

Reproductive Cycle of the Clam *Tellina petitiana* d'Orbigny, 1846, in Nuevo Gulf (Argentina)

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Abstract. *Tellina petitiana* inhabits the intertidal and upper subtidal zones of the Atlantic coast of South America, from Rio do Janeiro to northern Patagonia. Its gonads are diffuse and the sex cannot be detected with the naked eye. The application of histological techniques to individuals collected monthly for one year from a locality at the southern limit of the species distribution (Puerto Madryn, 42°46'S, 65°02'W) revealed a sex ratio not significantly different from 1:1 and no record of hermaphroditism. At vitellogenic maturity the oocytes reach a maximum diameter of approximately 70 µm and are surrounded by a dense basophilic substance of fibrous appearance. The spermatozoa, 16 µm in length, show a patchy distribution within the internal space of the alveoli. This species is iteroparous and displays an extended spawning period, from late spring to summer. Most specimens were in regression throughout fall, in multiplication from late fall to winter, and in maturation during spring. The development of the gonadal tissue was maximal in December and minimal in April. The yolk accumulation started in September. The vitellogenic oocytes reached their maximal estimated mean diameter in January and were present in few animals in March.

INTRODUCTION

Tellina petitiana d'Orbigny, 1846, inhabits sandy-muddy bottoms of the intertidal and upper subtidal of the Atlantic coast of South America from 23°S to 43°S, and is common in the gulfs of northern Patagonia (Castellanos, 1967; Rios, 1975; Scarabino, 1977; Barón, 1995). In some areas, the species is an important food item of scolopacid birds during inter-hemispherical migration (from February to April; Pagnoni, 1997).

Several descriptions of the reproductive cycle of tellinids from the Northern Hemisphere have been published to date (Lammens, 1967; Rae, 1978; Salzwedell, 1979; Brousseau, 1987; Harvey & Vincent, 1989; Kawai et al., 1993). However, the reproductive cycle has not been studied in tellinids from the southwest Atlantic.

The morphology and anatomy of *T. petitiana* have been reported in detail (Barón & Ciocco, 1997, 1998; Ciocco & Barón, 1998). The species is gonochoric, and its gonads have been characterized as "diffuse," macroscopically evident only at sexual maturity (Barón & Ciocco, 1998). The aim of this paper is to describe the reproductive cycle of the species for the first time.

MATERIALS AND METHODS

Samples of *Tellina petitiana* were randomly collected from the lower intertidal and upper meters of the subtidal

of a fine and medium grain sandy beach with low step (1.21°; Escofet, 1983) and semidiurnal tidal regime (average amplitude: 4.69 m), located at the waterfront of the city of Puerto Madryn (Mimosa Beach; 42°46'S, 65°02'W; Figure 1).

Twenty individuals of intermediate shell lengths were sampled once per month from April 1993 to March 1994. Once extracted from the sediment by digging and sieving, the clams were fixed in 10% formaldehyde in seawater and dehydrated in consecutive baths of 96% ethanol and a 1:1 mixture of 100% ethanol and xylene. Finally, 5 µm thick sections were cut with a microtome and stained with eosin-hematoxylin and Masson's trichromic stains.

Histological observations were made on the gonads. Cells from the germ line were observed under a microscope with a ×100 immersion objective, identified according to their size, shape, and arrangement, and photographed. Sex ratio was estimated from the total sample (n = 240), and a Chi-square test was used to verify differences from a 1:1 proportion. Gametogenesis was described according to the morphology of the cells observed. A scale of gonadal maturity was developed for *T. petitiana*, based on the stages assigned to the tellinids *Macoma balthica* (Linnaeus, 1758) (Lammens, 1967); *Macoma secta* (Conrad, 1837) and *Macoma nasuta* (Conrad, 1837) (Rae, 1978); *Tellina fabula* Gmelin, 1791 (Salzwedell, 1979); and *Tellina nitidula* (Dunker, 1860) (Kawai et al., 1993); and other bivalves, including *Aequipecten tehuelchus* (d'Orbigny, 1846) (Lasta & Calvo, 1978,

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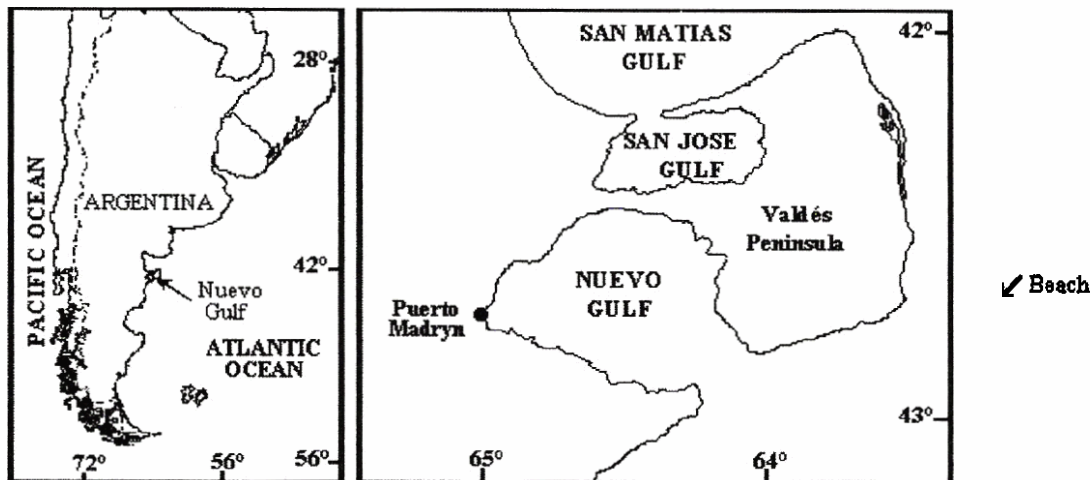


Figure 1. Location of the study area

as *Chlamys tehuélcha*); *Protothaca asperrima* (Sowerby, 1835) (Palacios et al., 1986); *Spisula solidissima* (Dillwyn, 1817); *Arctica islandica* (Linnaeus, 1767) (Jones, 1981); and *Spisula solidissima similis* (Say, 1822) (Kanti et al., 1993).

The sequence of gonadal stages was analyzed by comparing the percentages of specimens in different stages of maturity in the consecutive monthly samples. This process was compared with the percentage of alveolar area (PAA; Lasta & Calvo, 1978), an index reflecting the area occupied by gonadal alveoli relative to total area among the somatic organs (maximum area available for gonadal development) in histological sections. PAA was estimated for each individual from two microscopic fields under 10×10 magnification. A total of 480 fields were drawn on paper with a camera lucida. The outlines obtained were scanned (118×118 pixels/cm²) and the inter-alveolar and intra-alveolar areas were calculated by pixel counting (Aldus Photo Styler 2.0). The maturity index was then estimated as $PAA = (\text{intra-alveolar area} \times 100) / \text{total (inter-alveolar} + \text{intra-alveolar) area}$, following Lasta & Calvo (1978).

Additionally, monthly frequency distributions of vitellogenic oocyte diameters were estimated from September to February, the time period in which this cell type was present in the gonads. Due to the diversity of forms adopted by the vitellogenic oocytes during the process of maturation, the diameters were estimated through an adaptation of the technique used by Laruelle et al. (1994). The outlines of approximately 50 vitellogenic oocytes per clam were drawn from the histological sections under 100×10 magnification (immersion objective). Based on the assumption that each oocyte has the nucleolus placed in its center (Kennedy & Battle, 1964; Laruelle et al., 1994), only the cell sections showing this structure were selected to estimate oocyte diameters. The area delimited by each

outline was estimated with the technique used to calculate the PAA. Each area was treated as if it were the surface of a section passing through the center of a sphere, and the diameter of each oocyte was then estimated as $d = 2\sqrt{(\text{area}/\pi)}$. As a matter of comparison, a correlation analysis was performed between the average oocyte diameter per individual and the square root of the corresponding PAA.

For the sampling period, monthly means of surface water and air temperature recorded on an hourly basis were obtained from the Servicio de Hidrografía Naval de la Armada Argentina (1500 m from the sampling site) and the Servicio de Física Ambiental del Centro Nacional Patagónico, respectively. This information was supplemented with historical temperature registers supplied by the same institutions.

RESULTS

Sex Ratio

From a total of 240 individuals observed, 126 were females and 114 males. In the size range explored (33–40 mm), sex ratio did not significantly differ from 1:1 (Chi square test, $P = 0.44$, $df = 1$). No hermaphrodites were found.

Gametogenesis Characterization

Oogenic Series. In the females, primary germ cells (g, Figure 2), 10–12 μm in diameter (d), are imbricated in the alveolar walls and have a clear and light eosinophil cytoplasm and rounded nucleus ($d = 5\text{--}6 \mu\text{m}$) with the chromatin arranged as dispersed basophilic fragments. Oogonia 1 (o1, Figures 2.3) are adherent to the alveolar walls and have a similar appearance to that of the germinal cells. The nucleus ($d = 3\text{--}4 \mu\text{m}$) is clear and oc-

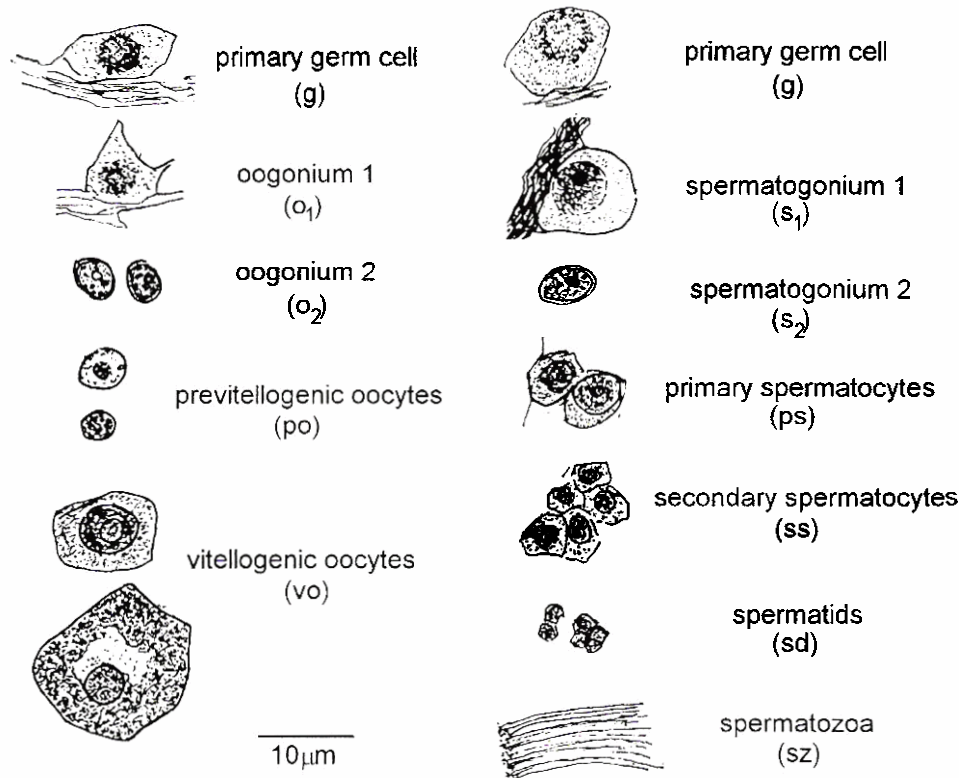
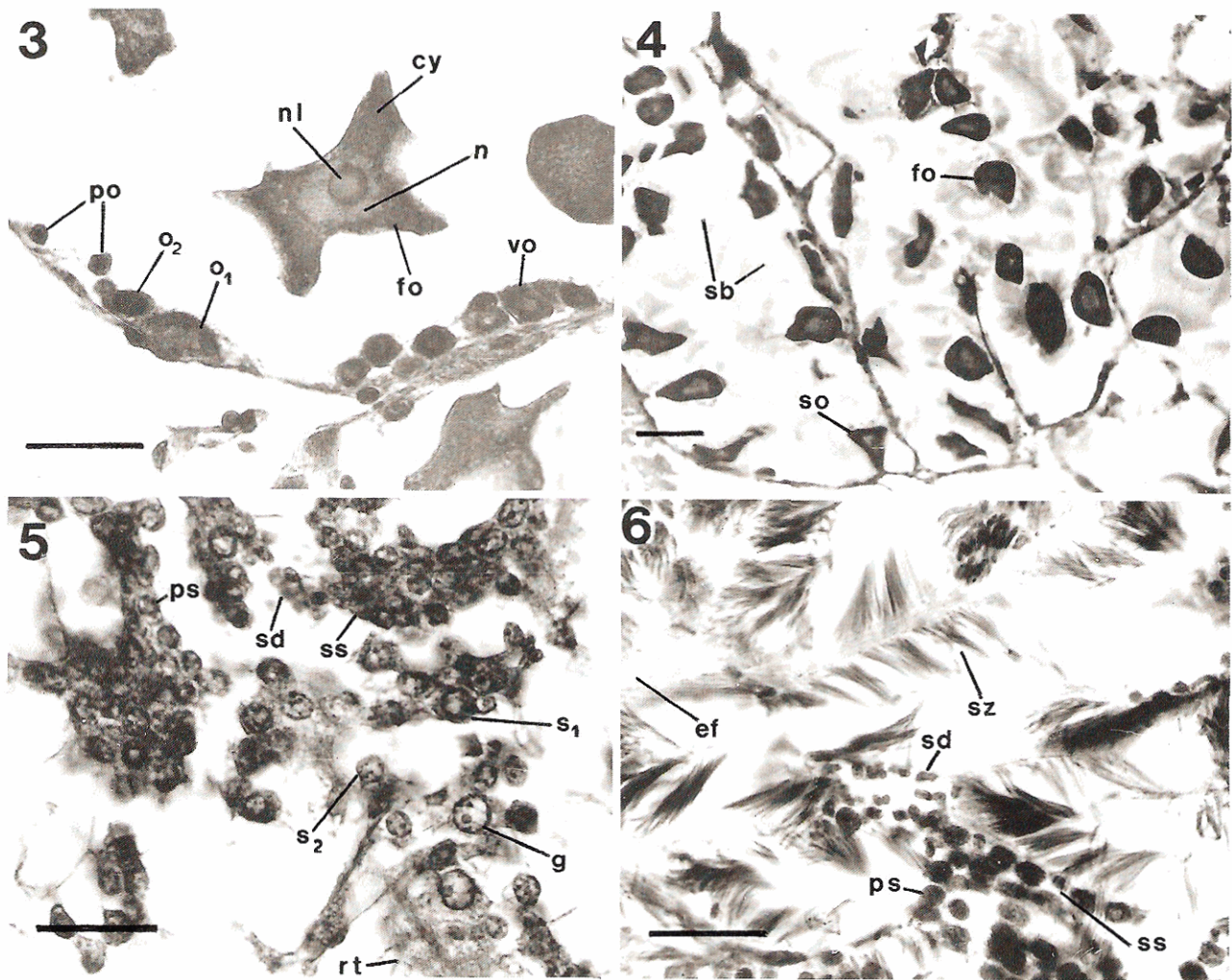


Figure 2. Schematic drawing of the sequence of gametogenic stages of *Tellina petitiiana*. Left: oogenesis; right: spermatogenesis.

copies a substantial part of the cell's section. Oogonia 2 (o_2 , $d = 3 \mu\text{m}$, Figures 2,3) have scarce cytoplasm. Previtellogenic oocytes (po , $d = 6 \mu\text{m}$, Figures 2,3) have basophilic nucleus and cytoplasm and are often tightly clustered, so that the plasmatic membranes take shapes ranging from rounded to polyhedral. Vitellogenic oocytes (vo , Figures 2,3) accumulate reserve substances, significantly increasing their size. These cells remain adherent to the alveolar walls until they reach approximately $20 \mu\text{m}$ in diameter. From this size up, cells start to detach, progressively taking stalked shapes and irregular outlines (so , Figure 4). Vitellogenic oocytes increase their diameter until they reach 40 to $75 \mu\text{m}$; their outlines become rounded, and their stalks become long, slender, and hardly detectable. In section these cells appear free in the alveolar lumen, even when they may still be attached to the alveolar walls by a thin stalk (fo , Figures 3, 4). Vitellogenic oocytes have acidophil cytoplasm (cy , Figure 3), a clear nucleus (n , Figure 3), and a conspicuous nucleolus (nl , Figure 3). Among the stalked (so , Figure 4) and free oocytes (fo , Figure 4) it is possible to observe a basophilic substance of fibrous aspect, occupying most of the intra-alveolar spaces (sb , Figure 4). This substance is dense, indistinguishable with Masson's trichomic staining, and can deform the oocytes when the intra-alveolar space is limited.

Spermatic Series. In males, primary germ cells ($d = 8-9 \mu\text{m}$) lie within the alveolar wall epithelium, and display a clear cytoplasm and a basophilic nucleus (g , Figures 2,5). Spermatogonia 1 (s_1 , $d = 7 \mu\text{m}$, Figures 2,5) remain attached to the alveolar walls and present a clear nucleus, with condensed chromatin of reticular aspect. Spermatogonia 2 (s_2 , Figures 2,5) are similar to spermatogonia 1, but their cytoplasm consists of a thin ring surrounding the nucleus. Primary spermatocytes (ps , $d = 6 \mu\text{m}$, Figures 2,5) have clear and very scarce cytoplasm, and a deeply basophilic nucleus. These cells are always crowded and their walls show hexagonal contours. Secondary spermatocytes (ss , Figures 2,5) show the same characters as primary spermatocytes, but are smaller ($d = 4 \mu\text{m}$). Spermatids (sd , Figures 2,6) are deeply basophilic cells ($d = 2 \mu\text{m}$), with no perceivable cytoplasm. Spermatozoa (sz , Figures 2,6) measure $16 \mu\text{m}$ in length and are heavily basophilic. The reticular tissue (rt , Figure 5), formed by "follicular cells," according to other authors' terminology (Coe, 1943; Lammens, 1967; Rae, 1978; Borzone, 1989), delimits several compartments within the alveoli of *T. petitiiana*. In each compartment it is possible to observe the different cellular types of the spermatic series lined up with the spermatozoa placed in the lumen, forming dense cell packs.



Figures 3–6. Appearance of female and male germ lines' cells. Figure 3. Detail of the female series. Figure 4. Alveoli containing mature oocytes. Figure 5. Detail of the first cellular stages of the male series. Figure 6. Detail of the advanced cellular stages of the male series. Key: cy, cytoplasm; ef, eosinophil fibers; fo, free oocyte; g, primary germ cell; n, nucleus; nl, nucleolus; o1, oogonia 1; o2, oogonia 2; po, previtellogenic oocyte; ps, primary spermatocyte; rt, reticular tissue; s1, spermatogonia 1; s2, spermatogonia 2; sb, basophilic substance; sd, spermatid; so, stalked oocyte; ss, secondary spermatocyte; sz, spermatozoa; vo, vitellogenic oocyte. Figures 3, 5, 6: scale bar = 20 μm ; Figure 4: scale bar = 50 μm .

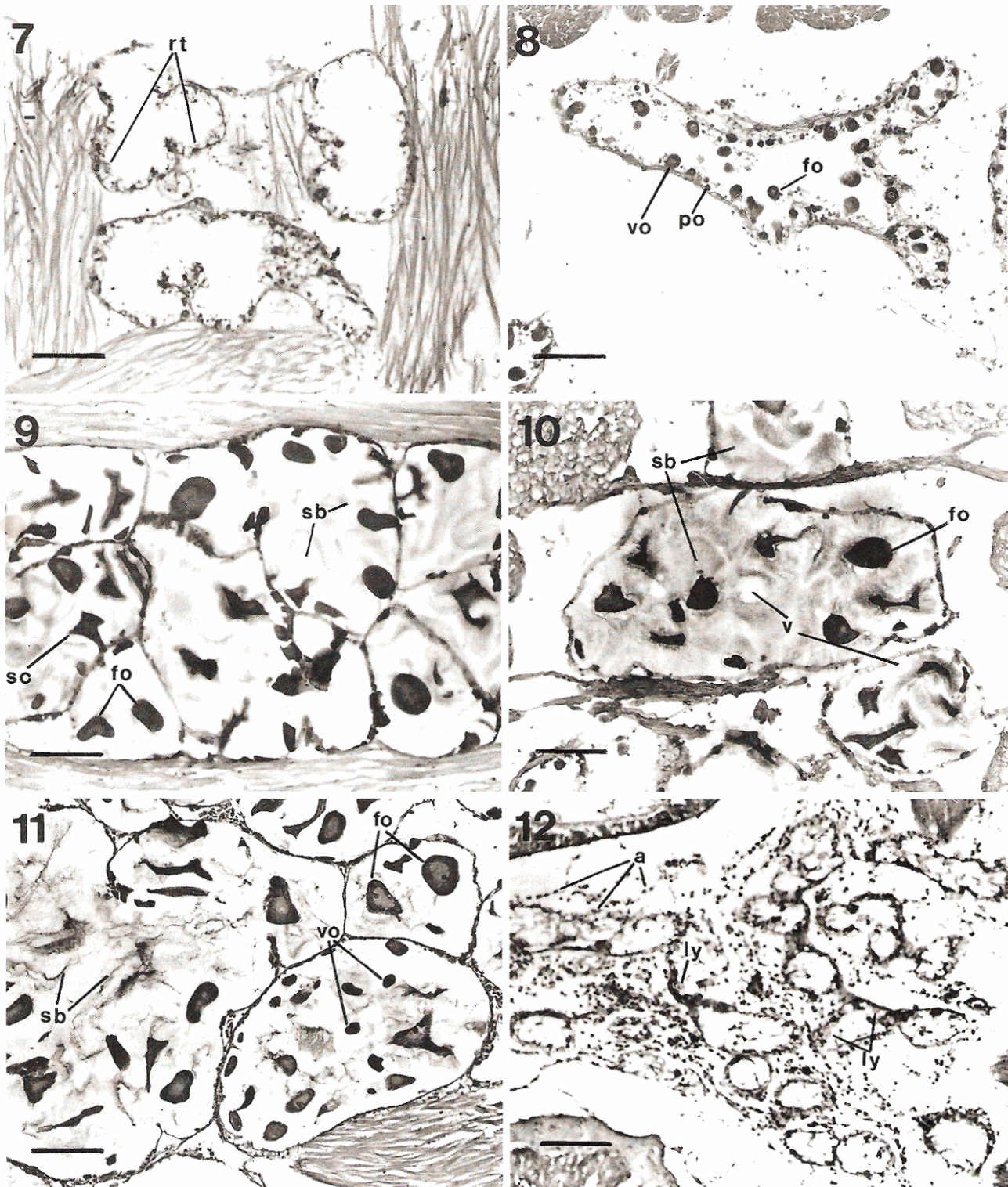
Maturity Scale in Females

Multiplication (Figure 7). Germ cells and abundant oogonia located in the reticulum of follicular cells (rt) form an inner annulus contiguous with the alveolar wall. There are also previtellogenic oocytes present. The fibers and cells as a whole confer a well defined aspect to the alveolar wall. The alveoli show irregular outlines and are dispersed, occupying 20 to 40% of the available inter-alveolar space. The lumen is spacious and generally represents more than 80% of the intra-alveolar space.

Early Maturation (Figure 8). Vitellogenic oocytes (vo) less than 20 μm in diameter are adherent to the acini walls, displaying rounded shapes. There is no material among these cells; oogonia and previtellogenic oocytes

(po) are abundant. Alveoli are rounded, occupying a percentage of the lumen similar to that of the preceding stage.

Advanced Maturation (Figure 9). Vitellogenic oocytes reach maximum diameters of 50 μm and become flattened, oval, or lobulated. Some of the cells, still attached to the alveolar walls, take stalked shapes (so). The basophilic substance (sb), contiguous with the vitellogenic oocytes' plasmatic membrane, is clearly visible, occupying most of the internal space of the alveoli. Oogonia and previtellogenic oocytes are abundant. Alveoli spread over 40 to 80% of the available space, in some cases deforming the adjacent muscular packs and imprinting irregular shapes on the neighboring digestive diverticula.



Figures 7–12. Appearance of the female gonads at different maturity stages. Figure 7. Multiplication. Figure 8. Early maturation. Figure 9. Advanced maturation. Figure 10. Maximum maturation with partial spawn. Figure 11. Spawning. Figure 12. Regression. Key: a, amoebocyte; fo, free oocyte; ly, lymphocyte; po, previtellogenic oocyte; rt, reticular tissue; sb, basophilic substance; so, stalked oocyte; v, vacuity; vo, vitellogenic oocyte. Scale bars = 100 μ m.

Maximum Maturation with Partial Spawn (Figure 10). Free oocytes (fo) reach maximum diameters and take compressed shapes. The basophilic substance (sb) around them shows well defined limits. It is possible to distinguish empty spaces (v) similar in shape and size to those of the cells remaining free in the lumen, suggesting that some of them have been evacuated. It is also possible to observe abundant oogonia, previtellogenic oocytes, and stalked oocytes. Alveoli spread over more than 80% of the available space and present polyhedral shapes due to the dense packing.

Spawning (Figure 11). The intra-alveolar space is ample, and some free oocytes (fo) still remain in it. Several vitellogenic cells (vo) of submaximal size ($d < 20 \mu\text{m}$) are free in the lumen, suggesting a massive detachment from the alveolar walls. Oogonia and previtellogenic oocytes are scarce. The alveoli recover rounded outlines, with a lobulated aspect in some cases, and lose contact with the adjacent organs and tissues.

Regression (Figure 12). Free oocytes have been fully evacuated; there are follicular cells in the lumen, and oogonia and oocytes among them. Eosinophil amoebocytes (a) are abundant, and lymphocytes (ly) appear grouped around the oocytes remaining in the wall. The alveoli occupy approximately 20% of the available space, dispersed among the other tissues, and appear flattened.

Maturity Scale in Males

Multiplication (Figure 13). There are primary germ cells in the alveolar walls. The most abundant cells are the spermatogonia (sg), especially among the follicular cells of the inner portion of the alveoli. In addition, there are several phagocytic cells (a) remaining from the inactivity phase (gonadal regression). The alveoli are irregular or rounded, abundant, small in diameter, and occupy 20 to 40% of the available space.

Early Maturation (Figure 14). The alveoli are filled with primary and secondary spermatocytes (sc), which appear grouped in dense packets among the spaces delimited by the follicular cells. At the periphery of the spermatocytes there are abundant spermatogonia. Spermatids and spermatozoa appear in some alveoli. The alveoli are rounded and have a greater diameter than those of the preceding stage, occupying 40 to 60% of the available space among the adjacent tissues.

Advanced Maturation (Figure 15). Dense cell masses detached from the alveolar walls fill the alveoli, occupying around 80% of the inner space. Spermatids and spermatozoa are abundant in all the alveoli, but they do not usually fill more than 40% of the space occupied by the cells of the entire spermatogenic series. Spermatocytes occupy the highest proportion of space within the alveoli. The spermatozoa (sz) appear in dense lines, in contact with septa of deep eosinophil conjunctive fibers (ef, Figures 6,15) formed at the inside of the alveoli. The recip-

rocal compression among alveoli produces a honeycomb pattern. The space occupied by the alveoli is 60 to 90% of the total.

Partial Evacuation with Recuperation (Figure 16). Spermatozoa present in the former stage have been evacuated. It is possible to observe several rounded and well defined vacuities among the cell mass (v). There are fewer spermatozoa than in the former stage, but it is possible to observe a dense mass of spermatocytes and spermatogonia. Other aspects are similar to those of the "advanced maturation" stage.

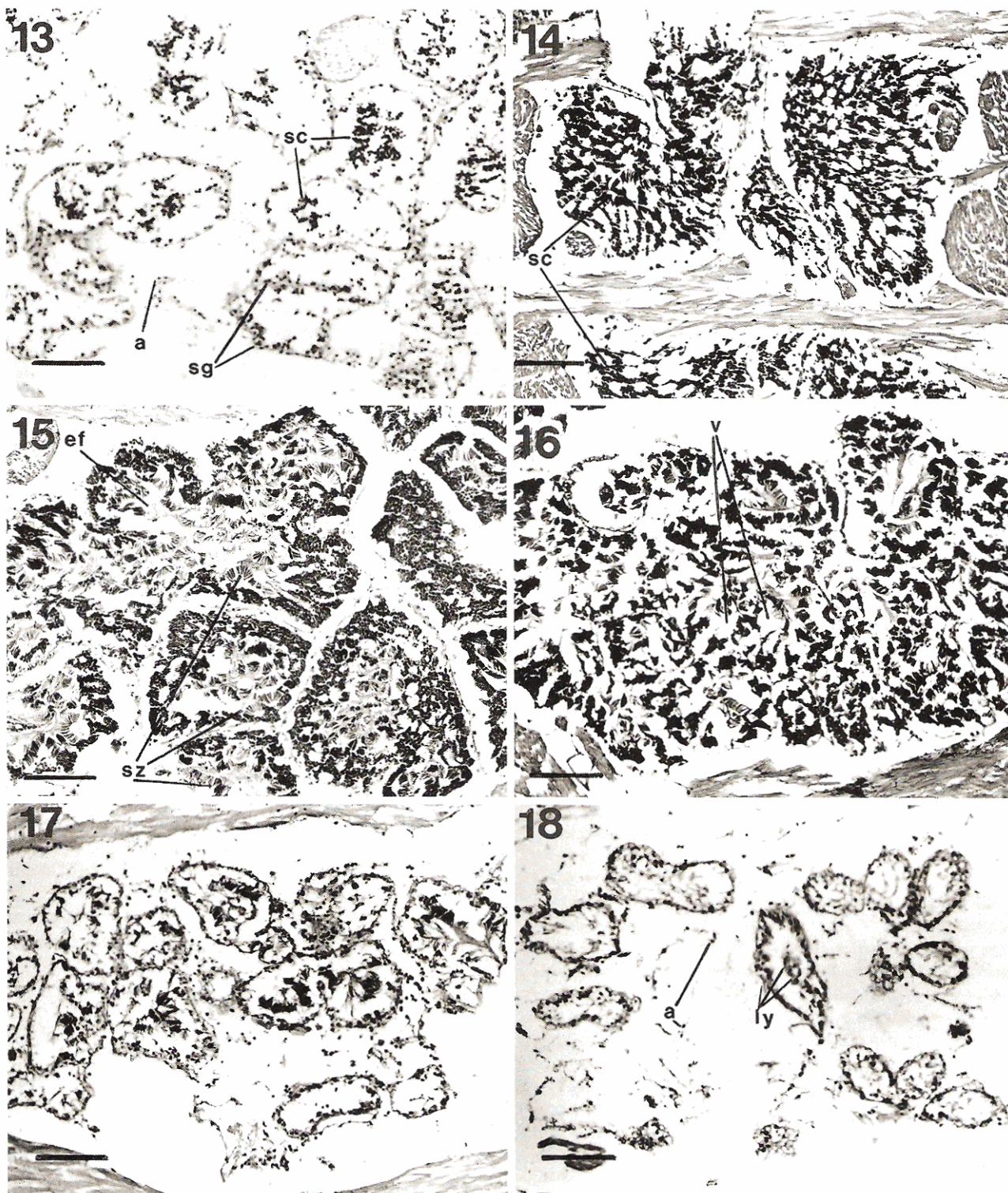
Evacuation (Figure 17). Spermatozoa, spermatids, and spermatocytes have nearly all been evacuated. The reticulum of follicular cells becomes more dispersed. A few remaining spermatogonia and spermatocytes appear attached to the alveolar walls. The alveoli are rounded, and the space among them has increased. The space occupied by the alveoli is 20 to 40% of the total.

Regression (Figure 18). The alveoli are nearly empty; it is not possible to observe spermatozoa or spermatids. There are abundant amoebocytes (a) and lymphocytes (ly) around the remaining spermatocytes and spermatogonia. The reticulum of follicular cells is absent or very scarce. The alveoli appear reduced in diameter and dispersed, occupying less than 20% of the available space.

Seasonal Variation of Gonadal Stages

In females (Figure 19), the multiplication began in June, and this stage was proportionally the most abundant in the winter samples. Between August and November, early maturation becomes advanced maturation. First partial spawnings were registered in November. Maximum maturation with partial spawning was the most abundant stage between November and February, but was scarce in March. Toward late summer and early autumn, female gonads were in regression, a stage that remained dominant until the beginning of the next winter.

In males (Figure 19), multiplication began in May and finished in September. Though the multiplication was, as in the females, the most abundant stage in winter, it was also possible to find males in early maturity after June. Early maturation was the most abundant stage toward late winter and early spring, whereas advanced maturation was the dominant stage during the spring months. First partial evacuation occurred in December, slightly later than the first partial spawning of the females. From December to February, most of the clams were in partial evacuation with recuperation stage. During the same period, it was still possible to find a considerable proportion of male gonads in advanced maturation. Final evacuation was detected in February and March, with a few delaying until April. Gonadal regression was initially detected in March; this stage was dominant in April and May, and it decreased gradually from June to August.



Figures 13–18. Appearance of the male gonads at different maturity stages. Figure 13. Multiplication. Figure 14. Early maturation. Figure 15. Advanced maturation. Figure 16. Partial evacuation with recuperation. Figure 17. Evacuation. Figure 18. Regression. Key: a, amoebocyte; ef, eosinophil fibers; ly, lymphocyte; sc, spermatocyte; sg, spermatogonia; sz, spermatozoa; v, vacuity. Scale bars = 100 μ m.

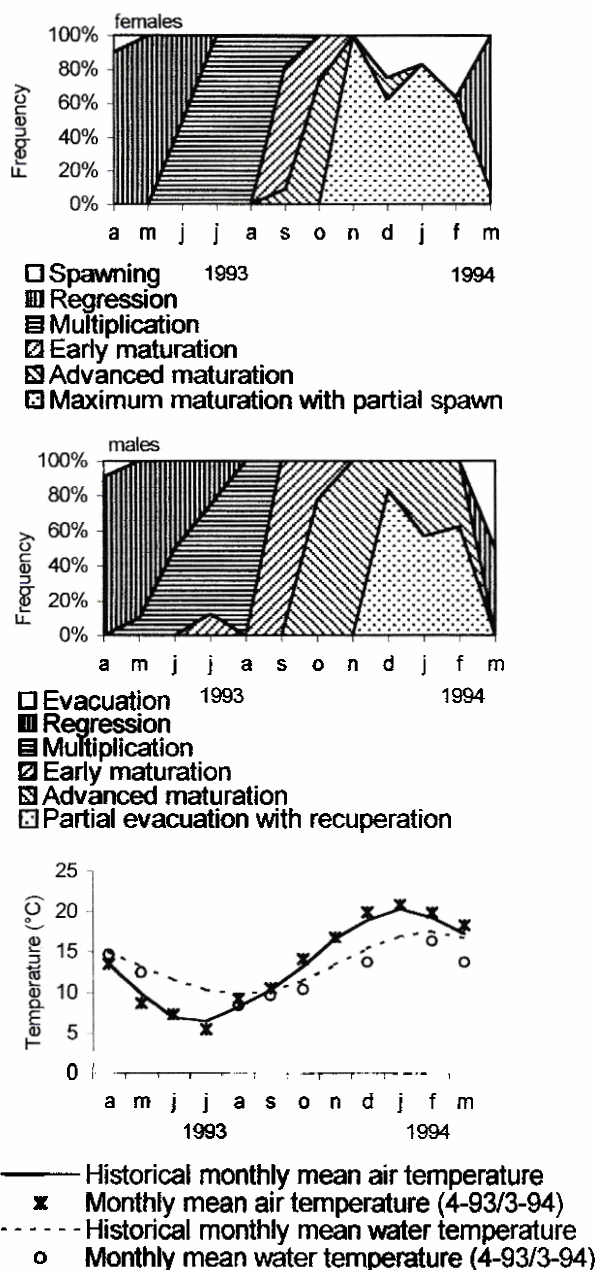


Figure 19. Percentage variations of occurrence of different gonadal stages by month, and monthly mean air and surface water temperature registers. Top: females; center: males; bottom: temperatures.

Seasonal Variation of the Percentage of Alveolar Area (PAA)

In females, PAA ranged between 13.9% (April) and 85.4% (December) (Figure 20). A gradual increase was detected during autumn and winter, except in September when the PAA was relatively low. After October, the PAA increased conspicuously until it stabilized at a maximum

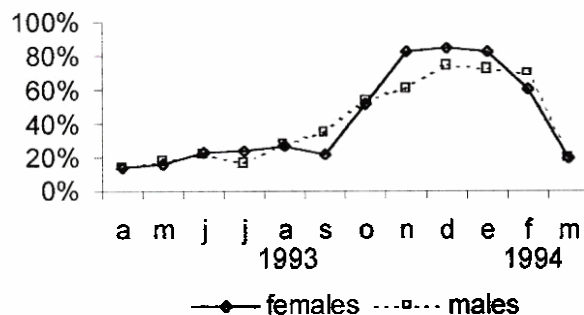


Figure 20. Monthly averages of the percentage of alveolar area (PAA) for both sexes.

from November to January. In February and March, the average PAA values decreased significantly.

In the males the lowest PAA average was observed in April (14.1%). After that, it increased gradually until December (80.4%) (Figure 20). During the subsequent months, higher values of PAA were detected. March was characterized by a conspicuous decrease in PAA.

Frequency Distribution of Vitellogenic Oocyte Diameter

Vitellogenic oocytes were present in the gonads of all females from September until February. Analysis of vitellogenic oocyte size frequency distribution by month shows the lowest values in September (6–39 μm , average = 17 μm), an important increase in October and November, and stabilization in December and January. Highest oocyte diameters were observed in January (16–71 μm , average = 43 μm), while a slight decrease was detected in February (Figure 21). In March, vitellogenic oocytes were only present in a small percentage of females (12.5%) due to full evacuation or reabsorption. A high correlation between average oocyte diameter per individual and the square root of the corresponding mean PAA was detected ($r = 0.90$, $n = 52$).

DISCUSSION

It has been reported that occasional hermaphroditic individuals occur in several species of bivalves defined as dioecious (Coe, 1945). However, this pattern is not frequent in Tellinidae (Lammens, 1967; Rae, 1978; Salzwedell, 1979; Brousseau, 1987; Kawai et al., 1993). Furthermore, individuals of *T. petitiiana* with both sexes were not detected during this study.

Sex ratio in *T. petitiiana* is not different from the 1:1 relationship reported for other tellinids and strict gonochoric bivalves such as *Macoma secta* and *Macoma nasuta* (Rae, 1978); *Tellina fabula* (Salzwedell, 1979); *Donax gouldii* Dall, 1921 (Fretter & Graham, 1964); *Mulinia lateralis* (Say, 1822) (Calabresse, 1969); *Spisula solidissima* (Jones, 1981); *Protothaca asperrima* (Palacios et al.,

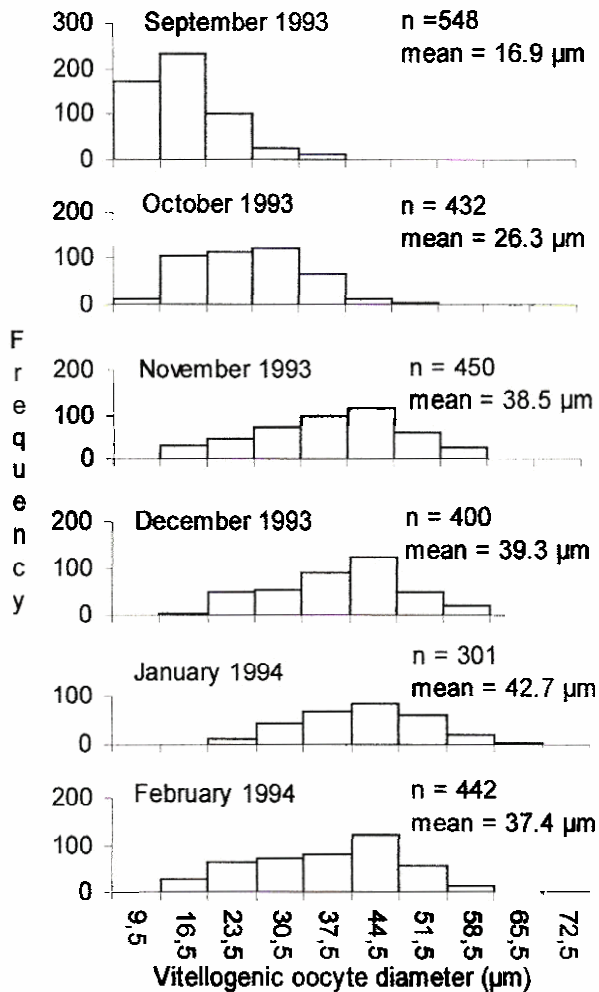


Figure 21. Monthly frequency distributions of diameters of vitellogenic oocytes.

1986), and *Spisula solidissima similis* (Kanti et al., 1993). Unlike the case in *Macoma balthica* (Brousseau, 1987), the macroscopic appearance (white to yellowish white color) of the *T. petitiiana* gonad during maximum maturity cannot be used to determine sex.

Size at sexual maturity has been reported in the tellinids *T. fabula* (10 mm; Salzwedell, 1979) and *N. nitidula* (14 mm; Kawai et al., 1993), and juvenile sexuality has been reported in 14–16 mm *Tellina serrata* Brocchi, 1814 (Lucas, 1975). Although the size range explored in this study (33–40 mm) does not include the size at maturity in *T. petitiiana*, mature females and males of 16 and 15 mm in size were identified from a reduced number of histological sections.

The aspect and the sequence of the oogenic series of *T. petitiiana* are similar to those described by Tranter (1958) for *Pinctada albina* (Lamarck). The change in the tinctorial affinity of *T. petitiiana* oocytes at the beginning

of the vitellogenic stage is similar to that described in *Aequipecten tehuelchus* (Lasta & Calvo, 1978). The material observed among the free oocytes of *T. petitiiana* is similar to the substance described in *Pecten maximus* Linnaeus, 1758 (Tang, 1941); *Placopecten magellanicus* (Gmelin, 1791) (Merrill & Burch, 1960); and *Macoma balthica* (Lammens, 1967). During the advanced maturation of these species, it is possible to observe a non-granular substance, possibly a component of the cell membrane among the oocytes (Sastry, 1979). It has been suggested that this substance is fibrillar material forming a vitelline envelope with unknown function (Beninger & Le Pennec, 1991).

Except for the arrangement of spermatozoa in the alveoli, spermatogenesis in *T. petitiiana* is similar to that described for *Pinctada albina* (Tranter, 1958). In *T. petitiiana* the spermatids and spermatozoa packs are irregularly arranged in an extensive area of the alveoli. In *P. albina*, in contrast, spermatids become spermatozoa, regularly arranged toward the lumen (Tranter, 1958). A pattern similar to the condition in *T. petitiiana* has been described for other bivalves. In *Macoma nasuta* (Rae, 1978), the more advanced sexual male products are compressed into cavities delimited by the follicular cells, giving the sections a patchy appearance. In *Protothaca asperrima*, the spermatids can be found lined along the inner edge of the alveoli or spread in the alveolar lumen forming "seed patches" without any order (Palacios et al., 1986).

T. petitiiana is an iteroparous species, with a single spawning period per year, as has been reported in other tellinids such as *Tellina tenuis* Da Costa, 1778 (Ansell & Trevallion, 1967); *T. fabula* (Salzwedell, 1979); *M. balthica* (Lammens, 1967); and *M. secta* (Rae, 1978). Multiplication stage is dominant during the winter, although in males this period starts in May. It is possible to observe several maturation degrees from middle winter (males) or early spring (females) until summer (February). The gamete evacuation starts in November and continues until April, with peaks in late spring (December, males) or summer (February–March, females). During autumn, gonadal regression is the dominant stage. The gametogenic cycle of *T. petitiiana* varies seasonally with the typical annual temperature variation of the cold-temperate seas. Since during the term of this study monthly water temperature averages were lower than historic registers (Figure 19), it is possible to expect inter-annual variations in the temporal range of each reproductive stage.

The seasonal variation of the average PAA values reflected the seasonal variation of the *T. petitiiana* gonadal stages. In females, maximum values from November–January coincided with the maturation peak prior to the beginning of spawning. Low values for April–May coincided with the gonadal regression period. The slight PAA increase detected in June–August matched the multiplication stage; the significant PAA increase after September

coincided with cytoplasmatic enlargement sizes due to advanced maturation. The males showed a similar pattern, with a very prominent PAA increase during October and November (advanced maturation), a decrease from January to April (evacuation with partial recuperation and evacuation stages), lower values in April and May (regression), and a moderate increase between May and August (multiplication). Variation and range of indexes similar to those of the PAA reported here for *T. petittiana* have been found in other bivalves. The proportion of the visual field occupied by gonad tissue in *Spisula solidissima* males ranged from 9.1–66.5% to 26.5–77.5% in 2 consecutive years (Kanti et al., 1993). In *A. tehuelchus* the female alveolar area increased from 30% to 97% between July and December, while the same variable represented about 40% during March-June (Lasta & Calvo, 1978).

There is a high correlation between the average diameters of vitellogenic oocytes per individual and the square roots of the corresponding PAA. In agreement with this, oocyte size matches the gonadal stage sequence detected in *T. petittiana*. The smallest average vitellogenic oocyte diameter agrees with early maturation stage found during September and advanced maturity of October. The larger oocytes observed between November and January are typical of the maximum maturation with partial spawn. The decrease in February coincides with the spawning registered in a large proportion of clams. The massive spawning detected between February and March is shown by the absence of vitellogenic oocytes from 87.5% of the individuals analyzed in the last month.

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