

Reproductive biology of ningu, *Labeo victorinus* (Pisces : Cyprinidae), in the Kagera and Sio Rivers, Uganda

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Synopsis

We investigated aspects of the reproductive biology of the cyprinid fish, *Labeo victorinus*, locally known as ningu, in the Kagera and Sio Rivers, Uganda. These rivers represent the last remaining refuges for this species within Uganda. *L. victorinus* is a highly fecund, potamodrometic fish that migrates upstream to spawn. Spawning is generally synchronised with the bimodal water level maxima observed within the rivers. There were, however, some deviations from this pattern. We caught sexually mature fish throughout the year in the Sio River, and noticed that spawning started before the second rainfall peak. Fish from the Kagera matured at significantly larger sizes than fish from the Sio River. Male and female fish, from both rivers, fed intensively during the non-breeding months accumulating significant fat reserves; a probable energy storage mechanism prior to their spawning migrations. The differences between the populations is probably a phenotypic response to differing abiotic factors such as river size, flow velocity and food availability.

Introduction

Lake Victoria, the world's largest tropical lake, faces numerous natural and anthropomorphic pressures such as the introduction of Nile perch *Lates niloticus* and over-fishing. This has resulted in species extinctions and declining fish population trends, particularly for cichlid fishes (Witte et al. 1992). Native non-cichlid species have also declined in abundance. The cyprinid fish *Labeo victorinus*, locally known as ningu, for example, once supported the most important fishery of all the potamodrometic¹ fishes (Cadwalladr 1965). This fishery has, in the last four decades, been greatly reduced to small catches at inflowing river mouths. In Uganda, the *L. victorinus* fishery is

now restricted to the Sio River on the Uganda–Kenya border (0°13'53" N, 34°00'30" E), and the Kagera River on the Uganda–Tanzania border (0°56'28.1" S, 31°46'18" E) (Figure 1) (Rutaisire et al. 2003) where populations of this fish are found in low densities. Submerged rocky cliffs and shelves near the river mouths are favoured by non-reproducing fish prior to migrating upstream to spawn.

Knowledge of aspects of the reproductive biology of a cultured or harvested fish is important for management. From an aquaculture perspective, market forces demand well-planned production of gametes and offspring to ensure all year-round production (Bromage 1995, Patino 1997). Manipulation of a fish's reproductive system under culture conditions requires an understanding of natural spawning patterns and other influential factors. Similarly, fisheries policies developed to

¹Organisms that migrate exclusively within freshwater.



Figure 1. Map of Uganda illustrating the locations of the Kagera and Sio Rivers.

assist harvesting rates are usually based on information of the species' reproductive biology such as size-at-sexual maturity, and the duration and periodicity of spawning.

The reproductive biology of *L. victorinus* is still largely unknown with information restricted to Cadwalladr (1965) and Fryer & Whitehead (1959). Cadwalladr (1965) described *L. victorinus* as a fish that migrates up the affluent rivers of Lake Victoria to spawn in lateral pools during rainy seasons, while Fryer & Whitehead (1959) reported on larval development, hatching of eggs and a description of spawning areas. No reproductive data have been collected in the last four decades during which period the lake's environment has changed. What is known is that fish migrate up the Kagera and Sio Rivers, twice a year in March–April and September–November, possibly to spawn (Figure 2). This study, therefore, contributes to the knowledge of this species' reproductive biology by investigating, and contrasting, important reproductive parameters such as sexual

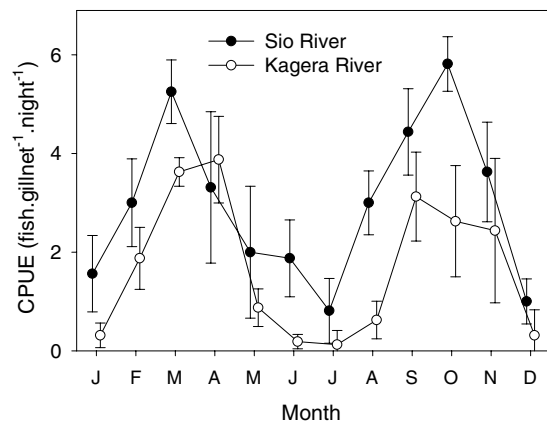


Figure 2. Mean monthly gill net catch-per-unit-effort (\pm standard deviation) for *L. victorinus* in the Kagera and Sio Rivers, Uganda from January to December 2000.

maturity, sex ratio, spawning seasonality and fecundity during spawning migrations. We compare two geographically isolated populations as they are the only remaining known populations

within Uganda, and the rivers are sufficiently different hydrologically from one another to provide insight into life-history responses.

Materials and methods

General

We caught a total of 138 and 188 female, and 254 and 215 male fish from the Kagera and Sio Rivers, respectively during the period from January to December 2000. Fish were sampled from both rivers each month. Information recorded for each specimen included measurements for fork length (FL) to the nearest 0.1 mm, and total mass (W) to the nearest 0.01 g. The mass of the excised ovary, liver, mesenteric fat and eviscerated fish (We) were later recorded. The sex of each specimen was recorded and gonads macroscopically staged (Table 1).

Sexual maturity and sex ratio

We calculated length-at-maturity, that length when 50% of the sampled fish in a size class are sexually mature, by fitting a logistic function to the proportion of reproductively active fish during the spawning season in centimetre size classes. The model predicted proportion of mature fish (P_L) in each length class (L) was described as $P_L = (1 + \exp(L - L_{50})/\delta)^{-1}$ where L_{50} is the length-

at-maturity and δ is the rate at which maturity is attained. The logistic parameters were estimated by non-linear minimisation of a negative binomial log-likelihood of the form

$$-\ln L = \sum_L y_L \ln \left(\frac{P_L}{1 - P_L} \right) + n_L \ln(1 - P_L)$$

where y_L is the observed numbers of fish mature in a total of n_L fish sampled in length class L . The null hypothesis that sex- and population specific estimates of L_{50} and δ were equal was assessed using a likelihood ratio test.

The sex ratio was determined for each river monthly. A significant departure from a 1:1 sex ratio was compared with a Bonferroni corrected Binomial distribution.

Indices

Each tissue's mass relative to eviscerated mass was calculated as an index. These included a gonadosomatic (GSI), a mesenteric fat (MFI) and a hepatosomatic (HSI) index. Due to the absence of a true stomach and the looping nature of labeine intestines, contents could not be easily squeezed out of the gut. We used a feeding index (FI), as employed by Gonçalves & Almada (1997), to calculate the proportion of the weight of entire gut to the fish's eviscerated weight. All indices were natural logarithm transformed and compared

Table 1. Macroscopic description of various stages of gonadal recrudescence in *L. victorinus*.

Stage	Males	Females
Juvenile	Testes threadlike translucent strap	Ovaries not distinguishable from testes. Also appears as a thin translucent strap
Maturing (Includes virgins and recovering spent fish)	Testes thick, straight and translucent	Ovaries straight. Ova white in colour and visible through the capsule.
Late-maturing	Testes enlarged, begin to form lobes and turn white. Mesenteric fat present around the testes	Ovaries increase in size, form lobes, is the largest organ in the abdominal cavity and is covered by mesenteric fat. Ova greenish in colour.
Ripe	Testes white convoluted and is the largest organ in the abdominal cavity. Mesenteric fat layer less than in Stage 3.	Ovaries are fully distended and fill the abdominal cavity. Oocytes olive green and easily shed on application of slight pressure on the belly.
Spent	Testes appeared as straight, thin, largely translucent strap on either side of the swim bladder ventral to the kidney.	Ovaries flaccid and often haemorrhagic if spawning was successful. Few oocytes visible, giving the ovary a speckled appearance.

across months using a Kruskal–Wallis test. Rain-fall data was obtained from the Meteorology Department, while hydrological data was from the Water Department, Uganda.

Fecundity and egg size

We estimated fecundity and egg size from fish in the ‘ripe’ macroscopic stage (Table 1) with only yolked eggs counted (Cambray 1982). Fresh ovaries were fixed in buffered 10% formalin for 12 h and stored in 70% ethanol. Ovary mass was recorded and all the eggs from one of the ovaries emptied into a beaker of water and shaken gently to cause uniform mixing. Volumetric subsamples of 1–2 ml were pipetted from the mixture and transferred to a Petri dish where all ova were counted using a tally counter. Fecundity was calculated as $F = n \times (V/v) \times (W/w)$ where n is the number of ova in the subsample V is the volume of ova and water, v the volume of subsample, W the weight of both ovaries, and w the weight of the ovary whose eggs were counted. Our second sample of ova was obtained from the ovary that was not used for fecundity studies, and their diameter measured along their median axis with a calibrated eyepiece micrometer fitted on a dissecting microscope at 20× magnification. After natural logarithm transformation, absolute fecundity was regressed against both eviscerated mass and fork length. We used Analysis of Covariance to test for the equality of the intercepts and slopes of both populations.

Results

Sexual maturity and sex ratios

Female length-at-maturity was estimated at 21.9 cm FL for the Kagera River population and 11.8 cm FL for the Sio River population (Figure 3), and were statistically different from one another (Table 2). The rate of sexual maturity, the parameter δ , did not differ significantly ($p > 0.05$). Male length-at-maturity was estimated at 22.1 cm and 12.8 cm FL for the Kagera and Sio River populations, respectively (Figure 3, Table 2). As with female fish, only the L_{50} parameter was significantly different between both populations (Table 2). Male and female fish

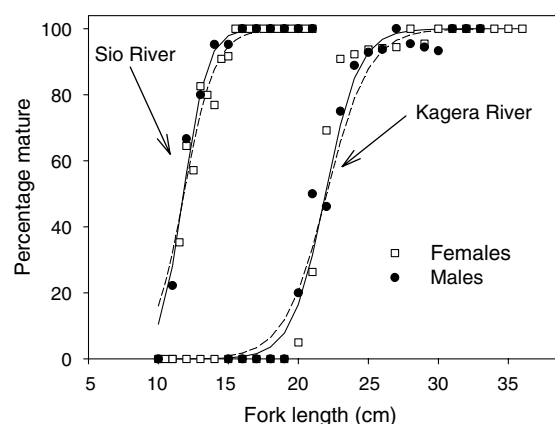


Figure 3. Observed (symbols) and predicted (lines) percent sexually mature male and female *L. victoriana* sampled from January to December 2000 from the Kagera and Sio Rivers, Uganda. Solid lines are for males and dashed lines for female fish.

Table 2. Logistic function parameter estimates for male and female *L. victoriana* sampled in the Kagera and Sio Rivers, Uganda from January to December 2000. Values with different superscripts are significantly different from one another ($p < 0.05$).

	Parameter	Males	Females
Kagera River	L_{50}	22.02 ^a	21.93 ^a
	δ	1.50 ^d	1.19 ^d
Sio River	L_{50}	10.79 ^b	11.83 ^c
	δ	0.84 ^d	1.11 ^d

from the Kagera River matured at the same length ($p > 0.05$), while in the Sio River, female fish matured at a larger length than males ($p < 0.05$). No difference was found in the maturity rate between males or females from either population.

For each river, the sex ratios were not significantly different from a 1:1 sex ratio ($p > 0.05$).

Reproductive seasonality

Female gonadosomatic indices (Figure 4) varied significantly across months for both the Kagera and Sio River populations ($p < 0.05$). Minimum observed GSI was in June ($10.44 \pm 2.8\%$) and July ($2.09 \pm 0.76\%$), while a maximum was reached in March for both the Kagera ($10.64 \pm 1.74\%$) and Sio River ($30.27 \pm 4.71\%$) populations. ‘Spent’

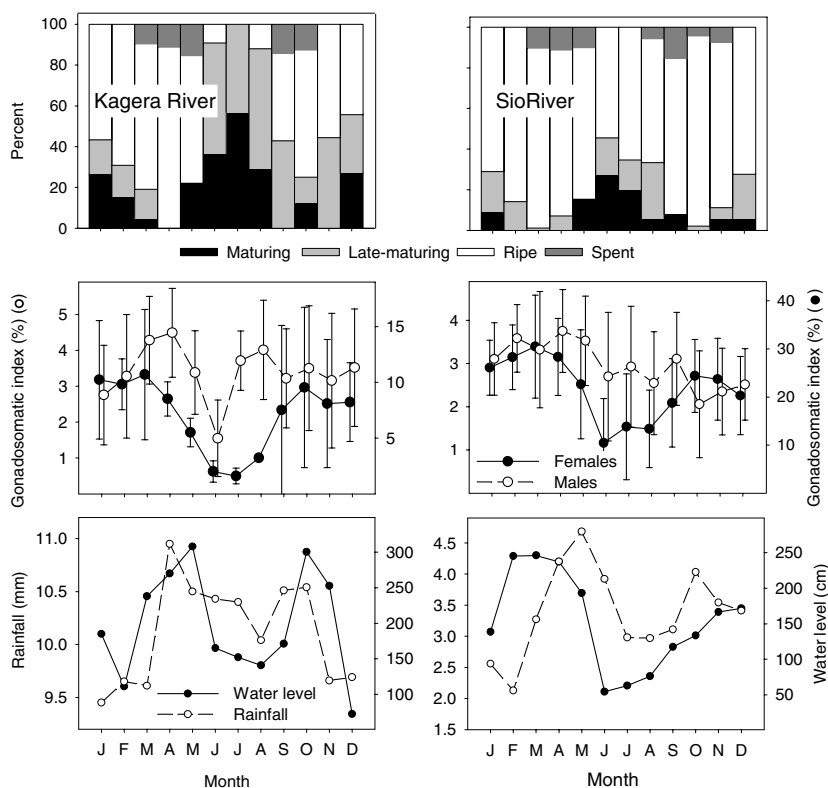


Figure 4. Monthly maturity stages for female *Labeo victorinus* (upper panels) and mean monthly (\pm standard deviation) male and female *L. victorinus* gonadosomatic indices (middle panels) sampled from the Kagera and Sio Rivers, Uganda from January to December 2000. The lower panels present mean water level and rainfall for the two respective rivers collected over the same time period as the data presented in the upper and middle panels. The data for mean monthly rainfall and water levels were provided by the Meteorology and Water Departments, Uganda.

gonads were observed in the March, April, May, October and November samples from the Kagera River population (Figure 3). In the Sio River population, the first spawning season corresponded to that of the Kagera River, but the second spawning period started in August, a month earlier. Freshly 'spent' fish were sampled in August from the Sio River population when all the fish from Kagera River had ovaries that were still in the 'maturing' and 'late-maturing' stages. The Kagera River samples displayed a clear distinct pattern of gonadal maturation with no 'ripe' ovaries sampled in July. In contrast, fish from the Sio River population had a high proportion of 'ripe' fish in the same month.

Similar to female fish, male GSI varied significantly across months in both populations ($p < 0.05$) (Figure 4). 'Spent' fish were rare, with only a few

specimens sampled in May–June, October and November in the Kagera River, and in May–August, October–November from the Sio River population. Fish with testes in the 'maturing' and 'late-maturing' stages were the most prevalent in both populations.

Fecundity and oocyte size

The regression of fecundity against eviscerated mass was linear and against fork length was curvilinear (Table 3). No significant differences were found in the relative rates of change in fecundity per unit increase in eviscerated weight ($p > 0.05$), or for mean fecundity adjusted to common body weight ($p > 0.05$). There was a weak relationship ($r^2 = 0.12$) between oocyte size and eviscerated mass in Sio River population. This relationship

Table 3. Regression relationships between fecundity (F) on fork length (FL) (cm) and eviscerated weight (We) (g), and oocyte diameter (OD) (mm) on eviscerated weight for *L. victorinus* in the Kagera and Sio Rivers, Uganda.

Population	Regression equation	r^2
Kagera River	$\text{Log}_e F = 0.66 + 3.16 \text{ Log}_e \text{FL}$	0.73
	$F = -1667 + 190\text{We}$	0.83
	$\text{OD} = 0.73 + 0.0005\text{We}$	0.75
Sio River	$\text{Log}_e F = 0.182 + 3.191 \text{ Log}_e \text{FL}$	0.93
	$F = -1013 + 168\text{We}$	0.95
	$\text{OD} = 0.8 + 0.0007\text{We}$	0.12

was stronger in fish from the Kagera River ($r^2 = 0.75$).

Feeding indices

There was significant variation in the feeding index across months for male and female fish from both populations ($p < 0.01$). Males and females from both populations had a similar bimodal pattern with maxima in June–July and December–January (Figure 5).

Mesenteric Fat Index

Deposition of fat in the mesentery varied significantly across months in both populations. In the Kagera River samples, there was a sharp rise in fat deposition in May peaking in June, and declining thereafter (Figure 6). A similar pattern was observed in fish inhabiting the Sio River except that a longer peak between June and August was observed. We noted that mesenteric fat deposition was mainly in 'maturing' and 'late-maturing stages.' In the 'ripe' and 'spent' stages, the fat deposits were already depleted. In males, the Mesenteric Fat Indices (MFI) also varied significantly across months (Table 3). In the Kagera River population, the MFI was bimodal and was lowest from April to June and during October–November period, while in the Sio River population the decline was only during May and November.

Hepatosomatic index

The hepatosomatic indices were not statistically significant across months for either sex or population ($p > 0.05$).

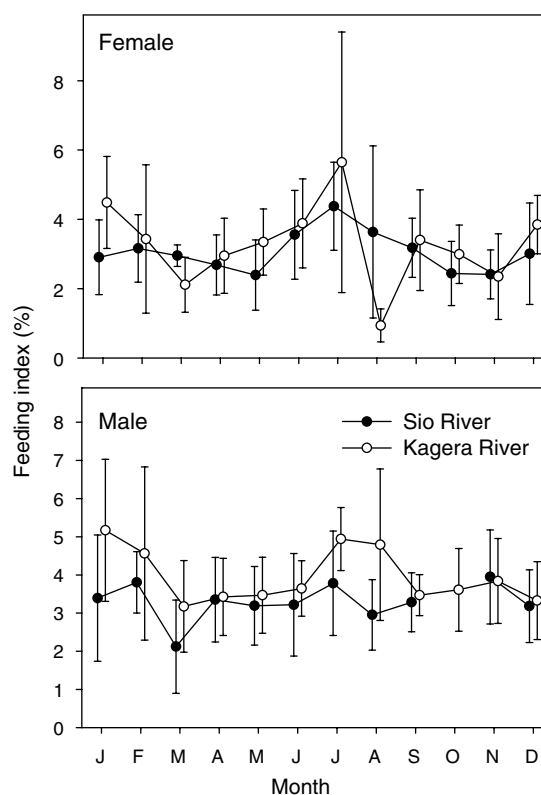


Figure 5. Monthly observed mean (\pm standard deviation) of female and male *L. victorinus* feeding indices sampled in the Kagera and Sio Rivers, Uganda from January to December 2000.

Discussion

Similarities and differences between the two populations of *L. victorinus* were clearly noticeable. Reproduction seemed to be synchronised with both rainy seasons, a finding confirming previous observations by both Fryer & Whitehead (1959) and Cadwalladr (1965). Synchronisation of sexual maturation and reproduction with onset of the rainy seasons has also been documented in other African labeines² (Jackson & Coetzee 1982, Skelton et al. 1991, Weyl & Booth 1999).

Non-spawning months were characterised by fish with full guts and high mesenteric fat deposits; a probable indication of feeding and accumulation

²Anon, 1965. Annual report of the Department of Agriculture and Fisheries¹ 1964. Fisheries Research, Part II. Government Printer, Zomba, Malawi.

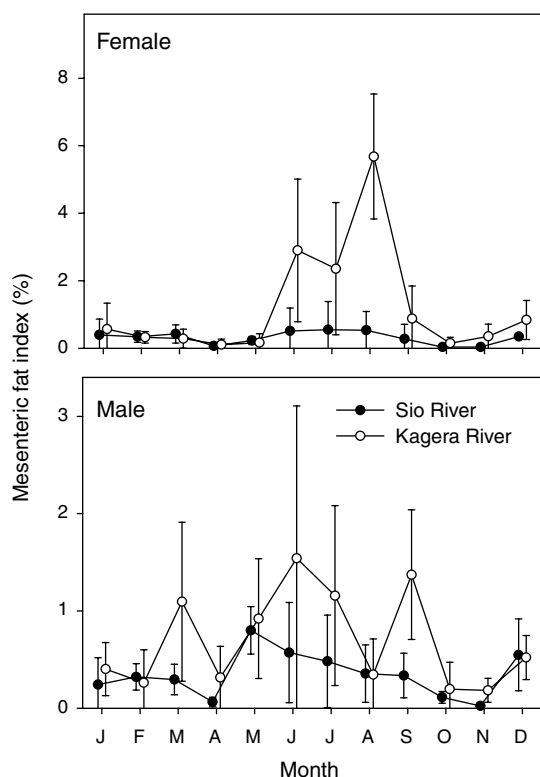


Figure 6. Monthly observed mean (\pm standard deviation) and female and male *L. victorinus* mesenteric fat indices sampled in the Kagera and Sio Rivers, Uganda from January to December 2000.

of fat reserves prior to upstream migration to spawn. The annual peaks in gut fullness in both populations were from June to July and from December to January. In the Sio River population, however, a sharp rise in the feeding index from May to June was followed by drastic fall in August. June was characterised by intense feeding by females in the Sio River whereas males, in contrast, did not exhibit much seasonality in their feeding patterns. In the Sio River population, reproduction did not seem to affect feeding as it did in the Kagera River population. Female mesenteric fat indices were either unimodal in the Kagera River (peaking between June and August) or bimodal in the Sio River (peaking between December and January and between June and August). The spawning period in the second half of the year was longer in the Sio River population than in the Kagera River population – as indicated by the presence of ‘spent’ ovaries. Spawning lasted

for four months (August–November), in the Sio River, while it lasted for two months (September–October) in the Kagera River. Sio River females appeared to feed rapidly in the adjacent lake and moved into the river to spawn shortly thereafter. This was noticed by the capture of freshly ‘spent’ females in August in the Sio River, a month prior to when fish in the same gonadal stage could be caught in Kagera River. The Sio River population could, therefore, have adjusted their feeding regime as to maximise chances of spawning at the earliest availability of suitable conditions.

The period between June and July was characterised by intense feeding and replenishment of energy reserves for spawning in both populations. This feeding period coincides with the complete mixing of the lake. It is known that complete mixing of Lake Victoria occurs during this period when the established thermocline breaks down under the seasonal onset of the South-East trade winds causing the lake to become isothermal with respect to depth (Talling 1966). It is therefore possible that mixing results in increased availability of detritus, epilithic algae, diatoms and crustaceans on which *Labeo* spp. are known to feed (el Moghraby & el Rahman 1984). Though *L. victorinus* had two non-spawning seasons, June and July is the only period when feeding and mesenteric fat indices were the highest and fish were considered to be in their best condition as defined by a high mass to length relationship. These indices started to decline shortly before the spawning seasons and indicated cessation of feeding and the subsequent utilisation of the deposited fat reserves during spawning. Cessation of feeding during the spawning season was also observed in *L. cylindricus* (Weyl & Booth 1999), and could be common behaviour in the African labeine lineage.

Utilisation of tissue reserves during oogenesis and subsequent reduction of deposits at the onset of spawning has been reported in several fish species. These include sockeye salmon, *Oncorhynchus nerka* (Idler & Bitners 1959), American plaice, *Hippoglossoides platessoides* (Mackinnon 1972), northern pike, *Esox lucius* (Medford & Mackay 1978), European plaice, *Pleuronectes platessa* (Dawson & Grimm 1980) and rainbow trout, *Oncorhynchus mykiss* (Nassour & Léger 1989). In the blennioid fish, *Salaria pavo*, reduction in feeding opportunities was reported to be the major

cost of reproduction (Gonçalves & Almada 1997). According to Fouda et al. (1993) nutrients foraged in one part of the year or area are expended at another time or place when optimal conditions for reproduction occur. The liver, muscle tissue and mesenteric fat have been reported to be the organs that store energy reserved for reproduction in the some fish species. Clearwater & Pankhurst (1994) attributed the increase of hepatosomatic index in red gurnard *Chelidonichthys kumu* prior to spawning, to the liver being the storage organ in that species. In *P. platessa* the main source of protein reserves was the carcass (Dawson & Grimm 1980). Okuda (2001) attributed a decline in the somatic condition, hepatosomatic and fat body indices in the cardinalfish, *Apogon notatus*, to reproductive costs during spawning. In *L. victorianus*, reproduction does not seem to exert energy costs on the liver as revealed by no significant variation in the monthly hepatosomatic index of both populations. Similar findings are reported in *O. mykiss* where the liver plays a small role in lipid storage (Nassour & Léger 1989). MacFarlane et al. (1993) investigated the role of accumulated lipids in the mesentery of the yellowtail rockfish, *Sebastes flavidus*, and showed that a greater proportion was incorporated in the developing ovaries. The sharp decline in the mesenteric fat index in *L. victorianus* during spawning periods suggests that the mesenteric fat deposits are the major source of energy for reproduction. Accumulation of mesenteric fat as reported in some fishes (MacFarlane et al. 1993, Okuda 2001) is important since lipids are known to play a number of roles such as formation of vitellogenin, insulation of organs, buoyancy and several other physiological functions (Weigand 1996).

Reproduction in the Kagera River population conformed to the 'normal' labeine reproductive pattern – synchronisation of spawning with the raining season. Deviations from this pattern, were, however observed in the Sio River population. Spawning occurred prior to onset of the rainy season. Further deviation from the 'norm' was inferred from the feeding patterns and catch-per-unit-effort. It is known that reproductive strategy of a species will be the summation of a suite of traits that enable an individual to produce the maximum number of offspring. These traits include age and size at first reproduction, size and

age specific fecundity schedules, reproductive effort and the timing of spawning (Mills 1991). 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 and enhanced survival through increased competitive ability. 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 rivers provide different environments; the Sio River is shallow (1–4 m deep), while the Kagera River is deep (10 m in depth) and fast flowing. Fishers take advantage of the shallow Sio River to set barriers that not only effectively target adult fish, but also impede upstream migration. 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 that poses a risk factor to the fishers. It is clear that the Sio River population is under intense fishing pressure and inhabiting an environment that is not adequately protective. The observed deviations, like spawning when there was no rainfall and the attainment of sexual maturity at significantly lower sizes than the Kagera River population, could also be differing phenotypic responses to both overexploitation and to differing abiotic environments.

A deviation from rainy season synchronised spawning has been previously reported in other African labeines. Mitchell (1984) noted that spawning in *L. umbratus* was not necessarily flood dependent as previously described by Jackson & Coetzee (1982) but rather breeds in the most suitable site available thus fitting into Balon's (1975) intermediate guild description. A deviation from the typical flood-spawning pattern in the African labeines was also reported by Cambray (1985) after observation of spawning of *L. capensis* in the Orange River without any rainfall and

flooding. It appears as though *L. victorinus* in the Sio River is on a similar plastic trajectory that involves spawning events that are not necessarily synchronised with the rainy season and at a smaller size-at-sexual maturity.

The fecundity of the two populations was also investigated since it is known to vary among populations, and at times, between strains of fish species (Jonsson & Jonsson 1999). The determination of the actual number of eggs produced would be more useful for analysis of stock dynamics (Mason 1985). Consideration of the actual number of oocytes produced would, therefore, account for incomplete spawning or interrupted maturation of cells during trophoblastic growth followed by resorption (Foucher & Beamish 1980), but is difficult in fishes that produce tens of thousands of eggs under lotic spawning conditions. Mason (1985) introduced the term 'Apparent Fecundity' to refer to the estimated number of oocytes undergoing trophoplasmic growth leading to cell maturity. In this study, fecundity was determined following Cambray's (1982) definition of absolute fecundity as the number of yolked ova (mature and immature) just prior to spawning. Increases in fecundity with found in this study are in general agreement with findings of other workers on teleost fishes (Barbini & McCleave 1997, Jonsson & Jonsson 1999). We found no significant differences in elevations and slopes of regressions of fecundity on eviscerated weight. This suggests that the rate of increase of fecundity with weight in both populations is not environmentally controlled.

In conclusion, we have shown that *L. victorinus* is a highly fecund synchronous fish with two spawning seasons. Disparities in reproductive patterns could be due to adaptive reproductive tactics in response to the uncertain environments or simply due to underlying genetic differences between both populations.

Acknowledgements

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