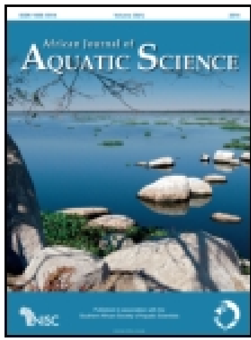

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African Journal of Aquatic Science

ISSN: 1608-5914 (Print) 1727-9364 (Online) Journal homepage: https://www.tandfonline.com/loi/taas20

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To cite this article: Justus Rutaisire & Anthony J Booth (2004) A histological description of ovarian recrudescence in two *Labeo victorianus* populations, African Journal of Aquatic Science, 29:2, 221-228, DOI: 10.2989/16085910409503813

To link to this article: https://doi.org/10.2989/16085910409503813

Published online: 07 Jan 2010.

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African Journal of Aquatic Science 2004, 29(2): 221–228
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AFRICAN JOURNAL OF AQUATIC SCIENCE
ISSN 1608–5914

A histological description of ovarian recrudescence in two *Labeo victorianus* populations

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Received 30 March 2004, accepted 5 August 2004

The ovaries of *Labeo victorianus* are paired organs situated in the peritoneal cavity and suspended on either side of the midline by a mesovarium. A capsule, composed of dense, regularly-arranged collagen and elastic fibres mixed with a few smooth muscle cells, enclosed the ovaries and gave off connective tissue septa, forming the ovigerous lamellae, which contained germ and follicle cells. Eight discrete stages of recrudescence were identified: oogonia, chromatin nucleolar oocytes, perinucleolar oocytes, primary yolk vesicle oocytes, secondary yolk vesicle oocytes, tertiary yolk vesicle oocytes, post-ovulatory follicles and atretic oocytes. Ovulation seemed to be synchronised with the onset of rainfall, with some deviations in the Sio River population. Gonadosomatic index variation followed a bimodal pattern, with maxima between January–February and between September–October for both populations. The same pattern was exhibited for both rainfall and water levels at the two study sites. Successful ovulation was followed by the formation of post-ovulatory follicles and Type I atresia, while failed spawning was characterised by Type II atresia. Clearance of post-ovulatory follicles was by phagocytosis and formation of melanomacrophage centres. There were variations in post-ovulatory changes between the two populations. Reproductive patterns in the Kagera River population conformed to the 'norm' in African labeines of the synchronisation of spawning with rainfall. Slight deviations from this pattern were, however, observed in the Sio River population where spawning occurred prior to the onset of rainfall.

Keywords: *Labeo victorianus*, oogenesis, ovarian recrudescence, spawning atresia

Introduction

Labeines are economically important food fish throughout the African continent (Reid 1985, Skelton *et al*. 1991). Ningu *Labeo victorianus* (Boulenger 1901) is limited in its distribution to the Lake Victoria basin, although the genus is widely distributed in Africa (Reid 1985). It is a potamodrometic species which migrates from the lake up rivers to spawn (Cadwalladr 1965a). The fish was once widely distributed in the Lake Victoria basin and supported the most important fishery of all the potamodrometic species in the lake (Cadwalladr 1965b). The introduction of gill nets, set at the river mouths during spawning migrations, has been reported to be responsible for the rapid decline of the species since the 1950s (Ogutu-Ohwayo 1990, Seehausen 1996, Rutaisire 2003). The fishery has collapsed, with fish having disappeared from some of their former habitats (Seehausen 1996). Recent surveys in Uganda have found only two distant populations; one in the Sio River on the Uganda-Kenya border (0°13'53"N, 34°00'30"E), and a second in the Kagera River on the Uganda-Tanzania border (0°56'28.1"S, 31°46'18"E) (Figure 1). The Sio River is shallow (c. 1–4m), while the Kagera River is deep (c. 10m) and fast-flowing. It was observed that fishers take advantage of the shallow Sio River to set barriers which not only effectively target adult fish, but also impede the upstream migration of those that survive the 'fishing gauntlet'. Seining was also observed during this study. Such indiscriminate fishing methods are not used in the Kagera River because of depth and high water flow, which pose a risk to the fishers.

Fisheries management is often concerned with the assessment of size at sexual maturity, patterns of spawning and fecundity, all of which require a thorough understanding of gonad microstructure and function. Knowledge of oogenesis, spawning seasons and behaviour is also important for the management of wild stocks and aquaculture. Such information is, however, available for only a small number of teleost species that are commercially important (Tyler and Sumpter 1996). In labeines, those reproductive studies conducted to date have predominantly been macroscopic in analysis (Cadwalladr 1965a, Siddiqui *et al.* 1976, Gaigher 1983, Van Zyl *et al*. 1995, Weyl and Booth 1999), with only two studies investigating ovarian histomorphology (Van der Merwe *et al*. 1988, Booth and Weyl 2000). From these studies *Labeo cylindricus* was found to be a synchronous iteroparous spawner, reproducing over a short period each year throughout its lifespan. It is acknowledged that histological studies provide precise information on oocyte development but are slow and expensive to undertake because they involve complex laboratory techniques (West 1992).

Published online 07 Jan 2010

Figure 1: Map showing the location of the Kagera and Sio Rivers

The importance of histological description of gametogenesis was emphasised by Booth and Weyl (2000), who noted that macroscopic staging must be validated if errors in the estimation of maturity and reproductive seasonality are to be minimised. This study investigated oocyte and ovarian changes during recrudescence in two distinct *L. victorianus* populations living under different environmental conditions.

Material and methods

A fleet of eight 45m gill nets with 27–75mm stretched mesh were set for 12 hours twice a week for 12 months in the Kagera and Sio Rivers during the period January–December 2000. Caught fish were removed from the nets and measured to the nearest 0.1mm for Fork Length (FL). Exposed gonads were classified macroscopically according to their maturation stage (Table 1). The excised ovary and the eviscerated fish were then weighed to the nearest gram. Ovarian tissue subsections were taken from the anterior, middle and posterior regions of the ovary and fixed in Bouin's fluid for 24 hours prior to transfer to 70% ethanol for storage. Preserved samples were routinely processed, following standard histological methods (Luna 1968). Transverse and longitudinal sections (5µm) were mounted on glass slides and stained in Ehrlich's Haematoxylin and Eosin (H&E). Oocyte stages were classified following Booth and Weyl (2000). Structural measurements were made on randomly selected and scanned sections from at least 10 fish per oocyte stage, using Sigma Scan Pro Image Analysis software. Seasonal changes in oocyte development were followed by measurement of area covered by each oocyte stage per microscopic field. Rainfall data were obtained from the Meteorology Department and hydrological data was from the Water Department, Uganda.

Differences in the median monthly Gonadosomatic Indices (GSI) and the ratio of ovary weight to eviscerated body weight were compared with a non-parametric Kruskal-Wallis test.

Results

Macromorphological description of the ovary

A total of 137 and 188 female fish were caught from the Kagera and Sio Rivers, respectively. *Labeo victorianus* ovaries are paired organs situated in the peritoneal cavity and suspended on either side of the midline by a mesovarium. Size and shape of the ovaries varied with the stage of development (Table 1). In 'juveniles', ovaries were yellowish, thin and translucent, while in 'regressed' fish, ovaries were flaccid, straight and translucent. As oogenesis progressed, the ovaries enlarged to become lobed, sac-like, greenish-cream organs filling the abdominal cavity.

A capsule, the tunica albuginea, composed of dense regularly-arranged collagen and elastic fibres mixed with a few smooth muscle cells, enclosed the ovaries. The capsule gave off connective tissue septa that invaded the ovary to form the ovigerous lamellae which projected towards the ovarian lumen. Germ cells and follicle cells were contained within the ovigerous lamellae. The follicle cells were spindle-shaped in the pre-vitellogenic and squamous in the vitellogenic ovary. An ovarian artery and vein were macroscopically visible along the entire length of both ovaries. Histological sections confirmed that the ovarian capsule and ovigerous lamellae were highly vascularised.

Microscopic description of oogenesis stages

The process of oogenesis was classified according to oocyte location and size, staining characteristics, number of nucleoli, presence of the follicular layer and the distribution of cytoplasmic inclusions. According to these criteria, oogenesis was found to proceed through six stages: oogonia, chromatin nucleolar oocytes, perinucleolar oocytes, primary yolk vesicle oocytes, secondary yolk vesicle oocytes and tertiary yolk vesicle oocytes.

Primary and secondary oogonia were discernable in ovarian nests where they occurred together with follicle cells (Figure 2a). Primary oogonia, the smallest germ cells noticeable, were characterised by a large nucleus:cell diameter ratio, chromatin granules on the nuclear envelope and one distinct nucleolus (Figure 2a). Secondary oogonia also had a high nucleus cytoplasm ratio and one nucleolus, but were larger than primary oogonia with their nuclei filled with basophilic chromatin threads (Figure 2b).

Chromatin nucleolar stage

Chromatin nucleolar oocytes were characterised by a large, centrally-located nucleus compared to the cell size, with clumps of basophilic chromatin on the nuclear wall and surrounded by a light basophilic cytoplasm (Figure 2a).

Perinucleolar stage

Growth of the chromatin nucleolar oocytes to the perinucleolar stage oocyte was accompanied by migration from the germ cell nests. Three types of perinucleolar oocytes were

Table 1: Macroscopic and histological description of various stages of oocyte recrudescence in *Labeo victorianus*

Stage	Macroscopic appearance	Histological equivalent
1. Juvenile	Ovary thick, straight, translucent, strap-like structure.	Oogonia, chromatin nucleolar and perinucleolar stage oocytes dominated the ovary. No post-ovulatory follicles.
2. Regressed	Ovary straight, flaccid, yellowish structure.	Oogonia, chromatin nucleolar and perinucleolar stage oocytes dominated the ovary. Post-ovulatory follicles and/or atretic oocyte visible.
3. Maturing	Ovary straight. Ova visible through the capsule. Ovary increases in size and starts forming lobes.	Primary yolk vesicle oocyte and secondary yolk vesicle oocytes stage present in the ovary.
4.Ripe	Ovary fully distended and fills the abdominal cavity. Oocyte olive green and easily shed on application of slight pressure on the ovary.	Ovary dominated by tertiary yolk vesicle oocytes. Few pre-vitellogenic stages begin to grow for the subsequent season.
5. Spent	Ovary flaccid and often haemorrhagic if spawning was successful. Few oocytes visible giving the ovary a speckled appearance.	Post-ovulatory follicles and Type I and II atretic oocytes, cohorts of previtellogenic oocytes visible.

recognised (Figure 2c). Pre-perinucleolar oocytes were close to the nests, polygonal in shape, and contained multiple nucleoli of varying sizes in the nucleus. Their cytoplasm was basophilic. Early perinucleolar oocytes were also polygonal in shape but had three to four large nucleoli and several smaller ones. Increase in size of these cells (Table 2) was accompanied by their becoming spherical and less basophilic in H&E. The late perinucleolar oocytes were the least basophilic and spherical in shape. Late perinucleolar oocytes were characterised by numerous nucleoli neatly arranged on the nuclear wall.

All perinucleolar stage oocytes had acellular zona radiata and were surrounded by two follicle layers, a theca and a granulosa. Yolk vesicles, or cortical alveoli, started to appear in the late perinucleolar oocytes marking the end of the primary growth phase.

Primary yolk vesicle oocyte stage

During this stage the cortical alveoli formed at the periphery of the oocyte and increased in number to fill the whole of the cytoplasm. The zona radiata and the follicular layer increased in thickness together with an increase in the number of nucleoli (Figure 2c).

Secondary yolk vesicle oocyte stage

Oocytes in this stage were characterised by the initial appearance of acidophilic yolk granules, staining red in H&E within the cytoplasm (Figure 2d). The prevalence of oocytes within this development stage was low when compared to other stages. Secondary yolk vesicle oocytes had similar follicular layers as the primary yolk vesicle oocytes.

Tertiary yolk vesicle oocyte stage

In tertiary oocytes (Figure 2e), the yolk granules that were initially at the periphery of the cytoplasm increased in size to form globules that occupied the entire central section of the cytoplasm. Cortical alveoli were only at the periphery of the cytoplasm, forming a ring around the ooplasm. The nucleus at this stage was centrally positioned and irregular in shape with several nucleoli on its membrane. The chromatin in the nucleus was no longer visible at this stage. As the oocyte developed further, the nucleus migrated from the centre to the periphery of the cell.

Post-spawned ovaries

After ovulation, the theca and granulosa layers remained in the ovary and hypertrophied to form the post-ovulatory follicles. The granulosa cells that were squamous prior to ovulation became cuboidal to columnar in structure with basophilic heterochromatin. The thecal layer became increasingly vascularised. Cohorts of basophilic developing oocytes were visible in 'spent' ovaries (Figure 3a). The post-ovulatory follicles were later invaded by macrophages to form melano-macrophage centres (Figure 3b). Oocyte atresia was common in the 'spent' fish and three forms were noted.

Type I atresia was characterised by fast fragmentation of the zona pellucida and dissolution of the cytoplasm contents (Figure 3a). This type of atresia was common in tertiary oocytes of successfully spawned ovaries. Type II atresia also occurred in vitellogenic oocytes and was characterised by the breakdown of yolk globules to smaller granules, together with vacuolar degeneration of the cytoplasm with an intact zona pellucida (Figure 3c). In some samples from the Sio River spawning was partial, as indicated by few post-ovulatory follicles among retained tertiary oocytes, while in others there were no post-ovulatory follicles. The presence of Type II atresia indicated failed spawning. In both spawning scenarios, the ovaries were cleared of the matured oocytes to facilitate gonadal recrudescence. In this case, ovigerous lamellae with germ cells surrounded and formed a ring around the 'unspawned' vitellogenic oocyte prior to onset of atresia (Figure 3d). The follicular layer of the 'unspawned' tertiary oocyte detached from the zona radiata and fragmented into small pieces accompanied by karyolysis (Figures 3e, 3f). The yolk globules in the oocyte cytoplasm fragmented into small granules followed by vacuolar degeneration of the oocyte and hyaline degeneration of zona radiata. Type II atresia occurred within 29 of the 32 'spent' ovaries from the Sio River (90.6%). It was also noted that it took over four months for an oocyte to be resorbed, by which time the younger oocytes had reached the primary yolk vesicle stage. Type III atresia was observed in samples from both populations and was characterised by cloudy swelling degeneration of the pre-vitellogenic oocytes.

Seasonal changes in the ovaries appeared to be synchronised with rainfall (Figure 4). The gonadosomatic indices of females varied significantly between months for

both the Kagera River (H = 35.7, n = 137, P < 0.01) and Sio River (H = 58.4, n = 188, P < 0.01) populations. Minimum observed GSI was in June (10.44 ± 2.8%) in the Sio River and in July (2.09 ± 0.76%) in the Kagera River. Maxima were reached in March for both the Kagera (10.64 ± 1.74%) and Sio River (30.27 ± 4.71%) populations. A similar pattern was noted for both rainfall and water levels in the two study sites.

Successful spawning was determined from the presence of extensive and tortuous vascularised post-ovulatory follicles (Figure 3a). In the Kagera River population, spawning occurred between March and May and from September to November. This period corresponded to the annual bimodal rainfall maxima and rising water levels. Synchronisation of spawning with rainfall was also reflected in the dominance of tertiary yolk vesicle oocytes prior to the rainfall. Whereas a similar pattern of spawning at the onset of rainfall was observed in the Sio River population, there was a major deviation during the second season exhibited by the presence of fresh post-ovulatory follicles in August, before the onset of rainfall (Figure 4). Atretic oocytes were observed in the Sio River population throughout the study period, with exception of March and April. In contrast, atretic oocytes were not found in the Kagera River population beyond two months post-spawning.

Microscopic investigation of *L. victorianus* ovaries indicated a typically cystovarian structure (Hibiya 1982), with oocytes developing in cohorts up to the tertiary yolk vesicle oocyte stage followed by ovulation or atresia. In the 'ripe' stage (Table 1), new cohorts of oocytes developing up to the pre-perinucleolar stage were visible in ovaries dominated by tertiary yolk vesicle oocytes. From this observation *L. victorianus* could not be classified as quiescent (Cadwalladr 1965b) as there was no period of inactivity between oogenetic cycles. Oogonia developing from the ovigerous lamellae of 'ripe' ovaries were not affected by post-ovulatory changes with only oocytes from the preceding cohort becoming atretic. Oocytes from fish sampled two months after peak spawning periods were at the primary and/or sec-

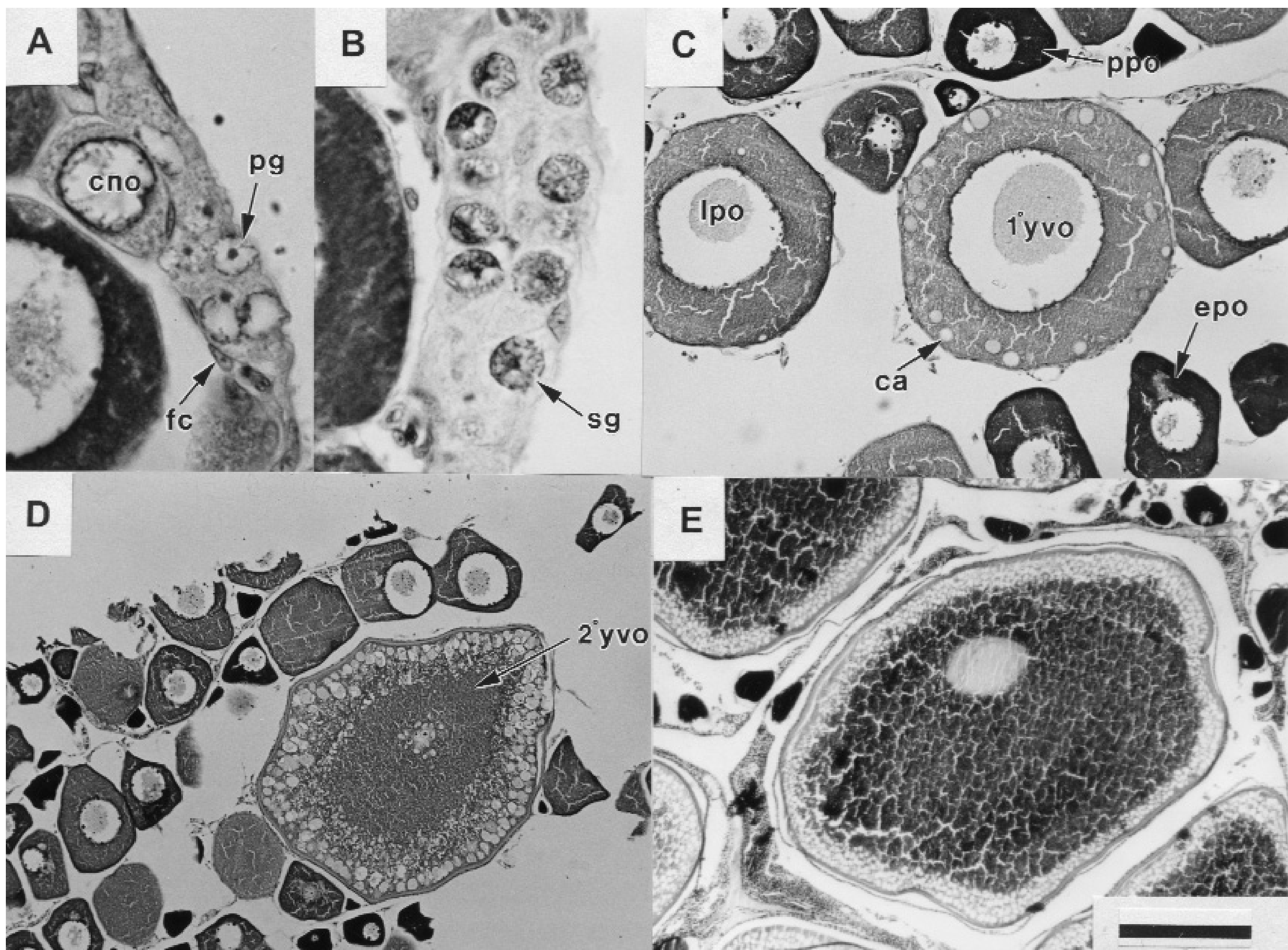

Figure 2: Transverse section through the ovary of *Labeo victorianus* showing the various oocyte stages. A, primary oogonia (pg), follicular cells (fc) and chromatin nucleolar oocytes (cno) in nests; B, secondary oogonia (sg); C, pre-perinucleolar oocyte (ppo), early perinucleolar oocyte (epo), late perinucleolar oocyte (lpo) and primary yolk vesicle oocytes (1°yvo) with cortical alveoli (ca); D, secondary yolk vesicle oocyte (2°yvo) with central cortical alveoli and yolk granules; E, tertiary yolk vesicle oocyte with migrating nucleus and peripheral cortical alveoli. Scale bar = A and B, 20μm; C and D, 100μm; E, 200μm

ondary oocyte stage. The low prevalence of secondary oocytes was possibly due to rapid oocyte development to the tertiary oocyte stage. Ovaries of fish caught four months post-spawning included the new cohort of oocytes that had reached the tertiary yolk vesicle stage. Based on these observations, it is proposed that development from oogonia to tertiary yolk vesicle oocyte takes four to five months in *L. victorianus*. Future studies involving repeated ovarian biopsy are, however, required to confirm this observation.

Discussion

In *L. victorianus*, Type III atresia of pre-vitellogenic oocytes was not characterised by invasion of follicles and phagocytosis (Hibiya 1982). In contrast, atresia followed a degenerative pattern as noted in *Cheimerius nufar* (Coetzee 1983). According to Hibiya (1982) the contents of vitellogenic oocytes liquefy and diminish during atresia, a description that conformed to Type I atresia noted in tertiary oocytes,

Table 2: Mean diameter (± standard deviation) of various oocytes stages from fixed ovaries of *Labeo victorianus*

Stage	Cell diameter (µm)	Nuclear diameter/cell diameter (µm)	Number of nucleoli	Number measured
Primary oogonia	10.42 ± 0.6	7.13 ± 0.5	1	29
Secondary oogonia	14.23 ± 1.2	10.60 ± 1.0	1	35
Perinucleolar oocytes				
a) pre-perinucleolar oocyte	65.29 ± 2.9	44.21 ± 2.4	8.30 ± 1.96	32
b) early perinucleolar oocyte	127.28 ± 0.5	69.06 ± 0.4	13.10 ± 1.05	34
c) late perinucleolar oocyte	216.78 ± 20.5	114.67 ± 9.9	25.30 ± 1.58	44
Primary yolk vesicle oocyte	294.04 ± 15.9	121.39 ± 14.9	22.60 ± 1.76	36
Secondary yolk vesicle oocyte	497.02 ± 0.40.6	178.06 ± 13.6	32.25 ± 2.02	26
Tertiary yolk vesicle oocyte	920.27 ± 27.23	204.00 ± 7.8	–	66

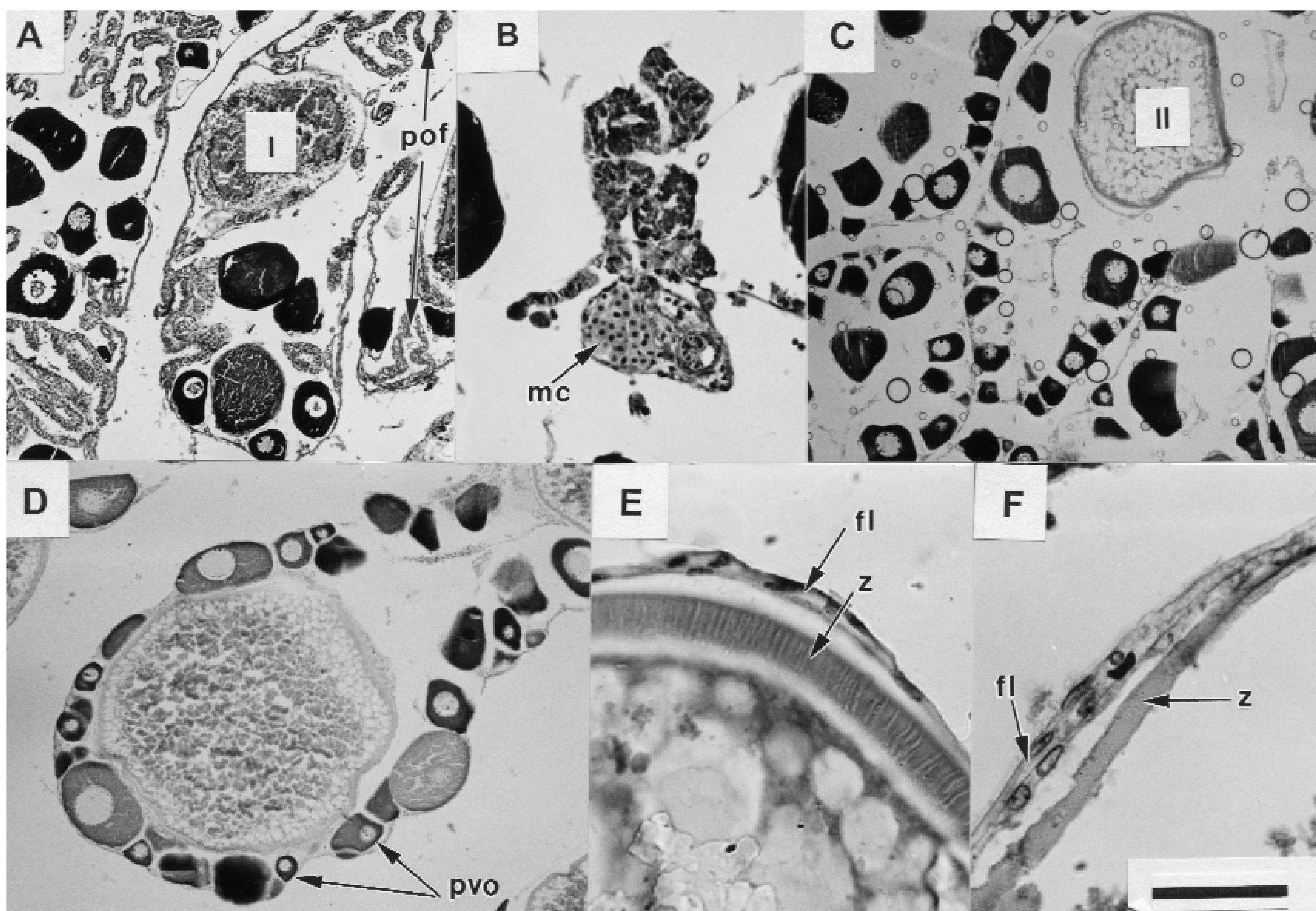

Figure 3: Transverse section through 'spent' ovaries of *Labeo victorianus* showing post ovulatory changes. A, Type I atretic oocyte (I), post-ovulatory follicles (pof), a cohort of previtellogenic oocytes; B, melanomacrophage centres (mc) in post- ovulatory follicles; C, Type II atretic oocyte (II); D, encircling of 'unspawned' tertiary yolk vesicle oocyte by pre-vitellogenic oocytes (pvo); E, normal follicular layers (fl) and zona radiata (z); F, hyaline degeneration of zona radiata and karyolysis of follicular layers. Scale bar = A, 100µm; B, 20µm; C and D, 100µm; E and F, 20µm

and also reported in *Mullus surmuletus* (N'da and Déniel 1993). Tyler and Sumpter (1996) observed that it was difficult to distinguish between an atretic follicle that failed to be ovulated in the previous spawning season, despite reaching full size, and a developing oocyte that becomes atretic before it reaches full size. In this study, atresia was observed in both successful and failed spawning attempts. In successfully spawned ovaries, fully developed i.e. tertiary yolk vesicle oocytes underwent Type I atresia, while Type II was most common at the secondary yolk vesicle stage of development. Type III atresia was observed in pre-vitellogenic oocyte stages only. In failed spawning attempts Type I atresia was absent but Type II occurred in all vitellogenic oocytes, and Type III in the pre-vitellogenic stages. During oocyte growth, Type III atresia was rare in both *L. victorianus* populations and does not seem to play an important role in determining the number of oocytes that develop to maturity.

Phagocytosis was characterised by areas staining brown in H&E and were similar to macrophage centres noted in teleost spleen (Hibiya 1982). It is reported that follicle cells

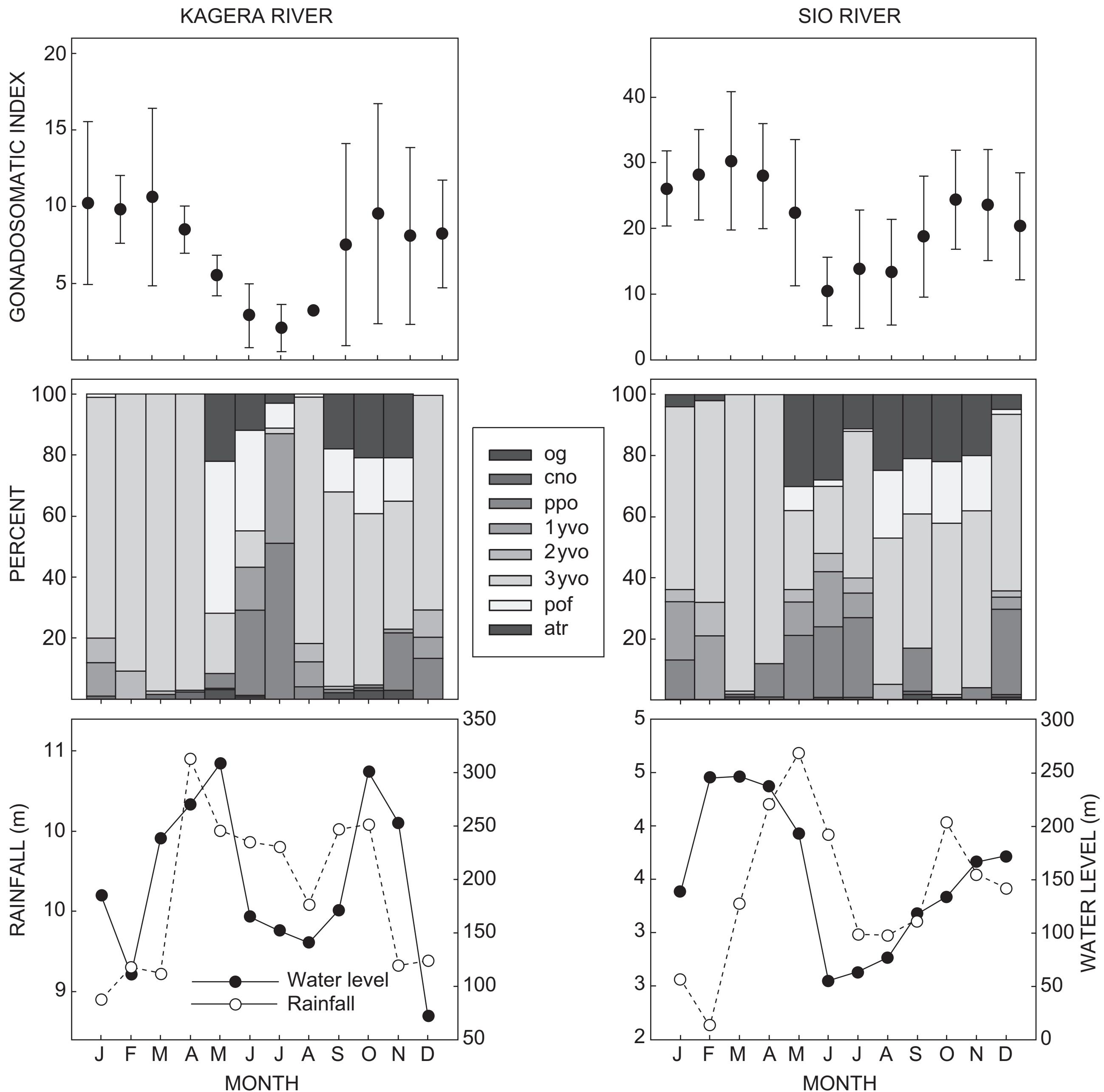

Figure 4: Seasonal changes in gonadosomatic index (mean ± standard deviation) and oocyte development stages in *Labeo victorianus* from the Kagera and Sio Rivers. og = oogonia, cno = chromatin nucleolar oocytes, ppo = perinucleolar oocytes, 1°yvo = primary yolk vesicle oocytes, 2°yvo = secondary yolk vesicle oocytes, 3°yvo = tertiary yolk vesicle oocytes, pof = post-ovulatory follicles, atr = atretic oocytes. Variations in rainfall and water levels are shown for both populations

have the ability to acquire phagocytic properties and have been observed to phagocytose atretic oocytes in some fishes (Hibiya 1982, Hoar 1969). In *L. victorianus*, phagocytosis was noted only in the post-ovulatory follicles and therefore appears to be the dominant process by which post-ovulatory follicles were cleared from the post-spawned ovaries. The presence of fresh post-ovulatory follicles before onset of rainfall was a deviation from the rainfall synchronised spawning pattern considered the norm for African labeines (Fryer and Whitehead 1959, Reid 1985, Skelton *et al*. 1991). Similar deviation from the typical flood-spawning pattern in the African labeines has, however, been reported by Cambray (1985) after observing the spawning of *Labeo capensis* in the Orange River in the absence of either rainfall or flooding.

The interruption of spawning was noted histologically by the low number of post-ovulatory follicles and Type II atresia that marked the end of oogenesis. This was evident in most Sio River samples. No phagocytosis was observed during this type of atresia but degenerative changes, characterised by the break-up of yolk globules, were followed by vacuolar degeneration. According to Hibiya (1982) and Bhagyashri and Saidapur (1996) there is a resorption of vitellogenin during this process. It could, therefore, be hypothesised that fish inhabiting the Sio River cope physiologically with failed ovulation by re-absorbing and recycling oocyte nutrients. The high prevalence of Type II 'atretic oocytes' in the Sio River population and the slow progression of this form of 'atresia' could be to facilitate nutrient transfer from the old oocyte, via the liver, back into the new cohort of developing oocytes. This process is possibly facilitated by the high degree of vascularisation noted in the ovaries. Further studies on the processes involved in nutrient resorption and recycling between the body and the developing oocytes are, therefore, recommended.

Histological investigations during this study have revealed differences in recrudescence patterns of the two *L. victorianus* populations. Spawning seems to proceed uninterrupted in the Kagera River population and is followed by Type I atresia and phagocytosis of post-ovulatory follicles. In contrast, there was over 90% spawning failure in the Sio River population, characterised by the predominance of Type II atresia. The incidence of follicular atresia is reported to be high under sub-optimal conditions (Tyler and Sumpter 1996). Unfortunately, those mechanisms which regulate follicular atresia are not properly understood as various factors, including environmental conditions, influence follicular atresia in fishes (Bhagyashri and Saidapur 1996). Atresia has been reported in *Cheimerius nufar* (Coetzee 1983), but differs in form and pattern from that in *L. victorianus*.

Reproductive effort also entails a cyclical demand for energy and material from the body, with bio-energetic expenditures needed for reproduction being closely related to other metabolic requirements (Miller 1984). Individuals must reach a threshold size before they are capable of distributing energy resources between somatic growth and gametogenesis in response to appropriate environmental cues (Munro 1990). The 'best' reproductive strategy is, therefore, a trade-off between a short generation time (r-selection) and enhanced survival through increased competitive ability (K-selection). Species that are exposed to unpredictable environments — like the Sio River population — tend to be generalist (*sensu* r-selected) and will favour a short generation interval and allocation of available energy resources to reproductive activities (Gunderson 1980).

The Kagera and Sio River systems present different environmental conditions, to which *L. victorianus* seem to have adapted accordingly. The Kagera River is a long, large and deep river (c. 10m deep and 20–30m wide) whereas the Sio River is shallow and narrow (<5m deep and c. 6–10m wide). Information gathered from the fishers, together with observations made during this study, indicated that the Sio River population is under intense fishing pressure. Steep banks and the inflow of large volumes of water into the Kagera River make fishing for *L. victorianus* using traditional gear difficult. In contrast, the Sio River is more suitable for seining, gill netting and deep-trapping. The conditions in the Kagera River can, therefore, be considered harsh for the fishers and stable to the fish, whereas the reverse is true in the Sio River. Type II atresia and a deviation from the 'normal' spawning pattern observed in the Sio River populations was possibly a compensatory response to over-fishing and the unpredictable environment, a character trait found in altricial/r-selected fishes. There is a need for further environmental investigation and for protection of the seemingly vulnerable Sio River *L. victorianus* populations.

Acknowledgements **—** The authors are grateful to the Lake Victoria Environmental Management Project, Makerere Research Grants and Andrew Mellon Foundation through Rhodes University for supporting this study.

References

BHAGYASHRI A and SAIDAPUR SK (1996) Atretic follicles and corpora lutea in the ovaries of fishes: structure-function correlations and significance. In: Munshi JSD and Dutta HM (eds) Fish Morphology. Horizon of new research. Science Publishers Inc., Enfield, New Hampshire, United States of America, pp 147–168.

BOOTH AJ and WEYL OLF (2000) Histological validation of gonadal macroscopic staging criteria for *Labeo cylindricus* (Pisces: Cyprinidae). African Zoology **35**: 223–231.

CADWALLADR DA (1965a) Notes on the breeding biology and ecology of *Labeo victorianus* (Boulenger) (Pisces: Cyprinidae) of Lake Victoria. Revue de Zoologie et de Botanique Africaines **72**: 109–134.

CADWALLADR DA (1965b) The decline in the *Labeo victorianus* (Boulenger) (Pisces: Cyprinidae) fishery of Lake Victoria and an associated deterioration in some indigenous fishing methods in the Nzoia river, Kenya. East African Agricultural and Forestry Journal **30**: 249–256.

CAMBRAY JA (1985) Observations on spawning of *Labeo capensis* and *Clarias gariepinus* in the regulated lower Orange River. South African Journal of Science **81**: 318–321.

COETZEE PS (1983) Seasonal histological and microscopic changes in the gonads of *Cheimerius nufar* (Ehrenberg, 1820) (Sparidae: Pisces). South African Journal of Zoology **18**: 76–88.

FRYER G and WHITEHEAD PJP (1959) The breeding habits, embryology and larval development of *Labeo victorianus* (Boulenger) (Pisces: Cyprinidae). Revue de Zoologie et de Botanique Africaines **59**: 33–49.

GAIGHER IG (1983) Reproduction of *Labeo umbratus* (Pisces: Cyprinidae) in Wuras Dam, a shallow, turbid impoundment. South

African Journal of Zoology **19**: 105–108.

Gunderson DR (1980) Using the r-K selection theory to predict natural mortality. Canadian Journal of Fisheries and Aquatic Sciences **37**: 2266–2271.

Hibiya T (1982) An Atlas of Fish Histology: Normal and Pathological Features. Kodansha Scientific Books, Tokyo, Japan, pp 104–110.

Hoar WS (1969) Reproduction. In: Hoar WS and Randall DJ (eds) Fish Physiology, Vol. 3: Reproduction and Growth Bioluminescence, Pigments and Poisons. Academic Press, London, United Kingdom, pp 1–20.

Luna LG (1968) Manual of Histological Staining Methods of the Armed Institute of Pathology. McGraw-Hill, New York, pp 5–46.

Miller PJ (1984) The tokology of gobioid fishes. In: Potts GW and Wootton RJ (eds) Fish Reproduction Strategies and Tactics. Academic Press, London, United Kingdom, pp 119–153.

Munro AD (1990) General introduction. In: Munro AD, Scott AR and Lam TJ (eds) Reproductive Seasonality in Teleosts: Environmental Influences. CRC Press, Boca Raton, Florida, United States of America, pp. 1–11.

N'da K and Déniel C (1993) Sexual cycle and seasonal changes in the ovary of the red mullet *Mullus surmuletus* from the southern coast of Brittany. Journal of Fish Biology **43**: 229–244.

Ogutu-Ohwayo R (1990) The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch *Lates niloticus* and the Nile tilapia *Oreochromis niloticus*. Environmental Biology of Fishes **27**: 81–96.

Reid GM (1985) A revision of African species of *Labeo* (Pisces: Cyprinidae) and a re-definition of the genus. Thesis Zoological. J Cramer Verlag Braunschweig **6**: 223–226.

Rutaisire J (2003) The Reproductive Biology and Artificial Breeding of Ningu *Labeo victorianus* (Pisces: Cyprinidae). PhD Thesis, Rhodes University, Grahamstown, South Africa, p 4.

Seehausen O (1996) Lake Victoria rock cichlids. Verdyun cichlids, The Netherlands, pp 263–264.

Siddiqui AQ, Chatterjee A and Khan AA (1976) Reproductive biology of the carp *Labeo bata* (Ham.) from the River Kali, India. Aquaculture **7**: 181–191.

Skelton PH, Tweddle D and Jackson PBN (1991) Cyprinids of Africa. In: Winfield IJ and Nelson JS (eds) Cyprinid Fishes: Systematics, Biology and Exploitation. Chapman and Hall, London, United Kingdom, pp 211–239.

Tyler CR and Sumpter JP (1996) Oocyte growth and development in teleosts. Reviews in Fish Biology and Fisheries **6**: 287–318.

Van der merwe W, Van vuren JHJ and Vermaak JF (1988) Cyclic histomorphological changes in the ovary of mudfish *Labeo capensis*. Aquaculture **72**: 349–358.

Van zyl BJ, Hay CJ and Steyn GJ (1995) Some aspects of the reproduction biology of *Labeo capensis* (Smith 1941) (Pisces: Cyprinidae) in relation to exploitation and extreme environmental conditions in Hardap Dam, Namibia. Southern African Journal of Aquatic Sciences **21**: 88–98.

West G (1992) Methods of assessing ovarian development in fishes: a review. Australian Journal of Marine and Freshwater Research **41**: 199–222.

Weyl OLF and Booth AJ (1999) On the life history of a cyprinid fish *Labeo cylindricus*. Environmental Biology of Fishes **55**: 215–225.