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Particular features of gonadal maturation and size at first maturity in *Atrina maura* (Bivalvia: Pinnidae)

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SUMMARY: The gonadal maturation of *Atrina maura* was examined by means of histological analysis and quantitative criteria. Particular features not previously described for this species are reported in this study: in both males and females the undifferentiated stage is absent and there is massive gamete resorption when the seawater temperature reaches 25°C; in males, there is continuous spawning concurrent with other gonadal development stages and the adipogranular cells surrounding the acini walls decrease with testis ripeness, which suggests they play an energetic role. Atresia displayed two stages: cytoplasmic structures with oocyte degeneration and digestion by hemocytes. The oocyte diameter was larger than that reported for cultured specimens. Size at first maturity was reached at 23.3 cm in shell height (SH) (12.2 cm in shell length, SL) in females and 22.8 cm SH (12.0 cm SL) in males.

Keywords: reproduction, resorption, adipogranular cells, size at first maturity.

RESUMEN: Aspectos particulares de la maduración gonádica y talla de primera madurez de *Atrina maura* (Bivalvia: Pinnidae). – Se analizó histológicamente y usando criterios cuantitativos el proceso de maduración gonádica de *Atrina maura*. Se reportan características particulares que no han sido descritas previamente para la especie: ausencia de la fase de indiferenciación y reabsorción masiva de gametos, tanto en hembras como en machos, cuando la temperatura del agua alcanza los 25°C; en los machos presencia de eyaculación continua simultánea con otras fases de desarrollo gonádico y células adipogranulares arregladas alrededor de las paredes de los acinos que disminuyen conforme avanza la maduración, sugiriendo un papel energético. La atresia presentó dos fases: estructuras citoplasmáticas con degeneración ovocitaria y digestión por hemocitos. El diámetro de los ovocitos fue mayor que los reportados para organismos de cultivo. La talla de primera madurez para las hembras se estableció en 23.3 cm de altura de la concha (AC) (12.2 cm de longitud de la concha, LC) y para los machos en 22.8 cm de AC (12.0 cm de LC).

Palabras clave: reproducción, reabsorción, células adipogranulares, talla de primera madurez.

INTRODUCTION

Pinnids, commonly called fan mussels or pen shells, are considered a delicacy in many countries (including Mexico and particularly in Asia). *Atrina maura* is found in littoral sand and mud habitats forming dense aggregations and is widely distributed along the temperate and tropical coasts of the east Pacific from Baja California Sur, México (including Gulf of California) to Peru.

Some species of the Pinnidae family have declined worldwide or are seriously threatened, which justifies including them in the listing of fully protected species (Cabanellas-Reboredo *et al.* 2009). Despite this, it is not yet the case for *A. maura* in Mexico, the catches of this species are increasing and there is no fishery management regulation.

As a result of the growing commercial demand for species of the Pinnidae family, most studies on these bivalves have focused on fishery assessment and development of mass culturing techniques (Kennedy *et al.* 2001, Lora-Vilchis *et al.* 2004, Safi *et al.* 2007). Relatively few studies have addressed taxonomic,

ecological, and physiological aspects of the species in this family (Butler *et al.* 1993, De Gaulejac *et al.* 1995, Urban 2001, Beer and Southgate 2006, Idris *et al.* 2008). The available information on *Atrina maura* mainly deals with the standardization of culturing techniques (Cardoza-Velasco and Maeda-Martínez 1997) and reproductive aspects in cultured organisms or under laboratory conditions (Rodríguez-Jaramillo *et al.* 2001, Enríquez-Díaz *et al.* 2003). In contrast, few investigations have been carried out on natural populations (Soria 1989, Ahumada-Sempoal *et al*. 2002, Ángel-Pérez *et al.* 2007, Ángel-Dapa *et al.* 2010).

Field observations usually provide the most reliable information about the onset of reproduction and the timing of spawning. However, observing spawning bivalves in nature is extremely difficult. On the other hand, observations of spawning under laboratory or experimental conditions have little meaning and might lead to dubious conclusions about the timeline of reproduction under field conditions. Therefore, microscopic analysis of gonads of wild specimens results in far more reliable information (Seed 1976).

In bivalves, histological analyses of gonadal tissue of individuals collected at regular intervals provide the most reliable method for determining seasonal gonadal changes. The timing of spawning and the percentage of spawning individuals in a natural population can also be determined with this method, which is useful for predicting the occurrence of seed settlement for use in aquaculture and for establishing fishery management measures (Brousseau 1987, Jaramillo and Navarro 1995, Alfaro *et al.* 2001). Moreover, studies that include direct sampling of wild populations may reveal histological, biochemical or metabolic changes that will lead to a deeper understanding of reproduction, and thus better management and optimization of bivalve production.

Determining gonadal development, size at first maturity and morpho-physiological indices not only improves the knowledge on these organisms but also provides monitoring tools. The size at first maturity is used to establish the minimum landing size, an important parameter for regulating fishing effort in many species. The minimum landing size should be larger than the size at first maturity to guarantee that the individuals can reproduce at least once, thus ensuring a parental stock that is large enough to maintain the population. Likewise, determining the reproductive season, the patterns of gonadal development and the type of spawning are also keys for broadening the knowledge on the species biology, and are also essential for further studies on fecundity and egg viability. Finally, information on the seasonality of the reproductive process and the factors affecting it (particularly seawater temperature and food availability) provides basic elements for fisheries management as well as for designing artificial environments for managing reproduction.

This study describes some histological features of the gonadal maturation of *A. maura* and investigates the relationship between gonadal maturation and seawater temperature in Ensenada de La Paz, B.C.S., Mexico. In addition, the size at first maturity is assessed for this species.

MATERIALS AND METHODS

Study area and sampling

Ensenada de La Paz (24°06'N-24°11'N and 110°19'W-110°26'W) is a shallow coastal lagoon (<10 m deep) located in the southern area of La Paz Bay in the Gulf of California, Mexico. This is the main *A. maura* fishing area inside the bay and one of the five fishing regions in the state of Baja California Sur. During 2008, 20-30 adult specimens of *A. maura* were collected monthly at depths from 3 to 8 m by semi-autonomous diving between 8:00 and noon. Seawater temperature at the time of sampling was recorded to the nearest 0.01°C with a BKPrecision 710 digital temperature meter. In the laboratory, the epibionts were cleaned off the specimens and the shell height (SH, in line straight distance from umbo to ventral margin of the shell) and shell length (SL, in line straight distance from anterior margin to posterior margin of the shell) were measured (±1 mm), as well as the total weight (TW) and flesh weight (FW) (±0.1 g). The visceral mass and adductor muscle were removed and their individual weights (VW and MW respectively) were also recorded (±0.1 g).

Sex ratio and size at first maturity

Since *A. maura* lacks sexual dimorphism, specimens were sexed through microscopic analysis of the gonads and the sex ratio was calculated monthly. In addition, the size at first maturity for each sex was estimated using Somerton's method (1980). Relative frequencies and cumulative relative frequencies for 1 cm size intervals were computed, and the latter was fitted to a logistic model from which the size at which 50% of the individuals are sexually mature was estimated. The estimate was based on the entire set of specimens sampled, since all showed evidence of gamete development. Both the SH and SL were considered as SH is biologically significant and SL is relevant for fisheries management.

Histological analysis and condition indices

Since *A. maura* has a diffuse gonad (the gonad infiltrates the digestive gland forming the visceral mass), a portion of the visceral mass containing gonadal tissue was extracted from each specimen and fixed in 10% formalin. A conventional histological technique was used (Humason 1979), consisting in dehydration through a sequence of alcohol solutions of increasing concentrations, followed by clearing with Hemo-De® and embedding in Paraplast-Xtra®. Sections 5 μm thick

were cut, stained with haematoxylin-eosin and examined under a light microscope.

The initial characterization of the gonadal development stages followed the proposal by Rodríguez-Jaramillo *et al*. (2001) for this species: early activity, development, late activity, maturity, spawning and post-spawning. These stages were modified based on acinus size, shape and extent of development; gamete occurrence and extent of development; gamete location in acini; oocyte size, and amount of connective tissue. In males, the presence of adipogranular cells (AGC) was also registered; these cells were identified by staining with Black Sudan. To support the assigned development stages with quantitative criteria, histological sections from 18 females and 18 males (six for each development stage detected in this study) were digitized and analysed using the software SIGMA SCAN PRO (V. 5.0, Systat Software, Inc.). In the ovaries of each studied female, the diameters of all oocytes found within 20 acini were measured. Afterwards, the proportion of each oocyte type per ovarian development stage was calculated. Oocytes were classified according to the four categories described by Rodríguez-Jaramillo *et al*. (2001) and Enriquez-Díaz *et al*. (2003) based on their extent of development: oogonia, previtellogenic oocytes, vitellogenic oocytes and post-vitellogenic oocytes. In males, the surface area occupied by AGC was measured in each testicular development stage. In both sexes, gonads undergoing gamete resorption were not considered quantitatively because this process affects the integrity of the gonadal tissue. The ovaric cycle in *A. maura* was determined considering the different development stages identified through histological analysis and their sequence in the ovarian ripeness.

In addition, monthly variations in the Condition Index (CI=FW/TW×100) and Muscle Yield Index (MYI=MW/FW×100) were examined.

Reproductive cycle

In order to describe the reproductive cycle, monthly relative frequencies of each gonadal development stage were calculated and plotted. To assess the effect of seawater temperature on the reproduction of *A. maura*, the relationship between temperature and the reproductive cycle was examined.

Statistical analyses

One-way ANOVA was used to examine the relationship between gonadal development stages and the frequency of different oocyte types or the percent area occupied by AGC. One-way ANOVA was also employed to examine monthly variations in CI and MYI. When the analyses of variance detected a statistically significant effect, *a posteriori* multiple comparison tests (Tukey) were conducted. Variables expressed as a frequency (%) were arcsine transformed (Zar 1996) to reduce the dependence of sample variances on the means and to normalize the data distribution. However, results are expressed as untransformed means and standard errors. All statistical analyses were performed using the software STATISTICA for Windows (Versión 6.0, Statsoft). Differences in sex ratios were tested using an χ^2 test with Yates' continuity correction (Zar 1996). A significance level of α=0.05 was set in all tests.

TABLE 1. – Size and weight (mean ± SE, range) of the whole female and male *Atrina maura* sample studied.

	Females	Males	ANOVA
Shell height (cm)	24.0±0.17 (19-28.1)	23.5±0.25 (16-28.2)	P=0.09
Shell length (cm)	13.1±0.13 (10-16.2)	12.9±0.15 (8.9-16.2)	P=0.35
Total weight (g)	282.9±8.34 (113.2-521.6)	290.9±11.45 (75.8-576.8)	P=0.57

RESULTS

Biometric analyses, sex ratio and size at first maturity

A total of 226 individuals, 52% females and 48% males, were examined. The overall sex ratio was 1.06F:1.00M. The sex ratio was significantly different (χ^2, P<0.05) from parity (1:1) only in February (3.00F:1.00M). The size and weight of specimens did not display significant differences between sexes (ANOVA, P>0.05) (Table 1).

Size at first maturity was reached at 23.3 cm SH and 12.2 cm SL (r^2=0.99) in females, and 22.8 cm SH and 12.0 cm SL (r^2=0.99) in males (Fig. 1). Nevertheless, mature females with a 19 cm SH (10 cm SL) and mature males as small as 16 cm SH (8.9 cm SL) were observed.

Gonadal development

Microscopic examination of gonads revealed the presence of gametes in different developmental stages in the same individual and even within individual acini. It was possible to determine that gamete production is continuous, particularly in males, while spawning is partial. The diameter of the 6618 oocytes measured changed with the extent of development. Oogonies measured between 7.0 and 20.8 μm (12.5±0.19 SE) and previtellogenic oocytes measured between 12.7 and 46.2 μm (27.9±0.33). Vitellogenic oocytes ranged between 23.7 and 56.5 μm (40.7±0.29), and postvitellogenic oocytes ranged between 29.4 and 56.0 μm (41.6±0.29).

Some features observed in the gonadal development of *A. maura* had not been previously described for this species. In females, ovaries that had started releasing oocytes and at the same time contained developing gametes (previtellogenic oocytes) adhered to the acinus walls were observed, thus indicating continuous gam-

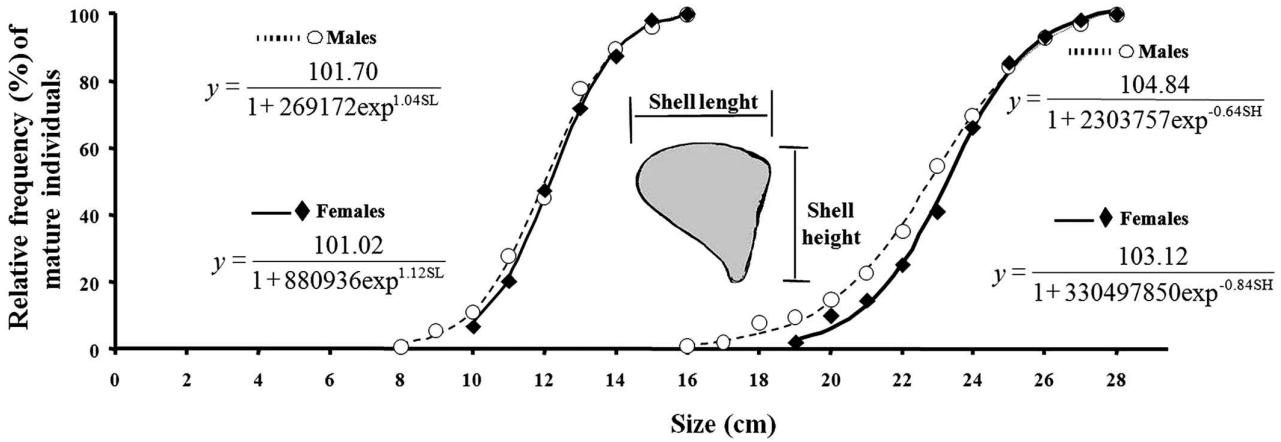

FIG. 1. – Size at first maturity for males and females of *Atrina maura* in Ensenada de La Paz, Mexico. Fitted models are included.

ete production and releases (Fig. 2). In males, most testes with spermatogenetic activity (gamete production) showed areas with clear evidence of gamete release (joint acini with abundant spermatozoids and partly emptied evacuating ducts). Continuous gamete production and releases (spawning with spermatic activity at the same time) was more persistent in males, only eight testes (of individuals measuring between 22.0 and 26.2 cm SH) showed no sperm development but contained abundant spermatozoids, apparently being released (Fig. 3). An interesting feature that persisted throughout the testicular development was the presence of a large amount of adipogranular cell-shaped structures surrounding the vesicular cells in each acinus (Fig. 4).

Massive lysis with deterioration and loss of acinus integrity was noted in both ovaries and testes (Fig. 5). This process was observed in 44 females (24.2±2.0 cm SH) and ten males (26.6±1.4 cm SH) and its frequency is described below as gamete resorption. These gonads displayed a large amount of mature atresic gametes (post-vitellogenic oocytes or spermatozoids). Numerous phagocytes (macrophage hemocytes) contributing to gamete lysis were observed both inside and between acini. Connective tissue invading the gonad was also observed.

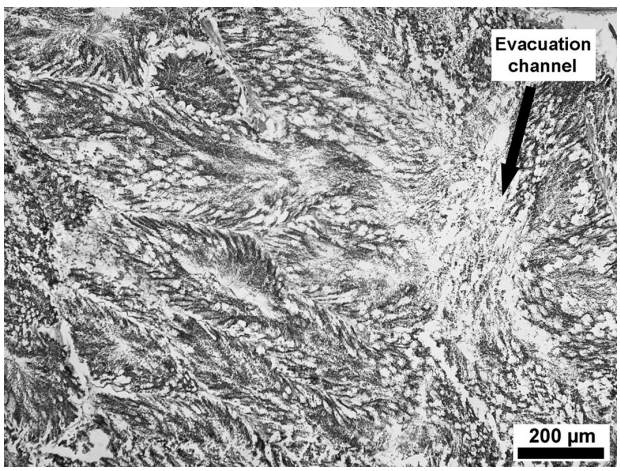

FIG. 3. – Photomicrograph of a spawning testis of *Atrina maura* with no evidence of sperm development.

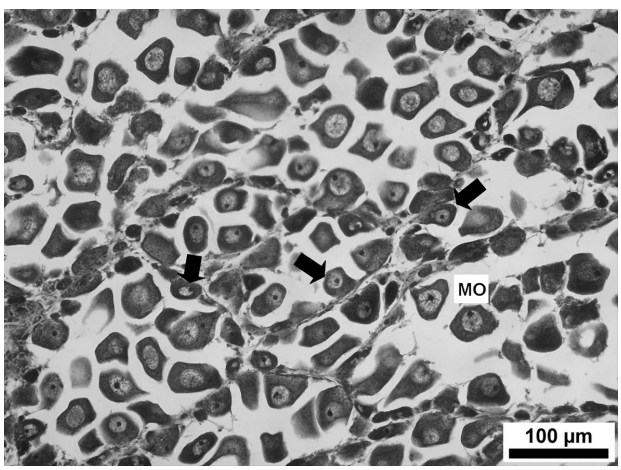

FIG. 2. – Photomicrograph of a spawning ovary with new development in *Atrina maura*. Arrows indicate some developing oocytes attached to acini wall. MO, mature oocytes.

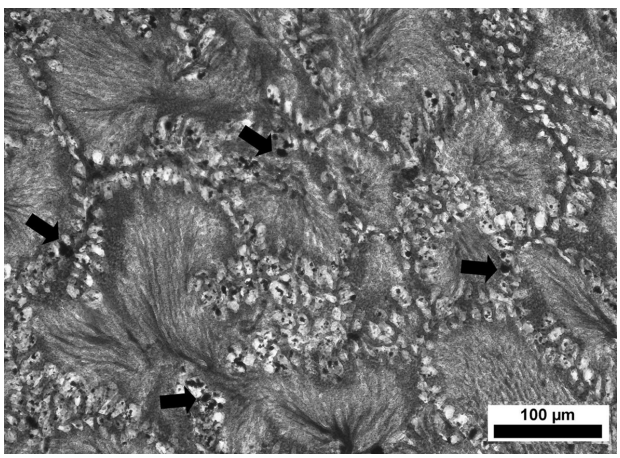

FIG. 4. – Photomicrograph of adipogranular cells (AGC) during testis development in *Atrina maura*. AGC (white cells) are evidenced by the lipid accumulations (black points, Sudan B stain), some of them are indicated by arrows.

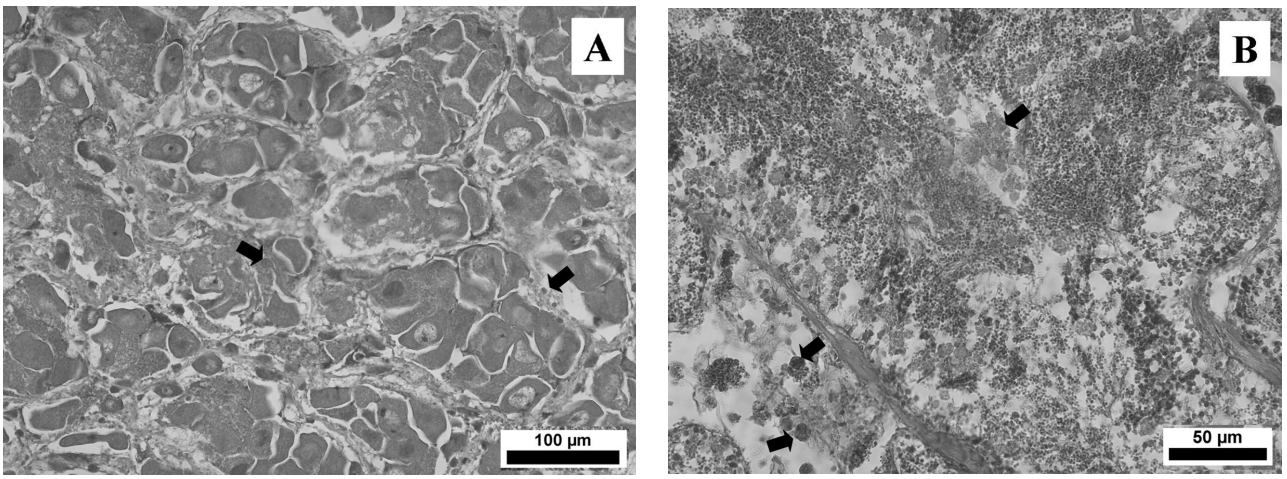

FIG. 5. – Photomicrograph of massive lysis (resorption) in gonads of *Atrina maura*: A) Ovary and B) Testis. Arrows indicate the presence of phagocytes.

Considering both our observations (described above), and the observations of gametogenic development reported for this species by other authors, three development stages were identified (Table 2) and no undifferentiated individuals were found. In females, these stages were: development, ripe and spawning. In males, since all specimens showed evidence of spawning but at the same time had gametes in different development stages, the definition of stages also considered these features: type-1, type-2 and type-3 spawning stages. In addition, in both sexes the resorption process was also considered as part of the reproductive cycle, since in some months all specimens were in gonadal resorption. Given that gamete production in *A. maura* was continuous, it was difficult to differentiate between gonads with advanced development and ripe gonads. Then, a given ovary was considered to be in the development stage when no post-vitellogenic oocytes were observed, whereas a testis was classified as type-1 spawning when the area occupied by AGC was higher than 15% and with evident spermatogenic activity.

The analysis of the frequency of occurrence by oocyte type and of percentage area occupied by AGC further confirmed the gonadal development stages identified in both sexes from histological observations. In females, the frequency of the different oocyte types changed significantly with the extent of ovarian development (ANOVA, $P<0.05$) (Table 3). The amount of oogonia was significantly higher in the development compared to the ripe stage; however, the spawning

TABLE 2. – Description of gonadal development stages in *Atrina maura*.

Females	Males
Development. Numerous oogonia and previtellogenic oocytes attached to acini walls. Presence of some oocytes entering the vitellogenic phase, evidenced by the increase in cytoplasmic surface area. In more developed ovaries, vitellogenic oocytes appear free in the lumen but postvitellogenic oocytes are never observed. Acini are found surrounded by connective tissue with little space between them.	**Type 1 Spawning**. Zones evidencing ongoing gamete release are visible: groups of acini and accumulation of spermatozoids, as well as emptying ducts. Evident stratification of gametes with different degrees of development. At the onset of this phase, thick layers of spermatogonia and spermatocytes occur in acini walls. As development progresses, spermatogonia become less abundant and the amount of spermatocytes, spermatids and spermatozoids increase. Presence of a large amount (>15% of gonad area) of adipogranular cells (AGC) between acini.
Ripe. Acini practically filled with free post-vitellogenic oocytes in the lumen. Because of their abundance, those oocytes acquire a polyhedral shape. Some previtellogenic oocytes attached to acini walls. Reduction of connective tissue without space between acini.	**Type 2 Spawning**. Zones evidencing ongoing gamete emptying are present. Acini filled with spermatozoids, with their flagella pointing towards the lumen. Layers of spermatogonia and spermatocytes have thinned and spermatogenetic activity continues. Presence of adipogranular cells (AGC) between acini (<15% of gonad area). Connective tissue barely evident.
Spawning. Partially empty acini, with variable amounts of post-vitellogenic oocytes depending on the progress of spawning. In some ovaries previtellogenic oocytes are present attached to the acinus walls, indicating the onset of a new development or rematuration. Connective tissue is evident, with a large space between acini.	**Type 3 Spawning.** Decrease in the number of spermatozoids in the centre of acini. Presence of emptying ducts. Some acini appear virtually empty, while others are still filled with spermatozoids. No spermatogenetic activity. Presence of adipogranular cells (AGC) between acini (<15% of gonad area). Connective tissue barely evident.
Resorption. Gonads show the same micro- and macroscopic characteristics than in the ripe stage, but contain large amounts of mature gametes undergoing lysis. Cellular degeneration is evident due to the loss of basic structural characteristics: deterioration of nuclei and breakage of plasma and vitelline membranes. Numerous phagocytes can be observed inside and between follicles.	

TABLE 3. Percentage occurrence (mean ± SE) of different oocyte types by phase of ovarian development in 18 females of *Atrina maura.* In rows, values with different letters are significantly different.

Oocyte type	Ovarian development phase			
	Development	Ripe	Spawning	ANOVA
Oogonia	16.3±2.8[b]	3.0±1.5[a]	10.0±3.2[ab]	P=0.022
Previtellogenic	43.3±10.3[b]	11.1±3.2[a]	27.4±4.1[b]	P=0.006
Vitellogenic	40.4±7.5[b]	6.4±2.2[a]	9.2±2.3[a]	P=0.004
Post-vitellogenic	0±0[a]	79.5±6.5[b]	53.5±5.2[b]	P<0.001

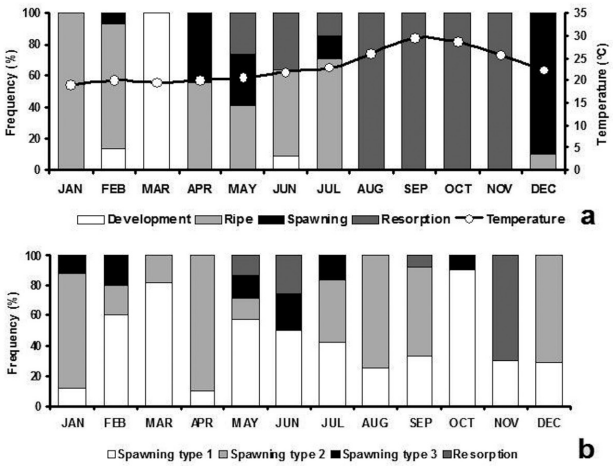

FIG. 6. – Seawater temperature variation in Ensenada de La Paz and reproductive cycle of *Atrina maura* females (a) and males (b).

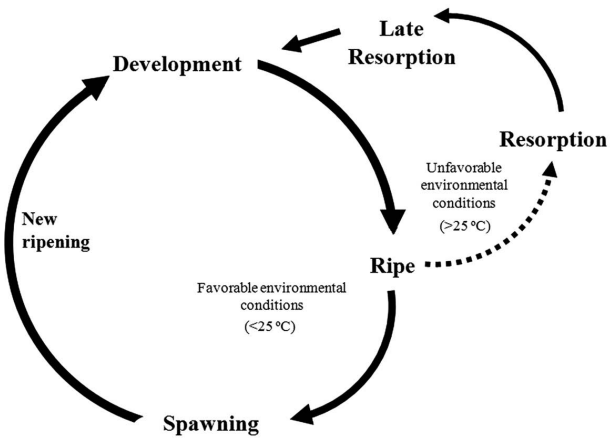

FIG. 7. – Schematic illustration of the ovaric cycle of *Atrina maura* in Ensenada de La Paz, Mexico.

stage did not significantly differ from the other stages in terms of oogonia frequency. However, previtellogenic oocytes were significantly more abundant during the development and spawning stages than in the ripe stage. The frequency of vitellogenic oocytes during the development stage was significantly higher than in the ripe and spawning stages. Finally, post-vitellogenic oocytes were more abundant in the ripe stage than in the spawning stage but the difference was not significant.

In males, the area occupied by AGC changed with the development stage. These structures were significantly more abundant (ANOVA, P<0.05) at the beginning of development (type-1 spawning stage: 21.10±3.76) and, although they decreased as ripening progressed, AGC remained throughout the entire gonadal cycle (type-2 spawning stage: 4.62±1.52; type-3 spawning stage: 8.31±4.03).

Reproductive cycle

The reproductive cycle of *A. maura* and the variation in seawater temperature in Ensenada de La Paz are shown in Figure 6. The seawater temperature had a seasonal variation with the lowest values from December to June (21.6-23.7°C) and the highest values from July to November (25.5-30.4°C) (Fig. 6a). A reproductively inactive period (resting phase) evidenced by the presence of undifferentiated individuals could not be identified. Ripe females were found from December to July with peak abundance in January and February (>80%). Spawning occurred from February to July and peaked in December (90%) (Fig. 6a). In males, spawning with different degrees of new ripening was observed throughout the study period (Fig. 6b).

In females, gamete resorption occurred in low percentages (between 14% and 36%) from May and throughout July; however, this condition appeared in all specimens observed from August to November, coinciding with the highest seawater temperatures (>25°C). Males also had gonads undergoing gamete

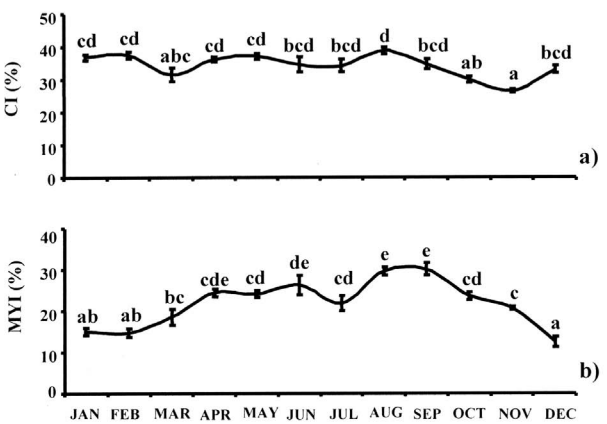

FIG. 8. – Monthly variations (means ± SE) in: a) Condition Index and b) Muscle Yield Index for combined male and female individuals of *Atrina maura*. Monthly samples with different letters are significantly different. Bars indicate the standard error.

resorption in the same periods, i.e. May, June and September (<25%), with a peak in November (70%).

The ovaric cycle (sequential occurrence of developmental stages) of *A. maura* is schematically illustrated in Figure 7. In Ensenada de La Paz the ovaric cycle of *A. maura* includes three development stages and a gamete resorption process, which are cyclically related and lead to two environment-dependent paths, apparently driven by seawater temperature.

Condition and muscle yield indices

Significant monthly differences (ANOVA, $P<0.05$) were detected in CI and MYI values, although a well-defined seasonality could not be recognized (Fig. 8). However, a significant decrease in both indices was observed from August to November in the case of CI, and to December in the case of MYI. Such reductions were related to the high frequency of gonads undergoing gamete resorption and, in the case of the MYI, also to spawning during December.

DISCUSSION

In Ensenada de La Paz, *A. maura* displayed continuous gamete production (only interrupted by the temperature dependent resorption process) with no evident seasonal pattern in the spawning process. However, gamete release only occurred when the temperature fell below 25°C.

Oocyte size is an important feature from both ecological and evolutionary viewpoints, as it reflects the maternal energy investment and influences the fitness of both the females and offspring. Oocyte size can be influenced by female size and origin (laboratory vs. natural conditions). In this sense, contrasting results have been found in different aquatic organisms, including positive correlations between female size or condition and egg or offspring size (sea star: George 1994, gastropods: Ito 1997, fish: Marteinsdottir and Steinarsson 1998), negative correlations (fish: Iguchi and Yamaguchi 1994), and no correlation (fish: Marsh 1984, echinoids: Lessios 1987, amphipods: Glazier 2000). Moreover, it has been demonstrated that stressed adult mussels produce smaller, lower-quality eggs and larvae (Bayne 1972). In the present study, the diameters of the different oocyte types of *A. maura* were larger than those reported in other studies performed under controlled conditions (Rodríguez-Jaramillo *et al*. 2001, Enríquez-Díaz *et al*. 2003). In this sense, Rodríguez-Jaramillo *et al*. (2001) studied laboratory-reared specimens that were smaller (9.8±0.1 cm SH) than those examined in this study (19 to 28.1 cm SH). Qualitative criteria are required to describe the reproductive processes related to gonadal development. However, detailed quantitative information reduces subjectivity and eliminates semantic problems inherent to qualitative descriptions, thus improving the ability to obtain ecologically meaningful information (Barber and Blake 1991). Accordingly, the three-stage gonadal development scheme proposed for males (type-1, type-2, and type-3 spawning stages) and females (development, maturity and spawning) are the combined result of qualitative analyses (microscopic observations and morphological criteria) and quantitative criteria (percentage area occupied by AGC and frequency occurrence of each oocyte type). This led us to establish that, even though *A. maura* males release gametes continuously in Ensenada de La Paz, development stages can be differentiated based on AGC abundance. Similarly, in females the frequency of occurrence of different oocyte types indicated the development stage (development, maturity and spawning). These criteria therefore seem more suitable for describing the gonadal maturation process in wild specimens of *A. maura* from the study area. In this case, the continuous gametogenetic activity observed in *A. maura* females (evidenced by the presence of oocytes in different developmental stages together with growing oocytes at the periphery of acini in spawning individuals) precluded a finer classification of specimens into intermediate reproductive stages (early activity, development and late activity). This phenomenon had already been reported to occur in this species, both in wild individuals (Ángel-Pérez *et al.* 2007) and in specimens reared or conditioned in the laboratory (Rodríguez-Jaramillo *et al*. 2001).

Contrary to reports for the Oaxaca coast (Ángel-Pérez *et al.* 2007), no undifferentiated specimens were observed in Ensenada de La Paz. The lack of a reproductively inactive period (resting phase) in this population might be a response to local environmental conditions, particularly food availability (Baqueiro and Aldana 2000, Villalejo-Fuerte *et al.* 2000). Ensenada de La Paz is a favourable area for continuous breeding of *A. maura* as there is a constant and immediate food supply for filter feeders. This zone displays high primary productivity (phytoplankton abundance and diversity); furthermore, its inner portion is a low-energy zone in terms of current strength, thus working as a natural trap for particulate organic matter (detritus) that can be re-suspended even by weak currents (Aguirre-Bahena 2002) and then consumed by benthic filter feeders.

Many proteins are synthesized during spermatogenesis, which involves a high energy expenditure (Lehninger 1975). The transport of nutrient reserves could occur either directly or through some cells located in acinus walls (e.g. Sertoli's cells) (Pipe 1987). In this sense, the presence of AGC surrounding acinus walls in males and their decrease with ripening suggest that AGC play a mediating role in the development and maturation of germ line cells. The relative proportion of storage tissue for germ cells has been reported to change depending on the gametogenic condition (Herlin-Houtteville and Lubet 1975, Lowe *et al.* 1982, Pipe and Moore 1985, Delgado and Pérez-Camacho 2007). The significant reduction in AGC over the course of testicular development supports the assumption that

their energy-supply role might be restricted to the earliest stages of spermatogenesis.

This is the first report of such an intense atresia in gonads of *A. maura* of both sexes. In oocytes, atresia apparently shows two clearly distinctive phases. Initially, lysis of the oocyte membrane and cytoplasmic structures takes place, which results in large masses of scattered cytoplasmic material with nuclei lacking nucleolus that appear more translucent compared to nuclei of normal oocytes. This is followed by the digestion of lysed materials by hemocytes. In spermatozoids, lysis is not as evident due to their almost total lack of cytoplasm. However, large masses of hemocytes that typically occur during the lysis process and loss of tissue integrity were also observed. This finding suggests there is spermatozoid degradation (Bayne *et al*. 1978), not previously described for *A. maura*.

Motavkine and Varaksine (1983) suggested three likely reasons for the occurrence of atresia: 1) a control mechanism of the number of cells in the acinus (which has a finite capacity) could explain physiological resorption (apoptosis); 2) a "self-cleaning" process, which prepares the gonad for a new gametogenic cycle; 3) unfavourable environmental conditions (e.g. pollution, nutritional deficit, anomalously low or high temperatures) which can restrain the ovaric cycle and impair spawning. In this study, high percentages of male and female gonads showing gamete resorption were observed from August to November, when the highest temperatures (>25°C) were recorded. This is further supported by another study showing that gamete resorption occurred at 25°C in *A. maura* females under laboratory conditions (Rodríguez-Jaramillo *et al*. 2001).

Oocyte atresia has been reported in other bivalve species such as *Corbicula japonica* (Baba *et al.* 1999), *Pecten maximus* (Paulet *et al*. 1988, Beninger and Le Pennec 1991), *Pinna nobilis* (De Gaulejac *et al.* 1995) and *Nodipecten subnodosus* (Arellano-Martínez *et al.* 2004), suggesting that lysis byproducts might be reabsorbed by ancillary cells, hemocytes and epithelial cells in gonoducts to be reused (Dorange and Le Pennec 1989, Le Pennec *et al.* 1991, De Gaulejac *et al.* 1995). In bivalves, the condition index (CI) is regarded as a quantitative indicator of soft tissue quality (i.e. nutritional status) (Crosby and Gale 1990, Abbe and Albright 2003). Moreover, CI is also a useful tool for assessing the reproductive condition in bivalves with diffuse gonads (as is the case of *A. maura*), in which assessing the gonadosomatic index is not possible. However, caution should be taken when the CI values are interpreted because these can be influenced by factors other than gonad size (e.g. adductor muscle size, amount of undigested food in the digestive gland, etc.). In *A. maura*, the adductor muscle represents approximately 20% of the flesh weight; therefore, the significant decrease in CI values observed late in the year can be accounted for a simultaneous reduction in MYI rather than by variation in gonadal maturity. In addition, a direct relationship between MYI or CI values and reproductive activity was not observed in this study. This, together with the high food availability in Ensenada de La Paz, supports the conclusion that the primary energy source for the reproduction of *A. maura* inhabiting this zone comes from recently ingested food (opportunistic tactic).

Determining the size at first maturity is particularly relevant for *A. maura* populations in Mexico since the National Fisheries Chart (Anonymous 2010) indicates that these are overexploited and deteriorating in all localities across its distributional range. In this study, both SH and SL were used to determine size at first maturity. Shell height was used for comparative purposes, as this is the parameter most frequently mentioned in bivalves that can be measured at the point of capture, and that can be returned to the environment without evident damage if they are below the minimum landing size. However, the SH of species belonging to the Pinnidae cannot be measured without causing considerable damage to the individuals, since these live almost completely buried, except for their rear end that protrudes a few centimetres above the sediment. Therefore, SL is the best alternative for fishery management measures, as this allows fishermen to measure the individuals without causing damage.

Size at first maturity in *A. maura* living in Ensenada de La Paz was reached at 12 cm SL. This differs from the only size at first maturity (16 cm SL) reported for this species at a locality in the Mexican Pacific (outlet of the Balsas River, Michoacán) (Soria 1989). Current regulations stipulate a minimum landing size of 14 cm SL for *A. maura* (Anonymous 2010), which is consistent with the present results. However, the size at first maturity decreases as a consequence of overexploitation, thus it should be monitored periodically to update the regulation if necessary.

The findings reported herein support the conclusion that *A. maura* displays an opportunistic reproductive strategy favoured by the large amount of food available in Ensenada de La Paz. Its reproduction combines several elements, including continuous maturation (no resting stage) and partial spawning, to ensure reproductive success. However, at temperatures above 25°C, massive gamete resorption occurs (mostly in females).

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