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Gonadal Structure and Gametogenesis of *Trigla lyra* (Pisces: Triglidae)

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Marta Muñoz, Maria Sàbat, Sandra Mallol and Margarida Casadevall (2002) Gonadal structure and gametogenesis of *Trigla lyra* (Pisces: Triglidae). *Zoological Studies* **41**(4): 412-420. The gonadal structure and development stages of germ cells of *Trigla lyra* are described for both sexes. The ovigerous lamellae of the saccular cystovarian ovaries spread from the periphery to the center of the gonad where the lumen is located. In addition to the postovulatory follicles and atretic oocytes, seven stages of development are described based on the histological and ultrastructural characteristics of the oocytes. Gonadal development is of the "synchronous group" type. This kind of development and the presence of postovulatory follicles in ovaries which still contain developing vitellogenic oocytes suggest that *T. lyra* spawns on multiple occasions over a relatively prolonged period of time. Drops of oil in the mature oocyte indicate that spawning is pelagic. The testes are lobular and of the "unrestricted spermatogonial" type. Male germ cells are divided into 8 stages that were principally analyzed by means of transmission electron microscopy. The morphological characteristics of the spermatozoon, as a short head and a barely differentiated middle piece with few mitochondria, indicate external fertilization. http://www.sinica.edu.tw/zool/zoolstud/41.4/412.pdf

Key words: Reproduction, Gametogenesis, Morphology, Ultrastructure, Triglidae.

Members of the family Triglidae inhabit continental and insular shelves of tropical and temperate seas; they are found on sandy and muddy substrates or rubble, using the free pectoral rays for support and to search for food. They can emit growling or grunting sounds with their swimbladder. After a pelagic phase, juveniles migrate to the bottom of shallow coastal waters. More specifically, the piper gurnard, *Trigla lyra*, is a benthonic species commonly encountered in the Mediterranean and East Atlantic. It lives in soft and rocky substrates off the coast at depths of up to 700 m (Whitehead et al. 1986). It is the most commercially important gurnard in Greece (Caragitsou and Papaconstantinou 1994). While some studies have referred to its growth (Mouneimne 1971, Papaconstantinou 1981 1983, Papaconstatinou et al. 1991) and feeding (Macpherson 1985, Moreno-Amich 1988, Caragitsou and Papaconstatinou 1994), almost all aspects of its reproduction are still unknown.

While a histological analysis of gonadal development is considered the most accurate method to determine the reproductive pattern in teleosts (Wallace and Selman 1981, West 1990), it is also the most time-consuming one. Furthermore, the reproduction of many species has only been studied in females, since the small-sized sex cells in males render ultrastructural analysis virtually necessary. This work documents the structure of the gonads in both sexes of *Trigla lyra*, through histological and ultrastructural analyses of different stages of development of male and female germ cells.

MATERIALS AND METHODS

Twenty-one females and 9 males of *T. lyra*, selected from catches made every month over a period of one year in different ports on the Costa Brava (northwestern Mediterranean) (Fig. 1), were used for the histological study of gonads and

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stages of development of their germ cells. Standard lengths ranged from 128 to 250 mm for females, and 123 to 289 mm for males. Fish were immediately fixed after capture in 10% formalin and then stored in 4% formalin. The gonads, once extracted and weighed, were kept in 70% alcohol. Histological methods followed those of Kiernan (1990). Ovaries were embedded in either Histosec 56-58 pF (Merck) or hydroxyethyl methacrylate, and were sectioned at 9-12 μ. Testes were embedded only in hydroxyethyl methacrylate and sectioned at 5 μ. Transverse and longitudinal sections were obtained in gonads of both sexes.

The following dyes were used for samples kept in Histosec: hematoxylin-eosin as general coloring, Mallory and Van Gieson as thrichromics, Gomori's argentic impregnation for reticular fibers and collagen, PAS reaction (periodic acid-Schiff) for demonstration of neutral muccopolysaccharides, and alcian blue coloring for acid muccopolysaccharides. Samples kept in methacrylate were stained with methylene blue-basic fuchsin, toluidine blue, and PAS as well. Lipids were detected in fixed non-embedded tissue sectioned with a cryo-microtome and stained with Sudan black B.

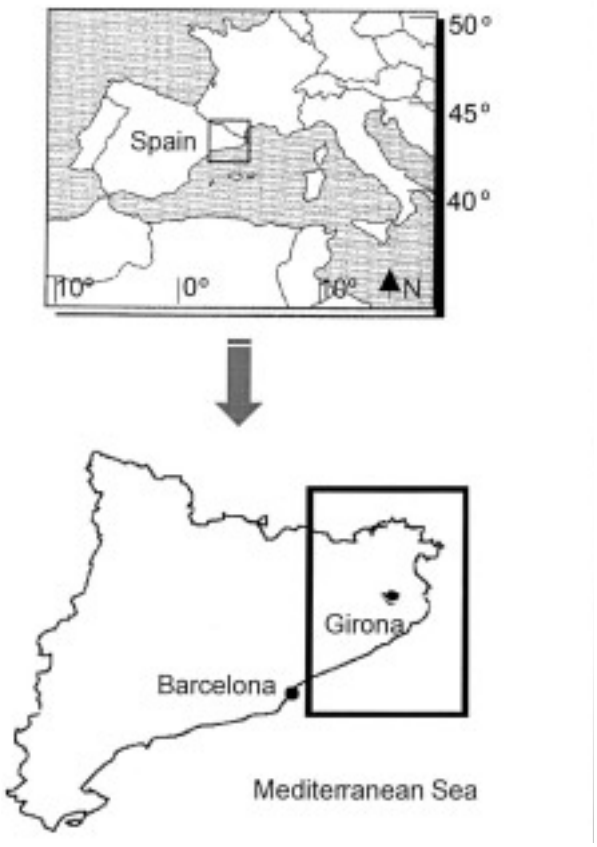

Fig. 1. Map of the sampling area, located in Spain. The enlarged area is the Costa Brava (41.51 N, 3.08 E) of the Mediterranean Sea.

Four ovary samples from 2 females caught in Jan. 1998 (195 and 243 mm in standard length) and 6 testicular samples from 2 males (220 and 270 mm in standard length) caught in May and Dec. 1998, were used for transmission electron microscopy (TEM). These samples were processed following methods of Glauert (1991) and Robards and Wilson (1993). They were fixed in a mixture of paraformaldehyde (2%)-glutaraldehyde (2.5%) with 0.1 M cacodylate buffer. Following fixing for 2 h at 4°C, they were washed several times with 0.1 M cacodylate buffer. Post-fixation was conducted in 1% osmium, also in cacodylate buffer, at 4°C for 1 h. Samples were washed several times, dehydrated through an alcohol series, and finally embedded in Spurr's mixture. Sections were examined with a Zeiss EM-910 transmission electron microscope.

Measurement of oocyte diameters was performed using an image analysis system (Image 1.41 VDM). The nucleoplasmic ratio (*NPR*) was calculated as $NPR = Vn/Vc - Vn$, where *Vn* is the volume of the nucleus and *Vc* that of the cytoplasm. Nuclear diameters of male germ cells were measured.

Oocyte developmental stages were determined following the criteria established by Selman and Wallace (1989) and West (1990). Grier's (1981) and Selman and Wallace's (1986) notes were applied for male germ cells.

RESULTS

Morphology of the gonads

Ovaries

The 2 ovaries are situated on the dorsal part of the peritoneal cavity, and are attached all along their dorsal surface by a mesovarium. They are saccular cystovarian ovaries (Hoar 1969) with a more-or-less triangular section. The ovigerous lamellae extend from the ovary wall to the center of the gonad, i.e., the lumen, where eggs are discharged during ovulation (Fig. 2a). Each lamella is suspended from the ovary wall by a fibromuscular cord containing blood vessels. This cord forms fibrovascular branches whose surfaces are covered by oocytes in different stages of develop-

ment. Their surfaces, and that of the cord, are coated by a single lamellar epithelium. Oocytes develop from numerous oogonia, located either in isolation or in groups, close to this epithelium.

The ovary wall is very thin and is composed of 3 layers. The outermost layer comprises a mesothelium and a submesothelial conjunctive layer of flat epithelial cells. The middle layer contains smooth muscle cells and numerous blood vessels. The innermost surface is coated with a flat, single layer of epithelium. The 2 ovary sacs are joined to the urogenital papillae such that the ovary duct consists of a short free part before passing to the outside.

Testes

Testes of *Trigla lyra* consist of 2 elongated structures, of a more-or-less triangular section, positioned dorsally (Fig. 2b). Seminiferous lobules have a blind end on the periphery of the gonad and contain spermatogonia all along the length of the testicular lobule.

Each gonad contains a main sperm duct which runs lengthwise along its lateroventral side, connecting to the lumen of the testicular lobules. The spermatogonia are always located on the periphery of the lobules. As they develop, the different spermatogenic stages penetrate into the

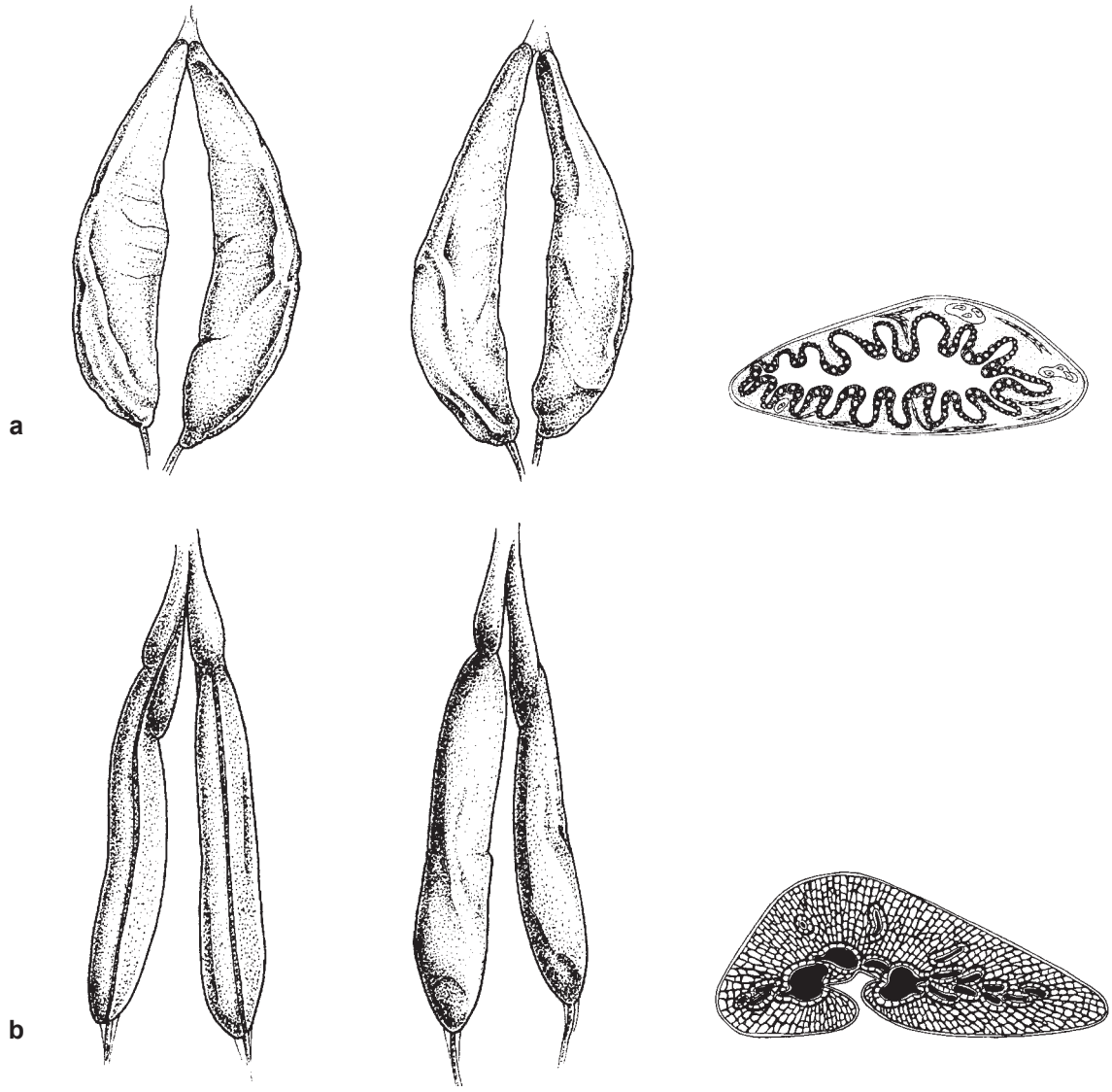

Fig. 2. Gonads of *Trigla lyra*. a. Ventral and dorsal views of the ovaries, with a transverse section. b. Ventral and dorsal views of the testicles, also with a transverse section.

lobule. The Sertoli cells envelop the germ cells forming spermatocysts which show characteristic synchronous development. Upon completion of spermiogenesis, the wall of the Sertoli cell opens up, and the spermatozoa are discharged into the lobular lumen, from where they head for the sperm duct. The testis wall consists of flat epithelium and a more-internal musculoconjunctival layer containing longitudinal muscular fibers and blood vessels. The 2 sperm ducts, coated by a single layer of epithelium, remain independent until they bind to the urogenital papillae.

Gametogenesis

Oogenesis

Progressive changes in cellular diameters and nucleoplasmic ratios during oogenensis are given in table 1.

Primary growth phase

The oogonia are small, rounded cells each with a pale, bulky sphere-shaped nucleus.

Oocytes of the chromatin-nucleolar stage have a nucleus that may contain several small nucleoli, although often there is an outstanding one located peripherally (Fig. 3a). Perinuclear chromatin can be observed ultrastructurally. The basophilic and homogeneous ooplasm contains 2 types of electron-dense material: “nuage” material, which remains independent and is always located close to the nuclear membrane, and material associated with mitochondria, known as the “intermitochondrial cement” (Fig. 3b). A single layer of flat follicle cells envelops the oocyte.

In the perinucleolar stage, the cellular volume of oocytes suddenly increases. The nucleus contains several nucleoli which vary in number and which migrate to the periphery. The presence of greatly varying nucleolar diameters indicates that nucleolar excision is not yet completed. In a more-advanced stage, the number of nucleoli stops increasing, stabilizing between 15 and 25 (per 9-μ section), all of which are approximately the same size and located around the nuclear membrane. The cytoplasm gradually loses its basophi-lia and becomes more granular. Formation of the Balbiani body can be observed as aggregations of basophilic material in a juxtanuclear position. Eventually it invades the majority of the cytoplasm. The ultrastructural study shows that membranous cellular organelles tend to migrate from the perinuclear area towards the cortical area.

Table 1. Mean cellular diameters and nucleoplasmic ratios (NPRs) of the stages of oogenesis of *Trigla lyra*

Stage	*n*	Diameter (μ)	NPR
Oogonia	10	6.92 ± 0.5[a]	0.31
Chromatin-nucleolar	30	15.25 ± 0.5	0.32
Perinucleolar	30	91.07 ± 3.1	0.27
Cortical alveoli	30	143.91 ± 4.5	0.15
Yolk I	30	207.08 ± 4.1	0.09
Yolk II	7	532.26 ± 13.3	—
Mature	10	596.24 ± 19.1	—

[a]Mean ± SE.

Secondary growth phase

Oocytes in the cortical alveoli stage have granular and more-acidophilic cytoplasm. Just before the cortical alveoli form, small lipid droplets can be seen on the perinuclear ooplasma, showing up on TEM images as being strongly osmophilic and having no external membrane. Immediately after their appearance, small cortical alveoli can be seen on the periphery of the cytoplasm, easily identifiable by virtue of their PAS+ reaction. Ultrastructurally, these electrolucent vesicles are characterised by their granulous content limited by an external membrane (Fig. 3c). The oocyte plasma membrane presents surface microvilli facing the microvilli which already project from the surface of follicle cells, and which have a cuboid shape. The zona radiata appears between these projections. This stage is very short, since the 1st yolk granules rapidly begin to appear.

The 1st vitellogenic stage is characterised by the appearance of small yolk granules on the periphery of the cytoplasm. The cortical alveoli are more extensively distributed than in the previous stage, and the lipid droplets have greatly increased in size and now occupy the central area of the cytoplasm (Fig. 3d).

During the 2nd vitellogenic stage, there are increases in the number, size, and distribution of yolk granules, which occupy nearly all of the cytoplasm at this point. Lipid droplets occupy the perinuclear area, and the cortical alveoli move to the periphery of the cytoplasm. Only a few cells at this stage could be detected, so nucleoplasmic ratios were not analyzed. The vitellogenic stages show an undulating nuclear membrane with nucleoli located on the periphery. The thickness of the

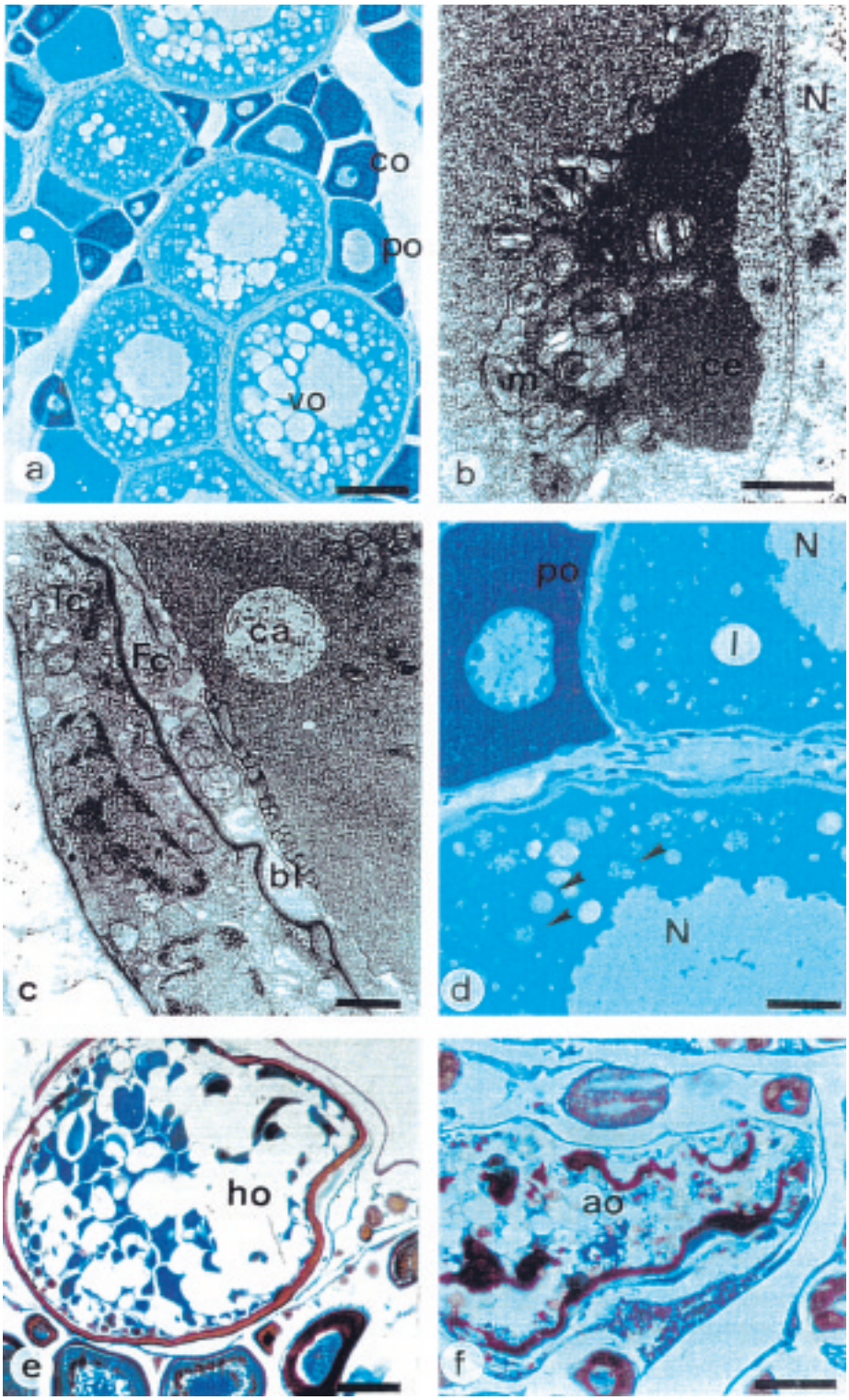

Fig. 3. Oogenesis. a. Oocytes at different stages of development. PAS staining. Bar = 80 μ. b. Electron micrograph showing the "intermitochondrial cement". Bar = 1 μ. c. Ultrastructure of the zona radiata in the cortical alveoli stage. Note the formation of microvilli. Bar = 1 μ. d. First vitellogenic stage. Arrows mark cortical alveoli. PAS. Bar = 20 μ. e. Oocyte in process of hydration. Mallory staining. Bar = 100 μ. f. Atretic oocyte. Note the cellular disorganization and fragmentation of the zona radiata. Mallory staining. Bar = 100 μ. (ao: atretic oocyte, bl: basal lamina, ca: cortical alveoli, ce: cement, co: chromatin-nucleolar oocyte, Fc: follicle cell, ho: hydrated oocyte, m: mitochondria, l: lipid droplet, N: nucleus, po: perinucleolar oocyte, Tc: theca cell, vo: vitellogenic oocyte).

zona radiata progressively increases up to about 18.9 μ in mature oocytes.

Maturity phase

Finally, oocytes undergo hydration (Fig. 3e), which is common in pelagic-spawning marine species. The follicle layer becomes thinner (7.2 μm) as a result of the rapid increase in oocyte volume. There is a change in the staining properties of the yolk granules, which are now merged together forming a single homogeneous and more-acidophilic mass.

Following ovulation, rapidly-degenerating empty follicular envelopes can be observed. They appear as structures folded over onto themselves, with dispersed PAS+ vesicles and eosinophilic granules in the lumen. The envelope collapses and disappears. Atretic oocytes can also be detected. At the beginning of atresia (α stage), the nucleus takes on an uneven and granular appearance until it disintegrates. In the cytoplasm, yolk granules are of various sizes and have rather uneven shapes. The oocyte loses contact with the granulosa, and the zona radiata also becomes uneven (Fig. 3f). In a more-advanced stage (β stage), large vacuoles and the remaining yolk granules can be seen. Finally, the structure collapses and becomes smaller, rendering it more difficult to discern the terminal postovulatory follicles.

Spermatogenesis

Spermatocysts at different stages of development are shown in figure 4a, and nuclear diameters are given in table 2.

Spermatocytogenesis phase

The primary spermatogonia appear individually or in small groups on the periphery of the lobule. They become weakly dyed and have a major round nucleus containing 1 or 2 nucleoli. Within the cytoplasm there are endoplasmic reticula, Golgi complexes, and mitochondria. It usually contains “intermitochondrial cement” and “nuage” material (Fig. 4b). Spermatogonia are always surrounded by Sertoli cells.

Secondary spermatogonia are now enclosed in a cyst. They have increased in number and are linked by intercellular bridges. Furthermore, the nucleus is smaller, and while it may still contain a nucleolus, the chromatin is much more heterogeneous and electron-dense than it was in the previous stage (Fig. 4c).

Table 2. Mean nuclear diameters for the stages of spermatogenesis of *Trigla lyra*

Stage	*n*	Diameter (μ)
Spermatogonia I	5	8.61 ± 0.66[a]
Spermatogonia II	9	6.15 ± 0.42
Spermatocytes I	19	4.96 ± 0.17
Spermatids I	17	3.02 ± 0.16
Spermatids II	13	2.35 ± 0.11
Spermatids III	8	1.76 ± 0.05
Spermatozoa	56	1.70 ± 0.03

[a]Mean ± SE.

Meiosis phase

The nucleus of the primary spermatocytes no longer contains nucleoli, and its morphology varies as the cell proceeds through the prophase. The pachytene stage is marked by synaptonemal complexes. The cytoplasm is rich in organelles, and some intercellular bridges continue to appear between the spermatocytes that form the cyst.

Secondary spermatocytes are difficult to observe because the time between the 1st and 2nd mitotic division is very short. They have only been detected by light microscopy, and they are characterized by their smaller nuclear size and by the patent cell division which converts them into spermatids.

Spermiogenesis phase

The initial spermatids have a rounded nucleus, where the chromatin has begun to condense heterogeneously. The cytoplasm contains some vesicles and large mitochondria, while the centriole complex is located at the periphery from where flagellar growth begins (Fig. 4d).

In a more-advanced stage, the spermatid takes on a more-uneven form, the nucleus becomes eccentric, and chromatin condensation advances. The amount of cytoplasm drops markedly, and the cytoplasmic organelles, basically mitochondria, tend to accumulate where the flagellum is growing. Cytoplasmic vesicles continue to increase in number.

Condensation of the nuclear chromatin continues in the final spermatid stage (Fig. 4e). The 2 centrioles are located in the nuclear fossa, and the cytoplasm is considerably reduced.

Spermatozoa have a round head, with uni-

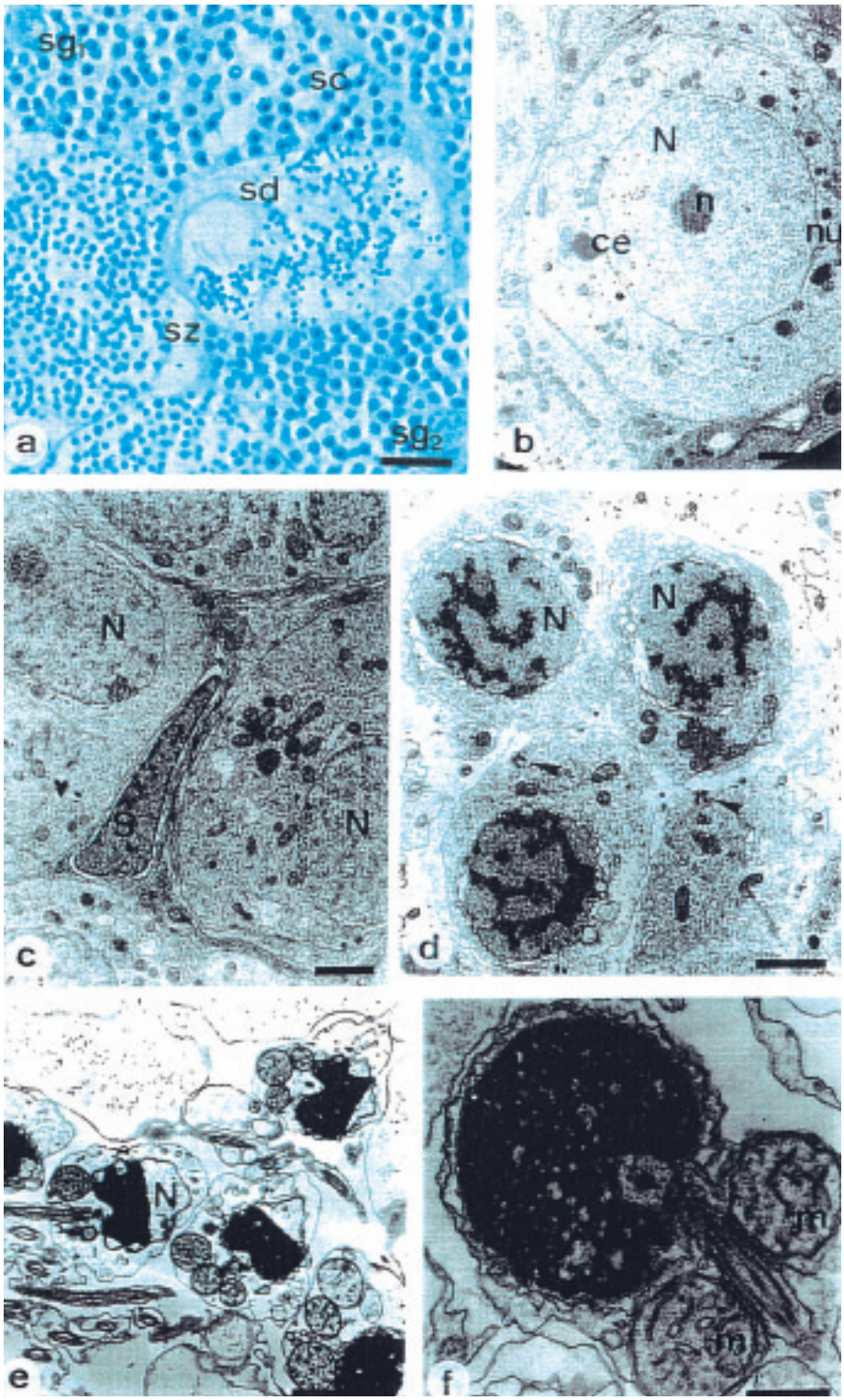

Fig. 4. Spermatogenesis. a. Light microscopic view of the testicle, containing cysts in several stages of development. PAS staining. Bar = 3 μ. b. Ultrastructure of a primary spermatogonium. Bar = 2 μ. c. Electron micrograph showing a Sertoli cell with secondary spermatogonia. Bar = 2 μ. d. Initial spermatids joined by intercellular bridges (*). Arrows show centriolar complexes. Bar = 2 μ. e. Final spermatids. Bar = 2 μ. f. Ultrastructure of the head and middle piece of the spermatozoa. Bar = 0.5 μ. (ce: cement, N: nucleus, n: nucleolus, nu: nuage, S: Sertoli cell, sc: spermatocytes, sd: spermatids, sg_1: primary spermatogonia, sg_2: secondary spermatogonia, sz: spermatozoa).

form density and no acrosome (Fig. 4f). The middle piece measures 0.9 μ and is made up of a ring of 3-4 sphere-shaped mitochondria. The flagellum presents a typical axonemal configuration, with 2 central microtubules and 9 peripheral doublets.

DISCUSSION

Ovaries of *Trigla lyra* contain oocytes in different synchronous groups of development which are discharged as they mature. Furthermore, we detected postovulatory follicles in ovaries which still contained developing vitellogenic oocytes. This type of ovarian development is of the "synchronous group" described by Wallace and Selman (1981). Similarly, mature testes contain germ cells in all stages of development, which indicates that spermatogenesis is also not totally synchronous. According to Miura (1998), this testicular description corresponds to a typical reproduction pattern of species having a relatively long spawning season, lasting for several months a year. Thus, the results agree with those obtained by Papaconstantinou (1983), who concluded that spawning of this species takes place between Sept. and Mar. However, in the northwestern Mediterranean, we have only observed mature ovaries with postovulatory follicles in Jan. and Feb.

The primary growth phase of oocytes is characterized by the nucleus undergoing major transformations such as an increase in size and the formation of multiple nucleoli which generate large quantities of ribosomal RNA (Takashima and Hibiya 1995). The electron-dense material of the cytoplasm consists of RNA and proteins (Selman and Wallace 1989) and seems to play an important role in mitochondriogenesis (Brusle 1980).

Lipid droplets begin to accumulate in the cytoplasm during the secondary growth phase. These may be involved in the formation of oil drops in fully developed eggs of the pelagic spawn of *T. lyra*, thereby guaranteeing their buoyancy. In this way, Potts (1984) pointed out that fish which are such as the triglids associated with soft substrates tend to lay pelagic eggs so that the eggs avoid being abraded or smothered by mobile particles. In fact, eggs of all Mediterranean species of this family which have been studied contain a drop of oil (Baron 1985).

Testes are of the lobular type as described by Takashima and Hibiya (1995), since the seminiferous lobules have a blind end. The presence of spermatogonia all along the testicular lobules characterize them as of the "unrestricted spermatogonial" type defined by Grier et al. (1980).

Fish spermatozoa present a great variety of shapes and structures. In teleosts, the only common aspect is the absence of an acrosome, which has been related to the presence of a micropyle in the egg (Mattei 1970). Energy required by the spermatozoon is supplied by mitochondria, which breathe and consume the endogenous substrate of the middle piece (Baccetti and Afzelius 1976). Internal fertilization can therefore be related to a long middle piece, and external fertilization to a short one (Favard and Andre 1970, Mattei 1991), as it is affected by the viscosity of the medium (Idelman 1967). The spermatozoon of *T. lyra* is of the type I anacrosomal "aquasperm" as defined by Jamieson and Leung (1991), which is typical of species with external fertilization, i.e., it has a short head, few mitochondria, and a barely differentiated middle piece.

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琴魴鰈*Trigla lyra* (魚綱：角魚科)的生殖腺結構及配子形成

Marta Muñoz Maria Sàbat Sandra Mallol Margarida Casadevall

本文描述琴魴鰈(*Trigla lyra*)雌雄兩性生殖腺構造及生殖細胞(germ cell)發育時期的形態。形成囊狀型(saccular cystovarian)卵巢的卵巢薄板(ovigerous lamellae)從生殖腺的周邊擴散到中央空腔(lumen)的位置。除了後排卵期的濾泡(postovulatory follicles)和萎縮的卵細胞(atretic oocytes)外，卵細胞由組織切片的微細構造可分成七個發育時期。生殖腺的發育是屬於「同步成熟」類型。這種發育類型的卵巢除了有後排卵期的卵黃泡之外仍含有發育中的卵黃生成期(vitellogenic oocytes)顯示琴魴鰈是屬於長期多次產卵魚類。其成熟卵中有油滴的存在表示牠們在水層中產浮性卵。精巢為小葉狀，精子生成係屬於非限制的類型。利用穿透式電顯可將雄性生殖細胞的發生分成八個時期。其精子(spermatozoon)的形態特徵為較短的頭部以及略為分化的中體(middle piece)，具有少數粒腺體顯示此魚種在體外受精。

關鍵詞：生殖，配子形成，形態學，微細構造，角魚科。

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