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Differentiated gonochorism in Nile perch *Lates niloticus* from Lake Victoria, Uganda

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Gonadal development and structure were examined in 317 Nile perch, *Lates niloticus*, of 4 to 157 cm SL taken from Lake Victoria, Uganda, in 2005–2006. Macroscopic and histological investigation showed a differentiated gonochoristic pattern, with no juvenile intersexuality. Oogonial cells (9.8 ± 3.0 µm) developed through six distinct stages: chromatin nucleolar oocyte (16.2 ± 3.3 µm), perinucleolar oocyte (33.8 ± 12.1 µm), late perinucleolar oocyte (74.8 ± 16.5 µm), cortical alveolar oocyte (122.6 ± 38.8 µm), secondary oocyte (260.9 ± 61.2 µm) and tertiary oocyte (475.5 ± 70.7 µm). *L. niloticus* was found to be an asynchronous spawner. The collection of female brood fish for induced spawning should aim at fish with an oocyte size of 475.5 ± 70.7 µm. Four main developmental stages were identified in the testis: spermatogonia (A and B), primary and secondary spermatocytes, spermatids and spermatozoa. Testicular structure conformed to the lobular and cystic type. Copious amounts of sperm were exuded from ripe males when slight pressure was applied on the belly. Milt could therefore be obtained by stripping.

Keywords: gonadal development, Latidae, oogenesis, spermatogenesis

Introduction

Lates niloticus (Latidae) is a large voracious predatory freshwater fish widely distributed in Africa, occurring commonly in all major river basins including the Nile, Chad, Niger, Senegal and Volta (Hopson 1972, Lipton 2003). It thrives under lacustrine as well as riverine conditions, with important populations occurring in Lakes Chad, Albert, Rudolf, and some Ethiopian lakes (Hopson 1972, Greenwood 1976). Originally, the species did not occur above the Murchison falls (Hopson 1972) but, following its introduction into Lake Victoria in the 1950s and 1960s, the species established itself in the new habitat and dominated fish catches in the late 1980s and early 1990s (Ogutu-Ohwayo 1988, Okaranon 2004). *L. niloticus* is Uganda's greatest fish export to the international markets (Balirwa 2007, Ministry of Agriculture Animal Industry and Fisheries 2009 unpublished data). However, demand exceeds the supply from the lakes and as a result fish processing plants have been reported to be operating at below 50% of installed capacity (Balirwa 2007).

The catches and mean sizes of *L. niloticus* have declined due to overfishing (Abila 1998). Recent observations of the fisheries trends of Lake Victoria indicated that the total contribution of *L. niloticus* to the annual fish catches have continued to decline despite increased fishing effort and stock management interventions (Muhoozi 2002). Clearly, there is a growing gap between supply and demand for *L. niloticus.* The only feasible way to increase its supply is through culture. For any fish species to be successfully farmed, well-planned production of seed is essential to sustain year-round culture and economic returns (Bromage 1995). Seed production entails understanding gonadal development and spawning patterns of the cultured species. Little information is available on gonadal development in *L. niloticus*, most work having been done on the related *Lates calcarifer* (Guiguen et al. 1994), which occurs throughout the coastal and fresh waters of the tropical Indo-West Pacific from the Persian gulf to Australia (Nelson 1994).

Gonadal sex differentiation broadly relates to all occurrences during development that lead to the expression of genetic sex via the appropriate phenotype and encompasses all the events that take place in the primordial gonad, including the migration of primordial germ cells (PGCs), the establishment of gonadal ridges and the differentiation of the gonads into testes or ovaries (Hendry et al. 2002). According to Devlin and Nagahama (2002), sex determination and differentiation in fish is a flexible process with respect to evolutionary patterns and is subject to modification by external factors. This process can be influenced by exogenous hormones and environment, which may override the genetically determined sex, thus modifying the sex during differentiation (Baroiller et al. 1999, D'Cotta et al. 2001). Exogenous steroids given during the gonadal development period can control the phenotype, overriding the expression of the genotypically-determined sex (Phelps and Popma 2000) leading to a phenotypic sex change.

Whereas some teleost species exhibit gonochorism, protandry has been reported in *Lates calcarifer* (Guiguen et al*.* 1994, Williams et al*.* 2004) and *Centropomus undecimalis* (Taylor et al. 2000). Although sex change has been postulated in *L. niloticus* based on skewed sex ratios (Hughes 1992), no histological validation has been done. According to West (1990), histological studies are required to validate macroscopic observations.

The present study examined macro and microscopic structures of the gonads of various size classes of *L. niloticus* to elucidate its gonadal development patterns. Information on gonadal development patterns can be used in the induction of sex change and spawning, which are common practices in aquaculture.

Materials and methods

Lates niloticus were randomly collected over a period of four months from October 2005 to January 2006 from various locations (32°35′ E, 00°10′ N; 32°28′ E, 00°03′ N; 32°34′ E, 00°09′ N; and 32°18′ E, 00°32′ S) in the Ugandan waters of Lake Victoria. Fishing gears included 5 mm mesh ‘lampara’ nets used in *Rastrineobola* fishing, beach seines (400 × 3 m, with 19 mm mesh wings and 25 mm mesh cod end), gillnets ranging from 127 to 228 mm stretch mesh, and long lines. A total of 317 fish (110 females, 122 males, 85 undifferentiated juveniles) of 4–157 cm standard length (SL) were collected, measured and dissected to expose the viscera and gonads. Gonadal and eviscerated weights were measured (g). Macroscopic staging was done based on a scale modified from Hopson (1972).

Sections of the gonad from the rostral, middle and caudal parts were fixed in Bouin’s solution. The tissues were embedded in pelleted molten paraffin wax and sections of 5–7 μm cut, stained with haematoxylin and eosin (H&E) or Masson’s trichrome (MT). The slides from all the three sections were examined under a Zeiss Axiostar Plus light microscope, but no location differences were observed. For measurements, the middle section was considered. The different cells and their nuclei were identified and measured using a fitted eyepiece calibrated for every objective lens with a stage micrometer or graduated slide. Microscopic oocyte stages were classified based on modified descriptions by Maldonado-Garcia et al. (2005), Ganais et al. (2004) and Wallace and Selman (1981). Thirty randomly selected oocytes were measured from each ovary by taking the average of maximal and minimal diameters as described by West (1990).

Results

Of the 317 fish caught, 117 were juveniles (4.0–29.9 cm SL) and 200 were adults (30–157 cm SL). Histological examination of the juveniles showed that 85 were undifferentiated and 32 differentiated (17 males and 15 females). A proportion of ripe running males (21.5%) and ripe females (6.5%) were present throughout the sampling period.

Macroscopic description of gonadal structure and development in **L. niloticus**

In the juveniles it was not possible to differentiate males from females using external features. However, in the mature fish, males were found to have two orifices, anal and urogenital, just anterior to the anal fin, whereas the females had three orifices; a genital orifice separate from the urinary orifice as well as the anal orifice (Figure 1). In ripe females the orifices were much clearer, whereas in the males, application of slight pressure on the belly caused exudation of milt. In dissected fish the gonads of juveniles were macroscopically visible even in the smallest fish caught (4 cm SL) as thin, transparent, indistinguishable paired tissue strands lying dorso-laterally along the length of the swim bladder, covered by a peritoneum and attached to the abdominal cavity by mesenteric tissue. In differentiated females the ovaries were paired structures located in the peritoneal cavity and suspended on either side of the midline by mesovaria. They were enclosed in a capsule, the tunica albuginea. The shape, size and appearance of the ovaries varied with the stage of development. In immature and spent fish, the ovaries appeared as thin, straight and translucent thread-like structures, but as oogenesis progressed the ovaries enlarged to become lobed, saclike, creamish-yellow organs filling the abdominal cavity. Mature ovaries were creamy yellow in colour and well vascularised. In transverse section the ovaries were oval shaped with numerous ovigerous lamellae from the tunica albuginea extending towards the centre of the ovary.

In males the testes were paired elongated structures situated in the dorsal region of the abdominal cavity. In sexually immature individuals the testes were threadlike, transparent paired structures running longitudinally along the dorsal wall of the body cavity, joining together at the caudal end. Macroscopically, sexual maturation was characterised by enlargement and convolution of the testes, which became grayish white, then whitish or pinkish with clear vascularisation, and finally to ivory white with well-rounded edges in the ripe running individuals.

Histological description of gonadal structure and development in **L. niloticus**

In undifferentiated juveniles the gonads contained primordial germ cells (PGCs) (Figure 2a) visible as large conspicuous cells (12.34 ± 1.79 μm [mean ± standard deviation]) with a large spheroid nucleus (7.28 ± 1.38 μm) containing a single nucleolus. The distribution of the primordial germ cells was sparse along the length of the gonad, interspersed with somatic cells. The somatic cells were spindle-shaped while some were ovoid (Figure 2a). Growth and development proceeded with the primordial germ cells proliferating to give rise to oogonia in ovaries and spermatogonia in testes. A differentiated ovary was characterised by a clear ovarian lumen and distinct basophilic oocytes, all enclosed in an ovarian capsule, the tunica albuginea (Figure 2b). The size at which the first indication of sex differentiation was visible was 9.7 ± 3.3 cm for females and 11.13 ± 2.7 cm for males. All fish above 30 cm were differentiated as either males or females, with no occurrences of intersex.

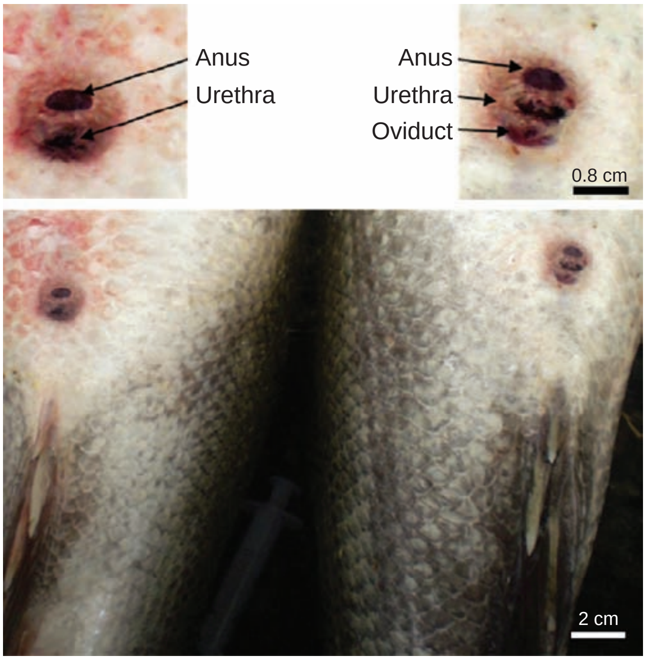

Figure 1: Nile perch male (left) with two orifices, female (right) with three orifices

Oogenesis

The primordial germ cells proliferated and later gave rise to oogonial cells. Oogonial cells in the ovary developed through six distinct cellular stages; chromatin nucleolar, perinucleolar, late perinucleolar, cortical alveolar, vitellogenic secondary oocyte and vitellogenic tertiary oocyte stage. The primary growth phase (previtellogenic) consisted of three cellular stages; chromatin nucleolar, perinucleolar and late perinucleolar. Chromatin nucleolar oocytes were characterised by a scanty cytoplasm and a centrally located nucleus containing a single nucleolus. The chromatin nucleolar oocytes (Figure 3a) measured 16.2 ± 3.3 µm in diameter. As the oocytes developed, the nucleoli increased in number and were arranged around the inner part of the germinal vesicle, defining another stage, the perinucleolar oocyte stage. The oocytes were polygonally shaped with a mean cell diameter of 33.8 ± 12.1 µm (Table 1, Figure 3a, b). The polygonally shaped perinucleolar oocytes with multiple nucleoli in the nucleoplasm became larger and more ovoid as development progressed to the late perinucleolar stage (Figure 3b). At late perinucleolar stage (at a diameter of 74.8 ± 16.5 µm) the nucleoli were arranged around the periphery of the nucleus like a beaded thread. The oocytes became more spherical at the late perinucleolar oocyte stage (Figure 3b).

The appearance of cortical alveoli in the cytoplasm (the cortical alveolar oocyte stage) (Figure 3c) marked the end of the previtellogenic phase. Vitellogenic stages consisted of secondary and tertiary oocytes. Secondary oocytes were characterised by a more acidophilic cytoplasm staining red in H&E stain (Figure 3d) with a mean cell diameter of 260 ± 61.2 µm (Table1). The tertiary oocytes contained numerous yolk granules and oil globules. The yolk stained red with H&E stain, but the oil globules remained colourless (Figures 3d, e). The tertiary oocytes were the largest cells with a mean diameter of 475.5 ± 70.7 µm. Tertiary oocytes undergoing maturation showed migrating nuclei (Figure 3e). Histological sections revealed the presence of all cohorts of all oocyte stages including the postovulatory follicles (POFs) in the same mature ovary (Figure 3d, f). In some ovarian sections, atretic oocytes were also visible (Figure 3g).

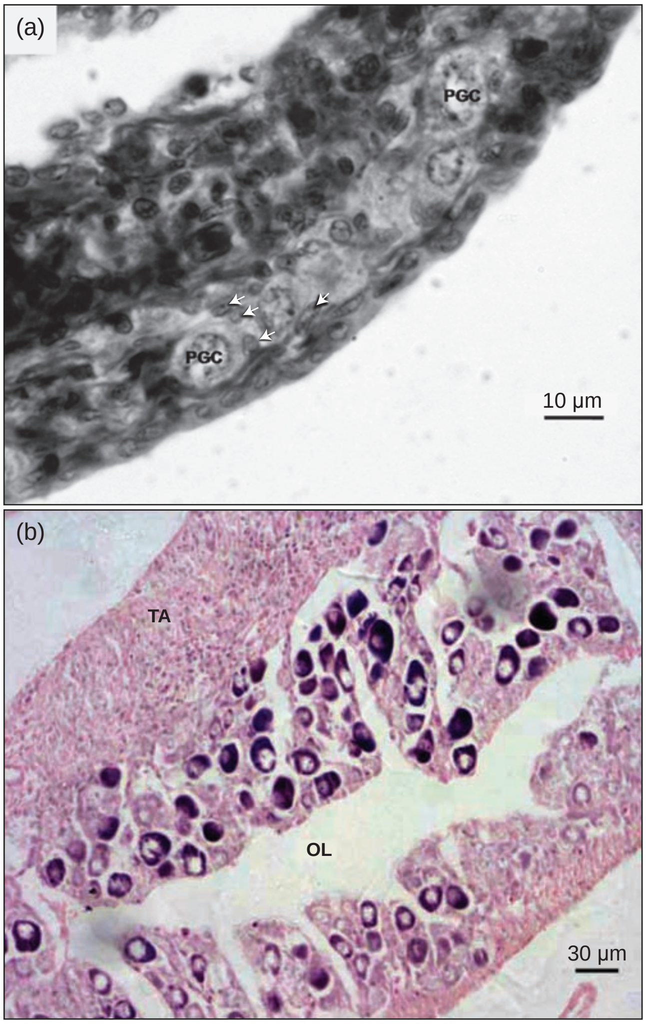

Figure 2: (a) Primordial germ cells (PGC) with large nucleus in an undifferentiated gonad from a fish of 5.6 cm SL. The PGCs interspersed with somatic cells (arrows). MT stain; (b) ovary of differentiated female (12 cm SL) with characteristic ovarian lumen (OL) and distinct basophilic oocytes**.** Ovary enclosed in a fibrous capsule, the tunica albuginea (TA). H&E stain

Spermatogenesis

In males the tunica albuginea extended septa into the testis, subdividing it into lobules (Figure 4a). Within the testis, spermatogenesis occurred in cysts and progressed through four main cellular stages; spermatogonia types A and B, primary and secondary spermatocytes, spermatids and spermatozoa.

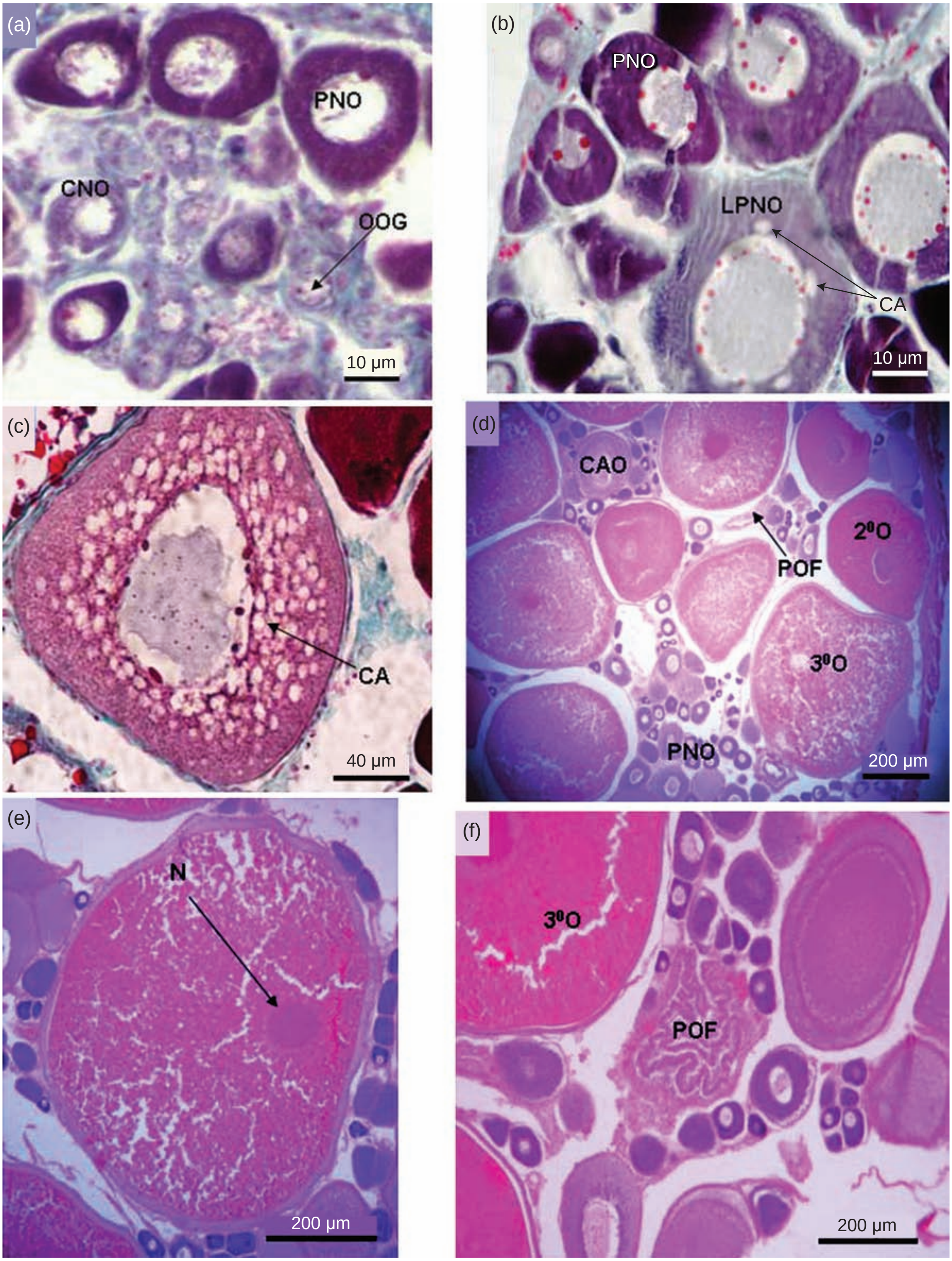

Figure 3: (a) Ovary with basophilic oocytes at various cell stages; oogonia (OOG), chromatin nucleolar oocyte (CNO) and perinucleolar oocyte (PNO). MT stain; (b) perinucleolar oocytes (PNO) and late perinucleolar oocytes (LPNO) with nucleus containing several nucleoli neatly aligned at the periphery of the nuleoplasm, cortical alveoli (CA) begin to appear at this stage. MT stain; (c) cortical alveolar oocyte with numerous cortical alveoli (CA) and changing cytoplasm from basophilic to acidophilic. MT stain; (d) ovary showing asynchronous oocyte growth, with oocytes at various stages: perinucleolar oocytes (PNO), cortical alveolar oocytes (CAO), secondary oocytes (2°O), tertiary oocytes (3°O) and post ovulatory follicle (POF). H&E stain; (e) oocyte undergoing maturation with migrating nucleus (N), moving towards the animal pole. H&E stain; (f) post ovulatory follicle (POF) together with previtellogenic and vitellogenic oocytes, i.e. tertiary oocyte (3°O). H&E stain

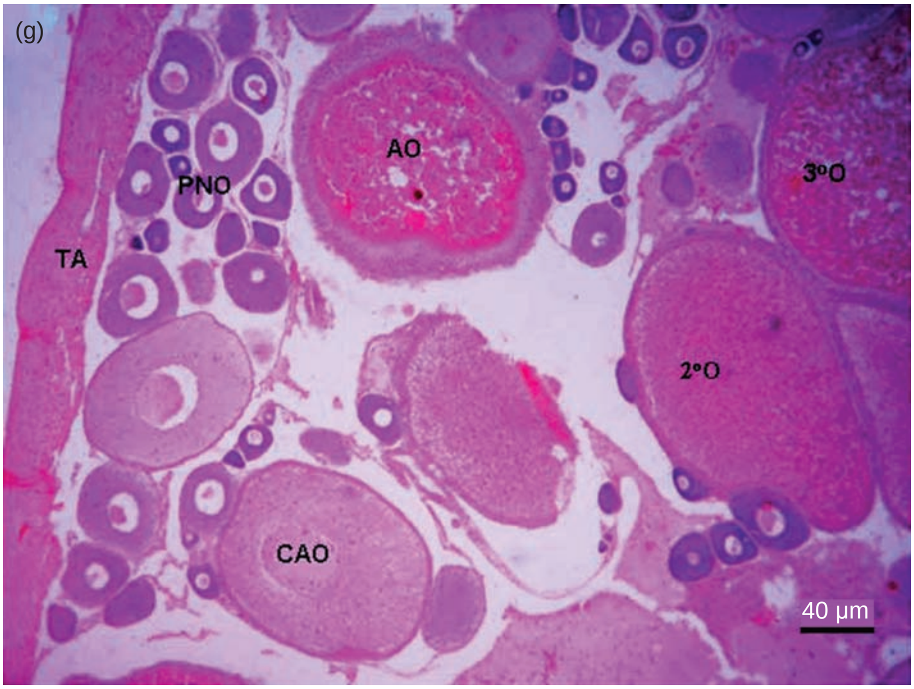

Figure 3: (cont.) (g) Ovary with altretic oocyte (AO) and other oocyte stages: perinucleolar oocytes (PNO), cortical alveolar oocyte (CAO), secondary oocyte (2°O) and tertiary oocyte (3°O). Ovary enclosed in a fibrous capsule, the tunica albuginea (TA). H&E stain

Table 1: Mean cell diameter ± standard deviation and histological description of cell stages from fixed ovaries of *L. niloticus*

Cell stage	Cell diameter (µm)	No. of fish measured (*N*)	Histological description
Oogonia (OOG)	9.8 ± 3.0	44	Cells stained lightly in H&E and MT, and located close to the ovigerous lamellae (Figure 3a)
Chromatin nucleolar oocyte (CNO)	16.2 ± 3.3	47	Oocytes consist of a limited cytoplasm densely stained with haematoxylin. Nucleus proportionally large, centrally located, and occupying the greatest part of the oocyte (Figure 3a)
Perinucleolar oocyte (PNO)	33.8 ± 12.1	37	Multiple nucleoli (2–16) appear in the nucleoplasm. Cells polygonal (Figure 3a, 3b)
Late perinucleolar oocyte (LPNO)	74.8 ± 16.5	44	Nucleoli arranged around the periphery of the nucleus like a thread with beads, oocytes more spherical
Cortical alveolar oocyte (CAO)	122.6 ± 38.8	34	Subcellular organelles appear, including cortical alveoli in the cytoplasm (Figure 3c)
Secondary oocyte (2°O)	260.9 ± 61.2	38	Encapsulated oocyte with follicular layers and an acidophilic cytoplasm staining red with haematoxylin (H&E)
Tertiary oocyte (3°O)	475.5 ± 70.7	37	Yolk deposits appear red in H&E, numerous oil globules remain colourless. In some fully grown oocytes undergoing maturation the nucleus is seen migrating to the animal pole (Figure 3e)

Spermatogonia type A measured 15 ± 1.84 µm and had a clearly defined ovoid central nucleus with heterochromatin granules around the nuclear wall. Two distinct nucleoli were discernible in the nucleoplasm. Spermatogonia type B, measuring 12.7 ± 1.43 µm, had an eccentric nucleus and a single nucleolus (Figure 4b). Generally, spermatogonia were distributed along the whole length of the lobule (Figure 4c).

The primary spermatocytes, 5.54 ± 1.84 µm, were smaller than spermatogonia type B (12.71 ± 1.46 µm) with dense basophilic chromatin strands. The primary spermatocytes were transformed into secondary spermatocytes whose nuclei were densely stained (Figure 4c). The primary and secondary spermatocytes developed in cysts and the latter gave rise to spermatids. The spermatids also developed

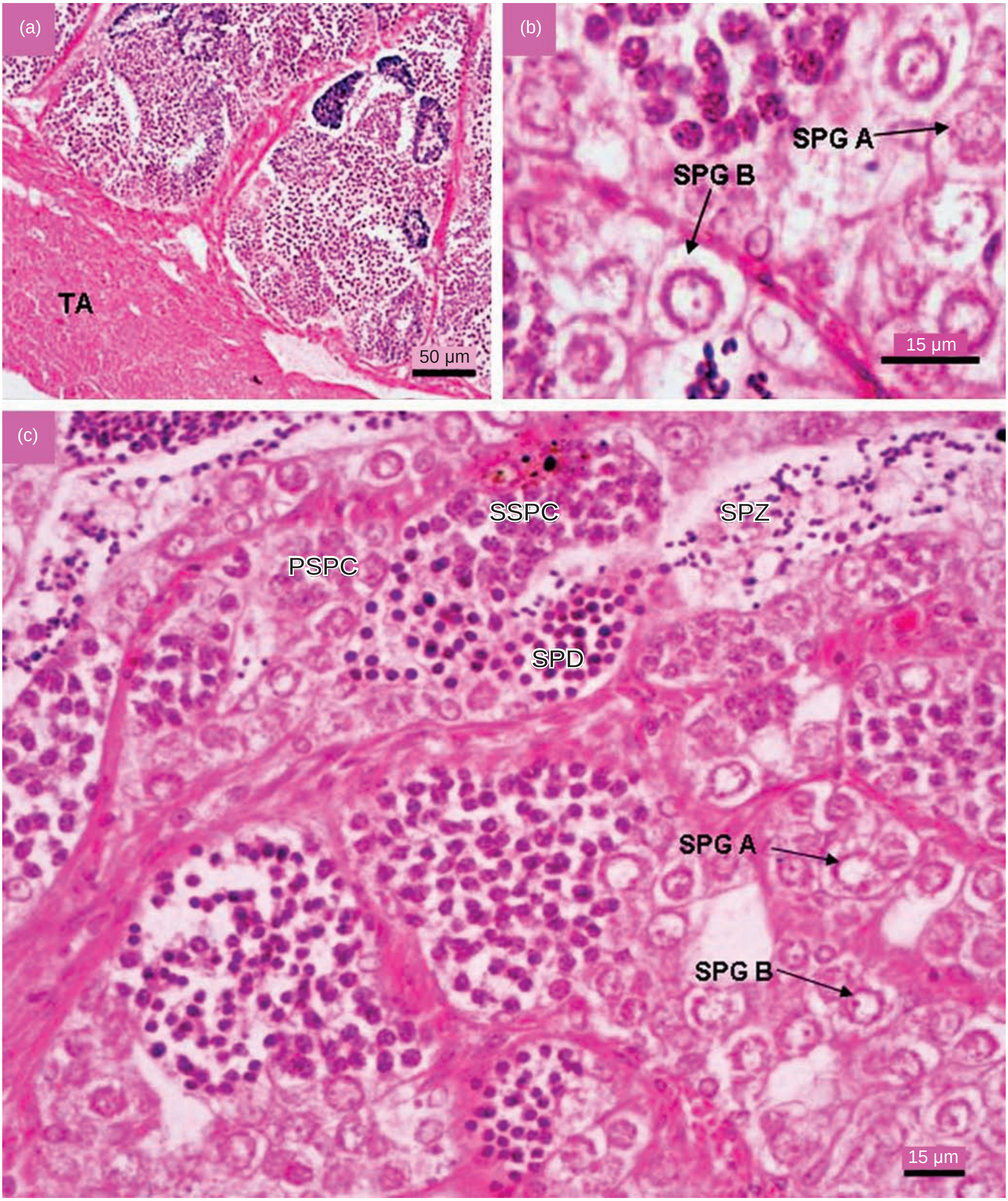

Figure 4: (a) Lobular *L. niloticus* testis covered by a tunica albuginea (TA) from which the septa arise to form lobules; (b) spermatogonia type A (SPG A) and spermatogonia type B (SPG B) with a single nucleolus; (c) testis of *L. niloticus* showing cystic spermatogenesis. All cell stages present spermatogonia type A (SPG A), spermatogonia type B (SPG B), primary spermatocytes (PSPC), secondary spermatocytes (SSPC), spermatids (SPD) and spermatozoa (SPZ) in the lumen of the lobule. H&E stain

in cysts, and ruptured to give spermatozoa, which were constantly shed into the lumen of the lobules (Figure 4c). Spermatozoa were found in the lumen of lobules and the sperm ducts. In ripe running males the entire lobule was filled with spermatozoa.

Discussion

The absence of intersex in the examined gonads from juveniles to adults (4–157 cm, SL) in this study indicated that *L. niloticus* is a gonochorist, exhibiting gonadal development of the differentiated type in which the gonads differentiate directly into female or male gonads (Yamamoto 1969, Sandra and Norma 2010). A similar pattern was found in Atlantic halibut *Hippoglossus hippoglossus* (Hendry et al. 2002), coho salmon *Onchorynchus kistuch* (Piferrer and Donaldson 1989) and common carp *Cyprinus carpio* (Komen et al. 1992). This type of gonadal development differs from undifferentiated gonochorism with juvenile intersexuality, as reported in the cyprinid *Labeo victorianus* from Lake Victoria (Rutaisire et al. 2008).

Sadovy and Shapiro (1987) reviewed the criteria for sexual categorisation of fishes as gonochorists or hermaphrodites, and suggested that a species can only be considered hermaphroditic if a substantial proportion of individuals in a population function as both sexes, either sequentially or simultaneously, which was not the case for *L. niloticus* in this study. No fish examined in this study had both ovarian and testicular tissue, and thus the possibility of hermaphroditism in *L. niloticus*, as hypothesised by Hughes (1992), was not confirmed. Hughes' (1992) conclusions of protandry in *L. niloticus* were based on size and distribution of males and females. The current histological investigations have clearly shown no occurrences of intersex in the species, although protandry has been reported in the closely related *L. calcarifer* (Guiguen et al. 1994) and in *Centropomus undecimalis* (Taylor et al. 2000).

Sex reversal is practiced in cultured fish species to favour development of the sex which has good and desirable culture characteristics (Phelps and Popma 2000). In order to cause functional sex reversal in fish, treatment for sex reversal using steroid hormones or environmental manipulations should be administered in sufficient doses during the undifferentiated stage of gonadal development and maintained up to the stage of sex differentiation (Nakamura et al. 1998, Scott 1987, Yamamoto 1969). From this study it can be inferred that intervention in sex change through the use of exogenous substances would be possible and appropriate in 0–9.9 cm SL size range, in which 98% of the juveniles examined were sexually undifferentiated.

Oocyte development

In *L. niloticus* the oocytes developed in cohorts with POFs among tertiary oocytes, suggesting that the species is an asynchronous iteroparous spawner. Tertiary oocytes in ripe females measured 475.5 ± 70.7 µm in diameter. To the aquaculturist, the appearance and diameter of the oocyte and the position of the nucleus in it are indicators of oocyte development, and hence are criteria in broodfish selection for induced spawning. Female fish are canulated and, if the oocyte nucleus exhibits migration from the centre to the periphery, ovulation can be induced by exogenous hormonal treatment. In *L. calcarifer,* females are canulated to obtain samples of oocytes, and females showing the most homogeneous batches of oocytes >400 µm are chosen for injection with luteinising hormone-releasing hormone analogue (Le Moullac et al. 2003). Based on procedures followed for induced spawning of *L. calcarifer*, and taking into consideration the findings from the current study, *L. niloticus* females showing homogeneous batches of oocytes 475.5 ± 70.7 µm should be selected for hormone induction for induced spawning trials. The size of tertiary oocytes in this study was about the same (about 0.53 mm) as that reported by Ogutu-Ohwayo (1988) for *L. niloticus* from Lake Victoria. However, it is smaller than that reported by Hopson (1972) from Lake Chad (0.67–0.92 mm).

Structure of the testis and spermatogenesis

The testis in *L. niloticus* conformed to the lobular description (Parenti and Grier 2004), of the unrestricted lobular type, where the spermatogonia are distributed along the whole length of the lobule. The type of testis in *L. niloticus* is similar to that in other Perciformes in families Centropomidae (*Centropomus undecimalis*: Taylor et al. 1998; *C. medius*: Maldonado-Garcia et al. 2005), and Percidae (*Perca flavescens*: Grier et al. 1980). The type of spermatogenesis in *L. niloticus* conforms to a cystic nature, where the spermatozoa develop in cysts (Mattei et al. 1993). Ripe males exuded milt upon application of slight pressure to the belly, which also happens in *L. calcarifer* (Tiensongrusmee et al. 1989) and *C. medius* (Maldonado-Garcia et al. 2005).

Conclusions

Lates niloticus is a gonochorist, with its gonads differentiating directly into ovary or testis. Mature *L. niloticus* were found to be sexually dimorphic, a feature that would facilitate identification and management of broodstock. Exudation of milt on the application of gentle pressure permits the collection and preservation of milt for artificial fertilisation without killing the male brood fish.

Using the current findings on the size of tertiary oocytes and the type of spawning in *L. niloticus,* female broodfish showing homogeneous batches of oocytes ≥475.5 ± 70.7 µm should be selected for induced spawning.

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