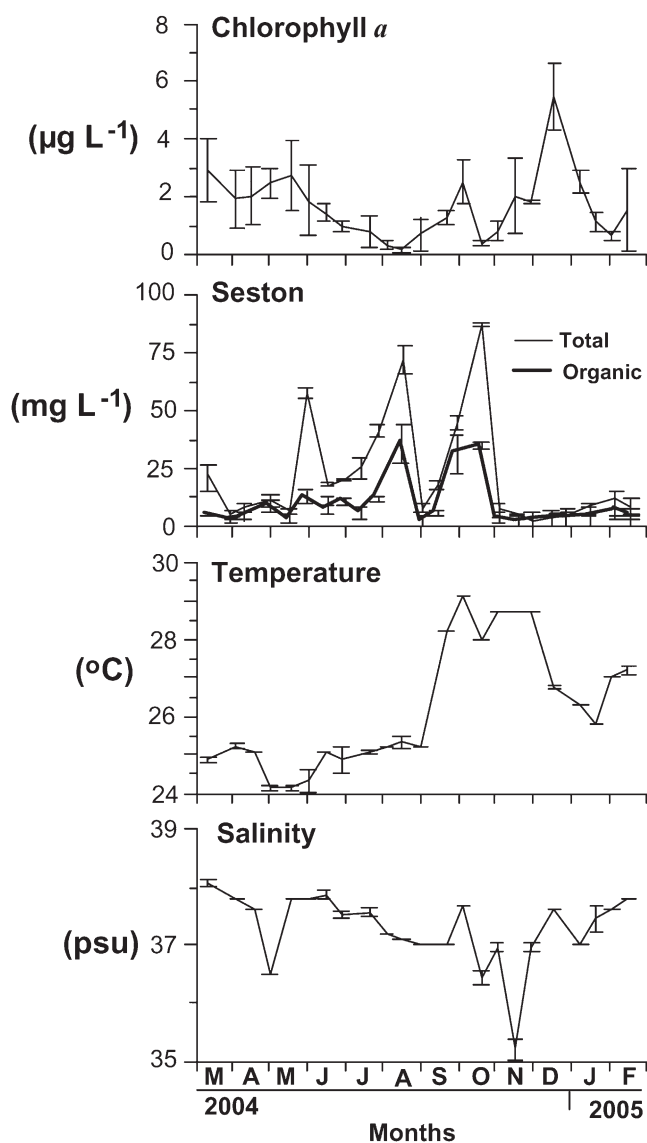
TPM values peaked in May ( $57.74 \pm 1.82\ \text{mg/L}$ ), August ( $72.10 \pm 6.00\ \text{mg/L}$ ), and October 2004 ( $87.23 \pm 0.45\ \text{mg/L}$ ); minimum values occurred in March, September, and from November onward ( $\sim 5\ \text{mg/L}$ ). POM changes (Fig. 2B) showed maximum levels between June ( $36.1 \pm 0.80\ \text{mg/L}$ ) and October ( $31.25 \pm 0.81\ \text{mg/L}$ ) and minimum levels in September ( $2 \pm 1.30\ \text{mg/L}$ ).

From March through August 2004, temperatures were low ( $24\text{--}25^\circ\text{C}$ ), then rapidly increased during the following months and peaked in October, thereafter remaining stable through December ( $28\text{--}29^\circ\text{C}$ ). Subsequently, temperature decreased gradually until mid January and started to increase again thereafter (Fig. 2C).

Salinity oscillated between 35.5–38.0 psu, with a maximum detected at the onset of spring 2004 (38.1 psu) and June 2004 (37.2 psu), and a minimum occurring at the end of autumn in November 2004 (35.2 psu; Fig. 2D).

In the ovary, changes in the POM levels explained 53% of the variance that occurred during gametogenesis. In terms of percentage, these changes are associated with temperature (69%) and TPM (72%) variations (Table 1). In addition, POM and temperature showed an inverse relation with the spawning events and explained 33% and 46% of the variance observed, respectively. The ripe and regression stages were not statistically associated with any environmental factor ( $P > 0.05$ ).

In the testes, 45% of the observed variance can be deduced from changes in the POM content, which occurs during



**Figure 2.** (A–D) Mean monthly variations in environmental parameters at the study area, including chlorophyll *a* (A), seston concentration (B), water temperature (C), and salinity (D).

gametogenesis. In contrast, 52% and 58% of the variance observed can be attributed to increases in Chl *a* and temperature values, respectively. For the ripe stage, changes in the TPM explained 26% of the variance, whereas those of POM and temperature explained, together, 50% of the variance of this reproduction stage, and that of Chl *a*, 57% (Table 1).

#### Condition Index

The CI decreased from March (109.4%) to August 2004 (90.9%), with maximum values from August through October 2004 (115.7–125.6%) and similar values from November 2004 through February 2005 (Fig. 4B).

#### Sex Ratio

Of 240 specimens analyzed, 137 were female (57%) and 103 male (43%), with an annual female-to-male sex ratio of 1.32:1. Sex ratio varied significantly between months ( $P < 0.05$ ), with

**TABLE 1.**

**Stepwise multiple regression analysis of *A. notabilis* females and males, considering gametogenesis and spawning reproductive stages and environmental factors (temperature, chlorophyll *a*, and organic and total seston).**

Parameters	Coefficient	SD	F partial	$r^2$	$P$
<b>FEMALE</b>					
Development					
Constant	-599.334				
Organic seston	41.489	0.404	9.304	0.532	0.003
Temperature	369.911	0.547	25.813	0.689	0.000
Total seston	26.807	0.408	4.158	0.715	0.046
$r^2 = 0.715, n = 60, F_{2,56} = 19.483, P < 0.05$					
Spawning					
Constant	541.575				
Organic seston	-51.882	-0.372	9.803	0.325	0.003
Temperature	-304.399	-0.330	7.752	0.461	0.007
$r^2 = 0.461, n = 60, F_{2,57} = 7.707, P < 0.005$					
<b>MALE</b>					
Development					
Constant	-21.640				
Organic seston	48.600	0.434	15.106	0.450	0.000
Chlorophyll <i>a</i>	-111.301	-0.280	15.106	0.515	0.015
Temperature	202.581	0.274	6.194	0.582	0.016
$r^2 = 0.582, n = 60, F_{2,56} = 9.555, P < 0.005$					
Ripeness					
Constant	5.159				
Total seston	23.376	0.258	4.120	0.258	0.047
$r^2 = 0.258, n = 60, F_{2,58} = 4.120, P < 0.005$					
Spawning					
Constant	515.699				
Organic seston	-56.036	-0.347	9.438	0.349	0.003
Temperature	-405.780	-0.380	11.679	0.496	0.001
Chlorophyll <i>a</i>	164.690	0.287	9.438	0.570	0.014
$r^2 = 0.570, n = 60, F_{2,56} = 8.971, P < 0.05$					

$P$ , statistical significance;  $r^2$ , regression coefficient; SD, standard deviation (SD).

females outnumbering males in March, August, September, and December 2004, and males dominating in May and June 2004 (Fig. 3).

#### Reproductive Cycle

Frequency histograms of female reproductive stages indicate that the ripeness stage was predominant throughout the year (Fig. 4A), with its highest percentage in March 2004 (60%) and the lowest percentage in November 2004 (11%). Similarly, spent gonads occurred almost all the year, with maximums in June (50%) and November (49%) 2004 and minimums at the beginning of November 2004 (14%). Maximum oogenesis was observed at the end of August 2004 (43%) and September 2004 (60%), and February 2005 (50%), whereas the inactive stage occurred at the beginning of November 2004 (71%) and January 2005 (67%; Fig. 4A). A detailed description of female gonad development is presented in Table 2.

Monthly male reproductive stages were similar to those of females. Ripe specimens were observed all year, with maximums occurring during the months of September (80%), May (71%), and October 2004 (67%), with one minimum in February 2005 (20%). The highest frequency of spawned



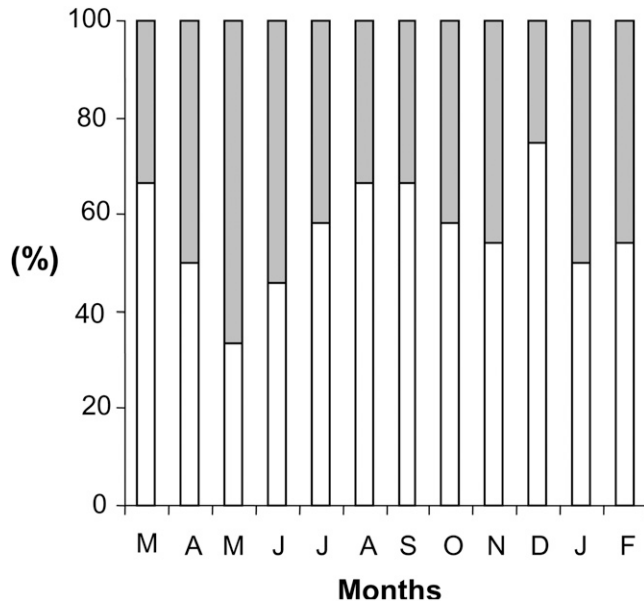


Figure 3. Mean monthly variations in sex ratio of *Anadara notabilis* from the Chacopata Peninsula, north of the Araya Peninsula, Venezuela, 2004 through 2005. ■ Male; □ Female.

specimens occurred in December 2004 (66%) and January 2005 (83%). The lowest frequencies were found in June and July (20%) and October (17%). The developing stage maximum was observed in August 2004 (60%), whereas its minimum was detected in November 2004 and the beginning of January 2005 (17%). The inactive stage was not observed for the male population (Fig. 4B). A detailed description of male gonad development is presented in Table 2.

#### DISCUSSION

In this study, POM and temperature were the main environmental regulating factors of reproduction in *A. notabilis* (Table 1). Changes in the POM content, particularly in May, July through August, and September through October were associated mostly with strong winds, which are reported to increase wave height (Okuda et al. 1978). This result is in agreement with findings by Narváez et al. (2000), who claimed that gametogenesis in bivalve species of tropical distribution such as *Pinna carnea* rely more on food availability than on water temperature. In contrast, most biological processes of temperate distributed species (e.g., *Pecten maximus*) are affected primarily by temperature and, second, by flow rate, rather than availability of food (Wilson 1987, Chauvaud et al. 1998).

During gonad development, there were significant differences in the female-to-male sex ratio throughout the year, which were slightly skewed toward female. Similarly, there were clear differences in the occurrence of female versus male gonad development stages, particularly for the ripe and spawning stages occurring during March and November (for females) and May, September, and October (for males). Previous studies of sex ratios close to unity have been reported for other members of the *Anadara* genus, including *A. granosa* (Pathansali 1966, Broom 1983, Broom 1984), *A. broughtoni* (Dzyuba & Maslennikova 1982), *A. tuberculosa* (Cruz 1984b), *A. similis* (Cruz 1984a), *A. notabilis* (Giles 1984), *A. antiquata* (Toral-Barza & Gomez 1985),

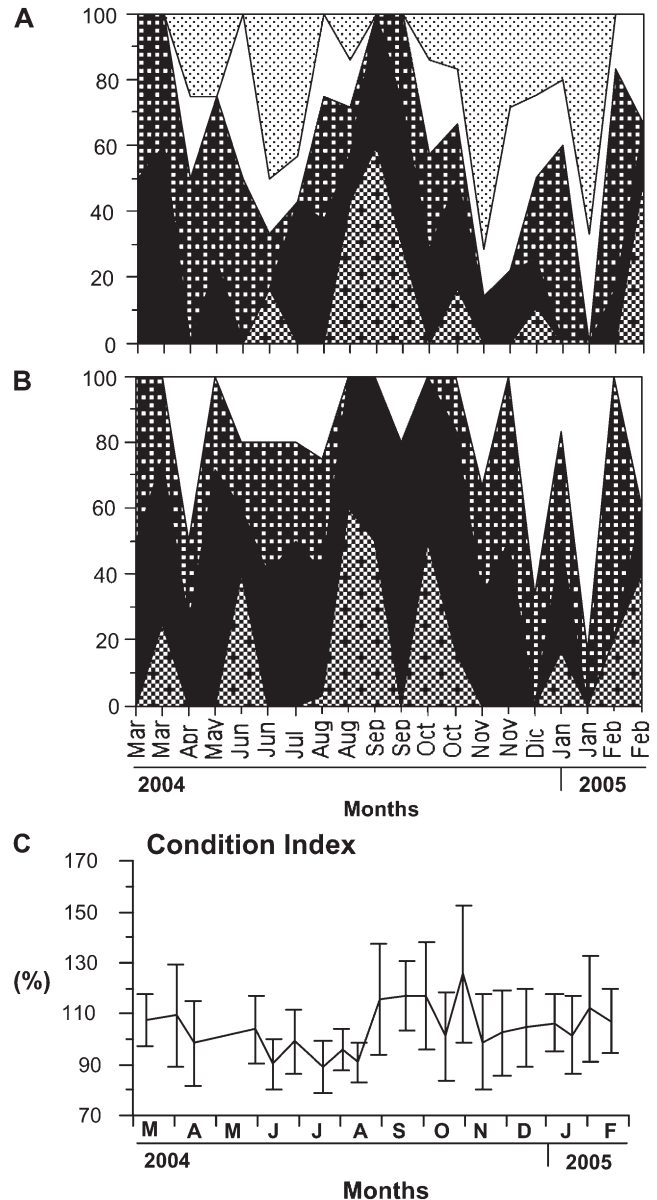


Figure 4. Relative percentages of gonad developmental stages of *Anadara notabilis* from the Chacopata Peninsula, north of the Araya Peninsula, Venezuela, 2004 through 2005. (A) Females. (B) Males. (C) Condition index. ■ Regression; □ Spent; ■ Partially spawned; ■ Ripe; ■ Active development.

*A. ovalis* (Power et al. 2004), and *A. inaequivalis* (Sahin et al. 2006). There are, however, contradicting results concerning sex ratios and the expression of maleness and femaleness in other Arcidae. For example, female populations dominate over male populations during reproduction in *A. senilis* in Africa (Yoloye 1974), *A. transversa* in Georgia (Walker & Power 2004), *A. antiquata* (Kastoro 1978), and *Arca noae* (Peharda et al. 2006), confirming the typical protandric sex reversal behavior (Mzighani 2005; Peharda et al. 2006). In contrast, sex ratio in *A. ovalis* showed marked dominance of males over females in temperate waters (Power et al. 2004, Power & Walker 2002). For other bivalve species, such as the pearl oysters *Pinctada mazatlanica* and *Pinctada margaritifera*, it was reported that female-to-male sex ratios are close to the unit when the animals are collected from the

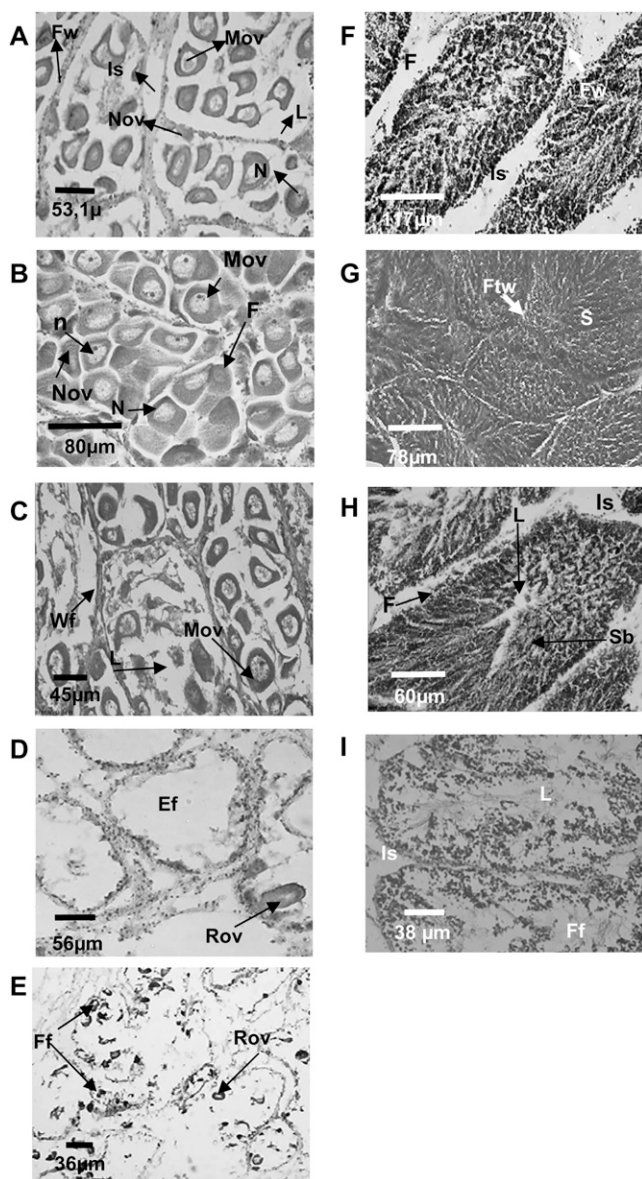


Figure 5. Gonad photomicrographs of *Anadara notabilis*, including females (A–E) and males (F–I). (A) Active development showing. (B) Ripeness presenting. (C) Partial spawning. (D) Spent. (E) Inactive stage. (F) Male active development. (G) Ripeness. (H) Partial spawning. (I) Spent stage. Ef, empty follicle; F, follicle; Ff, fragment follicle; Ftw, follicle with thick walls; Fw, follicle wall; Is, interfollicular space; L, lumen; Mov, mature oocytes; N, nucleus; n, nucleoli; Nov, nonmature oocytes; Rov, residual oocyte; S, spermatocytes; Sb, spermatocyte band.

wild, but tend toward dominance of maleness over femaleness under culturing conditions (Saucedo & Southgate 2008). According to Saucedo and Southgate, high stocking densities generate stressful conditions that favor the channeling of more energy reserves to produce the sex that is energetically cheaper: male.

*A. notabilis* experienced continuous reproduction throughout the year, including several spawning events in male and female gonads. This behavior represents the typical pattern of reproduction in tropical areas, where species adopt opportunistic strategies to build up their gonads from energy available from food rather than from energy stored within somatic tissues

(Bayne 1973, Baqueiro-Cardenas & Aldana-Aranda 2000). Similar opportunistic patterns have been reported for other bivalve species, including *P. perna* (Prieto et al. 1999) and *P. viridis* (Gúzman 2004). In addition to this pattern, we observed that gonad development proceeded more actively during the 2 periods of decreasing temperatures: one from March through July (26–25°C) and the other from August through November (29°C to 26°C). These suggest an inverse relation between water temperature and gametogenesis, and contradict previous findings by Giles (1984) that high CIs and ripest gonads in *A. notabilis* from the Gulf of Cariaco (North Venezuela) occurred at moments of decreasing phytoplankton concentration and increasing water temperature. The result, however, is consistent with data reported for other bivalve species exhibiting maximum reproductive activity at moments of decreasing water temperature. This is true for *Nodipecten nodosus* from the Chacopata populations in Venezuela (García et al. 2007) and *Pteria sterna* from Bahía de La Paz, Mexico (Saucedo & Monteforte 1997). Differences between these studies are relevant and cannot help confirm if gametogenesis in *A. notabilis* was supported from food intake (as a typical opportunistic behavior) or from stored reserves (as a conservative strategy).

Similar to *A. notabilis*, other tropical species (e.g., *Crassostrea rhizophorae*, *P. perna*, *P. viridis*, and *Arca zebra*) may take advantage of high food availability during the upwelling season that occurs from January through May to activate and sustain gametogenesis (Vélez 1977, Prieto et al. 1999, Lista et al. 2006). According to their latitudinal distribution, it is known that most bivalve species use different strategies for allocating acquired energy for reproduction (Bayne 1973). For example, when water temperature decreases and seston concentration increases in winter, some species follow a conservative strategy for allocating energy from reserves previously stored in somatic tissues. This is true for *P. fucata* in India (Desay et al. 1979), *P. mazatlanica* and *P. sterna* from Bahía de La Paz, Mexico (Saucedo & Southgate 2008), and the cockle *Cerastoderma edule* from northern Spain (Navarro et al. 1989). In contrast, when productivity increases in spring, other species adopt an opportunistic strategy for sustaining gametogenesis from food energy, as reported for the cockle *Glycymeris glycymeris* (Galap et al. 1997). Other species, however, are able to combine conservative and opportunistic strategies during reproduction. This is true for *Mytilus galloprovincialis* (Villalba 1995), *Argopecten ventricosus* (Racotta et al. 1998), and *C. gigas* (Kang et al. 2000).

Different from the synchronicity observed for overall development of the gonad, *A. notabilis* showed asynchrony in these stages within the same gonad sample. This pattern is typical of bivalves inhabiting geographical regions experiencing little seasonal fluctuations in water temperature, such as in the tropics and marine deep waters (Giese & Pearse 1974). In *A. notabilis*, male development of the gonad, with the exception of the spent stage, was continuous throughout the year, and specimens passed from the spawning stage to the active development stage without any evident pause. This result confirms the existence of short-term reproductive cycles occurring after a massive population spawning when environmental conditions are still suitable. Dribble spawning has also been reported in bivalve species such as *N. ponderosa* and *A. ovalis* (Power et al. 2004, Power et al. 2005), and *P. mazatlanica* (Saucedo & Southgate 2008) as a strategy to extend the spawning period and increase reproductive success.

TABLE 2.  
Description of developmental stages of oogenesis and spermatogenesis in *Anadara notabilis*.

Stage	Ovary	Testis
Resting	Also called inactive, undifferentiated, or stage 0. There is no trace of gonad development and specimens are unable to be sexed. It was not observed in this study.	
Active development	Follicles are filled with oogonia and developing oocytes anchored to the follicle wall, and display a broad range of sizes and irregular shapes. Some ripe oocytes with a large nucleus may be seen free in the lumen. Mean follicle diameter is $85.6 \pm 17.5 \mu\text{m}$ and mean oocyte diameter is $18.54 \pm 1.93 \mu\text{m}$ (Fig. 5A).	Follicles start to grow and enlarge, and connective tissue reduces. Starting from the outer layers to the center, all developmental stages are present: spermatogonia, abundant spermatocytes, smaller spermatids, and ripe spermatozoa with their pink tails (Fig. 5F).
Ripeness	Follicles are large, distended, and filled with free, polyhedral-shaped, ripe oocytes with a large nucleus and a small nucleolus. The interfollicular space decreases. Few oogonia and immature oocytes are still attached to the follicle wall. Mean follicle diameter is $146.2 \pm 28.9 \mu\text{m}$ ; mean oocyte diameter is $20.43 \pm 1.55 \mu\text{m}$ (Fig. 5B).	Follicles are enlarged and stratified. The dominant stage now is the spermatozoa, which strongly pack the follicle. Spermatogonia are restricted to a thin layer at the periphery of the follicle. Only a small amount of connective tissue is present. Mean follicle diameter is $138.6 \mu\text{m} \pm 31.7$ (Fig. 5G)
Partial spawning	Oocytes are expelled. Follicle walls look broken and empty, but still distended. Much residual material is seen. Some types of phagocytes appear in the space between the free residual oocytes, which now look rounded. Mean follicle and oocyte diameter are $146.2 \pm 28.9 \mu\text{m}$ and $15.83 \pm 3.15 \mu\text{m}$ , respectively (Fig. 5C).	Gamete release starts. Follicles show small, empty spaces with many free residual spermatozoa. Mean follicle diameter is $153.1 \pm 33.4 \mu\text{m}$ (Fig. 5H). Some follicles have irregular shapes with contracted membranes and a smaller diameter ( $125.6 \pm 32 \mu\text{m}$ ; Fig. 5I).

The eared clam *A. notabilis* from the Chacopata grounds has growing economic importance in northern Venezuela. The species exhibited continuous development throughout the year, which was regulated mostly by water temperatures and high POM concentrations. Gonad histology was the best predictor of reproductive activity, including spawning events and

sex expression. Despite this, we recommend that biannual studies of reproduction of this species be conducted to develop a broader understanding of its reproductive strategies based on interannual variations. This information can also help propose managing protocols of this species for aquaculture-based ventures.

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