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Stages of gonad development in the sea scallop Placopecten magellanicus (Gmelin) based on both macroscopic and microscopic observation of the gametogenic cycle.

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ABSTRACT

Stages of gonad development based on macroscopic observations and stages based on microscopic observations of Placopecten magellanicus gonads are presented. Due to the subjectivity of macroscopic observations of gonads, only four macroscopic development stages are identified : 1) spent/undeveloped, 2) early developing 3) late developing/full and 4) spawning. Microscopic observations based on histological sections of gonads allow the gametogenic process to be divided into seven stages: (I) differentiated, (II) developing, (III) filling, (IV) ripe, (V_1) spawning, (V_2) spent, (VI) latent.

RESUME

Les étapes du développement gonadique basées sur des observations macroscopiques et les étapes basées sur des obervations microscopiques de la gonade du Placopecten magellanicus sont presentées. À cause de la sujectivité des observations macroscopiques de gonades, seulement quatre étapes macroscopiques sont identifiées: 1) pondu/non-développé, 2) développment débutant 3) développement avancé/plein et 4) en cours de ponte. Les observations microscopiques basées sur des sections histologiques de gonades permettent de diviser le processus en sept étapes: (I) différencié, (II) en développement, (III) remplissage, (IV) mur, (V_1) en cours de ponte, (V_2) pondu et (VI) latent.

KEY WORDS: gametogenesis, Placopecten magellanicus, sea scallop, gonad stages.

INTRODUCTION

Gametogenesis of bivalve molluscs has been described by several authors for various species: Mya arenaria (Coe and Turner, 1938), Paphya staminea (Quayle, 1943), Pinctada albina (Tranter, 1958), Argopecten irradians, (Sastry, 1961), Chlamys varia, (Lucas, 1965). Sastry (1979) gives a detailed review of gametogenesis of the Pelecypoda.

According to Tranter (1958), both sexes are derived from large resting cells, (referred to as "stem cells") which are dispersed around the follicle walls of the gonads. These undifferentiated cells are referred to as "primary germ cells" by Coe and Turner (1938) and as "cellules mères" (= mother cells) by Lubet (1959). Each of these diploid germ cells undergoes a series of mitotic divisions before giving rise to spermatogonia or oogonia (Le Moigne 1979). Spermatogonia and oogonia multiply by means of mitotic divisions. After the last mitotic division the spermatogonia increase in size to become primary spermatocytes (spermatocytes I). The oogonia become primary oocytes (oocytes I).

Spermatocyte I and oocyte I maturation begins when they enter the first meiotic division. In male, spermatocyte I undergoes the first meiotic division to produce two haploid secondary spermatocytes (spermatocytes II). These then undergo the second meiotic division to produce four haploid spermatids which differentiate into spermatozoa (De Robertis and De Robertis 1980).

In most female molluscs, the first meiotic division of the oocytes I only reaches the end of the prophase or the beginning of the metaphase, unfertilized eggs are blocked at this stage (Raven 1966). Therefore only oocytes I are observed in the gonads. The oocytes I appear to enter a resting stage which is characterized by a vegetative growth (Tranter 1958). In Placopecten magellanicus the oocytes I grow from a 5 µm to 70 µm in diameter. After spawning, maturation continues only after the sperm enters the egg (Raven 1966).

The reproductive cycle of several bivalve and gastropod species has been described as comprising a series of stages based on histological examination (Mason 1958; Tranter 1958; Reddiah 1962; Sastry 1963; Lucas 1965; Smith 1966; Hennick 1970; Naidu 1970; Robinson et al 1981). Among these authors, Naidu (1970) and Robinson et al. (1981) worked on the sea scallop, Placopecten magellanicus. Naidu (1970) presented nine stages and described the macroscopic and microscopic aspects of the gonad for each stage. The application of stages described by Naidu (1970) is sometimes difficult because there is no way to differentiate between undeveloped adult and virgin juveniles stages. Robinson et al. (1981) briefly described six microscopic stages which were based on a shortened version of Naidu's (1970) stages. In this paper macroscopic and microscopic gonad development stages of the gametogenic cycle for adult P. magellanicus are presented.

MATERIALS AND METHODS

Scallops were collected in from five areas of the southern Gulf of St. Lawrence between April and November 1984 (Figure 1). After measuring shell height, gonads were photographed, then carefully dissected and stored for 48 hours in Bouin's fixative. Larger gonads were notched to allow better fixative penetration. After fixation, gonads were transferred to 70% ethanol until further processing. Following standard dehydration, clearing and parafin (Paraplast) embedding, specimens were sectioned (8 or 10 µm thickness) and stained with haematoxylin/eosin (Humason 1972). Examination of slides was made using a compound microscope and photographs were taken of each specimen at a magnification of 100x and x250.

Examples to illustrate each stage were selected from a total of 486 specimens. The scallop gonads chosen for illustration were taken from scallops with shell heights of 70mm or more. This selection insured that only adult scallops were studied. The macroscopic gonad development stages are based on observations made with the naked eye. The microscopic gonad development stages were developed based on histological sections. Features common to both sexes are presented first. Features which allow differentiation between males and females are then described. The percentage of follicle fullness and of interfollicular space at stages I, II and III for male and female were calculated using the "optical pattern recognition system" computer program by BioSonics Inc. Sections which were chosen for the representive photogragh were also chosen for percentage measurements. A representative area from males and females in stages I, II and III was selected and measured.

RESULTS

MACROSCOPIC STAGES

Four general macroscopic stages of gonad development were identified: 1) spent/undeveloped 2) early developing 3) late developing/full and 4) spawning.

1- SPENT/UNDEVELOPED

Male and female gonads can not be differentiated from one another. The gonads appear collapsed, translucent, flat and watery. The intestinal loop is clearly visible. If the above description is observed in winter or early spring the gonads are assumed to be undeveloped. If this stage is observed in late summer or fall, the gonads are believed to be spent. In some cases, the spent gonads are light pink in colour, suggesting the sex to be female.

2- **EARLY DEVELOPING**

The gonads are filling and appear to contain one quarter to one half their capacity. At this stage males can be differentiated from females. Portions of the male gonad contain cloudy white sex cells and some portions are transparent. Female gonads are pink to orange. The intestinal loop is visible but fading.

3-**LATE DEVELOPING/FULL**

Gonads are turgid and rounded and appear to have reached their maximum capacity. Follicles are packed and give the gonad a granular appearance. The colour of the male gonad varies from off-white to cream while the female gonad varies from pink to brick red. The intestinal loop cannot be seen unless it is near the gonad wall.

3- **SPAWNING**

Gonads are flaccid to varying degrees depending on the number of follicles emptied. Translucent islets can be seen in the cream or red gonads. The colour of the female gonads is fading to a pale pink and the male gonads are becoming more translucent as spawning progresses.

MICROSCOPIC STAGES

Seven microscopic gonad development stages were identified: 1) differentiated 2) developing 3) filling 4) ripe 5) spawning 6) spent and 7) latent.

STAGE I - DIFFERENTIATED

GROSS MORPHOLOGY (Figures 2A, 2B, 2C and 2D)

The follicles are well defined and in a typical section they occupy 42 to 46% of the gonads. The space between the follicle (interfollicular space) is highly visible. A large amount of connective and muscular tissue is dispersed within the interfollicular space. The ciliated gonoducts often appear to have a circular or an elongated irregular form. At this stage, the gonoducts do not usually have a visible lumen. The intestine may occupy most of the gonad, depending on where the section is taken. The lumen of the follicle may occupy up to 63% of the follicle.

MALE (Figures 2A and 2B)

The follicles contain only a few layers of cells along the follicle walls. Elongated germ cells which measure up to 10 µm in length and 5 µm in width are dispersed in the first layer of cells. The other layers of cells are made up of spermatogonia. Spermatogonia are spherical cells with no visible cytoplasm, they measure 3.2 to 4.3 µm in diameter.

FEMALE (Figures 2C and 2D)

A few germ cells, oogonia, and primary oocytes (oocytes I) are dispersed along the follicle wall. The germ cells are similar in size as male germ cells. The oogonia are round in section and have a diameter of 4.2 to 5.3 µm. They have no visible cytoplasm. The oocyte I has various appearance as it progresses through the prophase of the meiotic division. In the early development of the prophase the chromosomes of the oocyte I are densely stained clumps, the nucleolus is not visible and the oocyte I measures 5 µm. Towards the end of the meiotic prophase the nucleolus reappears in the oocyte I and the oocyte I measures 10 to 24 µm. The meiotic division of the oocytes I only reaches the end of the prophase or the beginning of the metaphase. At this stage, oocytes I never project into the lumen and appear to be incorporated with the follicle wall. The nucleus of a oocyte I measuring 24 µm, measures 17 µm and the nucleolus measures 4.2 µm.

STAGE II - DEVELOPING

GROSS MORPHOLOGY (Figures 3A, 3B, 3C and 3D)

Typicallly, the follicles occupy 42 to 46% of the gonad. The follicles contain proliferating sex cells. The follicular lumen can still be observed and may occupy up to 45% of the follicle volume. In the interfollicular space the connective muscular tissues are still visible. The intestine may still appear to occupy most of the gonad depending on where the section is taken. The gonoducts are similar in appearance to those observed in stage I but the gonoduct lumen may be observed more often.

MALE (Figures 3A and 3B)

The follicle walls are still lined with a few germ cells and spermatogonia. Several layers of spermatocytes I and II begin to fill the follicular lumen. The spermatocytes I measure 5µm in diameter and their nucleus measures 3 µm. The spermatocytes II measure 3.2 µm and their nucleus measures 2.2 µm. The spermatocytes I and II have very faintly stained cell membranes which surround the clear cytoplasm and the densely stained nucleus. Occasionally spermatids and spermatozoa can be seen near the follicular lumen.

FEMALE (Figures 3C and 3D)

The follicle walls may still contain a few germ cells, oogonia and smaller oocytes I (<24 µm). The majority of the oocytes I are attached to the follicular wall protrude into the follicular lumen. These attached oocytes measure 24-39 µm in diameter.

STAGE III -FILLING

GROSS MORPHOLOGY (Figures 4A, 4B, 4C and 4D)

Typically, the follicles occupy 82 to 88% of the gonad. The connective and muscular tissue may still be clearly observed between follicles. The intestine may also be observed depending on where the section is taken. The gonoducts are similar in appearance to those observed in stage II but may appear larger. At this stage virtually all the follicles are filled with sex cells. The follicular lumen has almost disappeared, only occupying 0.5 to 1% of the follicle.

MALE (Figures 4A and 4B)

Germ cells and spermatogonia may still line the follicle walls. The follicles are mostly filled with spermatocytes I and II and spermatids. Spermatozoa may be found in the center of the follicles. The circular-shape spermatids measure 2.2 µm in diameter, the spade-shape spermatozoa heads measure 1.2 to 1.4 µm in width and 2.2 µm in length and tails are 35 µm long. The spermatozoa tail take up the eosin stain. In some cases the spermatozoa have no visible orientation and in other cases the spermatozoa begin to orient their heads toward the follicle walls.

FEMALE (Figures 4C and 4D)

Smaller oocyte I (<24 µm) may still be present along the follicle walls. The follicles are filled with stalked and free oocytes measuring 40 to 60 µm in diameter. A oocyte I measuring 54 µm, contains a nucleus measuring approximately 32 µm and a 4.4 µm nucleolus. The stalked oocytes I are characterized by a peduncle or stalk which attaches them to the follicle wall. Chromatin associated with the nucleolus can be observed in the oocytes I. In rare cases the germinal vesicle in the oocytes I shows signs of breakage.

STAGE IV - RIPE

GROSS MORPHOLOGY (Figures 5A, 5B, 5C and 5D)

The follicles are full to capacity and adjacent follicle walls are touching each other. The interfollicular space is practically non-existent, except for a limited area around the intestine. The connective and muscular tissue can only be seen in this space surrounding the intestine. The gonoducts, when visible, appear similar to those observed in earlier stages.

MALE (Figures 5A and 5B)

Spermatozoa represent almost 100% of the follicular content. A thin layer of spermatocytes and spermatids may be seen along the follicle wall. The spermatozoa appear radially oriented with heads pointed toward the follicle walls and tails toward the center. This orientation gives the follicles a "cauliflower pattern" appearance.

NOTE (Figures 6A and 6B) Occasionally, in some areas of the gonad, follicle walls seem to have disappeared. Tightly packed spermatozoa with no orientation seem to be held in the interfollicular space by the pressure of the gonad wall and normal follicles from other areas.

FEMALE (Figures 5C and 5D)

The follicles are packed with free oocytes I measuring 50 to 70 µm in diameter. The germinal vesicle in most of the oocytes show signs of breakage. Only a few small oocytes I (<24 µm) remain near the follicle walls. The oocytes are so tightly packed that they assume a polygonal shape giving the follicles a "honey comb" appearance.

NOTE (Figures 6C and 6D) Abnormal islets of deformed oocytes may sometimes be observed. These oocytes do not have the regular polygonal shape described above. The abundance of these abnormal oocytes may vary from 0% to 100% of the oocytes in a given section.

STAGE V_1 -SPAWNING

GROSS MORPHOLOGY (Figures 7A, 7B, 7C and 7D)

The sexual products are in the process of being released. The follicles show varying degrees of emptiness and the gonoducts are enlarged. These enlarged ciliated gonoducts are circular or irregular in shape and usually have large lumen. The muscular and connective tissue may still be observed in the space around the intestine.

MALE (Figures 7A and 7B)

Radially arranged spermatozoa are the predominant sex cells present, however the follicle wall may still be lined with spermatocytes I, II and spermatids which form a thin, darker band along the follicle walls. Spermatozoa are often seen in the gonoducts.

FEMALE (Figures 7C and 7D)

Follicles contain varying proportions of stalked and free oocytes I. Few small ooctyes I (<24 µm) may be found along the follicle walls. Free oocytes I are rarely seen in the gonoducts.

STAGE V_2 -SPENT

GROSS MORPHLOGY (Figures 8A, 8B, 8C and 8D)

Most of the follicles are empty. The gonoducts are similar in appearance to those in stage V_1, however they may appear to be retracting because they may be more convoluted and the lumen may be smaller than in stage V_1. The intestine may or may not be observed depending on where the section was taken. The connective and muscular tissue can once again be seen in the interfollicular space. Phagocytic cells are abundant.

MALE (Figures 8A and 8B)

Residual spermatozoa are found along the follicle walls or in the follicular lumen.

FEMALE (Figure 8C and 8D)

Residual oocytes are present in a few follicles. Some oocytes I may show signs of autolysis and/or resorption. Some follicles appear to have failed to release their gametes.

STAGE VI - LATENT

GROSS MORPHOLOGY (Figure 8E and 8F)

At this stage it is impossible to distinguish between the sexes. The follicle walls are still conspicuous but there is no sign of gametogenic activity. The intestine may appear to occupy a large amount of space as in stage I. Gonoducts are similar in shape to stage I, loose connective and muscular tissue are present in the interfollicular spaces. Phagocytic cells may be observed.

DISCUSSION

For each macroscopic development stage of the gonads of P. magellanicus Naidu (1970) described a corresponding microscopic stage. Chipperfield (1953), Mason (1958), Reddiah (1962) and Sastry (1963) used the same approach when describing gametogenic stages in other pectinid species. In theory, this may be the most logical approach however, macroscopic characteristics are difficult to determine accurately because the key features are more subjective than those observed histologically. In this paper, the macroscopic stages were kept simple to reduce subjectivity. No attempt was made to relate macroscopic stages to corresponding microscopic stages. Hence, macroscopic examination allows only to distinguish between, spent/undeveloped, early developing, late developing/full, and spawning gonads.

Summarizing a continuous phenomenon, such as gametogenesis, in a number of step-like stages makes it easier to describe. In certain cases however, it is inevitably difficult to assign an observed histological image to one stage or another. The individual variability within a single population as well as between populations can make accurate comparisons difficult.

The microscopic gonad development stages, proposed in this paper are based on the presence, the abundance, and the arrangement of cell types in the follicles as they occur during gametogenesis in both males and females. Tranter (1958) described in detail the different cell types in gonad of male and female Pinctada albina. Similar cell types were observed in Placopecten magellanicus, however only general description are given in this paper, and the main differentiating characteristic is the cell measurement.

In stage I, primary germ cells and spermatogonia are predominant in males and in females, germ cells, oogonia and small (<24 µm) oocyte I.

Stage II is characterized by the appearance of spermatocytes I and II, occasional spermatids and spermatozoa in males and in females, stalked oocytes I.

In stage III, follicles are full of sex cells. Male follicles are filled mainly with spermatocytes I and II plus a few spermatids and spermatozoa. In females, follicles are filled with stalked and free oocytes I.

In stage IV the follicles are packed to maximum capacity. The characteristic feature of stage IV in males is the distinctive "cauliflower" pattern within the follicles formed by the radially arranged spermatozoa. In females a "honey comb" pattern is formed by the free oocytes I which are compressed into polygonal shapes due to crowding. The germinal vesicle is the enlarged nucleus of the primary oocyte (oocyte I) before reduction divisions are complete. As in other pectinid species (Sastry 1979), the germinal vesicle of a large number of oocytes shows signs of breaking down. This breakdown indicates the beginning of maturation as it occurs at the prometaphase of the first meiotic division (Raven 1966; De Robertis and De Robertis 1980). Germinal vesicle breakage occurring in the oocyte was also observed by Mason (1958) in Pecten maximus, by Tranter (1958) in Pinctada albina, by Lubet (1965) in Mytilus edulis and by Naidu (1970) in P. magellanicus.

In female stage IV gonads and less frequently stage III gonads, deformed oocytes are sometimes present. These abnormal oocytes appear to be in various degrees of lysis. The extent of the phenomenon is variable, affecting from 0% to 100% of the oocytes in a single tissue section.

In male stage IV gonads, abnormal areas where the follicle walls seem to have disappeared can occasionally be observed. Large amounts of spermatozoa with no defined orientation seem to be contained within the interfollicular space between the gonad wall and adjacent follicle walls. This could be a preparation artefact.

Spawning stages V_1 and V_2 are assigned the same stage number with different subscripts because they are really two phases of the same stage with no change in the cell type but a distinct difference in the numbers of gametes remaining.

During the latent or resting stage, (VI), sex cannot be deterrnined because no differentiated sex cells remain.

The microscopic (histologically-based) gonad development stages in this paper are similar to the stages proposed by Tranter (1958) who described the reproductive cycle of Pinctada albina and to the stages presented by Robinson et. al. (1981) for Placopecten magellanicus. However these two authors did not describe a latent stage as observed in

this study. Naidu (1970) who studied P. magellanicus in Port au Port, Newfoundland and Beninger (1987) who studied the same species in the Bay of Fundy, New Brunswick, did not identify a resting period. It is possible that gametogenesis of P. magellanicus in Port au Port, Newfoundland and in the Bay of Fundy, New Brunswick resumes immediately after spawning. Thompson (1977) who studied P. magellanicus from southeastern Newfoundland reported that the gonad enters the "resting stage" after spawning. A distinct resting period was observed in this study and similar interludes between successive cycles of gametogenesis have been observed in several species, e.g.: Chipperfield (1953) described a stage 0, "resting spent stage" for Mytilus edulis. Lubet (1959) identified a stage 0, as "repos sexuel" (= sexual rest) for Chlamys varia. Reddiah (1962) did not described a resting period but identified a stage 0, "immature" for the same species.

During the course of this study the latent stage (VI) was only occasionally observed. The latent stage does not appear to be obligatory. It can be hypothesized that individuals who successfully extrude all their sexual products due to ideal synchrony of environmental and physiological conditions will have completely emptied follicles. Their sex cannot be determined until re-development begins on the follicle walls. These conditions define the latent stage of gonad development. The resumption of gametogenesis will likely be dependent upon environmental stimuli. Usually, however, there are residual oocytes or spermatozoa in the follicles allowing sex determination and gonad development is, therefore, said to be in stage V_2. In some cases individuals with oogonia or spermatogonia developing on the follicle walls still contain residual gametes are in the lumen.

The gonad development stages presented by Naidu (1970) for P. magellanicus include virgin gonads. Mason (1958) and Reddiah (1962) also presented stages for other pectinids which included virgin stages. Lubet and Allarakh (1981) describe the spent gonads of Chlamys opercularis and C. varia as having the same histological characteristics as a juvenile gonad. However, Lucas (1975) found that juvenile sexuality can be distinguished from adult sexuality. A number of species strictly gonochoric as adults will exhibit a juvenile hermaphroditic sexuality (Ropes 1968, Lucas 1975, Worms and Davidson 1986). Gonad development stages which include virgins, juveniles and adults can be difficult to interpret because they mix the linear juvenile development phase with the cyclic gametogenic phases of adults. A greater comprehension of pectinid reproductive development would be achieved if the sexual development of juveniles is studied separately from the gametogenic cycle of the adults.

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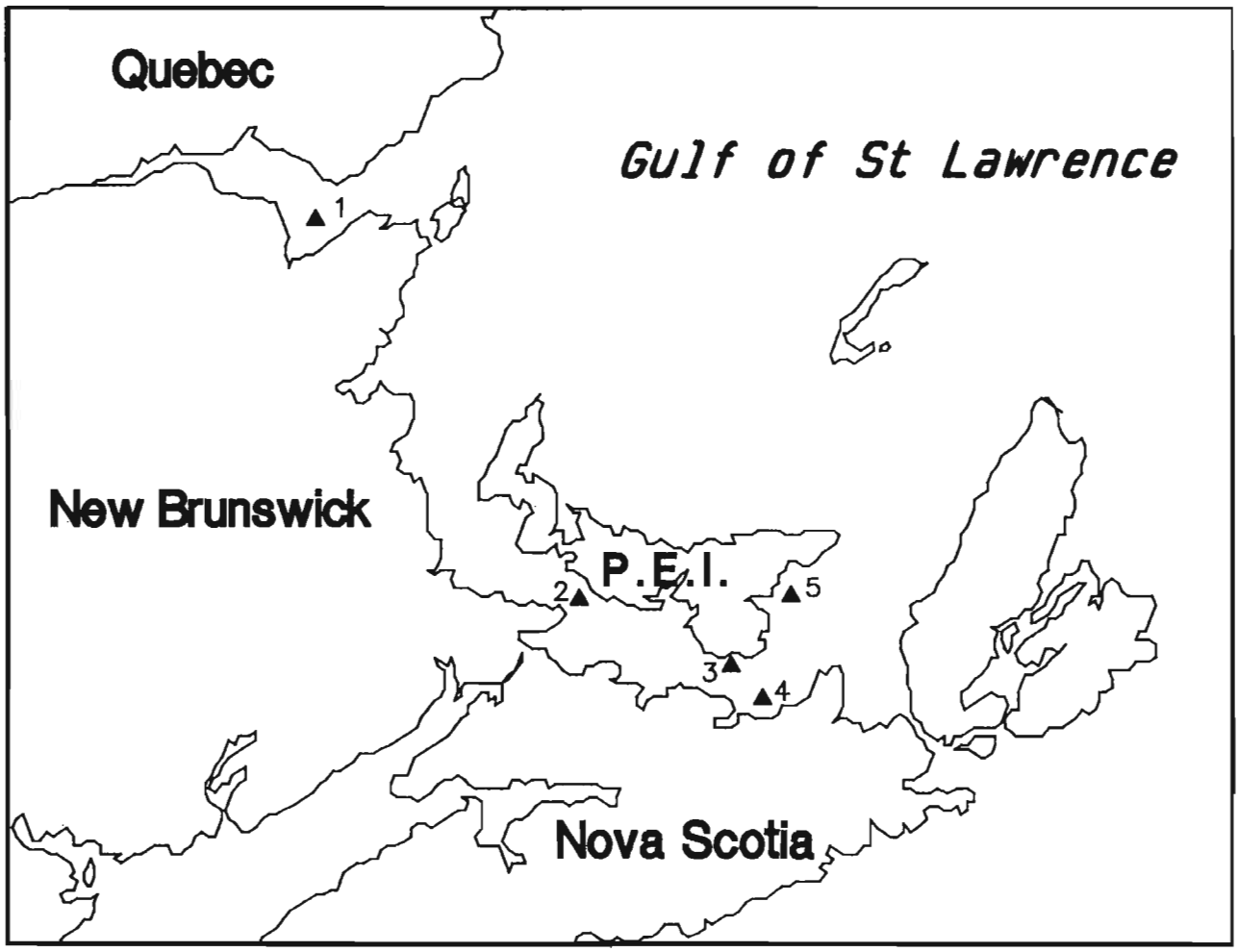

Figure 1. Map of the southern Gulf of St. Lawrence showing the location of sampling sites (▲). 1) Baie des Chaleurs 2) Cape Tormentine 3) Wood Islands 4) Pictou 5) Montague.

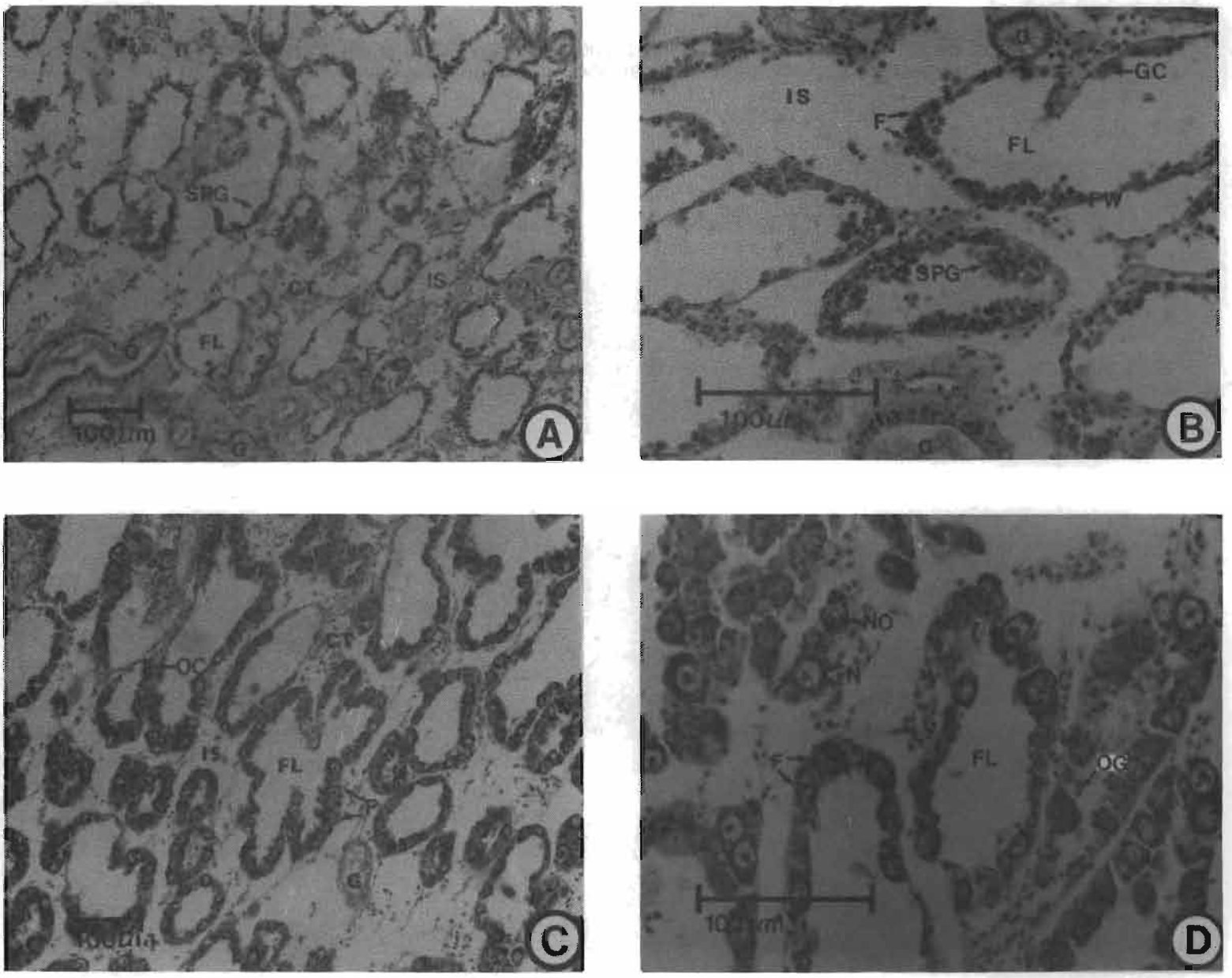

Figure 2. Gonad development stages of Placopecten magellanicus. A) Stage I, male at 100X magnification, B) Stage I, male at 250X magnification, C) Stage I, female at 100X magnification, D) Stage I, female at 250X magnification.

CT = connective tissue, F = follicle, FL = follicular lumen, FW = follicle wall, G = gonoduct GC = germinal cell, IS = interfollicular space, N = nucleus, NO = nucleolus, OC = oocyte I, OG = oogonium, SPG = spermatogonium.

Stages of gonad development in the sea scallop, Placopecten magellanicus (Gmelin) based on both macroscopic and microscopic observation of the gametogenic cycle.

Leslie-Anne Davidson and Jean Worms

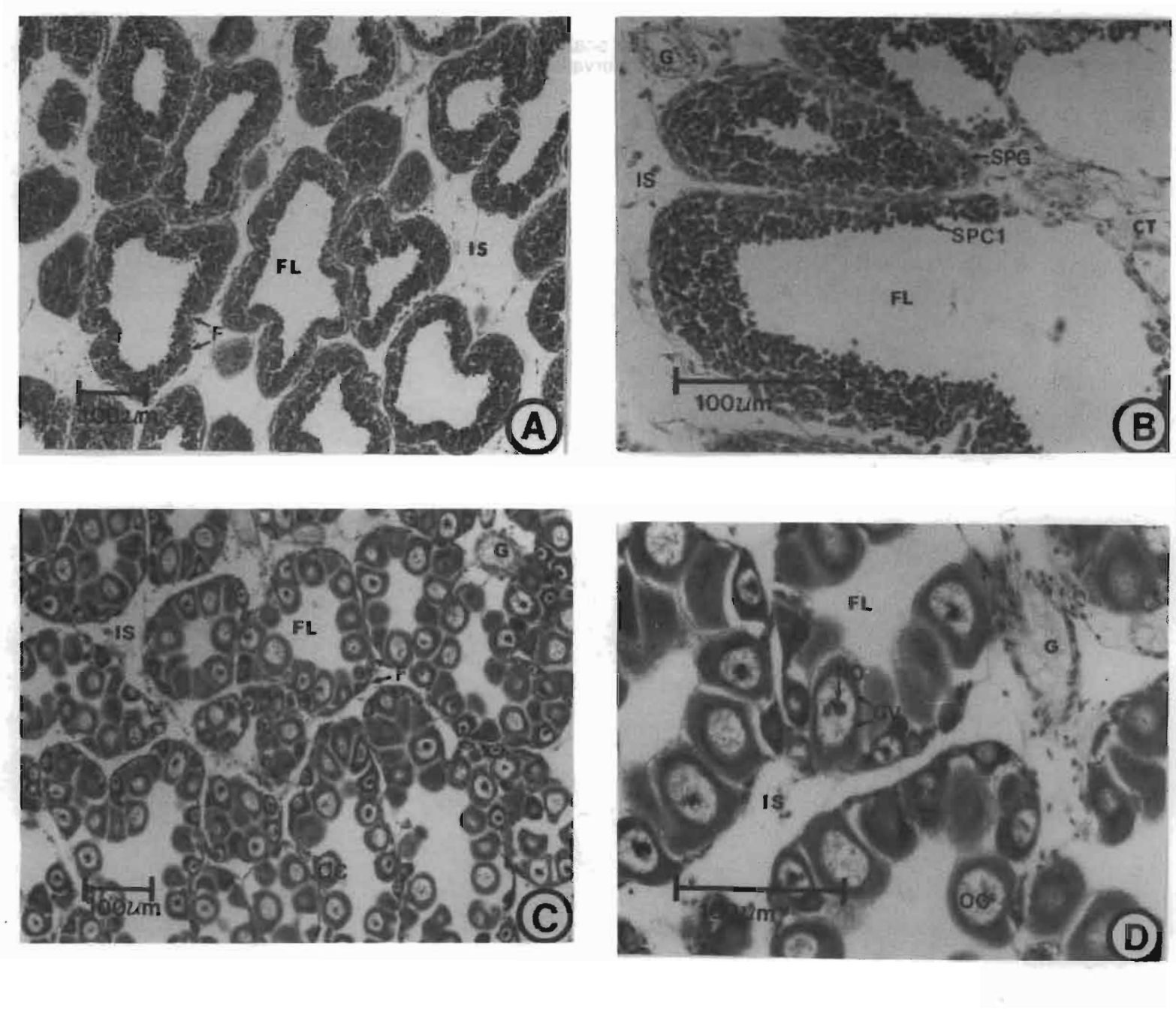

Figure 3. Gonad development stages of Placopecten magellanicus. A) Stage II, male at 100X magnification, B) Stage II, male at 250X magnification, C) Stage II, female at 100X magnification, D) Stage II, female 250X magnification.

CT = connective tissue, F = follicle, FL = follicular lumen, G = gonoduct,
GV = germinal vessicle (enlarged nucleus), IS = interfollicular space,
NO = nucleolus, OC = oocyte I, SPC1 = primary spermatocyte (spermatocyte I),
SPG = spermatogonium.

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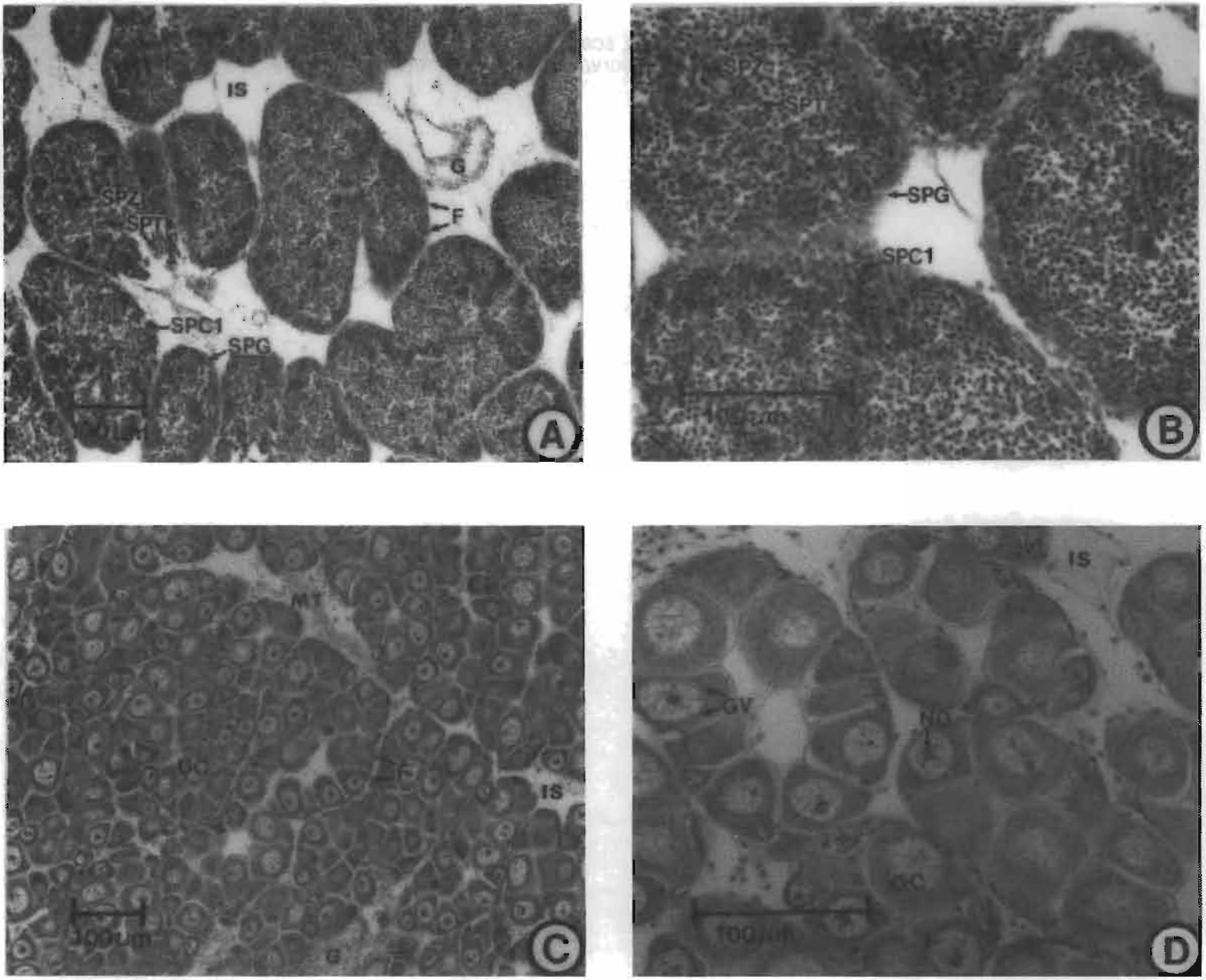

Figure 4. Gonad development stages of Placopecten magellanicus. A) Stage III, male at 100X magnification, B) Stage III, male at 250X magnification, C) Stage III, female at 100X magnification, D) Stage III, female 250X magnification.

F = follicle, G = gonoduct, GV = germinal vesicle (enlarged nucleus), IS = interfollicular space, MT = muscular tissue, NO = nucleolus, OC = oocyte, SPG = spermatogonium, SPC1 = primary spermatocyte (spermatocyte I), SPT = spermatid, SPZ = spermatozoa.

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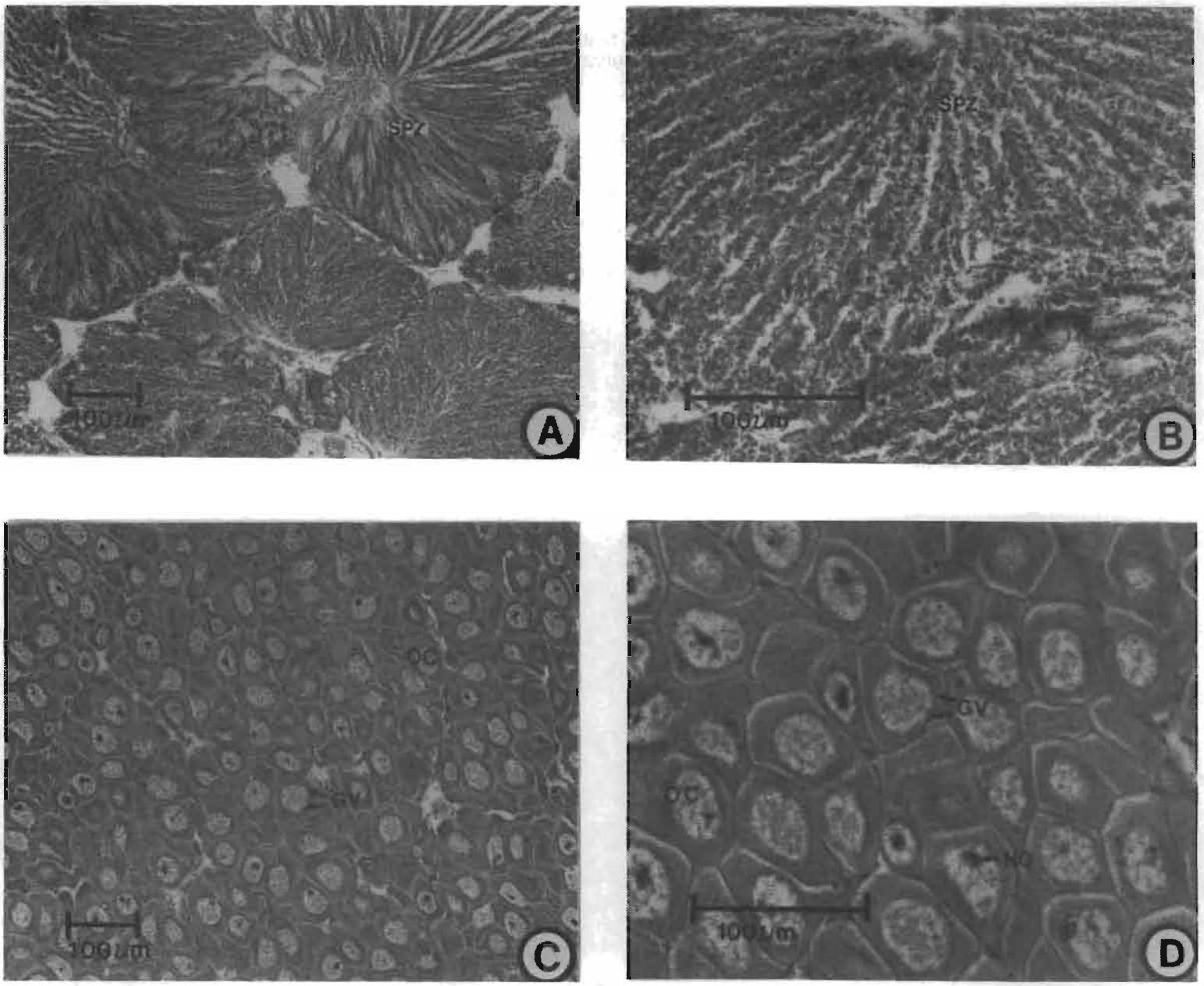

Figure 5. Gonad development stages of Placopecten magellanicus. A) Stage IV, male at 100X magnification, B) Stage IV, male at 250X magnification, C) Stage IV, female at 100X magnification, D) Stage IV, female 250X magnification.

GV = germinal vesicle (enlarged nucleus), NO = nucleolus, OC = oocyte I, SPZ = spermatozoa.

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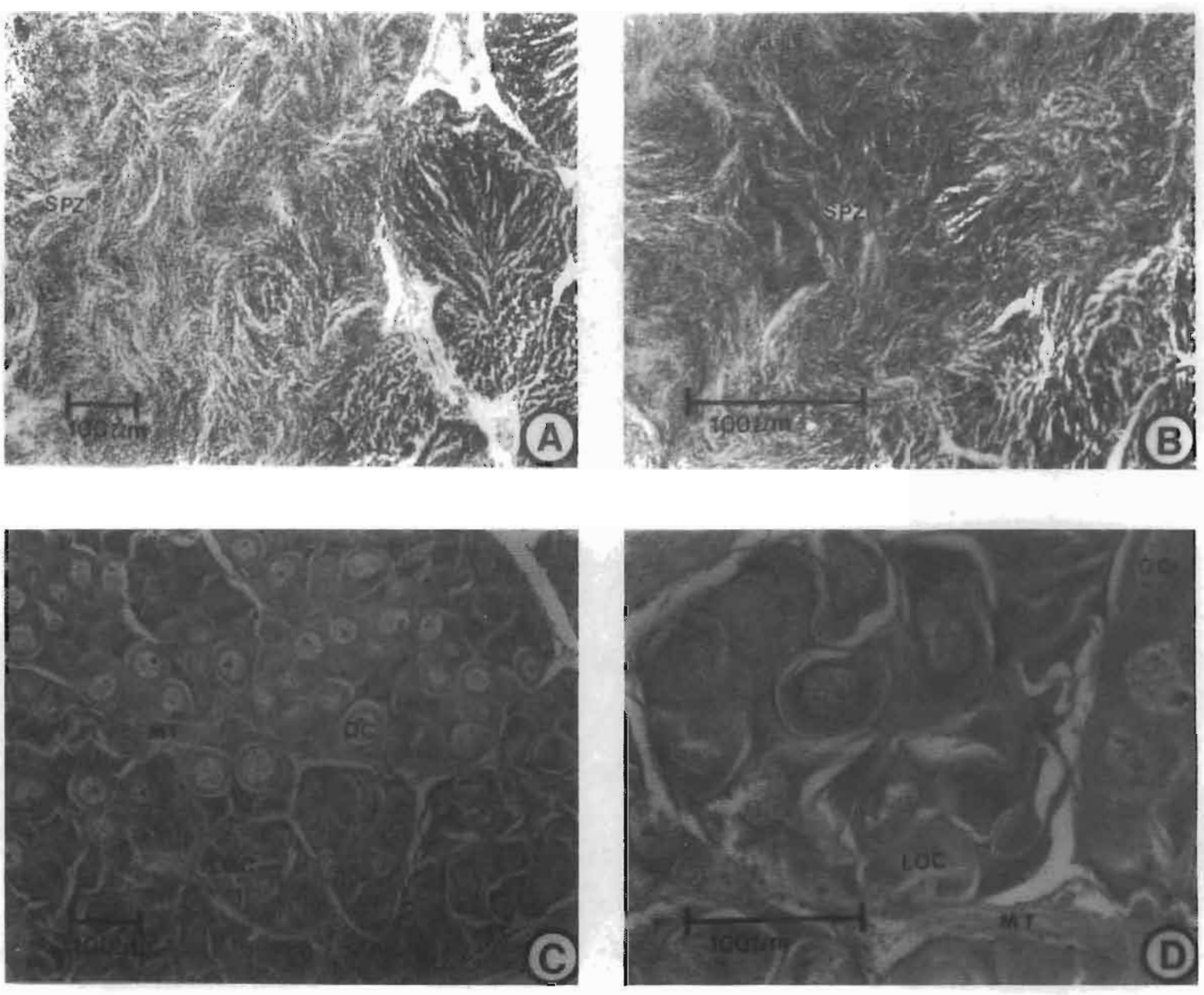

Figure 6. Abnormal gonad development occasionnally observed in Placopecten magellanicus. A) male at 100X magnification, B) male at 250X magnification, C) female at 100X magnification, D) female at 250X magnification.

LOC =lysed oocyte, MT = muscular tissue, OC = oocyte I, SPZ = spermatozoa.

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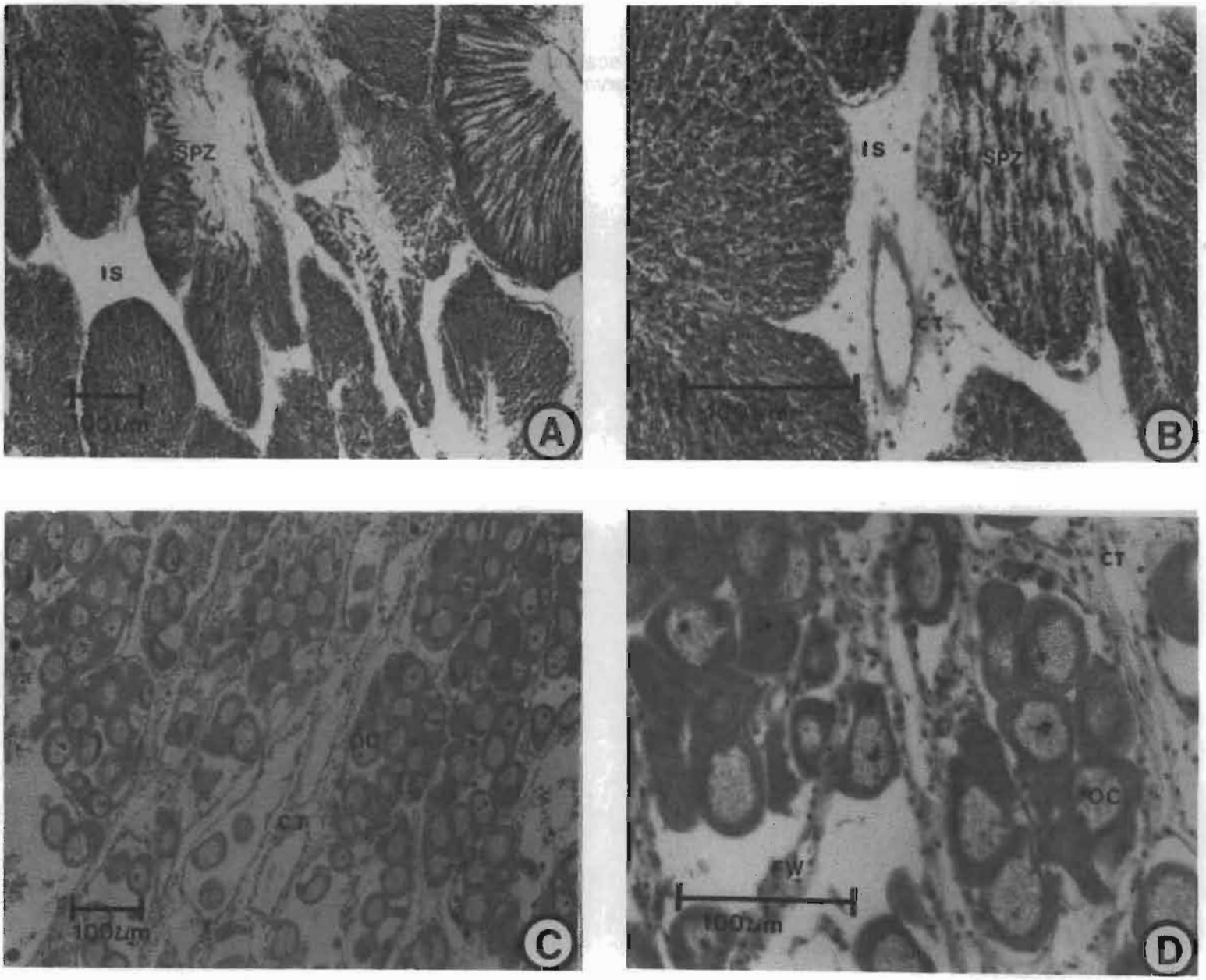

Figure 7. Gonad development stages of Placopecten magellanicus. A) Stage V_1, male at 100X magnification, B) Stage V_1, male at 250X magnification, C) Stage V_1, female at 100X magnification, D) Stage V_1, female 250X magnification.

CT = connective tissue, FW = follicle wall, IS = interfollicular space, OC = oocyte I, SPZ = spermatozoa.

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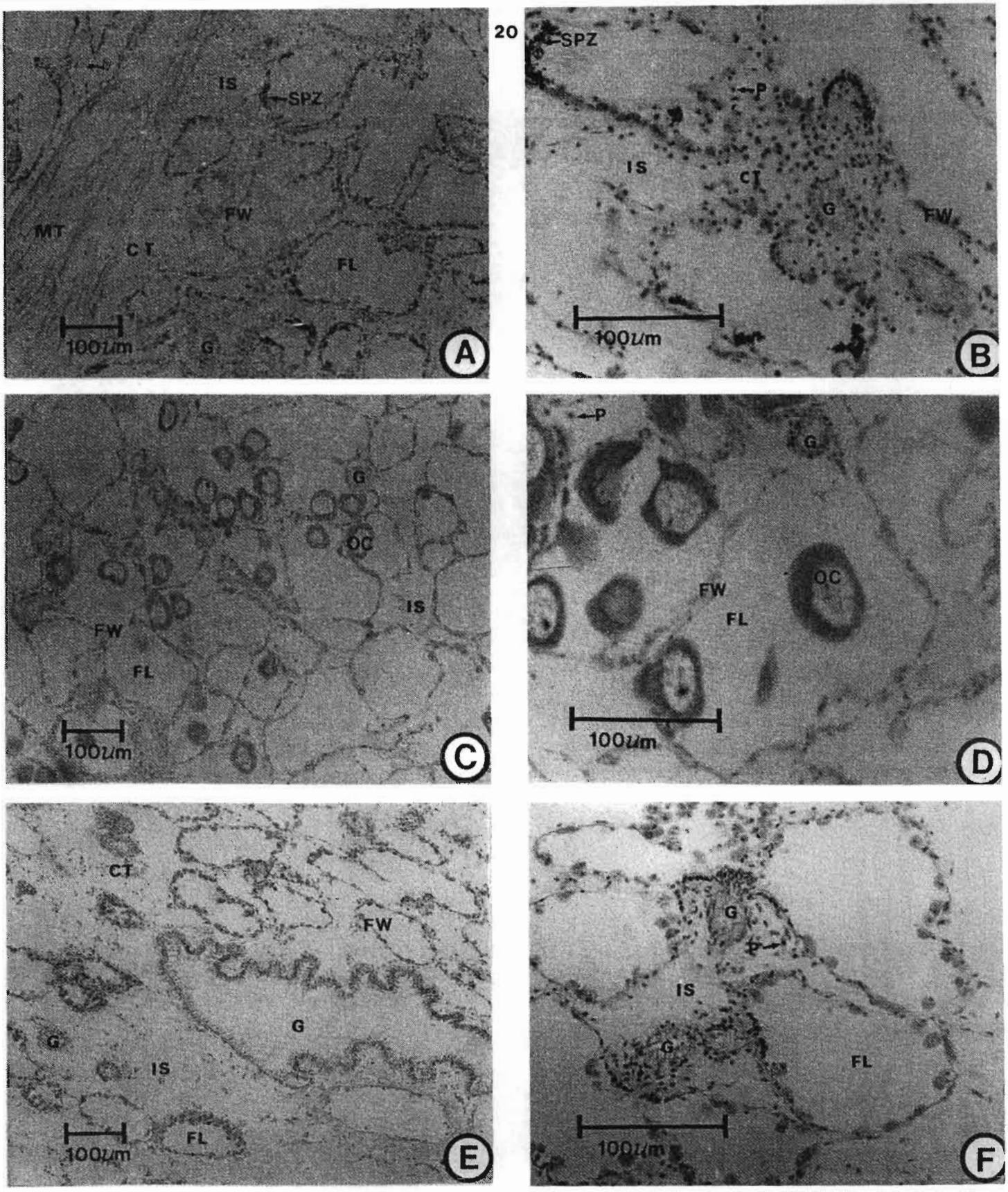

Figure 8. Gonad development stages of Placopecten magellanicus. A) Stage V_2, male at 100X magnification, B) Stage V_2, male at 250X magnification, C) Stage V_2, female at 100X magnification, D) Stage V_2, female 250X magnification, E) Stage IV, sex not determined, 100X magnification, F) Stage IV, sex not determined 250X magnification.

CT = connective tissue, FL = follicular lumen, FW = follicle wall, G = gonoduct, IS = interfollicular space, MT = muscular tissue, OC = oocyte I, P = phagocytic cell, SPZ = spermatozoa.

Stages of gonad development in the sea scallop, Placopecten magellanicus (Gmelin) based on both macroscopic and microscopic observation of the gametogenic cycle.

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