*J. Fish. Biol.* (1977) **11**, 437–445

# Aspects of the reproductive biology of *Hippopotamyrus pictus* from Lake Kainji, with notes on four other mormyrid species

B. F. BLAKE

*Department of Zoology, University of Reading, Whiteknights, Reading, Berkshire, England*

(*Accepted 6 August 1976*)

A method is described for the assessment of fecundity in mormyrid fish. In all species examined a tri-modal egg size distribution was found in the mature pre-spawning ovary. These modes represented one oocyte and two ova components. The significance of the presence of two sizes of ovum is discussed in relation to breeding periodicity in *Hippopotamyrus pictus*. Size and age at first maturity are estimated for this species. The probable effects of the formation of the lake on the breeding behaviour of mormyrids is discussed.

## I. INTRODUCTION

Daget (1954, 1957) and Banks, Holden & McConnell (1965) have made observations on the breeding biology of mormyrid fishes from the Niger River, but they did not carry out detailed investigations of individual species. Nawar (1959*a*) recorded the fecundity of *Hyperopisus bebe* (Gunther) in the Nile, and made observations on five other species of mormyrid from this river (Nawar, 1959*b*). Okedi (1969) described the size at first maturity, sex ratio, and spawning periodicity of five small mormyrids from Lake Victoria, and subsequently (Okedi, 1970) examined their fecundity otherwise few data are available for the breeding biology or fecundity of this family.

Since the impoundment of the Niger in 1968 and the consequent formation of Lake Kainji, it is likely that the breeding behaviour of some indigenous fish has been modified. The present study sought to discover the direction which such changes may have taken within the Mormyridae, and to investigate the fecundity and the breeding cycle of these fish.

## II. FECUNDITY ASSESSMENT

### METHOD

Bagenal (1971) reviewed the major methods available for the estimation of fecundity in fish. He defined fecundity as the number of ripening eggs in the female prior to the next spawning. These methods and this definition are not, however, readily applicable to many tropical species. As pointed out by Bagenal such fish are frequently multiple spawners and, as a result, a gonad may contain a wide range of egg sizes and maturity stages. This complicates both the assessment of total egg numbers and the recognition of ' mature ' eggs. Marked differences in the density, and consequently the sinking rates, of different egg sizes invalidates many conventional temperate water subsampling techniques. Gonad sectioning described for mormyrids by Okedi (1970) is similarly of doubtful value in fish where there is no apparent regular pattern of egg size distribution. The method described here avoids these problems to some extent.

Methods of capture are discussed elsewhere (Blake, in press). The fish were measured for total and standard lengths, weighed, sexed and assigned a maturity rating according to the scale of Nikolsky (1963). In the Mormyridae only the left gonad is developed, and this was removed and weighed. The outer ovarian wall was removed and the gonad split longitudinally and preserved in Gilson's fluid. The sample jar was subsequently agitated at irregular intervals to facilitate egg separation. Microscopic investigation revealed the presence of many very small eggs, and decanting of supernatent fluid for washing purposes required great care. It was, therefore, inevitable that some ovarian tissue debris remained in the sample, but egg separation was satisfactory and counting was not impeded.

After one month the eggs were sufficiently hardened to allow handling and an estimation of the numbers and sizes. At least three size ranges were present, two of which were yellow and yolky, and the third small and white. These were considered to be developing ova and oocytes respectively. As sub-sampling was necessary it was desirable to separate the eggs into three fractions according to diameter to avoid bias due to differences in sedimentation rates. The entire sample was poured into a sieve of 10 cm diameter with a zooplankton netting base of aperture 288 μm. The eggs were copiously washed and the filtrate preserved. The remaining eggs were then washed through a brass sieve of aperture 710 μm and the filtrate and residue preserved separately. These last two fractions were transferred to wide-necked jars and made up to 200 ml. Each fraction was poured back and forth between two similar jars four times to obtain a random distribution, and sub-sampled with a 5 ml Stempel pipette. The sub-sample was emptied onto a squared counting dish, counted and measured.

The filtrate from the 288 μm sieve contained many thousands of small oocytes, and it was not practicable to sub-sample 5 ml from a 200 ml volume. It was, therefore, made up to 250 ml in a stoppered, calibrated, separating funnel, shaken vigorously and a 10 ml sample run off into a wide-necked jar. This was then made up to 200 ml and sub-sampled as for the other fractions.

Initially, 90 eggs from each fraction were measured for all species giving a total of 270 eggs for each fish [Fig. 1(a)]. Subsequently this was reduced to 30 for each fraction for *Hippopotamyrus pictus*, and the size distribution analysed for the species rather than for individuals, [Fig. 1(b)]. Comparison of Fig. 1(a) and 1(b) indicates good agreement between individual and massed data in this species.

## RESULTS

Gonads were examined from five species of mormyrid: 62 *H. pictus*, 5 *Marcusenius senegalensis* Steindachner, 3 *Hyperopisus bebe* (Gunther) 3 *Campylomormyrus tamandua* (Gunther), 2 *Mormyrops deliciosus* (Leach).

### (a) *Hippopotamyrus pictus*

Few mormyrids of Lake Kainji were found with ripening gonads (see Discussion), and the present study relies on information derived from *H. pictus*. Table I illustrates the size range and numbers of oocytes and developing ova from the 62 fish examined. Primary and secondary oocytes were not differentiated but the overall size range of 0·034–0·33 mm diameter is in agreement with that reported for East African mormyrids by Okedi (1970) who considered primary oocytes to occupy the range 0·059–0·088 mm, and the secondary oocytes 0·09–0·35 mm. Okedi did not, however, differentiate egg size modes for the gonads as a whole. Figure 1(a) and (b) shows a clear trimodal

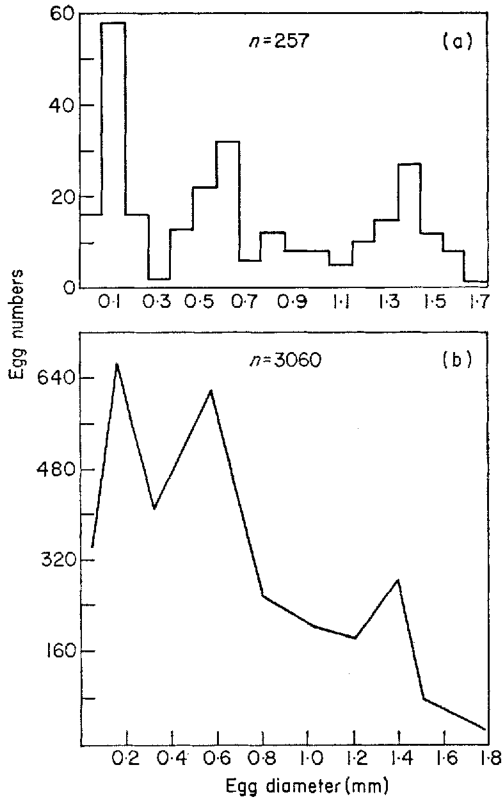


FIG. 1. (a) Egg size distribution in a single, female IV, *Hippopotamyrus pictus*. (b) Egg size distribution in a combined sample of 34 female IV *H. pictus*. Eggs were grouped in 0·2 mm diameter size groups and the mean plotted for each group.

TABLE I. Egg numbers and size ranges in *Hippopotamyrus pictus* at various stages of maturity

| Stage | Range of numbers: Oocytes (0·034–0·33 mm) | Small ova (0·34–0·80 mm) | Large ova (0·81–1·87 mm) | Fish $N = 62$ | Mean number for large and small ova fractions combined: Mean s.e. 95% confidence limits |
|---|---|---|---|---|---|
| ♀ III | 16 000–600 000 | 400–1880 | 0–800 | 10 | 520 ± 186·3 |
| ♀ IV | 10 000–330 000 | 1240–6400 | 1040–5760 | 34 | 3120 ± 329·18 |
| ♀ V | 14 000–172 000 | 1160–4080 | 1160–2400 | 10 | 2304 ± 406·8 |
| ♀ VI | 2000–30 000 | 480–1040 | 0 | 8 | 820 ± 123·8 (small ova only) |

pattern of egg size frequency for *H. pictus*, the oocytes having a peak at diameter 0·15 mm. Two distinct modes are apparent for the developing ova, one with a peak at 0·5 mm, and the second at 1·38 mm. Of the 62 fish examined, 34 had been assigned the maturity stage ♀ IV, and only these were included in the preparation of Fig. 1(b). According to Nikolsky (1963), this is the stage at which the gametes are ripe and the gonads have reached their maximum weight, but the gametes do not run out when light pressure is applied. This is necessarily an arbitrary division, however, it is an indication that all the gonads included in the figure had reached the immediate pre-spawning phase, and the egg size distribution should be close to that actually occurring at spawning. The relative magnitude of the modes in Fig. 1(b) is dependent on the sub-sampling technique. If it were possible to sample the entire gonad in a single step the oocyte mode would obviously dwarf the two ova peaks (Table I).

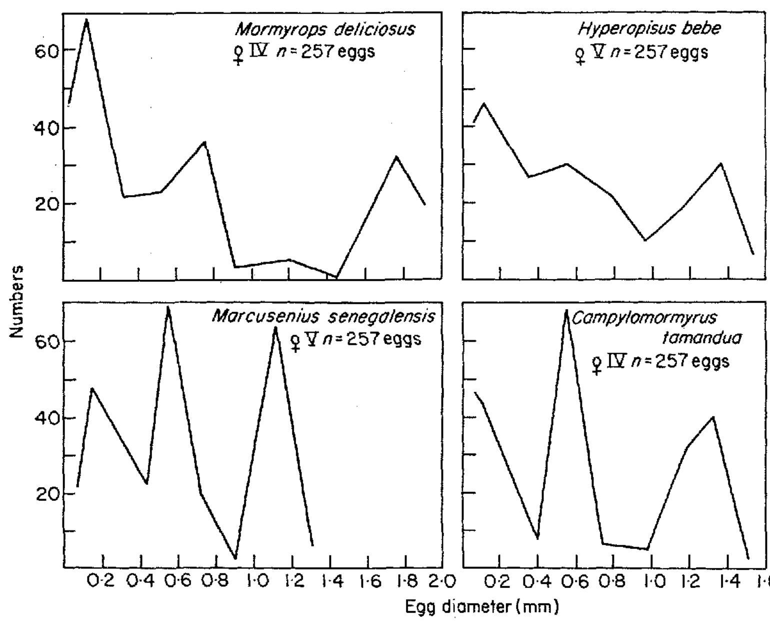


FIG. 2. Egg size distribution in four species of mormyrid. Eggs were grouped in 0·2 mm size groups and the mean plotted for each group.

The presence of two ovum size modes is interesting in that it seems to indicate either two spawning seasons or a single extended season. Nawar (1959*a*) noted the presence of two sizes of ova in *Hyperopisus bebe* and concluded that the nature of the breeding season required further study. The same author [Nawar 1959(b)] reported a four month breeding season for some Nile mormyrids, but suggested that most of these had a single spawning peak over one or two months. Okedi (1969), on the other hand, found several mormyrids from Lake Victoria bred twice a year, although the distinctness of the two cycles was apparently dependent on the duration of the rainy season. Nawar (1959*a*) also recognized the possibility that egg resorption may occur in *H. bebe* rather than a second spawning. Neither author, however, noted the presence of large numbers of oocytes such as were found in all maturity stages during the present study. The ratio of oocytes/ova varied with maturity (Table I) but even in completely spent fish up to 30 000 ocoytes were recorded. On the basis of gonad studies alone, it seems likely that either an extended or double spawning season occurs in *H. pictus*, and that an excess of oocytes is produced, which is resorbed after spawning. The advantage of such a system may lie in its flexibility. Possibly the number of ova ultimately developed to maturity is controlled by the environmental conditions. Thus in the rivers an extended rainy season could be exploited by the production of a large number of mature eggs late in the season, while the converse situation resulted in a more extensive resorption of oocytes and developing ova. One difficulty in determining if this situation exists is that of separating, by eye, virgin fish coming up to stage II for the first time, and mature fish recovering from a previous spawning.

(b) *Marcusenius senegalensis*, *Campylomormyrus tamandua*, *Mormyrops deliciosus*, and *Hyperopisus bebe*. Figure 2 shows the egg size distribution for these species. In view of the few fish involved little comment can be made on the Gonad composition. However, comparison with *H. pictus* indicates all species show the same basic trimodal pattern, although the necessity of combining different maturity stages tends to obscure this pattern. Thus the comments made in respect of *H. pictus* are relevant to the other four mormyrid species examined, although inter-specific differences in egg size and numbers are apparent, the mature ova of *M. senegalensis* being smaller than those of the other species. The results for *H. bebe* indicate agreement with Nawar (1969*a*) in the general size range of the large and small ova.

## III. BREEDING SEASON PERIODICITY

It is difficult to monitor the full breeding season of the mormyrids of Lake Kainji owing to marked seasonal fluctuations in the numbers of fish caught (Blake, in preparation). Maturing male and female *H. pictus* were frequently caught, but running and spent fish were relatively uncommon in the gill-net catches. It would, therefore, seem that the majority of this species move from the lake margins after reaching maturity stages III–IV, possibly undertaking a spawning migration. It is therefore difficult to ascertain if a single extended, or two separate, breeding seasons occur. By analysis of maturity stages from fish caught throughout the year from 1971–1975 it was, however, possible to deduce the timing and approximate extent, of the spawning season. As neither the effort expended nor the numbers of fish captured were constant from one month to the next it was necessary to express the abundance of a particular maturity stage in a given month as a percentage of the total adult fish caught. This necessitates an estimate of the size at first maturity. For this reason only females were analysed in detail as the various maturity stages were well defined and no wide variation was likely between the designation of stages II, III and IV by the present and previous workers. Such subjective differences could easily occur in the assessment of mormyrid testes. Figure 3(a) shows the analysis of standard lengths for 160 female III *H. pictus*, the first stage at which there can be no confusion between resting and virgin gonads. A clear peak exists, most of the fish being in the range of 16–19 cm standard length. This corresponds to age II fish as indicated by the length frequency histograms for 1974 [Fig. 3(b) and (c)]. Opercular bones and scales both showed ring formations in *H. pictus*, but these were extremely difficult to interpret, and did not give sufficiently consistent data to confirm or refute the length frequency analysis.

For the purpose of determining spawning periodicity only those female fish which were in excess of 16 cm standard length were considered, thus reducing the influence of fluctuating numbers of virgin fish on the percentages comprised by the various maturity stages.

## RESULTS

Table II shows the results of massed data from 817 fish collected between 1971 and 1975, and the analysis of 346 fish from a single year. In both cases a pattern is clear. The number of stage II fish decreases to a minimum in July, and is accompanied by an increase in the number of running or female V fish captured. No spent fish were recorded from January to July, but from August to December stage VI fish came in to the catches, reaching a maximum in November. It would thus seem that from January to June the fish are maturing, and spawn during and after July. The absence of spent fish in the first seven months of the year would seem a clear indication that only one spawning occurs. This may, however, be extended over several months as spent fish, apparently resorbing eggs, occurred from August to December in 1974. The onset of spawning in July–August is in agreement with the observations of Banks *et al.* (1965)

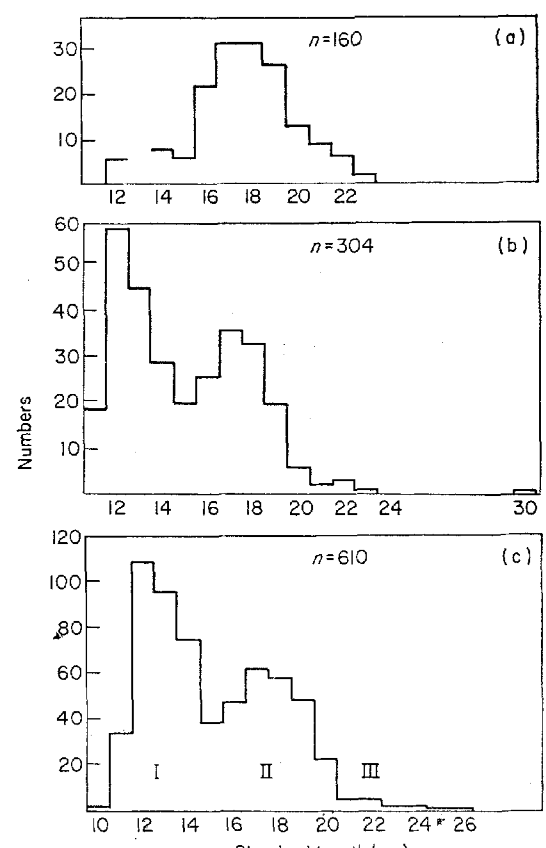


FIG. 3. (a) Standard length at stage III maturity for female *Hippopotamyrus pictus* Mean, with 95% confidence limits, 18·12±0·3528. (b) Length frequency histogram for female *H. pictus* in 1974. (c) Length frequency histogram for all *H. pictus*, male and female considered, for 1974. No significant difference was found in the mean standard lengths of 575 male and female fish sampled in 1974, i.e. $d$ (standardized normal deviate) = 1·4683 corresponding to $P = 0·1$. Similarly no significant difference was observed between the numbers of male and female fish in the sample: $X[ = 1·851$ with 1 df., $P = 0·5 - 0·1$.

TABLE II. Seasonal changes in the frequency of the various maturity stages of female *Hippopotamyrus pictus*. Each figure represents the percentage of the total number of females caught in a particular month. Only fish in excess of 16 cm standard length are included

| Month | $N$ ($n$ =817) | Maturity stage II | | III | | IV | | V | VI |
|---|---|---|---|---|---|---|---|---|---|
| J | 30 | 43·3% | (50·0%) | 43·3% | (40·0%) | 13·3% | (10·0%) | 0%(0%) | 0%(0%) |
| F | 69 | 28·9 | (30·0) | 53·7 | (40·0) | 17·4 | (30·0) | 0 (0) | 0 (0) |
| M | 55 | 43·6 | (69·0) | 49·1 | (23·0) | 7·2 | (7·7) | 0 (0) | 0 (0) |
| A | 250 | 23·6 | (25·0) | 58·0 | (59·7) | 16·0 | (12·5) | 0·8 (2·8) | 0 (0) |
| M | 61 | 21·3 | (24·1) | 47·5 | (42·6) | 24·6 | (24·1) | 6·6 (7·4) | 0 (0) |
| J | 14 | 28·6 | (20·0) | 50·0 | (70·0) | 21·4 | (10·0) | 0 (0) | 0 (0) |
| J | 40 | 15·0 | (5·6) | 40·0 | (55·6) | 30·0 | (27·8) | 15·0 (11·1) | 0 (0) |
| A | 85 | 22·4 | (16·9) | 36·5 | (34·0) | 24·7 | (26·4) | 11·8 (17·0) | 3·5 (5·7) |
| S | 69 | 16·0 | (9·7) | 52·2 | (32·3) | 21·7 | (35·5) | 1·4 (3·2) | 8·7 (19·4) |
| O | 42 | 35·7 | (36·8) | 28·6 | (5·3) | 19·0 | (31·6) | 7·1 (5·3) | 9·5 (21·1) |
| N | 74 | 33·8 | (35·9) | 29·7 | (15·4) | 13·5 | (10·3) | 2·7 (2·6) | 20·8 (35·9) |
| D | 27 | 48·1 | (47·1) | 14·8 | (11·8) | 11·1 | (11·8) | 7·4 (0) | 18·5 (29·4) |

Figures in brackets refer to 1974 only ($n$ = 346)

from the Niger prior to impoundment where *Marcusenius abadii* (Boulenger), *Mormyrus macrophthalmus* Gunther, and *Campylomormyrus tamandua* (Gunther) spawned during August. It seems likely that the time of spawning has not changed as a result of the formation of the lake. However, the fluctuations in numbers of mormyrids caught during the year are considerable (Blake, in preparation). In addition, of 648 maturing female *H. pictus* caught in the lake during 1974–1975 only 3·5% were at the running stage V. This indicates either that the spawning fish are not susceptible to capture by the methods employed, or that they leave the lake to spawn. The apparent scarcity of juvenile fish in the lake during the present study would support the idea of a spawning migration. Although the onset of spawning occurs at a similar time to that reported for other species in the river, the shallow swamps formerly created by the flooding of the river are no longer available and the need to locate such breeding sites may trigger the movements suggested. During 1974 and 1975 monthly sampling in two large rivers entering the west shore of Lake Kainji did not reveal any migration even when the lake began to rise in level during August–September. If a spawning migration does occur it is most likely to take the form of a run up the Niger itself.

## IV. DISCUSSION

Investigations into the breeding activities of mormyrids have yielded little specific information on the behavioural patterns involved. The nature of the spawning act is unknown as are the sites of egg deposition. Okedi (1970) suggested that parental care may be involved in reproduction, but this was based on the number, size, and yolky nature of the eggs, and not on observation. Aquarium observations by Okedi, (1968) failed to reveal spawning behaviour, although some ' nest building ' was observed. Some information is available on spawning movements. Whitehead (1959), and Okedi (1969) recorded anadromous behaviour in mormyrids from East Africa, and Daget (1957) recorded both anadromous and lateral movements in *Marcusenius*

(=*Gnathonemus*) *elongatus* (Pfaff) from the Niger system. Corbet (1961) also recorded anadromous activity in mormyrids from the Lake Victoria Basin, but suggested that one species; *Mormyrus kannume* Forskål, had adapted itself to breed in the Lake. From the present work on the Niger system at Lake Kainji it would appear that the species examined are anadromous. The breeding periodicity has only been studied in detail for *H. pictus*, but of the other six larger species regularly observed during 1974 and 1975 only four were found in a ripe condition (stage V), and these were represented by only 10 individuals. Similarly, electro-fishing, cast netting, and the use of small mesh static gill-nets failed to locate sites occupied by juvenile fish. Whether the suggested anadromous behaviour is a new activity induced by the formation of the lake is impossible to say in the absence of comparable preimpoundment data. Lateral movements into the flooded river margins certainly occurred at the site of Lake Kainji (Banks *et al.*, 1965), but it is not known if this followed an up-stream migration.

The site and the nature of egg deposition of Kainji mormyrids have not been studied. From the sinking rates and adhesive nature of the discharged ova it is apparent that the fish do not lay pelagic eggs.

The peak breeding season of *H. pictus* probably occurs from July to September, although the capture of running and spent fish up to December indicates that the overall period may be extended. The presence of both large and small eggs in the ovary of a fish does not necessarily indicate fractional spawning (Nikolsky, 1963), and it seems that the ability to spawn over an extended season may explain this situation in the mormyrids of Lake Kainji. Post-spawning gonads were flaccid and brown in colour, often containing large numbers of oocytes and some small ova. It would appear that these eggs are resorbed during the resting phase, and in the Mormyridae fecundity, expressed as the total number of eggs in the ovary, is not an indication of the reproductive potential. The number of eggs laid is difficult to assess as the proportion of small ova and oocytes which ultimately mature may vary according to the age of the fish (Nikolsky) and environmental influence. As pointed out by Corbet (1961) problems of this nature require a contemporary study of both lake and river habitats.

I wish to thank the staffs of the Shagunu field station and the University of Ife, Department of Biological Sciences for their assistance in the collection of data. This work was carried out as part of the Kainji Research Project financed by the Overseas Development Ministry of the British Government.

## References

Bagenal, T. B. (1971). Eggs and early life history, Part I. Fecundity. In *Methods for assessment of Fish Production in Fresh Waters.* (W. E. Ricker, ed.). Oxford: Blackwell.

Banks, J. W., Holden, M. J. and McConnell, R. H. (1965). Fishery Report. In *The First Scientific Report of the Kainji Biological Research Team.* (E. White, ed.). University of Liverpool.

Corbet, P. S. (1961). The food and feeding of non-cichlid fishes in the Lake Victoria Basin, with comments on their evolution and adaptation to lacustrine conditions. *Proc. Zool. Soc. Lond.* **136,** 1–101.

Daget, J. (1954). Les poissons du Niger Supérieur. *Mém. de l'I.F.A.N. Dakar*, No. 36. 391 pp.

Daget, J. (1957). Donnees recantes sur la biologie des poissons dans la Delta Central du Niger. *Hydrobiologia* **5,** 321–347.

Nawar, G. (1959*a*). A study of the fecundity of the Nile mormyrid *Hyperopisus bebe* Lacepede. *Ann. Mag. nat. Hist.* (13) **2,** 493–504.

Nawar, G. (1959*b*). Observations on the breeding of six members of the Nile Mormyridae. *Ann. Mag. nat. Hist.* (13) **2,** 603–606.

Nikolsky, G. V. (1963). *The Ecology of Fishes*. London & New York: Academic Press.

Okedi, J. (1968). Notes on the behaviour of the small mormyrid fishes of Lake Victoria. *E.A.F.F.R.O., Ann. Rep.,* 1967, 42–48.

Okedi, J. (1969). Observations on the breeding and growth of certain mormyrid fishes of the Lake Victoria Basin. *Rev. Zool. Bot. afr.,* **79,** 36–64.

Okedi, J. (1970). A study of the fecundity of some mormyrid fishes from Lake Victoria. *E. Afr. agric. For. J.* **XXXV,** 436–442.

Whitehead, P. J. P. (1959). The anadromous fishes of Lake Victoria. *Rev. Zool. Bot. afr.* **59,** 329–363.