THE BIOLOGY OF ALESTES IMBERI PETERS (PISCES: CHARACIDAE) IN LAKE McILWAINE, RHODESIA

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ABSTRACT

The population of Alestes imberi in Lake McIlwaine increased greatly in late 1974, but the species is of little economic importance in the lake. The breeding season is short and coincides with the main river floods. Females are larger than males and fecundity is extremely high. Like other Alestes species it is a very versatile feeder, and utilizes mainly insect alates from April to November, and chironomid larvae and pupae from December to March. It is able to take advantage of periodic insect emergences and to utilize some plant material. Zooplankton and fish are not important food items. Condition factors appear to be related to spawning. Growth rates could only be assessed indirectly but appear to be more rapid in Lake McIlwaine than in Lake Kariba.

INTRODUCTION

Alestes imberi Peters is a small characid fish with a wide distribution in eastern Central Africa. It occurs throughout the middle and lower Zambezi River systems, including Lake Malawi, as well as in the Sabi, Limpopo and Pongola systems to the south and in the upper Congo to the north (Jackson 1961; Crass 1964; Jubb 1967; Balon 1971; Bell-Cross 1972). Although once abundant in Lake Kariba (Jackson 1961) it now appears to have been largely replaced there by A. lateralis Boulenger (Balon 1971). This species was thought to be an invader from the upper Zambezi, but recent information suggests that this is not so (G. Bell-Cross pers. comm.), and there is also some doubt about its identity (Jubb 1976).

As a relatively small species A. imberi is of little economic importance in areas where the commercial fishery is based on large-mesh gill nets, and thus relatively little is known of its biology. General accounts, with some discussion on its feeding and angling, were given by Jackson (1961), Crass (1964) and Jubb (1967). Growth rates and standing crop in Lake Kariba were assessed by Balon (1971, 1972), whilst Munro (1967) examined some stomach contents from fish from Lake McIlwaine, and Donnelly (1971) made biological observations on the species in Lake Kariba.

Lake McIlwaine is situated about 37 km south-west of Salisbury, Rhodesia, and although eutrophic (Marshall & Falconer 1973; Mitchell & Marshall 1974) is an important commercial fishing and angling centre. The population of A. imberi in the lake increased

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enormously towards the end of 1974 (Figure 1) and this paper presents the results of a preliminary study of its biology in the Lake.

MATERIALS AND METHODS

Most fish were taken from a continuing routine gill-netting programme which began in July 1974. A fleet of nets with stretched-mesh sizes from 25 mm (1 inch) to 178 mm (7 inches) increasing by 12,5 mm ($\frac{1}{2}$ inch) increments was used. Each net was 25 m long and about 2 m

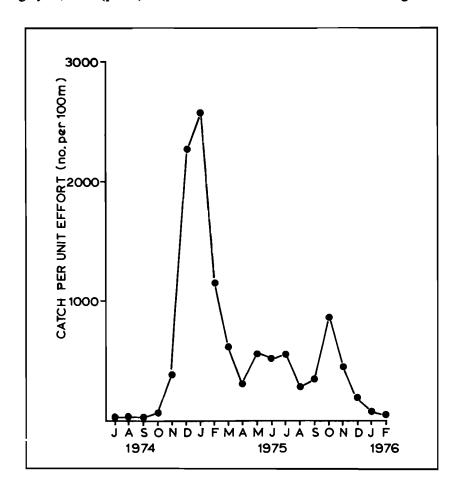


FIGURE 1

The catch of A. imberi taken in 25 mm nets (no. 100 m⁻¹) during the period July 1974 to February 1976. This figure clearly illustrates the population increase that occurred at the end of 1974.

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deep. These nets were laid each week at one of four stations (Figure 2); each was therefore sampled every fourth week, or at least once per month.

A. imberi was only taken in the four smaller-meshed nets (25,38,51 and 64 mm stretched mesh). A few specimens were also taken in small-mesh seine nets or recovered during the course of a fish-poisoning programme (Marshall & Lockett 1976).

Fork length, standard length, weight, sex and gonad condition were recorded from each fish taken from the gill nets, using standard methods given by Ricker (1968). Only standard length has been used in this paper and was measured to the nearest millimetre, whilst mass was taken to the nearest gram. A. imberi of the size captured in gill nets can be easily sexed externally as the distal portion of the anal fin is concave in the female and pointed in the male (illustrated in Crass 1964). Gonad condition was assessed as:

Immature (no evidence of sexual activity, testes and ovaries indistinguishable);

Inactive (gonads larger, testes and ovaries distinguishable);

Active (testes greatly enlarged, ovaries enlarged and eggs clearly visible);

Ripe (gonads of maximum size);

Ripe-running (sexual products being shed, eggs can be extruded).

In practice, however, it was found that the Active, Ripe and Ripe-running categories could be combined when assessing breeding condition. A small proportion was categorised as Spent, a condition in which some eggs are being reabsorbed after the others have been shed, but these were combined with Inactive fish.

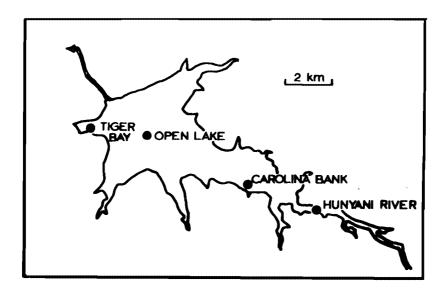


FIGURE 2

Lake McIlwaine, showing the four gill-netting stations used during this study.

A subsample of up to thirty fish (if available) was taken from each net on every sampling and weighed, correct to 0,1 g, for assessment of condition factors. Ovaries were also taken for estimating fecundity and stomachs were collected for food analysis. Entire ovaries were preserved in Gilson's fluid (Ricker 1968) and the eggs were later separated from the ovarian tissue and dried. Their number was then estimated from the weight of a counted subsample.

Stomach contents were difficult to analyse, for two main reasons. Firstly, this fish has two series of sharp multicuspidate teeth in the upper and lower jaws (Jubb 1967) and it is able to bite most food items into small pieces. Secondly, like other Alestes species it has extremely efficient digestive capabilities (Bowmaker 1969) and food was often in an advanced state of digestion after the fish had remained overnight in the gill-nets. Food was analysed by the numerical method (Hynes 1950) and only whole organisms or heads were counted in the case of Cladocera and insects. Polygonum seeds were always bitten into two or three pieces and their numbers were estimated by attempting to count the distal portions which bear a distinctive bifurcated structure. Each piece of plant detritus, usually grass, was counted.

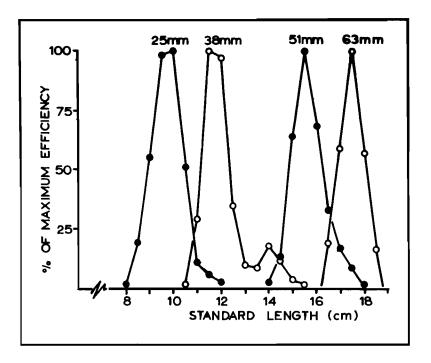


FIGURE 3

Retention curves for A. imberi in the four smallest nets used in the routine programme. Data for the period July 1974 to June 1975 are used.

RESULTS

Gear selection

The retention curves for A. imberi in the four smallest gill-nets are shown in Figure 3, in which the percentage of maximum efficiency for each net is plotted against standard length (grouped in 0,5 cm length classes). Fish of about 12 to 14 cm standard length were not taken in large numbers but it is not clear whether this was caused by low sampling efficiency or whether the population in this size range was small. No fish were taken in 76 mm nets although some are taken in commercial nets of this size (0,07 fish 100 m⁻¹ in 1975). The number and mean length of fish taken in each gill net during the period July 1974 to March 1976 are given in Table 1.

TABLE 1

The number and mean length of A. imberi taken in gill nets (July 1974 to March 1976).

Mesh size (mm)	Number	Percentage	Mean length (cm)
25	11 098	56,58	9,78
38	6 237	31,79	12,57
51	2 157	11,00	15,66
63	124	0,63	17,56

Breeding

The sex ratio for all size groups was easily calculated as the sexes can be distinguished externally. The sex ratio in relation to size is shown in Figure 4 and is based on data from all stations. Up to 11,5 cm length the ratio is fairly constant with rather more than 50% females. The proportion of males then rises rapidly to 95% at 12,5 cm. It declines to about 50% at 14,5 cm and at 16,0 cm or more the population consists entirely of females.

The breeding season was determined by calculating the percentage of fish showing breeding activity (i.e. with Active, Ripe or Ripe-running gonads) in each month. Males and females were plotted separately and the results are shown in Figure 5. This figure does not include fish taken in the 25 mm nets as they were almost always immature and showed no evidence of breeding activity. Females appear to come into breeding condition sooner than males with maximum breeding activity in October and November, compared to December and January for males. The number of females taken in breeding condition declined rapidly and their breeding was over by February, whereas males showed considerable breeding activity in January and February. These fish were not, of course, taken at their actual spawning sites and there may be a time lag which accounts for the apparent discrepancy in

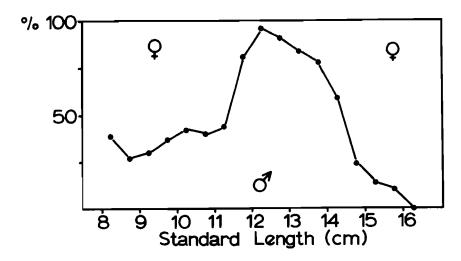


FIGURE 4

The sex ratio in relation to size of fish. Data taken from 2 500 fish caught between July 1974 and February 1976.

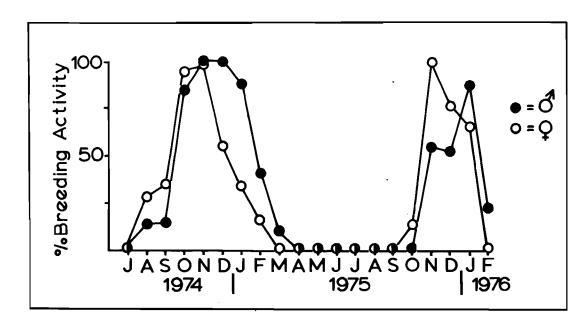


FIGURE 5
Breeding season of A. imberi. Males and females are shown separately but no fish taken in 25 mm nets have been included.

Figure 5, where females seem to breed earlier than males. Neither sex showed any breeding activity from March to September, a period which includes the coldest months of the year and when river flows are declining.

The size at which breeding begins in this species was estimated by determining the percentage breeding activity in each 0,5 cm length group during the months of maximum breeding activity which were November-December for males and October-November for females (Figure 6). Males begin breeding at about 11 cm whilst females begin at about 12,5 cm. The age of these fish was not accurately determined but it is suggested that they breed at two years old (see later).

Fecundity is high and the number of eggs in relation to length is shown in Figure 7. A large female of over 16 cm in length could produce 50 000 eggs but an average of 30 000 to

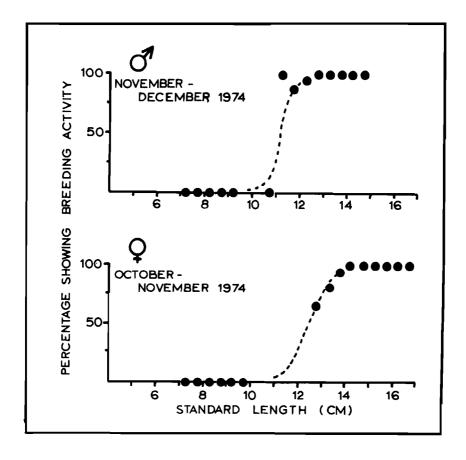


FIGURE 6

The size at which breeding commences. Data are taken from the months in which maximum breeding activity occurs.

40 000 is more typical. As would be expected smaller fish produce fewer eggs and no suitable ovaries could be collected from fish below 12 cm in length. This confirms the data shown in Figure 6, which suggests that females do not usually breed below 12 cm in length.

No evidence of a breeding migration was found, although this species is known to be potamodrometic (Bowmaker 1973). This was probably because of the nature of the sampling programme.

Feeding

A. imberi is able to utilize a wide variety of food and Figure 8 shows the seasonal variation of food items during the period July 1974 to June 1975. Insect alates were the most important food from July to December and from April to June. A wide variety of insects was taken, amongst the most abundant being small cicadellid leaf-hoppers. Other groups included aquatic Diptera (principally chironomids), terrestrial Diptera, Hymenoptera,

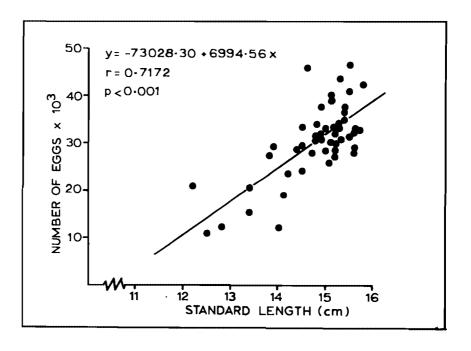
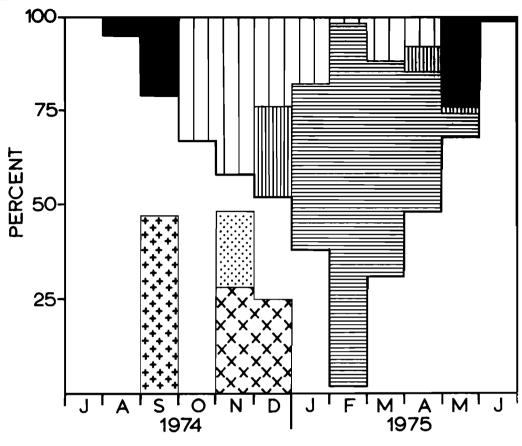


FIGURE 7
The number of eggs produced in relation to standard length. A total of 54 ovaries was collected for egg counts.

FIGURE 8 (on opposite page)

Seasonal variation of food taken by A. imberi. The data from all stations have been combined, and a total of 480 stomachs was examined.



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	Ants (CAMPONOTUS sp.)	
×××	Termites (MACROTERMES sp.)	TES
++++	Beetles (Melasoma quadrilineata)	ALATES
	Other groups	
	Chironomid and Chaoborus larvae &p	upae
	Cladocera	
	Polygonum seeds	
	Plant material	

Coleoptera, orthoptera, Ephemeroptera and Hemiptera. A few small spiders were also taken.

The fish were particularly able to take advantage of seasonal emergences of adult insects and these could sometimes be distinguished. In September 1974 a small chrysomelid beetle Melasoma quadrilineata was an important component of the diet. This insect appears to live on new foliage (produced in September) on the Brachystegia trees which surround the lake. Termite alates emerge in large numbers during the wet months and these were an important food item in November and December. Similarly, ant alates (Camponotus sp.) emerged and were utilized in November. It should be pointed out that Figure 8 combines data from all stations throughout the month. When particular insect emergences occurred the fish fed exclusively on these insects. However, these emergences were generally shortlived and the fish were then forced to utilize other food.

Seeds of *Polygonum senegalense*, a common marginal plant, were extensively utilized from October to January, and in November made up almost 50% of the food taken. They were most frequently found in fish taken at Tiger Bay (Figure 2). The seeds presumably floated to this area under the influence of the prevailing wind which blows down the axis of the lake into this bay. Other plant material taken included grass and a few grass seeds. Grass was most important in December 1974 and was probably made available when the lake level rose and covered marginal vegetation. It is not known whether the fish tore off pieces of grass for themselves or whether they took small pieces detached by other means.

Chironomid and chaoborid larvae are most abundant in the lake from January to April (Marshall 1971) and they were an extremely important food item during this period. In February 1975 they formed over 95% of the diet but the number then declined until they made up only 5% in May.

Zooplankton was generally unimportant except in September and May when considerable quantities of *Daphnia* and *Bosmina* were utilized. Fish were even less important and only once was a small cichlid fish found in a stomach (although 480 stomachs were examined). Unidentified fish eggs were sometimes found but were not significant.

This food analysis was, of course, carried out on fish from gill nets, and stomachs of smaller fish could not be examined. It is not yet known what the latter feed on, as too few were taken to permit stomach content analyses.

Length-mass relationship and condition

The length-mass relationship for A. imberi from Lake McIlwaine is shown in Figure 9. Although the largest fish recorded was 18,9 cm in length and weighed 140,3g, relatively few fish over 17 cm were collected. No significant differences in length-mass relationships for males and females could be detected and the data for both sexes were combined.

The length-mass relationship can be represented by $W = al^b$ where a and b are derived by plotting the log mass against log length and calculating the regression line by the method of least squares (Ricker 1968). For A. imberi from Lake McIlwaine this becomes W = 0,0098 1^{3,285}. This was then used to calculate condition factors using the formula

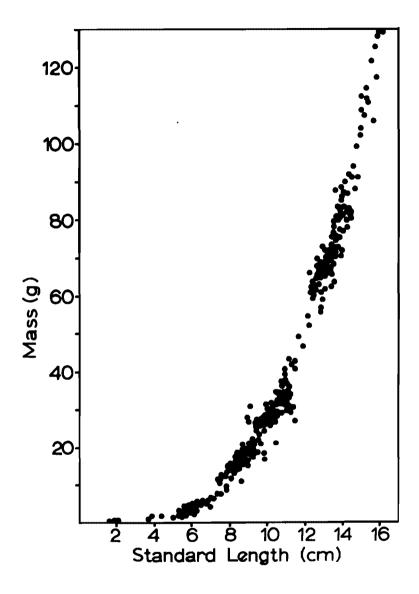


FIGURE 9

Length-mass relationship of A. imberi from Lake McIlwaine, based on 1 500 fish. There appeared to be no significant difference between males and females.

$$CF = \frac{W.100}{1^{b}} = \frac{W.100}{1^{3,285}}$$

Condition factors were calculated for fish taken from July 1974 to June 1975 and are shown in Figure 10. Data for male and female fish less than 10 cm in length were combined and are shown in the lower part of the figure. Their condition factor was between 1,45 and 1,50 for most of the year, except for February when it rose to 1,62, and July and August when it was well below 1,40.

Condition factors for both males and females over 10 cm in length were initially little over 1,30 but rose to a maximum in October for males and in November for females. Both then showed a rapid decline until January. The condition factor for females fluctuated between 1,35 and 1,45 for the rest of the year. In males, however, the condition factor varied rather more and reached a peak of over 1,50 in May.

Growth

Detailed studies of growth have not yet been carried out, but an indication of growth rates can be gained from field data. Some small fish with a mean standard length of 1,8 cm were collected in March 1974, whilst others were collected in September (mean SL 5,7 cm) and October (mean SL 6,7 cm). It is assumed that these were spawned in December 1973 which would give them a mean growth rate of 0,63 cm month⁻¹ or 7,56 cm yr⁻¹.

Further information can be obtained from the numbers of fish taken in the 25 mm and 38 mm gill-nets. The mean numbers of fish taken per month at three-month intervals are shown in Figure 11, and it appears that the fish taken in 25 mm nets (mean SL 9,78 cm) during January-March 1975 were being taken in 38 mm nets (mean SL 12,57 cm) a year later. If these fish were from the December 1973 spawning then they would be about 14 months old in 1975 and about 26 months old in 1976. Using this information, growth can be shown as in Table 2.

From this it appears that the fish grow to about 8 cm in their first year, which is the size at which they begin to be taken in 25 mm gill-nets. The growth rate is considerably slower in their second year when they reach about 12 cm, which is the mean size for capture in 38 mm nets and the approximate size at which they can breed. Too few fish were taken in 51 mm and 63 mm nets to enable a clear picture to be drawn but it is likely that these were mostly three-year-old fish. Fish taken in the 63 mm nets (mean SL 17,56 cm) were entirely females and this suggests that they have a faster growth rate than males. Although males were more numerous in the 51 mm nets they were smaller (mean SL 13,74 cm) than the females (mean SL 14,78 cm), which suggests that females grow faster than males. It would appear, therefore, that females can reach about 16,0 cm in their third year whilst males reach about 14,0 cm.

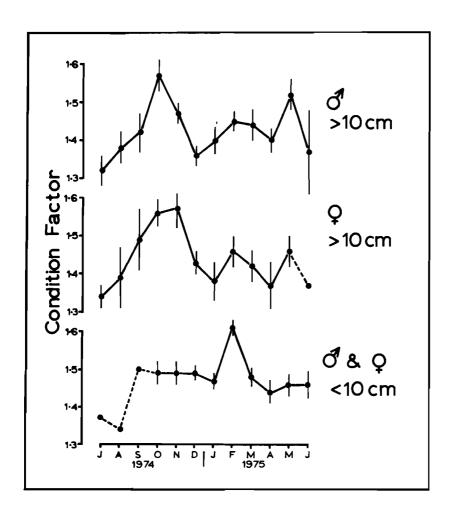


FIGURE 10

Condition factors for the period July 1974 to June 1975. Males and females greater than 10 cm standard length are plotted separately. Both sexes are combined for fish of less than 10 cm Standard Length. The vertical lines show \pm twice the standard error of the mean, whilst points connected by broken lines were calculated from less than 10 fish.

TABLE 2
Estimation of growth of A. imberi in Lake McIlwaine

Date			Growth		
	Age (months)) Mean SL	cm month-1	cm yr	
March 1974	3	1,8	0,60	7,20	
September 1974	9	5,7	0,67	8,04	
October 1974	10	6,7	0,63	7,56	
January-March 1975	13-15	9,8	0,65-0,75	7,8-9,0	
January-March 1976	25-27	12,6	0,47-0,50	5,6-6,0	

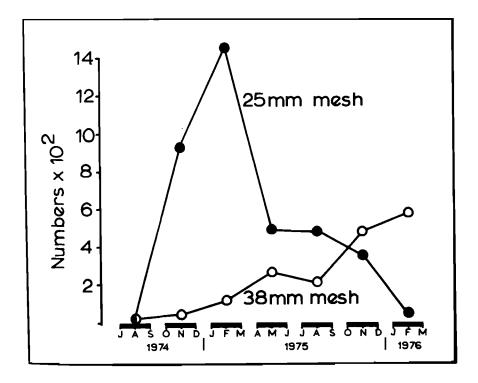


FIGURE 11
The mean number of fish taken per month for three-month periods from July 1974 to March 1976. The decline in number of fish taken in the 25 mm nets is matched by a corresponding increase in the number taken in the 38 mm nets.

DISCUSSION

Interest in A. imberi in Lake McIlwaine was initially stimulated by its vast increase in numbers in late 1974 (Figure 1) when it was clear that very successful breeding had occurred. The data suggest that these fish were spawned in the 1973 spawning season in which exceptionally heavy river flows followed an extremely severe drought in the previous season. It is known to be potamodrometic (Bowmaker 1973), like other Alestes species (Jackson 1961; Lauzanne 1973), but no evidence of a breeding migration was found during this study (this was probably because of the sampling methods). The heavy inflow from the tributary rivers and streams in 1973/74 probably enabled the species to breed most successfully, thus accounting for the large number of fish taken in late 1974. A similar population explosion of this species also occurred in the Sebakwe Dam, about 140 km south of Lake McIlwaine, at this time (unpublished data). This lake was also affected by the 1972/73 drought which was followed by exceptionally heavy rains, thus suggesting that river flow conditions provided good breeding conditions. However, the factors that affect breeding in this species are not fully understood. Although the population of A. imberi fluctuates in Lake Kariba, it has not been possible to relate this to any environmental factors (S A Mitchell pers. comm.).

The breeding season of A. imberi was short and is probably geared to the main river floods in January and February and there is no evidence to suggest that it bred more than once. This is in contrast to A. macrophthalmus, living under lacustrine conditions, which had a long breeding season and probably bred twice (Bowmaker 1969). It was noted in both species, however, that males maintained breeding condition longer than females.

Fecundity was extremely high and appeared to be higher than southern populations of this species, as Crass (1964) noted that a Natal specimen contained only 14 000 eggs. It was also considerably higher than in the larger A. nurse, A. dentex (Lowe-McConnell 1975. quoting Daget 1952) and A. macrophthalmus (Bowmaker 1969). Bagenal (1973) has shown that fecundity can vary considerably in response to various environment conditions. The most important of these appeared to be an increase in fecundity in low-density populations, but this does not apply to A. imberi in Lake McIlwaine. The cause of this high fecundity is not yet known, nor is it known whether it will persist in subsequent years.

Condition appears to be related to spawning although there was considerable fluctuation (some of which may be accounted for by the level of accuracy in weighing). However, condition in larger males and females seems to improve as they come into breeding condition, only to decline when spawning takes place. The increase in condition amongst smaller fish in February and in larger males in May cannot be explained but may be caused by increased food availability or other external factors.

A. imberi is similar to other members of the genus, such as A. macrophthalmus (Bowmaker 1969) and A. baremoze (Lowe-McConnell 1975 quoting Hopson 1972) in that females grow faster and are larger than males. This has been confirmed for A. imberi by Balon (1971). It has been suggested that this is a mechanism to ensure greater egg production as these species do not care for their young (Kenmuir 1973a).

The growth rates postulated in this paper are considerably higher than those given for Lake Kariba fish by Balon (1971), which only reach 6 cm in their first year, as compared to 8 cm for McIlwaine fish. It is possible that competition with the much more abundant A. lateralis has adversely affected the growth rate in Lake Kariba.

A number of papers refer to the feeding habits of Alestes species, and a feature of these fish is their versatility and ability to utilize a wide variety of food (Corbet 1961; Petr 1967; Bowmaker 1969; Lauzanne 1973; Reynolds 1973). A. imberi is no exception. Its most distinctive food source in Lake McIlwaine is terrestrial insects, a feature noted by Munro (1967), and in this respect it is similar to A. sadleri and A. jacksoni (Corbet 1961), and to A. macrolepidotus and A. nurse (Reynolds 1973). In Lake Kariba it showed a preference for the seeds of Potamogeton pusillus but it also took insects, snails and small fish (Donelly 1971). Plant material is an important food item for most Alestes species and they have been found to utilize a variety of seeds. Fish are not an important food item in Lake McIlwaine although larger species are piscivorous. Even this, however, is not constant and A. baremoze provides an example of the wide-ranging food habits of the genus. In Lake Volta it is largely piscivorous (Reynolds 1973), whereas in Lake Tchad it feeds on plankton, but turns to plant material in the rivers on its breeding migration (Lauzanne 1973).

The large numbers of A. imberi in Lake McIlwaine stimulated interest in its possible commercial utilization, although it is normally too small to be of commercial importance. However, the only method of capture so far available is by the use of gill-nets, but the cost of these nets is high and there is also a danger of affecting stocks of the valuable commercial species (of which the most important are Sarotherodon macrochir, Labeo altivelis, Clarias gariepinus and Hydrocynus vittatus). The percentage of Alestes and of commercial species taken in the small-mesh nets is shown in Table 3, and it can be seen that the species most endangered by small-mesh nets are L. altivelis and S. macrochir. The population of H. vittatus is smaller but this species would also be under severe pressure as it is known to be

TABLE 3

Composition of catch in small-mesh gill-nets (percentage by numbers) during the period

July 1974 to December 1975.

	25 mm	38 mm	51 mm	63 mm
Hydrocynus vittatus	2,49	3,70	3,28	5,97
Labeo altivelis	11,38	46,78	51,19	35,51
Alestes imberi	85,96	48,29	40,00	7,19
Clarias gariepinus	0,01	0,03	0,45	1,66
Tilapia rendalli	0,02		0,48	5,42
Sarotherodon macrochir	0,14	1,20	4,60	44,25

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greatly affected by small-mesh nets (Kenmuir 1973b). So far no other suitable method for cropping *Alestes* has been found, and, in any event, it is probably only economical to utilize it during periods when it is extremely abundant.

The role of A. imberi in the ecology of the lake has not yet been fully determined. It appears to be the only species that utilizes terrestrial insects but it competes with a number of other species for chironomid larvae (Munro 1967). However, when available the latter are an abundant food source and A. imberi is unlikely to be adversely affected by competition for them. Because of its small size, it could be expected to be an important forage fish, but Munro (1967) found none in Hydrocynus vittatus stomachs taken from Lake McIlwaine.

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REFERENCES

- BAGENAL, T B 1973. Fish fecundity and its relations with stock and recruitment. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, 164: 186-198.
- BALON, E K 1971. Replacement of Alestes imberi Peters, 1852 by A. lateralis Boulenger, 1900 in Lake Kariba, with ecological notes. Fish. res. Bull. Zambia 5: 119-162.
- BALON, E K 1971. Replacement of Alestes imberi Peters, 1852 by A. lateralis Boulenger, 1900 in Lake Kariba, with ecological notes. Fish. Res. Bull. Zambia 5: 119-162.
- BELL-CROSS, G 1972. The fish fauna of the Zambezi river system. Arnoldia, (Rhodesia) 5 (29): 1-19.
- BOWMAKER, A P 1969. Contribution to knowledge of the biology of Alestes macrophthalmus Gunther (Pisces: Characidae). Hydrobiologia 33: 302-341.
- BOWMAKER, A P 1973. Potamodromesis in the Mwenda river, Lake Kariba. In Man-made lakes: their problems and environmental effects, ed. Ackermann, W C, White, G F & Worthington, E B. Geophys. Monogr. 17: 159-164.
- CORBET, PS 1961. The food of non-cichlid fishes in the Lake Victoria basin, with remarks on their evolution and adaptation to lacustrine conditions. *Proc. zool. Soc. Lond.* 136: 1-101.
- CRASS, R S 1964. Freshwater fishes of Natal. Pietermaritzburg: Shuter & Shooter.
- DONNELLY, BG 1971. The fish population changes on Lake Kariba between 1960 and 1968: Part 2, Characidae and Citharinidae. Mimeographed report, Lake Kariba Fisheries Research Institute.
- HYNES, H B N 1950. The food of freshwater sticklebacks (Gasterosteus aculeatus and

- Pygosteus pungitius), with a review of methods used in studies of the food of fishes. J. anim. Ecol. 19: 36-58.
- JACKSON, PBN 1961. The fishes of Northern Rhodesia. Lusaka: Government Printer.
- JUBB, RA 1967. Freshwater fishes of Southern Africa. Cape Town & Amsterdam: Balkema.
- JUBB, RA 1976. Letter to the editor. J. Limnol. Soc. sth. Afr. 2: 35-36.
- KENMUIR, DHS 1973a. The ecology of the tigerfish Hydrocynus vittatus Castelnau in Lake Kariba. Occ. Pap. natn. Mus. Rhod. B. 5: 115-170.
- KENMUIR, D H S 1973b. The commercial exploitation of stocks of tigerfish Hydrocynus vittatus Castelnau, in Lake Kariba, Rhodesia, by means of small-meshed gill nets. Rhod. J. agric. Res. 11: 171-179.
- LAUZANNE, L. 1973. Etude qualitative de la nutrition des Alestes baremoze (Pisces, Characidae). Cah. Off. Rech. Sci. Tech. Outre-Mer (Hydrobiol.) 7: 3-15.
- LOWE-McCONNELL, R 1975. Fish communities in tropical freshwaters. London & New York: Longman.
- MARSHALL, BE 1971. Ecology of the bottom fauna of Lake McIlwaine (Rhodesia). M. Phil. thesis, Univ. London.
- MARSHALL, BE & FALCONER, A C 1973. Eutrophication of a tropical African impoundment (Lake McIlwaine, Rhodesia). Hydrobiologia 43: 1-123.
- MARSHALL, B E & LOCKETT, C A 1976. Juvenile fish populations in Lake McIlwaine, Rhodesia. J. Limnol. Soc. sth. Afr. 2: 37-42.
- MITCHELL, DS & MARSHALL, BE 1974. Hydrobiological observations in three Rhodesian reservoirs. Freshwat. Biol. 4: 61-72.
- MUNRO, J. L. 1967. The food of a community of East African freshwater fishes. J. Zool., Lond. 151; 389-415,
- PETR. T 1967. Fish population changes in the Volta Lake in Ghana during its first sixteen months. Hydrobiologia 30: 193-220.
- REYNOLDS, J.D. 1973. Biology and fisheries potential of four species of *Alestes* (Pisces Characidae) in the new Volta Lake, Ghana. *Revue Zool. Bot. afr.* 87: 298-310.
- RICKER, WE (Ed.) 1968. Methods for assessment of fish production in fresh waters. *IBP Handbk* 3.