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# Reproductive cycle in an imposex-affected population of *Olivancillaria deshayesiana* (Gastropoda: Olividae) from Mar del Plata, Argentina

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ABSTRACT: *Olivancillaria deshayesiana* (Gastropoda: Olividae) is distributed from Ilha Grande (Rio de Janeiro, Brazil) to Necochea (Buenos Aires, Argentina). Apart from some descriptions of the embryonic development and the egg capsules, little is known about the reproduction and ecology of this species. In this 2 yr study (October 2005 to September 2007), the reproductive cycle of *O. deshayesiana* was examined in a population highly affected by imposex, from the Mar del Plata coast, Argentina. Males exhibited seasonal reproductive activity, with a major spawning period from September to January (spring to early summer) for the 2 yr, which coincided with an increase in seawater temperature and photoperiod. In contrast, females were mature and capable of spawning year round, with a major spawning period from September to January (spring to early summer), simultaneous with the major spawning period of males.

KEY WORDS: Imposex · Mar del Plata · *Olivancillaria* · Olividae · Reproduction

## INTRODUCTION

The neogastropod genus *Olivancillaria* d'Orbigny, 1840 includes soft-bottom species that inhabit shallow waters up to 70 m depth in the Argentine Malacological Province (AMP), extending from Bahia state, Brazil (12° 15′ S, 37° 47′ W) to Punta Pardelas (42° 37′ S, 64° 15′ W), Chubut province, Argentina (Teso & Pastorino 2011). Eight *Olivancillaria* species inhabit the southwestern Atlantic (Teso & Pastorino 2011), some of which are the target of subsistence fisheries (Scelzo et al. 2002, Narvarte 2006). This genus and some volutids (i.e. *Adelomelon, Zidona*) and nassarids (i.e. *Buccinanops*) represent the most important endemic and abundant gastropods on sandy bottoms in the AMP.

*Olivancillaria deshayesiana* is commonly found from Ilha Grande (23° 09′ S, 44° 13′ W), Rio de Janeiro state, Brazil, to Necochea (38° 33′ S, 58° 44′ W), Buenos Aires province, Argentina, up to 60 m depth (Teso & Pastorino 2011). Individuals are semi-buried, and their shell is partially covered by the mantle. Little is known about the reproduction and ecology of this species. Borzone (1995) described the embryonic development and the egg capsules of *O. deshayesiana*, which are attached to the shells of other live gastropods (i.e. *Buccinanops monilifer* and *B. duartei*); a single embryo hatches from each egg capsule (Borzone 1995). *O. deshayesiana* is a bycatch of the fisheries for the prawn *Artemesia longinaris* and the shrimp *Pleoticus muelleri* (Scelzo et al. 2002), rather than being a direct target of artisanal fishermen. Recently, Teso & Penchaszadeh (2009) reported the occurrence of imposex (masculinization of females caused by the presence of tributyltin [TBT] in the water) in an *O. deshayesiana* population from the Mar del Plata area, and Arrighetti et al. (2012) determined through a von Bertalanffy growth model that

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this species may grow to a total shell length of 31 mm in about 10 yr. The aim of our study was to describe the gonadal structure and reproductive cycle of *O. deshayesiana*, and to provide new information on the occurrence of imposex in a population in the Mar del Plata area, Argentina.

## MATERIALS AND METHODS

### Sampling

Mar del Plata (38° 20′ S, 57° 37′ W) is an open coast and the site of the most important coastal fishery fleet of Argentina (Penchaszadeh et al. 2001). In this area, water temperature ranges seasonally between 8.4 and 20.8°C and salinity is rather constant at 33.8‰ (www.iafe.uba.ar/tele/Antares_argentina/; Guerrero & Piola 1997).

Specimens of *Olivancillaria deshayesiana* were collected monthly by bottom trawling (3 m mouth opening, 15 mm mesh size) off Mar del Plata City between 5 and 12 m deep from October 2005 to September 2007. Approximately 20 snails were caught each month and taken to the laboratory, where the shell was separated from the soft body. Shell length (SL) was measured with a Vernier caliper to the nearest 1 mm, and the shell-free wet mass (SFWM) was weighed to the nearest 0.1 g. To establish the morphometric relationship between SL and SFWM for each sex, linear regression analyses were performed using $\log(\mathrm{SFWM}) = \log(a) + b \times \log(\mathrm{SL})$. Parallelism tests and analysis of covariance (ANCOVA) were performed to compare the relationship between SFWM and SL between sexes (Sokal & Rohlf 1995). A chi-squared test was used to test for significant differences in sex ratio. Statistical analysis was carried out with the software Statistica v. 6.0.

Recently, Teso & Penchaszadeh (2009) reported that this population is affected by imposex, and on this account animals were sexed by differences in gonad color and the presence (females) or absence (males) of internal sexual glands such as capsule and albumen glands. Sex was confirmed by the histological examination of gonad sections under a Zeiss Axio Imager Z1 microscope. The frequency of imposex was calculated as the proportion of females with imposex compared to the total number of females in the sample. The following values were calculated: mean female penis length, mean male penis length, and relative penis size index (RPSI), defined as (mean length of female penis)$^3$/(mean length of male penis)$^3$ × 100 (Gibbs & Bryan 1994).

### Gonadal structure and reproductive cycle

The gonads of each individual were fixed in Bouin's solution, dehydrated in a graded ethanol series (70, 80, 96, and 100%), embedded in paraffin and resin, cut at 5 µm thickness, and stained with Harris' hematoxylin and eosin. Gonad sections were examined histologically under a Zeiss Axio Imager Z1 microscope and photographed with an SV Micro-Sound-Vision digital camera. To study oocyte growth, the mean of 2 oocyte diameter measurements (taken at right angles to each other) was calculated for 15 to 35 oocytes containing a nucleus with nucleolus, from each female. In addition, the different stages of gonadal development were analyzed for both sexes.

## RESULTS

Sex could be distinguished in 470 snails. The overall sex ratio of 1:1.4 (female:male) differed significantly from 1:1 ($\chi^2 = 7.53$, df = 1, $p < 0.01$). Total SL ranged from 16 to 33.3 mm in females and from 19.5 to 35 mm in males. The relationships between total SL and total SFWM are shown in Table 1. The parallelism test revealed a statistically significant difference between sexes ($F = 312.8$, $p < 0.01$), with males being significantly larger than females (parallelism test, $p < 0.01$).

The incidence of imposex-affected females of *Olivancillaria deshayesiana* was 81.9%, and the mean RPSI was 3.56. Most of them had a single vas deferens and penis (Fig. 1a,c), and the remaining individuals (3.6%) presented malformations such as 2 penises (Fig. 1b). None of the imposexed females had a vas deferens obstructing the vagina.

Table 1. *Olivancillaria deshayesiana*. Relationship between shell length (SL) and shell-free wet mass (SFWM) for males and females. Values are ±SD

| Sex | Mean SL (mm) | Mean SFWM (g) | Regression equation | $R^2$ | p |
|---|---|---|---|---|---|
| Male | 28.3 ± 2.6 | 3.0 ± 1.4 | $\log(\mathrm{SFWM}) = 3.24 \times \log(\mathrm{SL}) - 5.23$ | 0.76 | <0.01 |
| Female | 26.9 ± 2.6 | 2.3 ± 0.8 | $\log(\mathrm{SFWM}) = 3.24 \times \log(\mathrm{SL}) - 4.26$ | 0.78 | <0.01 |

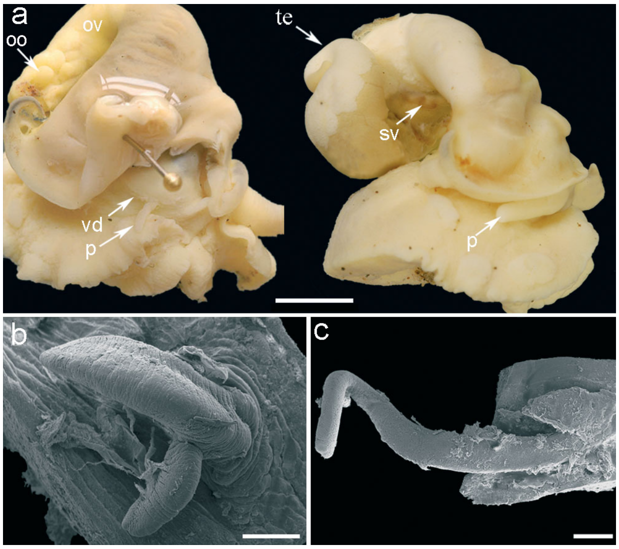

Fig. 1. *Olivancillaria deshayesiana*. (a) Female (left) with vas deferens (vd) and penis (p); note the presence of numerous oocytes (oo) in the ovary (ov). Male (right) with a normal penis (p); te: testicle, sv: seminal vesicle. Scale bar = 5 mm. (b) Scanning electron microscopy (SEM) image of a female with multiple penises. Scale bar = 200 µm. (c) SEM image showing detail of a female penis. Scale bar = 1 mm

## Gonadal structure and reproductive cycle

In both sexes, gonads were located distally in the visceral mass, intruding into the digestive gland. This made it impossible to calculate the gonadosomatic index (see Figs. 1a, 2d, 5a).

### Males

The male gonad extended from the apex to almost the end of the body whorl (Fig. 1a, right). The testis was conspicuous, varying from dark brown and branched (resorption stage) to cream (ripe stage). The seminal vesicle was light brown, inconspicuous, and contiguous to the testis, embedded in it. In histological sections, the testis consisted of numerous spermatogenic tubules separated from each other by connective tissue (Fig. 2). Spermatogenesis occurred within the spermatogenic tubules, each of which was surrounded by a membrane (Fig. 2).

Based on histological observations, the male gametogenic cycle was divided into 4 developmental stages: proliferation and growth, pre-evacuation, evacuation, and resorption. The stage of proliferation and growth was characterized by the presence of spermatocytes and spermatogonia near the tubule walls (Fig. 2a); spermatids were also found, and the lumina of the spermatogenic tubules and the seminal vesicle were empty. In the pre-evacuation stage, spermatozoa were placed in the center of the tubule lumen (Fig. 2b); spermatogonia, spermatocytes, and spermatids were located near the tubule walls, and the seminal vesicle was empty. In the evacuation stage, the lumina of the tubules and the seminal vesicle were full of spermatozoa (Fig. 2c). The resorption stage was characterized by the complete absence of spermatozoa, with the spermatogenic tubules and seminal vesicle appearing collapsed (Fig. 2d); yellow bodies and signs of degradation were found.

The monthly frequency of males in each developmental stage is summarized in Fig. 3. Males at the stage of proliferation and growth were found between May and September, reaching a maximum number between May and June (autumn) of the second year. The pre-evacuation stage took place be-

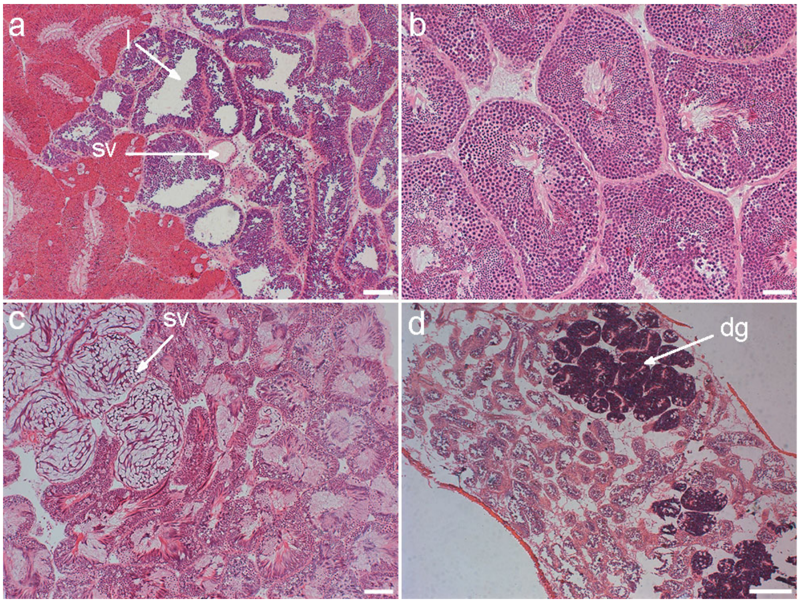

Fig. 2. *Olivancillaria deshayesiana*. Histology of male gonad at different developmental stages. (a) Proliferation and growth: tubules filled with spermatogonia and spermatocytes; no spermatids or spermatozoa were observed. The lumina (l) of the spermatogenic tubules and seminal vesicle (sv) are empty. (b) Pre-evacuation: spermatogenic tubules with the entire spermatic series. (c) Evacuation: spermatogenic tubule full of spermatozoa, note the seminal vesicle (sv) full of spermatozoa. (d) Resorption: degrading spermatozoa free in the testis; dg: digestive gland. Scale bars = 200 µm (a); 100 µm (b,c); 300 µm (d)

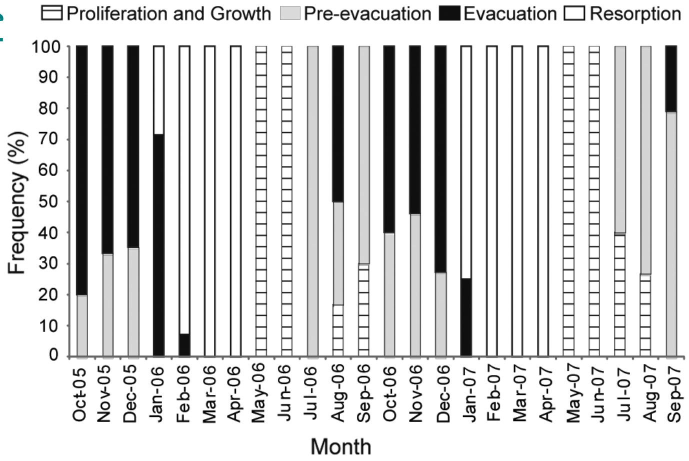

Fig. 3. *Olivancillaria deshayesiana.* Monthly frequency of different gonad developmental stages of males for the study period (October 2005 to September 2007)

tween July and December (winter to spring); spermatozoa were released from the gonads between September and January (spring to early summer), simultaneously with an increase in surface water temperature and photoperiod (Fig. 4). The resorption stage occurred between January and April, with a maximum proportion of individuals between February and April (summer to autumn), when the photoperiod becomes shorter.

### Females

The female gonad extended from the apex to almost the end of the body whorl (Figs. 1a & 5a). The ovary was light yellow (ripe) and conspicuous; it was composed of many tubules where oogenesis was taking place (Fig. 5a). Each tubule was surrounded by connective tissue and contained companion cells in close contact with the oocytes.

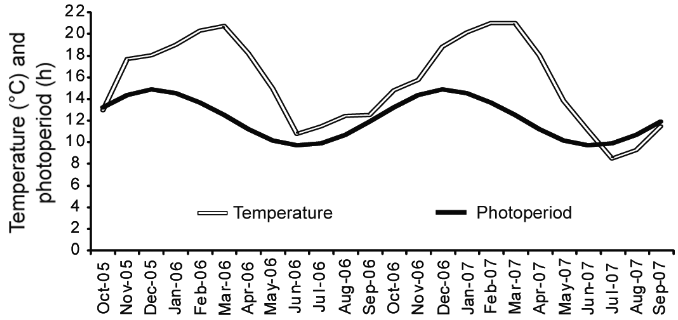

Fig. 4. Mean values of surface seawater temperature (°C) and photoperiod (hours of light) for the study period (October 2005 to September 2007). Data from Red ANTARES (www.iafe.uba.ar/tele/Antares_argentina/) and Servicio de Hidrografía Naval (www.hidro.gov.ar)

The female gametogenic cycle was divided into 4 developmental stages: early vitellogenesis, pre-evacuation, evacuation, and resorption. The first stage (early vitellogenesis) was characterized by a larger proportion of oogonia and pre-vitellogenic oocytes (up to about 200 µm in diameter) near the tubule walls and the presence of companion cells (Fig. 5b); a few vitellogenic oocytes were found in the lumen (Fig. 5c). In the pre-evacuation stage, the ovary increased in size and the tubules were full of vitellogenic oocytes measuring between 250 µm and 1 mm in diameter (Fig. 5d); oocytes were free in the lumen, ready to be released. In the evacuation stage, most of the oocytes were released but a few of them remained (Fig. 5e); no pre-vitellogenic oocytes were found in the tubule walls. The resorption stage was characterized by empty tubules with a decrease in size and the presence of new oogonia in the tubule walls (Fig. 5f).

The monthly frequency of females in each developmental stage is summarized in Fig. 6. In contrast to males, females showed a fully active gonad and gamete liberation over almost the entire study period. The early-vitellogenesis stage occurred between February and June (summer to autumn). The pre-evacuation stage took place throughout the study period, except for January and February of both years and March 2006. The evacuation stage continued throughout the study period except for May (2006 and 2007) and February 2006. The largest proportion of individuals (≥60 %) at this stage was recorded in spring, between October and December 2005 and September (2006 and 2007), simultaneously with an increase in surface water temperature and photoperiod. The resorption stage extended between January and February of both years (summer) and, in contrast to males, it was absent in some individuals. Fig. 7 shows the monthly frequency of oocyte diameter obtained during the 2 yr study period (from October 2005 to August 2007).

## DISCUSSION

### Population structure

In the studied population of *Olivancillaria deshayesiana*, total SLs ranged from 16 to 35 mm, with males being significantly larger than females. Specimens smaller than 16 mm escaped through the net (mesh size: 15 mm). The population showed a female:male sex ratio of 1:1.4, with a clear predominance of males.

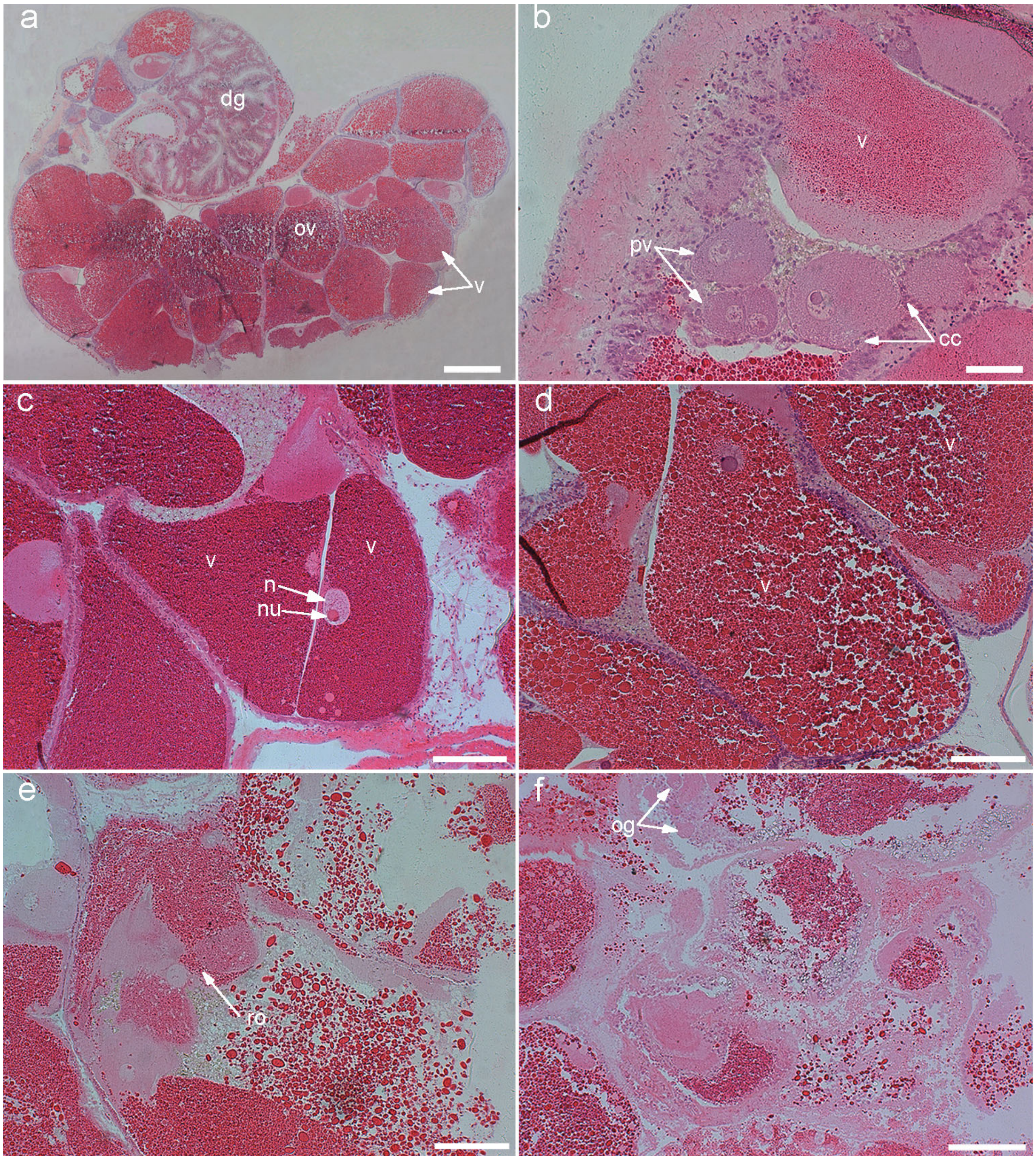

Fig. 5. *Olivancillaria deshayesiana*. Histology of female gonad at different developmental stages. (a) General view of a mature female ovary (ov) full of vitellogenic oocytes (v) in close contact with the digestive gland (dg). (b,c) Early vitellogenesis: pre-vitellogenic oocytes (pv) surrounded by companion cells (cc) and vitellogenic oocytes (v); note the presence of nucleus (n) and nucleolus (nu). (d) Pre-evacuation: vitellogenic oocytes occupying the entire tubule. (e) Evacuation: tubules almost empty, with residual oocytes (ro). (f) Resorption: empty tubules with new oogonia (og). Scale bars = 600 µm (a); 300 µm (b); 100 µm (c); 200 µm (d–f)

This pattern is quite uncommon in gonochoristic gastropods, among which females predominate over males with a male:female sex ratio of up to 1:2 (Feare 1970, McGwynne & van der Horst 1985, Gibbs et al. 1988, Martel et al. 1986, Olabarria & Ramirez-Llodra 2004, Narvarte 2006), or with females being at least as frequent as males (Fretter & Graham 1994, Giménez & Penchaszadeh 2002, Cledón et al. 2005).

The presence of imposex in *Olivancillaria deshayesiana* throughout the study period provides evidence of the negative influence of the port of Mar del Plata on the local gastropod population, confirming previous results (Teso & Penchaszadeh 2009). This is in line with the study of Bigatti et al. (2009), who recorded TBT pollution in the sediments in Mar del Plata. In this study, no histological alterations in

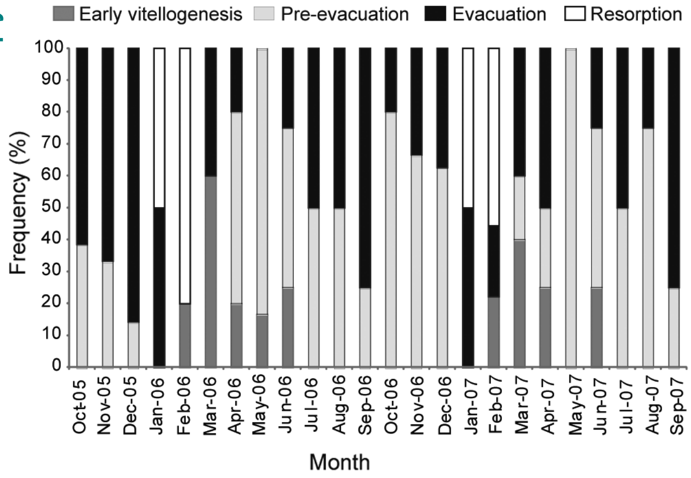

Fig. 6. *Olivancillaria deshayesiana*. Monthly frequency of different gonad developmental stages of females for the study period (October 2005 to September 2007)

gonad structure were observed, and in consequence the gonadal cycle was not affected. Similar results were found by Cledón et al. (2005) in a population of the snail *Adelomelon brasiliana* in the same area. On the other hand, the neoformation of multiple penises in females indicates that the sensitivity to TBT is higher in *O. deshayesiana* than in other snails from the same area, such as *Buccinanops monilifer* and *A. brasiliana*, which had lower percentages of imposex and RPSI values (Cledón et al. 2006, Averbuj & Penchaszadeh 2010).

## Gonadal structure and reproductive cycle

This study represents one of the first reports on the gametogenic cycle in species of the family Olividae, along with the report of Rocha-Barreira (2001). The

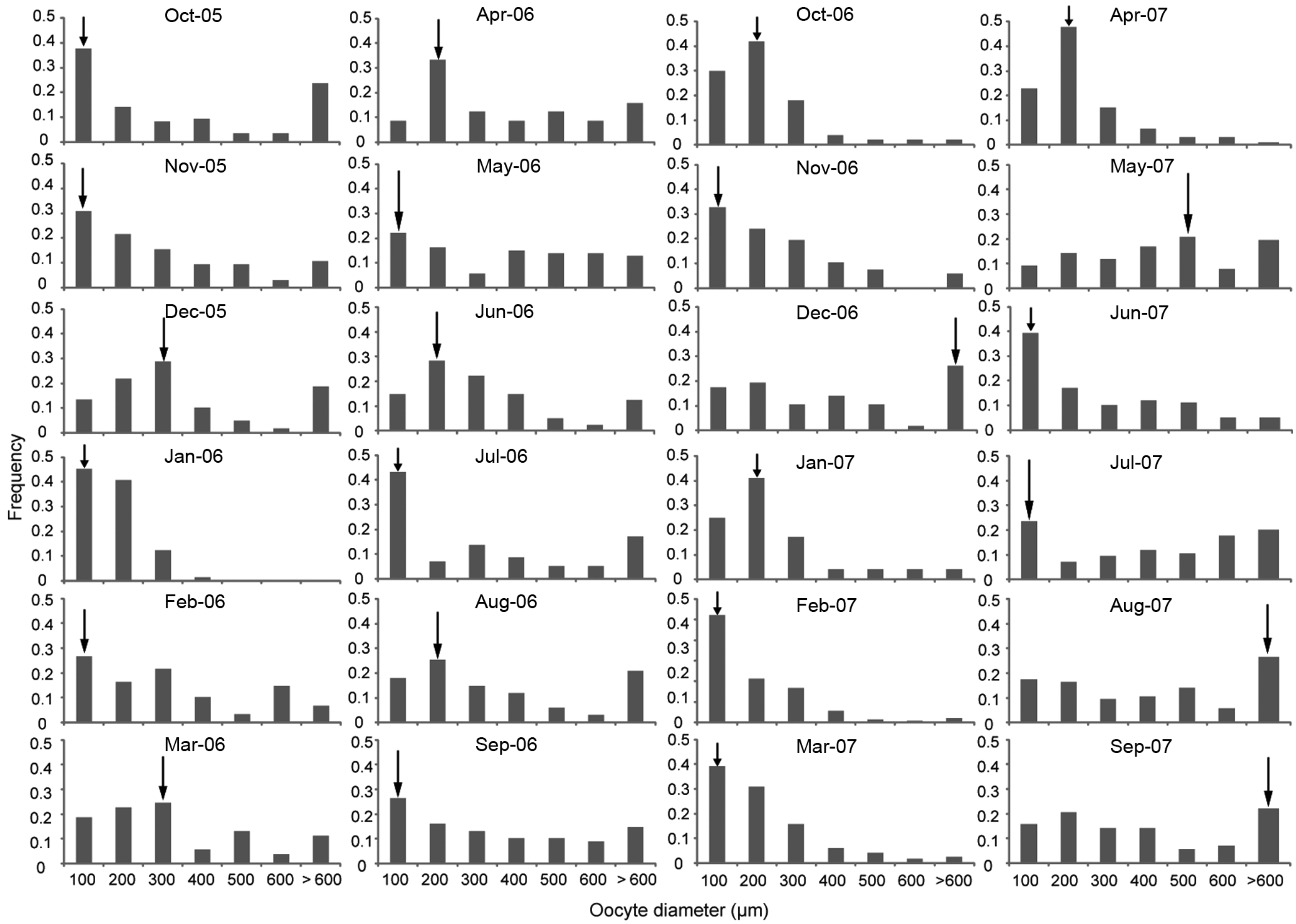

Fig. 7. *Olivancillaria deshayesiana*. Monthly relative frequency of oocyte diameter (October 2005 to September 2007). Arrows indicate the modal monthly oocyte diameter

general structure of the gonads of *Olivancillaria deshayesiana* is similar to that of other olivids (Marcus & Marcus 1959, Rocha-Barreira 2001, Pimenta 2005). Its testis and ovary are of the same color as in *O. auricularia* (Rocha-Barreira 2001) and extend from the apex to almost the end of the body whorl.

### Males

Male reproduction is seasonal, with a major spawning period between spring and early summer (September to January) of both years. This pattern may be related to an increase in seawater temperature and photoperiod, which are important environmental factors regulating gonadal development and spawning in many gastropod species (Fretter & Graham 1994, Giménez & Penchaszadeh 2002, Cledón et al. 2005, Bigatti et al. 2008, Penchaszadeh et al. 2009, Arrighetti & Penchaszadeh 2010, Averbuj & Penchaszadeh 2010). Males exhibited a pronounced resting period from summer to autumn (February to April), in accordance with a decrease in these variables. From May to June, all individuals underwent a stage of proliferation and growth. Seasonal reproduction in males was also found in *Buccinum undatum* by Martel et al. (1986) and in *Olivancillaria auricularia* (as *O. vesica auricularia*) by Rocha-Barreira (2001). However, this pattern is unusual in males of other Neogastropoda species, whose testes seem to produce mature sperm year round without a resting period, e.g. the volutids *Zidona dufresnei* (Giménez & Penchaszadeh 2002), *Adelomelon brasiliana* (Cledón et al. 2005), and *A. beckii* (Arrighetti & Penchaszadeh 2010) in Mar del Plata, *Odontocymbiola magellanica* (Bigatti et al. 2008) and *A. ancilla* (Penchaszadeh et al. 2009) in Golfo Nuevo, and the nasarid *Buccinanops cochlidium* in Golfo San José (Averbuj et al. 2010), among others.

### Females

In contrast to males, females were mature and spawning year round, with a major spawning event between September and January (spring to early summer). This period coincided with the major spawning period of males. No females in the stage of proliferation and growth (exclusive presence of oogonia and pre-vitellogenic oocytes in the tubules) were found. The resorption period was short (January to February) and was only observed in some individuals. As a general rule in Caenogastropoda, tropical species often have extended spawning periods while a seasonal pattern is common in temperate species (Webber 1977). The latter is the case for the volutids *Zidona dufresnei* (Giménez & Penchaszadeh 2002) and *Adelomelon brasiliana* (Cledón et al. 2005) from Argentina and a population of *Buccinum undatum* from Canada (Martel et al. 1986), among others. However, as observed in the present study, the females of some Caenogastropoda species of temperate areas have a continuous reproduction with different spawning intensities, such as *A. beckii* (Arrighetti & Penchaszadeh 2010) and *Odontocymbiola magellanica* (Bigatti et al. 2008) from Argentina, *Olivella biplicata* (Edwards 1968) and *Nucella emarginata* from California (USA), and *Nucella lapillus* from France (Webber 1977). Moreover, Borzone (1995) reported the occurrence of egg capsules in a population of *Olivancillaria deshayesiana* from Rio Grande do Sul (Brazil) throughout the year, with higher abundances between August and October. The continuous reproductive activity of females observed in this study is consistent with the continuous occurrence of egg capsules in the population from Brazil (Borzone 1995). This, in turn, reinforces the hypothesis of continuous reproduction.

It was difficult to measure a representative number of vitellogenic oocytes larger than 600 µm (ready to be spawned) because only a few of them had a nucleus with nucleolus in the histological preparation of the gonad. This resulted in an underestimation of the frequencies of large oocytes, and therefore the use of oocyte size appears to be unfeasible for determining the reproductive cycle in *Olivancillaria deshayesiana* and other species showing the same type of reproduction.

## General remarks

The seasonal reproductive activity of males (with a clear resting period) suggests that females store sperm in the seminal receptacle for several months. This same pattern was suggested for *Buccinum undatum* (Martel et al.1986) and other species (e.g. Fretter & Graham 1994, Bigatti et al. 2008). The occurrence of egg capsules year round and the development of a single egg of between 800 and 900 µm within each egg capsule (Borzone 1995) may indicate an extended period of vitellogenesis during which each female deposits a few egg capsules per year. A similar pattern was reported for *Olivancillaria auricularia* from southwestern Brazil (Rocha-Barreira 2001). This pattern implies high energetic costs of reproduction, explaining the smaller body size of females. Similar observations of body size and reproductive pattern were reported for *Olivella biplicata* (Edwards 1968).

All individuals sampled in this study were mature, because the sampling method excluded individuals <16 mm in SL. According to the von Bertalanffy growth model of *Olivancillaria deshayesiana* (Arrighetti et al. 2012), mature individuals of 16 mm in SL correspond to an age of about 1 yr. This result may indicate that this population attains first sexual maturity before other gastropods, such as *Haliotis rubra* (6 to 7 yr; Prince et al. 1988), *Buccinum undatum* (6 to 7 yr; Gendron 1992), *Zidona dufresnei* (8 to 9 yr; Giménez et al. 2004), *Adelomelon brasiliana* (7 yr; Cledón et al. 2008), and *Odontocymbiola magellanica* (8 yr; Bigatti et al. 2007).

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