Fish population changes in the Sanyati Basin, Lake Kariba, Zimbabwe

D.H.S. Kenmuir

Lake Kariba Fisheries Research Institute, Department of National Parks and Wildlife Management, Zimbabwe

Large-fish population changes in the Sanyati Basin of Lake Kariba between 1960 and 1975 are evaluated and discussed. The early lake population following closure of the dam wall in 1958 was similar to the pre-impoundment riverine population with *Labeo* spp., *Distichodus* spp., *Clarias gariepinus* and two characid species dominating gill-net catches. Exceptions were mormyrids, scarce in the new lake although abundant in the river, and *Oreochromis mortimeri*, scarce in the river but expanding rapidly in the lake. Productivity in the new lake in terms of ichthyomass relative to later years was high. In later years following closure several of the early abundant mostly potamodromous species declined rapidly (*C. gariepinus, Labeo* spp., *Distichodus* spp.,) and by 1975 they were unimportant. Mormyrids, cichlids and two silurid species increased significantly in catches as did the characin, *Hydrocynus vittatus*; the latter as a result of the expansion of the freshwater sardine population, from 1970. While early populations were essentially herbivorous later populations were largely insectivorous/molluscivorous. Concomitant with these changes new species appeared, while a few disappeared. Possible sources of origin of the new arrivals are discussed. Salient features of the entire evolutionary process are summarized, while some of the lessons learnt from Kariba, and a few recommendations arising from this, are listed in the conclusion.
S. Afr. J. Zool. 1984, 19: 194 – 209

Bevolkingsveranderinge van grootvis tussen 1960 en 1975 in die Sanyati-kom van die Karibameer word geëvalueer en bespreek. Die bevolking net nadat die meer tot stand gekom het na die voltooiing van die wal in 1958, het ooreengestem met die rivierbevolking voor opdamming, en *Labeo* spp., *Distichodus* spp., *Clarias gariepinus* en twee spesies van die Characidae het die kiefnetvangste oorheers. Uitsonderings was die Mormyridae wat skaars was in die nuutgevormde meer maar volop in die rivier, en *Oreochromis mortimeri* wat skaars was in die rivier maar wat in die meer vinnig in getalle toegeneem het. Produktiwiteit in die nuwe meer, gemeet in vismassa, was hoog relatief tot latere jare. Met verloop van tyd het van die vroeë volop en meestal riviervissoorte in die meer vinnig skaars begin raak (*C. gariepinus, Labeo* spp., *Distichodus* spp.,) en teen 1975 was hulle onbelangrik. Mormyridae, Cichlidae en twee spesies van die Siluridae het betekenisvol in vangste toegeneem asook *Hydrocynus vittatus*; laasgenoemde as gevolg van die toenemende sardientjiebevolking vanaf 1970. Waar die vroeë bevolkings hoofsaaklik plantvretend was, was lateres hoofsaaklik insek/skulpvretend. Gepaardgaande met hierdie veranderings het nuwe spesies bygekom, terwyl 'n paar verdwyn het. Moontlike plekke van oorsprong van die nuwe aankomelinge word bespreek. Die hoof kenmerke van die veranderings word opgesom terwyl sommige van die lesse wat by Kariba geleer is en 'n paar aanbevelings wat hieruit voortvloei, in die gevolgtrekkings gegee word.
S.-Afr. Tydskr. Dierk. 1984, 19: 194 – 209

D.H.S. Kenmuir
Present address: 7 The Fold, Northwood, Mount Pleasant, Harare, Zimbabwe

Received 13 October 1983; accepted 1 February 1984

This paper considers the major natural large-fish population changes in the Sanyati Basin of Lake Kariba (Figure 1) between 1960 and 1975. With the exception of Jackson (1960) who dealt with the immediate effect of dam closure on the river fish population, nothing empirical has yet been published on this aspect of the biology of Lake Kariba fish, despite the lake being in existence now for 25 years. The subject has, however, been discussed partially and in general terms by van der Lingen (1973), Bowmaker, Jackson & Jubb (1978) and Kenmuir (1978, 1983), while unpublished data on some aspects are those of Donnelly (1971), and the report of Kenmuir (1977), from which this paper is derived.

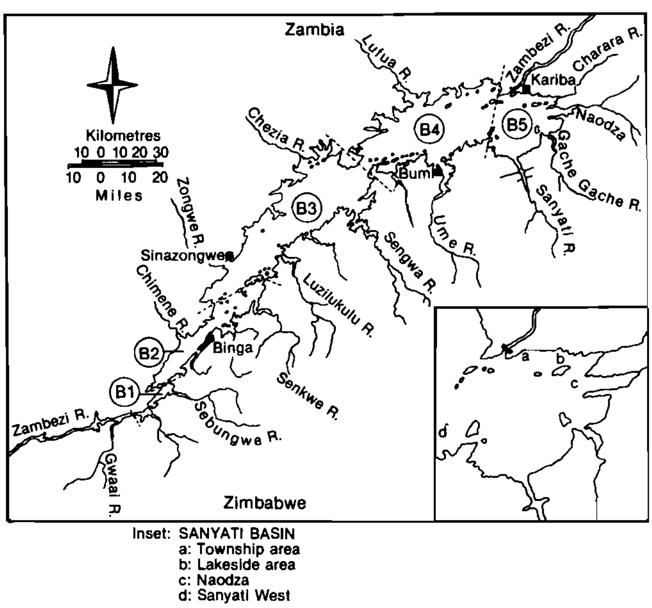

Figure 1 Map of Lake Kariba showing the Sanyati Basin (B5) in relation to the rest of the lake. Basins 1 and 2 are essentially riverine, whereas Basins 3 to 5 are lacustrine and probably showed the same fish population change characteristics. Inset is B5 enlarged to show netting areas.

The period under discussion encompasses the lake's formative years after dam-wall closure in December 1958 and leads to the beginning of the period of intensive sardine fishing operations in the Sanyati Basin in 1976, when the first thousand tons of fish were netted. Subsequently nearly 30 000 tons were caught between 1976 and 1981, of which some 80% were taken from the Sanyati Basin. Prior to this, slightly over 1 000 tons were netted in exploratory commercial fishing between

1973 and 1975 following the introduction of sardines in 1967/1968.

The annual removal of large quantities of fish nutrients from one area of the lake must have an effect, directly or indirectly, on other consumer organisms in the aquatic environment. Considering that nutrients are already lost to the lake fairly rapidly because of the high outflow to volume ratio an additional and imposed loss must affect the nutrient budget, and will ultimately have ecological consequences of one sort or another. Thus prior to the recent high sardine catches it was suggested that a change in nutrient flow caused by the development of the freshwater sardine population could be a contributory cause for the decline of *Salvinia* and sudd mats in the lake (Kenmuir 1978, p.44), a subject elaborated on more recently by Marshall & Junor (1981). Submerged aquatics might similarly be detrimentally affected if the phytoplankton → zooplankton → sardine → fishermen chain monopolizes and removes open water nutrients circulating after turnover before these become available to the littoral zones through wind and current action. This in turn could affect other populations, such as those of marginal fish and freshwater mussels. Thus cognizance should be taken of Balon's warning (1974a) that the sardines are liable to attain their high density at the price of other taxa. Beadle (1974) also recognized the ecological ramifications of intensive commercial fishing.

The year 1975 can be regarded as the end of the period when observed fish populations reflected the outcome of mainly natural evolutionary processes, probably not greatly affected by the widely dispersed marginal multi-species gill-net fishery, and 1976 as the beginning of a period of intensive mono-species commercial fishing, when further evolutionary and largely man-induced trends were probably put into motion.

This paper deals with the first period and presents the fish population changes that have been determined from experimental and, to a lesser extent, from commercial gill-netting, prior to the advent of the sardine fishing industry. It serves as a baseline against which further population changes may be measured. Data on the composition of subsequent fish populations are being collected by the Kariba Fisheries Research Institute.

Brief history of the lake

The lake started filling in December 1958 and reached peak level in September 1963. This phase was marked by an increase of total dissolved solids from 26 ppm in the old river to a recorded 65 ppm in the new lake (Harding 1966) and represented one of extremely high productivity characterized by an explosive growth of organisms, including plankton blooms, the water fern, *Salvinia molesta* Mitchell, and various species of fish (Balinsky & James 1960; Jackson 1960; Hattingh 1961; Boughey 1963; Harding 1966).

After filling, the lake level has fluctuated annually by 1,5 to almost 6 metres, caused by evaporation, release of water through the power station turbines and sluice gates, inflow from the Zambezi and other rivers, and direct precipitation (Figure 2). This phase was marked by a decline in total dissolved solids (Harding 1966); development of aquatic weedbeds and a corresponding change in the invertebrate fauna (McLachlan 1969); changes in the composition of fish taxa (Donnelly 1971; Kenmuir 1977); appearances of species hitherto unrecorded in the lake (Bell-Cross 1972; Balon 1974a,b,c); axial distribution of fish species in relation to basin limnology (Begg 1974); the decline of *Salvinia molesta* (Mitchell & Rose 1979; Marshall & Junor 1981); and development of large mussel beds

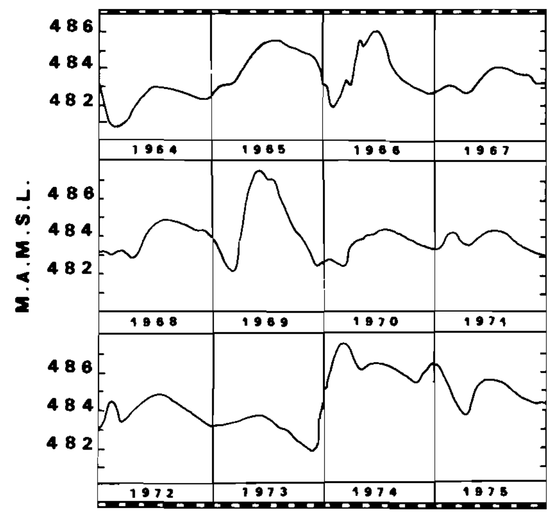

Figure 2 Lake level fluctuations from 1964 to 1975. The lake filled in 1963 and then dropped several metres in 1964 before beginning the annual regime of fluctuating lake level.

(Kenmuir 1980a,b, 1981). Several of these events are summarized and discussed by van der Lingen (1973), Bowmaker (1975) and recently more comprehensively by Kenmuir (1978, 1983).

Human activities with a bearing on the biology of the lake have involved cichlid stocking from 1959 to 1961 (Parnell 1960, 1961); commercial gill-netting in the littoral areas from 1960 and 1962 on the north and south banks respectively (Harding 1966; Minshull 1973); introduction of freshwater sardines (*Limnothrissa miodon* Boulenger) in 1967/1968 (Balon 1971a; Bell-Cross & Bell-Cross 1971; Junor & Begg 1971); introduction of a grasshopper to feed on *Salvinia* (Mitchell & Rose 1979); and the development of a commercial sardine fishery (Cochrane 1976, 1978; Kenmuir 1978, 1981, 1982b; Langerman 1979; Marshall & Langerman 1979; Marshall & Junor 1981; Marshall *et al.* 1982).

The river and the fish population before impoundment

Jackson (1961) described the Zambezi in the area to be flooded as a sandbank river, rising to great heights during and shortly after the rains and then dwindling in size as the dry season advanced to a fraction of its former size between alluvial river banks. As a result aquatic vegetation of any type was scarce. Fish spawning took place in adjacent flooded areas when the river was high, but once the river receded the population was forced back into the river proper, to lead a competitive and precarious existence in ecologically unfavourable conditions.

The predatory tigerfish was probably partly responsible for the scarcity of small species in this section of the Zambezi River compared with the Upper Zambezi. Only eight small species were recorded, these being *Alestes imberi, Micralestes acutidens, Chiloglanis neumanni, Aplocheilichthys johnstonii, Pharyngochromis darlingi, Opsaridium zambezensis, Barbus barotseensis* and *B. fasciolatus*, while large fish recorded were *Anguilla nebulosa labiata, Protopterus annectens, Mormyrus longirostris, Mormyrops deliciosus, Marcusenius macrolepidotus, Hydrocynus vittatus, Distichodus mossambicus, D. schenga, Labeo altivelis, L. congoro, Barbus marequensis, Eutropius depressirostris, Synodontis zambezensis, S. nebulosus, Clarias gariepinus, Heterobranchus longifilis, Malapterurus electricus, Oreochromis mortimeri, Tilapia rendalli, Serranochromis codringtoni.*

The bulk of the large-fish catch was made up of *Labeo* species, *Distichodus* species, *Hydrocynus*, *Mormyrus* and *Clarias*. Cichlid species, the mainstay of nearly all African freshwater fisheries, were scarce. Of the smaller species, *Alestes imberi* and *Micralestes acutidens* were abundant, while the small *Barbus* species were not particularly common, and the only small cichlid recorded, *P. darlingi*, was present in moderate numbers.

Jubb (1961) recorded 53 species in the Middle Zambezi system between the Victoria Falls and the Cabora Bassa rapids, excluding the whole Kafue River system above the Kafue Gorge and the escarpment rivers of Northern Rhodesia (now Zambia), while Bell-Cross (1972) lists 58 species as occurring in the Middle Zambezi from the Kariba dam wall to the Cabora Bassa dam wall, including tributaries, but excluding the Upper Kafue. By contrast the Upper Zambezi and Kafue systems have 84 and 67 species respectively.

Sampling methods and sources of data

Data from experimental gill-netting using mixed-mesh nets at two stations in the Sanyati Basin show fish population changes during 1960 – 1975 (Tables 1 & 2). In the early years netting effort was more intensive than later, when it was scaled down mainly for economic and logistic reasons.

A fleet consisted of ten 6-ply nylon nets, each mounted by the half in lengths of 45,7 m ranging in mesh size from 38 to 152 mm at 12,7 mm increments, all 2,1 m deep except the 38-mm mesh net, which hung about 1 m deep. Most of the netting up to 1965 was with top-set nets, whereas later netting was mainly with bottom-set nets. However, since netting was conducted in shallow water this inconsistency should not unduly affect results, although it is taken into account when interpreting the data.

Following political events in 1965 which resulted in staff upheavals, the regular netting programme lapsed, but was resumed again on a regular basis in 1972, although some netting was done at the Lakeside Station in 1967/1968. While this lapse in data-collecting is regrettable the interval does serve to emphasize sharply the differences in the two netting periods. The netting results have been used only to compare relative abundance of species from year to year, and not to try and effect comparison between species. To compare catches from year to year the results have been reduced to the numbers of fish caught *per fleet setting* per year.

The Lakeside Station is in a flat cleared area (cleared of bush prior to the lake filling to facilitate commercial gill-netting), while the Kariba Station is situated on a fairly steep, shelving shoreline adjacent to the Kariba Township, and not subject to commercial fishing. Commercial netting ceased at the Lakeside Station in July 1972 because of increased pleasure-boat usage pressure in this area.

In the Lake's formative years experimental netting was also done at other stations in the Sanyati Basin. To show the basic similarity of fish populations from different areas at that time, data from these are shown in Tables 3, 4 and 5, the latter being from the 1961 Annual Report (No. 11) of the Joint Fisheries Research Organization. The data are supplemented by figures from the commercial gill-net fishery and personal observation.

The fish population changes

Results for each station have been treated separately (Tables 1 to 4). To show the trends more clearly data from the Kariba and Lakeside Stations and the axial netting done in 1961 (Table 5) are also shown in graph form (Figures 3 to 7).

Mormyridae

Figures 3 to 6 show that mormyrids increased significantly in catches in the Sanyati Basin after 1964. Between 1961 and 1964 only 20 mormyrids involving three species were netted at Kariba Station in over 150 000 m of net set, while between 1972 and 1975 over 800, involving four species, were netted in approx-

Table 1 Number of fish netted per fleet setting from the Kariba Station

Species	1961	1962	1963	1964	1972	1973	1974	1975
Hippopotamyrus discorhynchus	–	–	–	0,03	8,23[a]	4,57	8,40	5,58
Marcusenius macrolepidotus	–	–	–	–	1,12	2,23	0,95	0,58
Mormyrus longirostris	0,19	0,01	0,01	–	1,41[a]	3,19	9,45	7,00
Mormyrops deliciosus	0,01	–	–	–	–	0,15	0,68	–
Alestes imberi	14,01[a]	13,54	6,90	1,55	7,88[a]	3,07	3,13	18,47
Hydrocynus vittatus	29,35[a]	25,76	20,45	14,84	55,53[a]	27,38	44,59	39,73
Distichodus schenga	3,99[a]	1,70	0,51	0,21	0,18	–	0,22	0,10
D. mossambicus	2,80[a]	1,15	0,36	0,09	–	–	–	–
Labeo altivelis	12,79[a]	9,61	3,50	0,78	0,18	–	0,22	1,05
L. congoro	29,45[a]	12,25	4,47	0,92	–	–	–	0,05
Oreochromis mortimeri	12,08[a]	4,89	1,98	0,48	2,35[a]	5,61	10,22	13,98
O. macrochir	0,31	0,14	0,02	–	–	–	–	0,63
Tilapia rendalli	1,15	0,31	0,10	–	0,47	0,38	1,22	–
Serranochromis (Sa) codringtoni	0,16	0,07	0,05	0,01	6,18[a]	4,57	11,72	7,68
Synodontis zambezensis	–	0,12	–	–	1,59[a]	2,03	10,27	4,05
Eutropius depressirostris	0,15	0,07	1,05	0,12	1,53[a]	1,73	3,68	3,26
Clarias gariepinus	8,02[a]	4,37	2,63	0,26	0,47	0,11	2,77	0,63
Heterobranchus longifilis	–	–	–	–	0,06	0,11	0,36	0,21
Number of settings	80	83	94	89	17	26	22	19

[a] = 8 most common species.

Table 2 Number of fish netted per fleet setting from Lakeside Station

Species	1960	1961	1962	1963	1964	1967/68	1972	1973	1974	1975
H. discorhynchus	–	–	–	–	0,26	0,40	18,06[a]	18,44	10,76	3,19
M. macrolepidotus	–	–	–	–	–	1,80	6,21	5,59	5,15	1,30
M. longirostris	–	–	0,09	–	0,08	–	1,16	1,62	4,53	8,42
M. deliciosus	–	–	–	–	0,63	–	0,05	0,33	0,34	0,11
A. imberi	63[a]	44	19,36	24,66	3,59	2,20	0,84	0,33	4,11	20,49
H. vittatus	58[a]	40	55,45	65,16	41,16	27,40	101,42[a]	62,29	139,73	84,30
D. schenga	3[a]	4	2,18	0,91	1,49	1,00	0,10	0,07	0,26	0,04
D. mossambicus	5[a]	9	3,55	1,25	0,77	–	–	–	–	–
L. altivelis	216[a]	74	29,64	16,41	9,54	–	0,10	–	0,03	0,42
L. congoro	17[a]	18	12,27	11,25	3,57	–	–	–	–	–
O. mortimeri	38[a]	1	21,00	8,16	2,78	9,60	15,32[a]	13,40	50,84	40,07
O. macrochir	–	–	–	–	–	–	–	–	0,03	0,23
T. rendalli	–	3	0,45	0,91	0,11	0,80	1,37[a]	1,11	4,38	4,34
S. (Sa) codringtoni	–	1	1,00	0,41	0,18	2,80	15,37[a]	23,03	39,15	47,73
S. zambezensis	–	–	–	–	0,52	–	0,79	1,92	3,11	1,69
E. depressirostris	–	–	0,91	2,91	0,36	1,60	11,68[a]	6,03	12,11	3,81
C. gariepinus	12[a]	29	16,55	13,33	0,90	1,80	2,95[a]	1,85	10,96	6,46
H. longifilis	–	–	–	–	–	–	0,05	0,03	0,07	0,19
Number of settings	1	1	11	12	61	5	19	27	26	23

[a] = 8 most common species.

Table 3 Number of fish netted per fleet setting from Naodza cleared area

Species	1960	1962	1963	1964	1964/65[a]
H. discorhynchus	–	–	–	0,05	0,14
M. macrolepidotus	–	–	–	0,15	0,14
M. longirostris	–	–	–	–	0,05
M. deliciosus	–	–	–	–	–
A. imberi	20,50	49,57	7,54	2,31	0,09
H. vittatus	78,00	56,71	55,54	51,60	35,60
D. schenga	7,50	4,42	0,45	2,30	3,05
D. mossambicus	5,50	7,71	1,54	0,57	0,52
L. altivelis	137,00	53,14	6,63	3,21	1,28
L. congoro	7,00	10,00	3,45	4,26	1,38
O. mortimeri	87,00	53,28	2,27	14,05	2,24
O. macrochir	–	–	–	–	–
T. rendalli	5,00	0,85	0,72	0,15	0,47
S. (Sa) codringtoni	–	–	0,18	0,26	0,42
S. zambezensis	–	–	–	0,26	0,33
E. depressirostris	–	–	6,72	11,78	10,52
C. gariepinus	49,50	6,14	5,09	1,26	1,71
H. longifilis	–	–	–	–	–
Number of settings	2	7	11	19	21

[a] = bottom set.

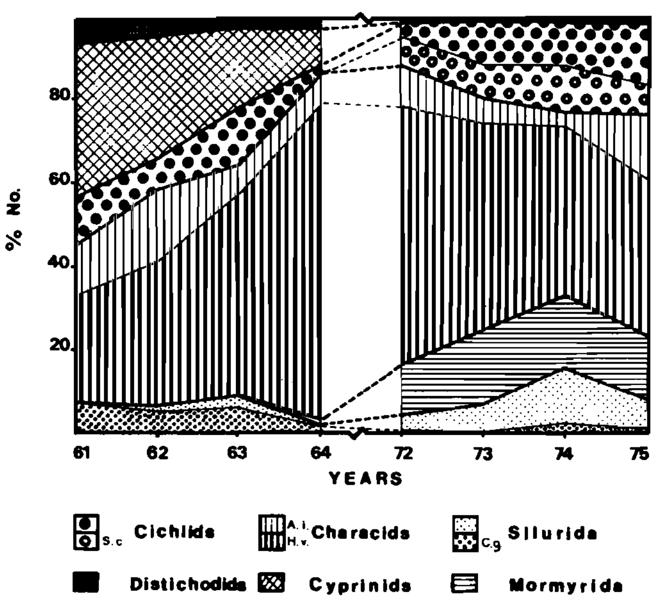

Figure 3 Annual percentage proportions (number) of the families for the two periods, Kariba Station. Distichodids and cyprinids are combined for the 1972 – 1975 years. Key abbreviations: *C. gariepienus* (C.g.); *H. vittatus* (H.v.); *A. imberi* (A.i.); *S. codringtoni* (S.c.).

imately 29 000 m (Table 1). For the same period, an increase also occurred at Lakeside, where improved catches of *M. longirostris* in 1975 possibly resulted to a certain extent from the cessation of commercial gill-netting there in 1972 (Figure 6). Netting results from the Naodza and Sanyati West Stations show a similar scarcity of mormyrids in catches from 1960 to 1965, in bottom- and top-set nets (Tables 3 & 4), while Figure 7 indicates they were scarce throughout the lake in 1961. Their scarcity is also shown in the analysis of African village catches in the Sinazongwe area of Zambia in 1962, where *M. longirostris*, *M. deliciosus* and *Hippotamyrus discorhynchus* combined formed only 1,1% of the total catch (Fisheries Research Bulletin, Zambia, 1965). In 1974, however, *Mormyrus* and *Mormyrops* combined formed 10,5% of the catch of African fishermen from Kariba to Sengwa.

With the development of aquatic macrophytes and sediments

Table 4 Number of fish netted per fleet setting from Sanyati West cleared area

Species	1962	1963	1964	1965	1963[a]	1964[a]
H. discorhynchus	–	0,53	0,19	1,60	0,65	0,14
M. macrolepidotus	–	0,11	0,03	8,20	0,20	0,04
M. longirostris	0,12	0,11	–	–	0,15	–
M. deliciosus	–	0,03	–	–	0,20	–
A. imberi	17,12	1,38	0,11	0,50	0,50	–
H. vittatus	77,62	51,23	42,79	28,00	38,15	36,00
D. schenga	5,80	2,73	2,38	1,80	10,30	4,19
D. mossambicus	17,50	5,65	1,23	0,30	4,30	2,19
L. altivelis	52,90	42,46	16,49	5,30	88,80	27,19
L. congoro	28,70	7,42	8,38	1,50	9,35	14,04
O. mortimeri	49,10	4,88	2,23	2,80	7,10	4,33
O. macrochir	–	–	–	–	–	–
T. rendalli	0,50	0,46	0,07	0,50	0,10	0,14
S. (Sa) codringtoni	0,12	0,42	0,46	0,80	1,05	0,52
S. zambezensis	–	2,30	0,15	0,70	0,75	0,19
E. depressirostris	0,75	0,73	–	1,70	1,35	–
C. gariepinus	25,20	4,92	0,46	1,80	1,65	0,71
H. longifilis	–	–	–	–	0,05	–
Number of settings	8	26	26	10	20	21

[a] = bottom set.

Table 5 Percentage proportion (No.) of various species caught from different areas in January 1961 (see Figure 7)

Species	Open lake	A San west clearing	B Sibilobilo River	C Chezia River	D Luzilukulu River	E Sinazongwe estuary	F Chimene estuary	G Binga clearing	Sanyati gorge
H. discorhynchus	–	–	–	–	1,37	3,65	–	–	–
M. macrolepidotus	–	–	–	–	–	–	–	–	–
M. longirostris	–	–	–	–	–	–	–	–	–
M. deliciosus	–	–	0,12	–	–	–	–	–	0,14
A. imberi	2	1,26	34,22	32,15	26,93	16,05	56,48	12,00	62,41
H. vittatus	17	21,33	1,99	14,28	17,26	29,92	5,13	30,30	1,77
D. schenga	10	–	0,75	7,15	2,07	0,73	0,29	4,74	0,14
D. mossambicus	3	1,59	2,62	3,57	–	8,75	1,72	2,52	–
L. altivelis	3	53,21	35,08	–	6,21	0,73	2,28	2,21	9,69
L. congoro	12	0,58	19,74	–	4,15	10,22	5,14	6,94	22,64
O. mortimeri	42	7,08	3,12	7,15	1,37	1,45	17,24	1,26	–
O. macrochir	–	–	–	–	–	–	–	–	–
T. rendalli	–	0,92	0,12	–	–	–	0,57	–	–
S. (Sa) codringtoni	–	–	–	–	–	–	–	–	–
S. zambezensis	–	–	0,37	–	3,45	10,94	–	10,10	0,27
E. depressirostris	–	–	0,24	10,72	25,45	13,86	7,99	28,40	0,41
C. gariepinus	11	13,70	1,49	24,99	6,21	2,18	2,57	1,26	2,51
H. longifilis	–	0,30	–	–	5,52	1,45	0,57	–	–
B. marequensis	–	–	–	–	–	–	–	0,32	–
L. cylindricus	–	–	0,12	–	–	–	–	–	–

after 1964 when the lake reached a relatively stable level and there was an increase in the invertebrate fauna as a result (McLachlan 1969), conditions probably improved for the benthic-insect-eating mormyrids, resulting in an increase in population numbers. Recent research (Joubert 1975; Mitchell 1976) has shown the mormyrids of Kariba, with the exception of *M. deliciosus*, to be heavily dependent on benthic organisms for food.

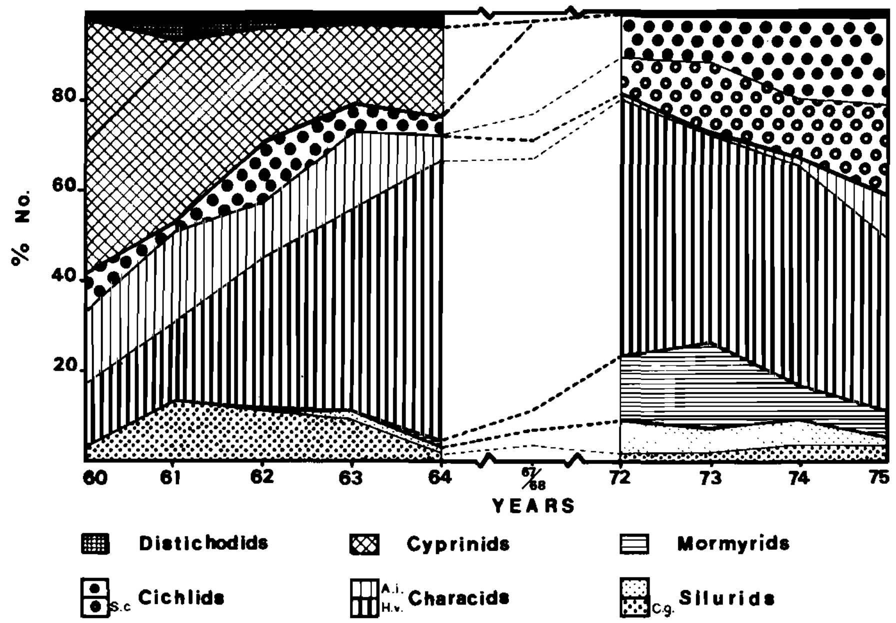

Figure 4 Annual percentage proportions (number) of the families for the two main periods, Lakeside Station. Distichodids and cyprinids are combined for the 1972 – 1975 years. Key abbreviations: *C. gariepinus* (C.g.); *H. vittatus* (H.v.); *A. imberi* (A.i.); *S. codringtoni* (S.c.).

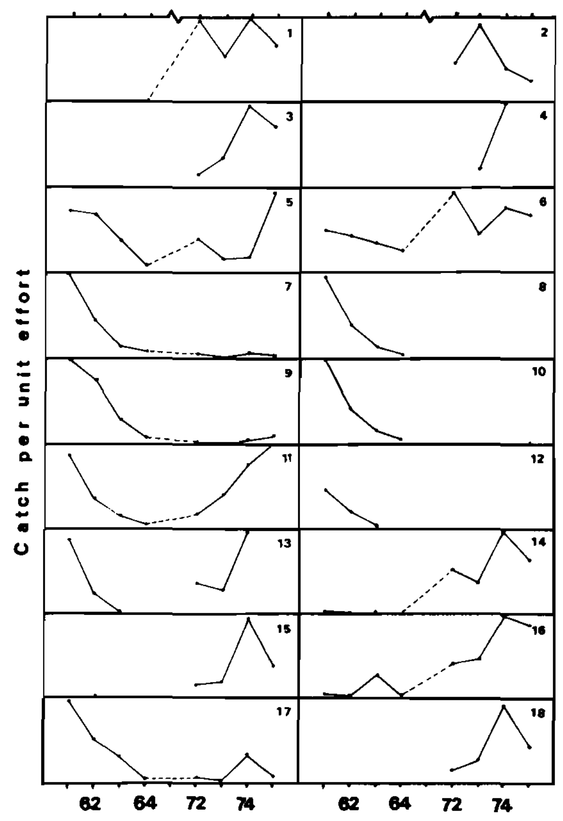

Figure 5 Annual C/E for individual species to show trends, Kariba Station. (Vertical axis scales for different species are not similar.) Dashed line connects two main periods. Unconnected dots on baseline indicate species only fractionally present. 1. *H. discorhynchus*; 2. *M. macrolepidotus*; 3. *M. longirostris*; 4. *M. deliciosus*; 5. *A. imberi*; 6. *H. vittatus*; 7. *D. schenga*; 8. *D. mossambicus*; 9. *L. altivelis*; 10. *L. congoro*; 11. *O. mortimeri*; 12. *O. macrochir*; 13. *T. rendalli*; 14. *S. (Sa) codringtoni*; 15. *S. zambezensis*; 16. *E. depressirostris*; 17. *C. gariepinus*; 18. *H. longifilis*.

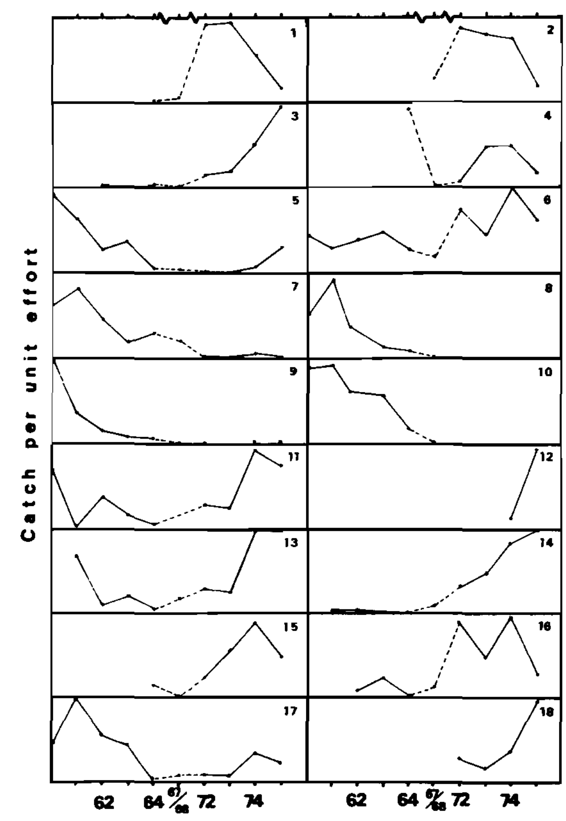

Figure 6 Annual C/E for individual species to show trends, Lakeside Station. (Vertical axis scales for different species are not similar.) Dashed line connects two main periods. Unconnected dots on baseline indicate species only fractionally present. Enumeration as in Figure 5.

Characidae

A. imberi were abundant after closure of the dam wall, but by 1964 the population had declined. By 1975, however, their numbers had increased significantly particularly at the Kariba Station, contradicting Balon's assertion that 'The indigenous *Brachyalestes i. imberi*, for example, was replaced by *Alestes lateralis* in enormous density and in a very short time'. While some degree of inter-specific competition might influence the relative status of the two species at any one time there is little evidence to support Balon's assertion that the one replaced the other (1971b, 1974a). On the contrary the data suggest that

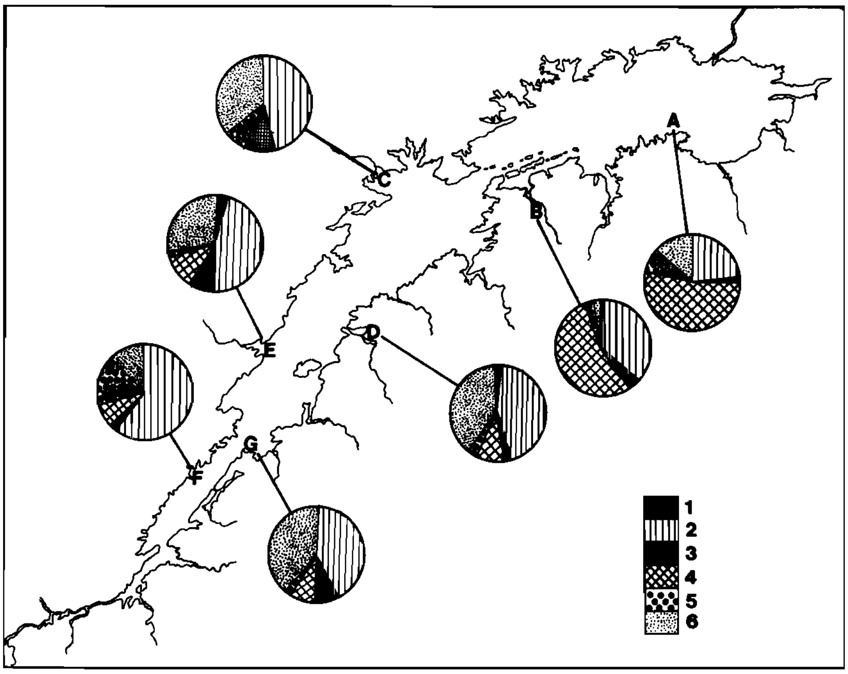

Figure 7 Percentage proportions (number) of families as indicated by gill-netting in various areas of the lake in January 1961. A: Sanyati West; B: Sibilobilo; C. Chezia; D: Luzilukulu; E: Sinazongwe; F: Chimene; G: Binga. Key: 1 Mormyrids; 2 Characids; 3 Distichodids; 4 Cyprinids; 5 Cichlids; 6 Silurids.

no such replacement of *A. imberi* by *A. lateralis* took place. According to Balon (1971b) specimens of *A. lateralis* were first recorded in the lake as late as 1963, and yet Figures 5 and 6 show that *A. imberi* started declining very early in the lake's history, as also occurred in the Volta Lake (Petr 1971). By 1964/1965 when *A. imberi* stocks were very low, *A. lateralis* only formed 5,3% of the food eaten by tigerfish (Matthes 1968), as opposed to 54% by 1967/1968 (Donnelly 1971) and 20,6% by 1969/1970 (Kenmuir 1973a). Clearly the decline of *A. imberi* stocks (from 1960 – 1964) took place before the expansion of the *A. lateralis* population (1964 – 1968) and the two events appear not to have co-incided at all. If anything, the temporary demise of *A. imberi* stocks may have created a vacant semi-pelagic niche for a few short years, which *A. lateralis* was then able to exploit. As shown, *A. imberi* increased again in the 1970s and both species are now fairly common in the lake and evince little indication of a 'replacement' phenomenon, or the 'competitive exclusion' phenomenon which Bowmaker *et al.* (1978) suggest may occur on a regional basis.

If this species spawns on newly flooded grassland (Balon 1971b) their success may depend on whether lake level is rising or falling during their breeding season, which is from about December to March (L.K.F.R.I. records, Burne, pers. comm.). In Lake McIlwaine an exceptionally strong year class in 1974 was attributed to very successful spawning in 1973, when heavy rain flows created suitable breeding conditions (Marshall & van der Heiden 1977). Thus the strength of year classes may vary considerably from year to year. Reference to Figure 2, for example, shows that only two summers, 1964/1965 and 1973/1974, had lake level rises corresponding with the breeding season, providing flooded margins for spawning activities. Perhaps not coincidentally the species showed increases in 1967/1968 (Donnelly 1971) and in 1975, three and two years respectively after these favourable lake level rises.

In the Volta Lake *Alestes* species were similarly common but also declined soon after closure in commercial catches in the north-west, where small-mesh nets were used to catch them (Petr 1968, 1971). Restrictions on using small-mesh nets in Kariba (Soulsby 1963) prevented the early population explosion of *Alestes* being exploited.

The *H. vittatus* population, after an initial expansion, appeared to decline (Figures 5 & 6) so that by 1964 catches were lower than in earlier years. A possible reason was an absence of suitable fodder species in this intermediate and unstable phase of the lake's existence, or perhaps because of dilution of the population in a greatly expanded water body. Following this period the population increased beyond its earlier level. At the Kariba Station, for example, the lowest catch in the second period (1973) was almost equal to the highest catch of the first period (1961). The 1974 catch at Lakeside is more than twice the highest first period catch in 1963.

This later increase was probably related to food supply. Freshwater sardines (*Limnothrissa miodon*) introduced to the lake from Lake Tanganyika in 1967/1968 bred successfully and spread, and by 1970 had become well incorporated into the diet of *H. vittatus* in the Sanyati Basin (Kenmuir 1971a, 1973a). Commercial gill-net catches of tigerfish rose to a peak in 1974 while the developing sardine fishery tigerfish catches in sardine nets rose to a peak in 1977 and then declined (Marshall *et al.* 1982).

Distichodontidae

Distichodids, common in catches from 1960 to 1962, particularly at the Naodza and Sanyati West Stations (Tables 3 & 4) and also throughout the lake (Figure 7), soon showed a steady decline (Figures 5 & 6) and by 1967/1968 only occasional specimens were recorded at the Lakeside and Kariba Stations. Between 1972 and 1975 no *D. mossambicus* were recorded at the Kariba and Lakeside Stations and only a very few *D. schenga*, while they are now rarely netted in commercial catches in the Naodza cleared area, despite their early abundance there.

Both species are potamodromous and once they reached adult size in the lake they probably migrated from the marginal shorelines to riverine areas of suitable habitat. Being essentially fluvial they become progressively more common in commercial gill-net catches towards the more riverine western end of the lake (Begg 1974). They are herbivorous, utilizing attached algae, but also feeding on molluscs, and 'dredging' food from the lake floor (Donnelly 1971).

Reference to Figure 8 shows that in the new lake growth was rapid, with the populations of *D. mossambicus* and *D. schenga* showing fork-length frequency peaks at 32 and 30 cm by 1961. Thereafter growth slowed and by 1963 the peaks were at 35 and 33 respectively. Lack of recruitment to the nets in the later period is clearly shown (Figure 8) and is one of the reasons for their decline in experimental catches, and for their small contribution to commercial catches in the eastern basins. In 1974, for example, they formed only 2,3% of the catch (mass) from Kariba to Sengwa as opposed to 19,5% in the remaining western half of the lake. Despite their scarcity they attain masses of 6 kg or more in the lake, appreciably larger than fish recorded from the river.

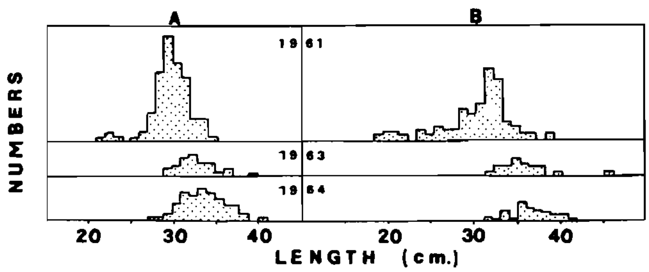

Figure 8 Structure of netted populations of *D. schenga* (A) and *D. mossambicus* (B) for various years. Note the lack of recruitment for both species, particularly evident by 1964, and faster growth rate of *D. mossambicus*.

Cyprinidae

Prominent in catches in 1960 and 1961 (Figures 5 & 6), particularly *L. altivelis*, cyprinids soon declined at all four stations, and by 1967/1968 they had entirely disappeared from the catch at the Lakeside Station. *L. altivelis* is now largely restricted in distribution to the three major affluent rivers of the Sanyati Basin — the Naodza, Gache Gache and Sanyati (Kenmuir 1971b), while a small population has been recorded from the mouth of the Charara River (Burne, pers. comm.). Their decline in commercial catches is shown by the declining purchases of 'nchila' (*Labeo* spp.) from Dandawa and Monga villages near the Sanyati Gorge, from 53% in 1964 to 15% in 1975. Like *Distichodus* they are essentially fluvial and potamodromous (Bowmaker 1973), and are more common in commercial catches towards the more riverine western end of the lake (Begg 1974). In 1974 they formed only 6,2% of the total landings and purchases of fish from Kariba to Sengwa, compared with 22,5% in the western third from Sengwa to Mlibizi.

Figure 9 shows growth of *L. altivelis* was rapid in the first few years with the population mode (fork length) reaching 28 cm in 22 months, and 40 cm in 58 months (October 1964). There is evidence to suggest that this early population did not breed until the 1964/1965 rainy season, which probably explains the general lack of recruitment up to this date (Kenmuir, unpublished data). *L. congoro* also showed a lack of recruitment up to 1964, with a concomitant decline in the largely single year class spawned after wall closure (Figure 9).

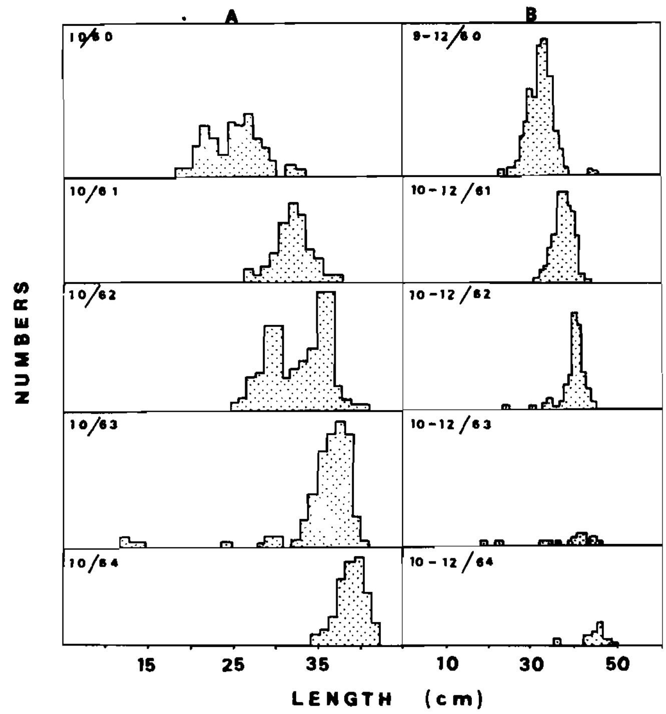

Figure 9 Structure of netted populations of *L. altivelis* (A) and *L. congoro* (B) for the same months of various years. Note the lack of recruitment for both species.

Growth in the new lake was rapid, with the population mode reaching 32 cm by the end of 1960 (Kenmuir 1971c). In Cabora Bassa populations of *L. congoro* and *L. altivelis* grew rapidly, reaching 12 – 18 cm within nine months of dam-wall closure (Jackson & Rogers 1976).

Cichlidae

This family has shown some interesting changes. *O. mortimeri* is the mainstay of the commercial fisheries. In 1962 it formed 35% of commercial catches at African fishing villages in the Sinazongwe area (Fisheries Research Bulletin, Zambia, 1965) while in 1974 it formed 38% of catches between Kariba and Sengwa.

The species initially bred successfully with a high survival rate during the filling phase, as shown by experimental net catches in 1960 and 1961 (Figures 5 & 6). By 1964 the population had reached a total length of 34 – 43 cm, but little or no recruitment was taking place, indicated by the extreme scarcity of juveniles in the experimental net catches in 1964 (Figure 10A). This resulted in the rapid decline of catches in the experimental nets up to 1964 (Figures 5 & 6). This lack of recruitment has been attributed by Donnelly (1971) to decreasing areas of shallow water as the lake rose, with increasingly steeper profiles and reduced habitat for fry and fingerlings. *Hydrocynus* and possibly *Clarias* predation may have reduced fingerling numbers as well. By 1968 the dominant part of the commercial catch was composed of large females of 37 to 43 cm and males of 40 to 49 cm (Donnelly 1971). These fish, caught in large numbers in experimental and also commercial nets, were probably remnants of the population spawned shortly after closure of the dam wall. By this time smaller fish started appearing in experimental gill-nets and it is probable that successful spawning and recruitment only took place after 1964, when the lake had stopped rising. Thus the species shows an almost classical decline followed by a rapid increase in catches, particularly evident in Figure 5. The increase of this species after 1972 might also be attributable to the cessation of commercial netting in the area in July 1972, as the catch of 50 fish per setting in 1974 at Lakeside is exceptionally high. Nevertheless the increase also shows successful adaptation to the lacustrine conditions after 1964.

The structure of the netted population in 1975, showing the preponderance of smaller fish in relation to earlier years is shown in Figure 10A.

Serranochromis (Sa) codringtoni, uncommon in experimental catches from 1961 to 1964, increased rapidly after this and by 1972 they figured prominently in catches at both the Lakeside and Kariba Stations, and also formed 5,2% of the commercial catch from the Kariba to Sengwa fishing camps. By 1975 they formed approximately half of the cichlids caught at both stations (Figures 3 & 4). Table 5 shows that *S. codringtoni* was uncommon throughout the lake in the early years.

The success of this mollusc and insect-feeding species (Mabaye 1980) possibly resulted from expansion of aquatic macrophytes from 1964 with a concomitant increase of invertebrate food (McLachlan 1969). Minshull (pers. comm.) notes a possible correlation between the high catches of the species in the Sanyati West area in the early 1970s and the presence in this area of large numbers of the mollusc, *Melanoides tuberculata*. A second factor, possibly, was the availability of nursery areas for the young after 1964 in the developing macrophyte beds. *Serranochromis (sargochromis)* species have a lower temperature tolerance than young *Tilapia* and *Oreochromis* and the existence of cover for young *S. codringtoni* in deeper, cooler water might also have contributed to their increase (Donnelly 1971).

Figure 10B depicts the structure of the netted population at Lakeside in 1972 and 1975. The majority of these are adult fish (22–32 cm), with good recruitment evident. This is a smaller species than *O. mortimeri* with a maximum mass of about 1,3 kg and total length of 38 cm. *O. macrochir*, considered extinct following its introduction to the lake between 1959 and 1961, reappeared in catches at the Lakeside Station in 1974 and 1975 and at the Kariba Station in 1975. Its future success could depend on whether or not it is occupying a niche not occupied by other species, or whether evolutionary changes in the aquatic environment favour its increase. Bowmaker *et al.* (1978) suggest that increased predation by sardines on zooplankton, with a resultant increase in phytoplankton, could benefit *O. macrochir*. Another possibility is that the large mussel beds of the lake, contributing ammoniacal excretory products, could benefit phytoplankton and ultimately *O. macrochir* (Kenmuir 1980a).

T. rendalli are caught infrequently in gill-nets in relation to their abundance, and the low numbers shown in the tables do not necessarily indicate their true status. Nevertheless they declined at both stations up to 1964, and then increased in the 1970s when diving observations and spear-fishing and angling catches showed they were abundant, occupying a wide range of habitats, but particularly common in areas of extensive submerged aquatic-macrophyte beds (pers. obs.). They feed on various plants, particularly the soft-leaved *Potamogeton* species and *Vallisneria aethiopica*; the lake grass *Panicum repens* (Caulton 1977); and also the periphyton on submerged trees (Kenmuir 1978). They also breed successfully in the shallows from September through the summer months till winter, when nesting colonies can be seen along the shoreline. Their potential fertility was shown by a pair which spawned eight times in one year in an experimental tank at Kariba (Kenmuir 1973b). These factors, plus the fact that they are not cropped heavily by commercial gill-netting, would have favoured an increase, particularly after 1967 when *P. repens* established on the lakeshore (Mitchell 1969; van der Lingen 1973). Conversely, any decline in aquatic macrophytes over a long period could adversely affect this important angling and spear-fishing species.

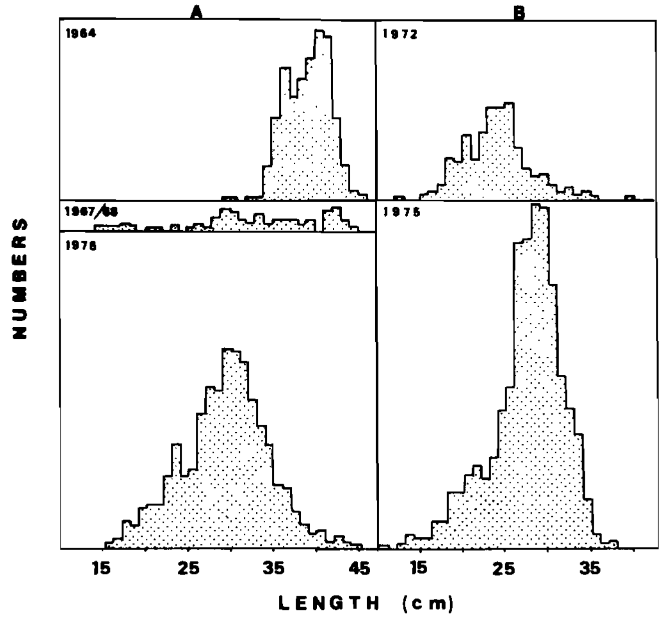

Figure 10 Structure of netted populations of *O. mortimeri* (A) and *S. (Sa) codringtoni* (B) for various years. Note first indications of recruitment in 1967/1968 and well-established recruitment by 1975 in *O. mortimeri* population. Note also smaller maximum size of *S. (Sa) codringtoni* and good recruitment of this species.

Clariidae

C. gariepinus was initially common in catches up to 1961 (Figures 5 & 6), particularly at the Naodza and Sanyati West Stations (Tables 3 & 4), but subsequently all four stations showed a sharp decline as a result of lack of recruitment to the population (Figure 11). Catches increased slightly at Lakeside from 1973 to 1975 with cessation of commercial netting, but did not compare with earlier abundance and their proportion in the overall catch remained low (Figures 3 & 4). Even greater numbers may have been recorded in the early years if bottom-set nets had been used. Both Lake McIlwaine and Lake Robertson, outside Harare, showed similar increases and then decreases of *C. gariepinus* following the closure of their dam walls (McIlwaine Research Centre Records). In the Hendrik Verwoerd Dam this species increased after impoundment, but also showed lack of recruitment (Hamman 1980). Growth rate in the new lake was rapid, with the population as a whole reaching 50 to 80 cm by 1961 (Figure 11).

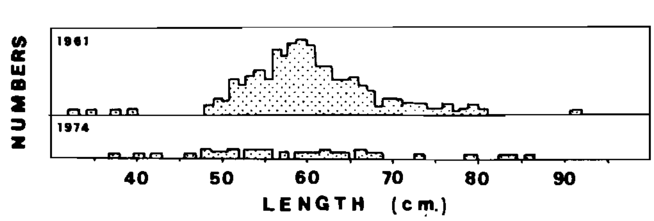

Figure 11 Structure of netted populations of *C. gariepinus* in 1961 and 1974. A mode of 60 cm by 1961 shows rapid growth rate, but lack of recruitment to the population is evident.

No *H. longifilis* were caught from 1961 to 1964 at any of the stations, and only in recent years has there been an upward trend in their numbers at both stations (Figures 5 & 6). They are uncommon in Kariba, and formed only 1,5% of the commercial catch in 1974 from African fishing camps east of the Sengwa River. Similarly in Cabora Bassa they were very uncommon in catches after closure of the dam wall (Jackson & Rogers 1976). Little is known of their biology. Kariba anglers catch them in some muddy river estuaries during the rains, while divers below the Kariba dam wall report they are fairly common in the stilling pool, and also in the clear fast-flowing water of the Kariba Gorge.

Schilbeidae

E. depressirostris was uncommon in early catches at the Kariba and Lakeside Stations, but increased considerably up to 1975 at both stations (Figures 5 & 6). The top-set nets used in the early years probably did not underestimate their abundance, as catches at Lakeside in 1967/1968 in bottom-set nets were also low (Donnelly 1971). As they are largely insectivorous in Kariba the development of aquatic macrophytes on the cleared areas and consequent increase of invertebrates since 1964 probably favoured their expansion in the Sanyati Basin. Early populations present in riverine areas (Table 5) presumably served as the source from which this latter expansion derived.

Mochokidae

S. zambezensis was absent or not common in catches from 1960 to 1965 although being essentially benthic the top-set nets may have underestimated their abundance. Nevertheless they have increased since then with fairly good catches at the Kariba Station (up to 10 per setting) in 1974, compared with no returns at all for the years 1961, 1963 and 1964, and improved catches at Lakeside compared with the early years. They favour a rocky or treed habitat, and Lakeside is not a prime habitat area, while the Kariba Station is more favourable. They feed largely on molluscs (Kenmuir, unpublished data; Begg 1968) and since these are abundant in the lake, habitat, rather than food, is probably a factor limiting their expansion.

Changes in catch per effort

Concomitant with changes in the fish taxa composition were yearly changes in productivity, indicated by the catch per unit effort. At the Kariba Station catches dropped from 119 fish/fleet in 1961 to 20 fish/fleet by 1964, or from 73 kg/fleet to a mere 8,5 kg/fleet. This low was then followed by an increase to 85 fish/fleet in 1972, and 103 fish/fleet in 1975, or 17,5 kg and 38,5 kg/fleet respectively. Similarly, at the Lakeside Station catches dropped from 412 fish/fleet in 1960 (one setting) to 161 fish/fleet in 1962 (126 kg/fleet) to 66 in 1964, and then rose again to 225 fish/fleet in 1975 (87 kg/fleet).

At both these stations therefore the trend has been a drop from the initial high productivity followed by a build-up to a level considerably higher than the low period, but not as high as the earlier period. Also of interest is that the average mass per fish was appreciably higher in the early years than in the later years. At the Kariba and Lakeside Stations in 1962 this was 0,65 and 0,78 kg respectively, compared with 0,38 kg at both stations in 1975. This lower average mass reflects the greater numbers of smaller species caught in later years. It is obvious from these results that Kariba has followed the pattern of increased-decreased-increased productivity characteristic of man-made lakes (Bowmaker 1975).

Appearance of species

Jackson (1961) envisaged that once Kariba had filled, new species might invade the lake as ecological niches became available to them, while others would disappear. New species have in fact appeared and others disappeared, but the extent and mechanics of the invasion is the subject of some controversy (Jubb 1976a,b; Bowmaker *et al.* 1978; Kenmuir 1978; Marshall 1979). Most of these species have appeared in the more westerly basins of Lake Kariba (Balon 1972, 1973) and have yet to appear either regularly or at all in catches in the eastern basins (Mitchell 1976, 1978).

Balon states (1974a,b,c) that during his work on Lake Kariba the original list of 28 fish species was increased to 40, and on the basis of this and investigations of the fish fauna on the edge of the falls he concluded that the Victoria Falls are not a physical barrier to the downstream invasion of Upper Zambezi species, as suggested by Jubb (1961, 1964). Balon's contention is an important and controversial one and requires additional comment to that of Bowmaker *et al.* (1978), since these authors point out that if he is correct his argument has implications regarding the effectiveness of even the largest waterfalls as a barrier to fish movements.

Balon lists the following 14 species as invaders: *Alestes lateralis, Serranochromis (Sargochromis) giardi, S. (Sa) carlottae, S. (Serranochromis) macrocephalus, S. (S) robustus, Marcusenius macrolepidotus, Barbus poechii, B. paludinosus, B. unitaeniatus, B. lineomaculatus, L. cylindricus, Schilbe mystus, Oreochromis andersoni, Pseudocrenilabrus philander.*

Jubb (1976a) points out that eight of the species mentioned above (*L. cylindricus, M. macrolepidotus, S. mystus, P. philander, A. lateralis* and all the *Barbus* species except *Barbus poechii*) were in fact present in the Middle Zambezi system prior to Kariba and were not recorded by the pre-impoundment surveys, which concentrated on the river proper, and the lower stretch of the Sanyati. However, since Balon himself recorded *B. poechii* in the Lusito River (1974c), a tributary entering the Zambezi below Kariba, this species was also present in the Middle Zambezi area (Kenmuir 1977). These species could well have entered Kariba from affluent streams or even been present in streams/rivers drowned by the lake, and as such may not be invaders at all. *L. cylindricus*, for example, is a common species in the stilling pool and gorge below the dam wall, where they reach a mass of 1 kg. They are also present in the affluent Umniati and Naodza Rivers at the river/lake interfaces, as well as at Mana Pools (Kenmuir 1976, 1977). Clearly the species has always been present in these areas, some portions of which were covered by the new lake (e.g. the Kariba and Sanyati Gorges), and they cannot possibly be regarded as invaders.

Of the remaining five species in Balon's list, Jubb notes that while some or all may be true invaders they may have originated either from affluent rivers or from the Chilanga fish ponds, which provided *O. macrochir* and *T. rendalli* for stocking purposes. As far back as 1952 *S. (S) robustus* and *O. andersoni* were being stocked in dams in Rhodesia, some of them in the Middle Zambezi River catchment (Toots 1970). Bell-Cross (1976) lists introduced *S. (S) robustus* from the Middle Zambezi below Kariba and also records *S. (S) robustus* and *O. andersoni* from the Kalomo River, a tributary of the Middle Zambezi. The annual report (1961) of the Joint Fisheries Research Organization (p.99) records *S. (S) robustus* from dams and weirs on the Middle Zambezi system in Zambia, notably the Zongwe, Chezia and Lufua Rivers, all of which now flow into Lake Kariba, while *S. (S) macrocephalus* is recorded from a dam or weir on the Zongwe River, and *S. (S) robustus* (1,59 kg) is recorded from Poole Dam on the Umfuli River, a major tributary of the Umniati, which discharges into the Sanyati Basin of Lake Kariba (Kenmuir 1977). Thus these species may have invaded Kariba from any of a number of sources, and it is certainly not true, as Balon states (1974c), that their only place of occurrence in the Middle Zambezi is in Kariba, implying that they originated from above the falls. In this connection it is interesting to note that *S. (S) robustus* and *Micropterus salmoides* established without any known introduction taking place in Lake Robertson on the outskirts of Harare within a few years of the dam's formation in 1976 (McIlwaine Research Centre Records). Similarly in Lake Kamburu in Kenya, *Cyprinus carpio* appeared in catches a few years after the lake formed, possibly invading from ponds via a major affluent river (Dadzie, pers. comm.).

The accidental introduction of species to Kariba from the Chilanga fish ponds is also a possibility. According to the 1958 annual report (p.44) of the J.F.R.O. several cichlid species, other than the introduced ones, were present in the eight Chilanga dams between 1952 and 1955. These were *Serranochromis (S) thumbergi, S. (S) angusticeps, P. philander, O. andersoni* and *O. mossambicus* (Kenmuir 1977). Bowmaker *et al.* (1978) point out that the Chilanga fish ponds had breeding stock seine-netted from Kitwe, in which it was inevitable that a significant proportion of the more than one million fish stocked were of species other than the two tilapiines intended. In addition, water from these ponds was pumped from a tributary of the Kafue, which contains numerous species, including members of the genus *Serranochromis (Serranochromis)* and *Serranochromis (Sargochromis)* not recorded from the Zambezi. Bell-Cross (pers. comm.) points out that the feeder stream of the Chilanga ponds did not contain adult *Serranochromis* but this does not preclude juveniles. I have observed juvenile *S. (S) robustus* in a small dam next to a head-water tributary of the Gwebi river which flows into Lake Robertson.

Burne (pers. comm.) found that various ponds at the McIlwaine Research Centre became infested by small species pumped from the nearby Lake McIlwaine, showing that unwanted entries of this nature are possible. Similarly, prawn ponds at Kariba were infected by unwanted fish species from the nearby lake via the pump (Caulton, pers. comm.). Hence the accidental introduction of other species into Chilanga ponds, and thence to Kariba, cannot be ignored.

Even if some species have come from above the Victoria Falls they may have come via a route other than dropping over the falls. According to Jubb (1976b) a more logical route is via the feed to the Victoria Falls hydro-electric power-station — either down the rapids and minor waterfalls from the outflow of the header dam to the river below, or via the feed to the turbines.

Thus Balon's assertions (1974c) that 'Some recent invaders into Lake Kariba. . . disprove the assumption that no fish are able to survive the drop over the edge of the Falls', and 'Most of the new species are clearly invaders from the Upper Zambezi via the Victoria Falls' are seriously undermined by several alternative explanations for the arrival, or appearance, of new species in the lake. The true invasion, if there is one, appears to be on a very minor scale as opposed to the large-scale invasion proposed by Balon. Nevertheless, in view of the fact that *Limnothrissa miodon* have successfully negotiated the Kariba dam wall to invade the Zambezi River (Kenmuir 1975), and apparently are now in Cabora Bassa (Bruton, Jackson & Skelton 1982), one cannot claim the Victoria Falls are a complete barrier to downstream fish movements. It is possible that downstream movements have occurred from time to time in the past, but establishment of new species was unsuccessful because of the relatively harsh ecological conditions in the Middle Zambezi. With the creation of a new and more favourable environment in the form of Lake Kariba a few species may have been able to establish successfully. If this is true it suggests that the erstwhile unsuitable ecological conditions below the falls were the real barrier to mixing of some elements of the upper and lower ichthyofaunas, and not the falls themselves. Could this apply to other rivers where distinct faunas live in distinct environments, ostensibly because of geographic barriers, but in reality because of inability to penetrate different environments where natural selection has already filled all available niches? This possibility has also been put forward by Bell-Cross (1968) who considered that some falls might be 'ecological' barriers, rather than physical ones, and is also suggested by Balon (1974a). Balon's dogmatic but largely unfounded assertions on the invasion have at least served to focus attention on this aspect of zoogeography, and additional research is required on this interesting question.

Disappearance of species

The disappearance or semi-disappearance of species from Lake Kariba was on a small scale. As indicated by Bowmaker *et al.* (1978), early victims were *C. neumanni* and *O. zambezensis*, both current-loving species, the latter now found only in the two western basins (Balon 1974a). *B. marequensis* and *S. nebulosus* have also largely disappeared. I have seen a small population of the former species in recent years at Mica Point, while occasional specimens of the latter have been caught in gill-nets in rocky areas below the Kariba township. Balon (1972) and Mitchell (1976) recorded *S. nebulosus* and not *B. marequensis* in marginal fish-fauna sampling programs. However, Burne (1977) recorded one *B. marequensis* in an estuarine station, while I netted occasional specimens in the upper reaches of the Sanyati Gorge in the early 1970s, and one or two off the Sanyati West coastline.

M. acutidens has not in fact disappeared from the lake (Bowmaker *et al.* 1978), as they were recorded by Balon (1972) and Mitchell (1976), and have also been seen in several localities in the Sanyati Basin (when diving) by the author. They have a preference for clear water, often moving or turbulent, and generally over rocks or sandy substrates, rather than in 'weed' areas where *A. lateralis* occur. *P. darlingi* is probably one of the most ubiquitous of all Kariba species, occurring from very shallow water to depths of 20 or more metres, and in a variety of habitat types, including aquatic vegetation (pers. obs.; Mitchell 1976). The latter author comments: 'This ubiquitous small fish appeared to be most common amongst rooted vegetation marginally'. Thus it is not generally correct that the species was displaced from shallow weedy habitats by *P. philander*, or that it only occurs in deeper and rockier areas (Bowmaker *et al.* 1978). This latter species was found by Mitchell (1976) to be generally uncommon, while Balon (1972, 1973) found it to be approximately four times less common numerically than *P. darlingi.*

Discussion

Since comment has already been made on particular species, this section will analyse in general terms the overall and more salient features of the changes that have occurred in the Sanyati Basin.

The J.F.R.O. surveys of the Zambezi River in 1956 and 1957 showed that only a handful of species made up the greater part of the samples. These were the two *Labeo* spp., the two *Distichodus* spp., *H. vittatus, M. longirostris, C. gariepinus,* and *A. imberi.* Cichlids were poorly represented in catches. *O. mortimeri* were present 'in fair, but by no means large quantity', *T. rendalli* occurred in 'moderate quantity' though not as abundant as *O. mortimeri*, while only a few specimens of *S. codringtoni* were recorded (Jackson 1961).

Following closure of the wall in December 1958, the early large-fish fauna was similar to the situation found in the old river, with *A. imberi, H. vittatus,* the two *Labeo* spp., *C. gariepinus*, the two *Distichodus* spp., and *O. mortimeri* occurring most abundantly in catches. This was the case throughout the lake as shown in Table 5, although in some areas, particularly river estuaries, *S. zambezensis* and *E. depressirostris* were also important components of the catch.

The early lake fauna differed from the river picture in that *O. mortimeri* were common, while *M. longirostris* were uncommon. This is similar to the Volta Lake situation where towards the end of the first year of the lake's existence, *Labeo, Distichodus, Lates* and characids were the most abundant fish by numbers in catches, particularly *Alestes nurse.* In addition cichlids established rapidly in the lake, notably *Tilapia* species, and by early 1966, approximately 18 months after the dam started to fill, they constituted three-quarters of the total catch at two stations in the southern half of the lake (Petr 1968, 1971). As in Kariba, mormyrids practically disappeared from the lake catches, except in the north, even though they had been common in the river, and most characids, after their initial abundance, rapidly declined. Jackson & Rogers (1976) remark on the absence of mormyrids in early catches in the Cabora Bassa dam, while in Lake Kainji mormyrids represented only a small part of the catch in the new lake, although they had been important in the river (Lelek 1973; Lewis 1974). Citharinidae, Characidae, Serranidae, Schilbeidae and Mochokidae were the most common early families in catches. Future years might well see the re-emergence of mormyrids as important components of the ichthyomass in these lakes. In fact Blake (1977) notes a gradual increase in numbers of mormyrids in Lake Kainji between 1972 and 1975. It seems probable that a general feature of the fish fauna of new African lakes will be the early disappearance of benthic invertebrate feeders during the filling phase, followed by their re-appearance as substrates stabilize and benthic life establishes.

At Kariba closure of the wall during the rains in December was a fortuitous time for summer breeders, and not surprisingly the majority of the early abundant species in the lake were fecund potamodromous species with breeding seasons coinciding with the flood season. They spawned successfully in the flood waters and their offspring enjoyed a high survival rate in the ever-expanding lake, where cover and food abounded. The old conditions, where juveniles were forced back into the river during the dry season, disappeared. Had the wall closed during the dry months the early fish picture might have been different. Similarly in Cabora Bassa closure of the wall during the rains (December 1974) led to a high survival rate and rapid population increase of certain silurids, characids and cyprinids (Jackson & Rogers 1976).

Early successful species in Kainji and the Volta in general were also fecund species, e.g. Characidae, Cyprinidae and Citharinidae. In both lakes a rapid increase of characids took place as in Kariba, and in Kainji the early build-up of citharinids and cyprinids was followed by a decrease in both numbers and weight of individuals caught as occurred in Kariba.

Petr (1967) suspected that Kariba would stabilize after the third year of its existence. As indicated by the data presented this was not the case, and the population in Kariba continued to change noticeably. Of the early very abundant species mentioned above the majority had dwindled in importance or disappeared entirely from certain localities by 1972. In Tables 1 and 2, for example, of the eight most commonly caught species in 1960 and 1961 at the two stations, only two remained common at both stations by 1972, these being *O. mortimeri* and *H. vittatus.*

To digress for a moment it might be suggested that commercial netting rather than natural or evolutionary processes influenced the downward trend of the larger nettable species. It seems probable that commercial netting pressure from 1962 onwards did assist the decline, but on the other hand several factors indicate that the process was natural and would have occurred regardless of commercial netting. Commercial netting only started in late 1962 and netting pressure could not have had much influence until at least 1963, since a very small tonnage was recorded in 1962 (Minshull 1973; Marshall *et al.* 1982). Reference to Figures 5 and 6 and Tables 1 – 3 shows that the decline of various species was well advanced by 1963. Secondly the almost total lack of recruitment among the large nettable species suggests they were ill-adapted to conditions establishing in the lake, and natural replacement of stocks was not taking place. Thirdly, if netting was responsible for the decline then cessation of commercial netting in the area in July 1972 should have allowed all stocks to re-establish substantially from immigration and recruitment. Only *O. mortimeri, T. rendalli* and *C. gariepinus* showed increases at both stations, whereas both stations recorded insignificant quantities of *D. mossambicus* and *L. congoro* after 1964 right up to 1975; and only occasional specimens of *D. schenga* and *L. altivelis.* They also showed increases of species that were not common in early years and were not commercial species, suggesting that the increases seen in several species were natural responses to the environment rather than influenced by the lack of netting. Finally, if commercial netting depressed stocks of certain species then this should have taken place throughout the lake, and not only in the Sanyati Basin. The high proportion of riverine fish in commercial catches in Basins 1 and 2 (Begg 1974; L.K.F.R.I. unpublished data) shows that the species concerned are well capable of maintaining their stocks in the face of commercial netting pressure if conditions are right, and their decline in the Sanyati Basin was obviously due to other causes.

As mentioned above, in place of the unsuccessful species, fish appeared which were seldom or never caught in the early years but by the 1970s figured prominently in catches. These were *S. (Sa) codringtoni, M. longirostris, H. discorhynchus, M. macrolepidotus, E. depressirostris,* and *S. zambezensis.* Of interest here is that these late-comers are predominantly benthic invertebrate feeders whose debut probably awaited the development of suitable food resources, dependent in turn on improved substrate conditions for benthic fauna.

The river estuaries supported invertebrate feeders (*Eutropius, Synodontis*) early in the lake's history which tends to support this idea, as presumably conditions here were more suitable for invertebrate life. In the Volta Lake mormyrids were only common in the north where Petr (1968) states: 'Some correlation can be drawn between the occurrence of mormyrids and the advance of the muddy flood waters into the north-western arm of the lake'. McLachlan (1974) points out that a large increase in sedentary animals and plants follows the arrival of the annual flood waters in Lake Volta with their load of detritus. In Kariba the establishment of submerged aquatics after 1964 (McLachlan 1969) must have favoured the mormyrids and some of the silurids, (e.g. *E. depressirostris*) by boosting invertebrate life and also by providing cover for these essentially nocturnal or crepuscular species (Mitchell 1978).

The fish population changes in the Sanyati Basin between 1960 and 1975 can thus be grouped into two definite categories. Firstly, fish which were initially successful as a result of spawning success and high survival rate following closure of the dam wall, with subsequent decline owing to lack of recruitment and possibly localization to certain areas; and secondly, fish which were initially scarce or non-existent but which have subsequently established successfully and now appear frequently in catches. These two categories fall conveniently into the two phases of the lake's history as outlined by McLachlan (1974) — the filling phase, characterized by an explosive growth of organisms, and the post-filling phase, characterized by the development and exploitation of existing habitats. With regard to fish fauna, Kariba has followed the normal pattern of development of lake ecosystems throughout the world. The three phases are an initial brief productive period during filling followed by a less productive trough, and then a slow rebuilding (Bowmaker 1975). This trough might be likened to a biological pause as living elements of the ecosystem start their readjustment to new conditions, and it coincides with the vulnerable-stable period described by Balon (1974a,d) as following an unbalanced eutrophy phase.

The early successful species were mostly fecund algae or detritus feeders, while later successful species in terms of numbers were mostly benthic invertebrate feeders. Seven of the eight most common species caught at Lakeside and Kariba in 1975 were predators and only one a 'vegetable' feeder (*O. mortimeri*) as compared with five 'vegetable' feeders and three predators in 1962. Similarly in the Volta Lake early predominating elements were herbivorous and plankton feeding fish (Lowe-McConnell 1975), while in Kainji an early trend also was the increase of algae/detritus feeders (Lelek 1973; Lewis 1974). A fairly general feature of new African lakes might be not only the decline of the benthic invertebrate feeders, but an early predominance of primary consumers, utilizing the abundant primary production food resources stemming from nutrient-rich waters.

An interesting feature of Kainji and Volta was the early development of clupeid populations. From this, and the success of *L. miodon* in Kariba, and apparently now also in Cabora Bassa, it is obvious clupeids are well adapted to surviving and thriving in man-made lakes even during the unstable phase and hence could play an important role in fish production in African lakes in the future. Lake Kariba, for example, produced over 11 000 tons of sardines in 1981 (Marshall, pers. comm.), and as a result of Kariba's success it has been suggested that smaller lakes should also be recipients of experimental introductions of freshwater sardines (Kenmuir 1982a). At the same time, however, the impact of such introductions (and their consequent exploitation) on other elements of the aquatic environment needs to be better understood.

The annual removal of nutrients from Lake Kariba through intensive commercial sardine fishing might cause further fish population changes, through alterations in nutrient cycling, for example. Since such changes might not necessarily be of a beneficial nature in the lake's multi-use context (angling species could suffer), continuing monitoring of marginal fish populations is necessary, and future research could profitably examine nutrient flows in the Sanyati Basin with a view to predicting possible long-term effects of the mono-species fishery on the lake. This information is important as successful clupeid fisheries could well develop in several major and lesser African lakes in future years.

Yet a third category in Kariba involved species which underwent a decline in numbers after initial success, but then showed an increase in numbers as reflected in gill-net catches. These were *O. mortimeri* and the characids, *H. vittatus* and *A. imberi*.

O. macrochir stands on its own, representing an artificially introduced species whose existence was not known or recognized following its apparent failure until the first specimens were officially recorded in 1974. The reappearance of this species stresses the unreliability of forming conclusions about the fish fauna of a newly created impoundment based on short-term investigations. Several authors prematurely commented on the failure or apparent failure of *O. macrochir* in lake Kariba.

Another category includes those fish whose existence was not recorded either in the river or in the lake in the early years, but whose presence is now known. The five *Serranochromis (Serranochromis)* and *Serranochromis (Sargochromis)* species — *S. (S) robustus, S. (S) macrocephalus, S. (S) angusticeps, S. (Sa) giardi*, and *S. (Sa) carlottae* — are examples. None of these were recorded either by Jackson or Jubb in the Middle Zambezi or its tributaries, but have now been recorded in Kariba (Donnelly 1971; Balon 1973). The possible origin of these species has been discussed earlier. Their presence complicates the issue in that it is likely to prolong the final phase, if one will ever exist, where the lake has 'settled down'. Only one of these species *S. (S) macrocephalus* has been recorded in the easterly basins of the lake, (Marshall, pers. comm.; Kenmuir 1978, 1983) their distribution so far being confined mainly to the westerly basins. Will they eventually establish in the Sanyati Basin, and if so, what effect will this have on the fish populations there? Similarly, will the artificially introduced *O. macrochir* expand beyond its present low level, and if so, what effect will this have on other species? Will it move into an unoccupied niche, or will it compete with other species? In Lake McIlwaine the introduced *O. macrochir* has virtually replaced the original *O. mossambicus*, while in Lake Kyle the introduced *O. macrochir* outweighs *O. mossambicus* in commercial catches (Lake Kyle Fisheries Statistics 1975; Minshull, pers. comm.).

Whereas the changes recorded here, with the exception of the appearance of new species, pertain mainly to the Sanyati Basin the same sequence of events in varying degrees must undoubtedly have occurred throughout the lake, with species declining in importance and others increasing as conditions changed for or against them. The early picture with regard to the fish composition seems to have been much the same throughout the lake, as indicated in Table 5 and Figure 7. The characid and cyprinid components clearly dominated these gill-net catches, with silurids important particularly in river areas. The cichlid component at this stage is relatively minor while mormyrids are insignificant.

However, while changes have undoubtedly taken place throughout the lake, it is evident from experimental and commercial netting that the greatest changes have taken place in the more lacustrine basins, where the large river-breeding cyprinids and citharinids have largely been replaced by the lake cichlids. The species cline, showing the gradual increase of cyprinids from their lowest value in the east (commercial data) to their highest in the west, and conversely the gradual increase of cichlids from low values in the extreme west to much higher values in the three large eastern basins has been shown by Begg (1974). Thus while most African man-made lakes may show a transition in time of riverine-type fish to lacustrine-adapted cichlids, there is also likely to be a species cline from one end of the lake to the other. This was evident early in the Volta Lake (Petr 1968).

The results presented here confirm Rzoska's statement (1966) that the successional changes in a newly created lake occur over a period of the order of ten to twenty years. Future years and published data will undoubtedly show further changes as a result of artificial introductions (*Limnothrissa miodon*), intensive sardine commercial fishing, accidental or natural introductions such as of the genus *Serranochromis*, and poaching of breeding stocks in rivers. Finally, regardless of what may occur in Lake Kariba itself, either naturally or by design (management), the ultimate ecological fate of the lake may be decided by events occurring outside its confines.

In the absence of any control or concern, agricultural and possibly industrial developments and practices occurring or liable to occur in the catchment areas of the lake will ultimately affect part or the whole lake if pollutants are allowed to flow unchecked into its waters. Although the possibility of a 'dead lake' might seem remote at present, pesticide contamination of both fish eagle and crocodile eggs is already established, and there are indications that pesticide residues are accumulating in some localities (Whitwell *et al.* 1974; Wessels *et al.* 1980). Taking into account Kariba's value as a local and international tourist asset, and as a producer of over 80% of Zimbabwe's fish, the situation needs to be monitored closely.

To summarize briefly, the salient features of the evolutionary process in the Sanyati Basin were the rapid increase in fish biomass; development of species which were able to utilize the initial flooding for spawning purposes; the decline of the same largely herbivorous species later when lacustrine conditions established; eventual development of a diverse and essentially lacustrine or still-water fauna dominated numerically by insectivorous/molluscivorous species; decreased production after the initial high productivity, followed by increased production later because of an increase in the variety of species caught; appearance of new and disappearance of old species; and increase of at least one species owing to a new food source introduced by man.

Conclusions

Several points of international interest arise from the experience of Lake Kariba. Since the creation of medium to large dams is becoming a feature of Africa these may be of use to fishery planners and are discussed below.

From a commercial point of view the formation of a new lake creates eutrophic conditions which will usually result in the rapid development of a large and exploitable fish resource. It not exploited immediately the potential for good catches from the initial high productivity is lost. This happened in Southern Rhodesia where commercial fishing started four years after the dam wall was closed, with a resultant loss of several thousand tons of fish (Kenmuir 1978).

In view of the rapid build-up of fish stocks and an equally rapid decline (shown also in Volta, Kainji and Cabora Bassa) it is unwise to plan long-term fishing operations based on the early fish resources. Plans should be tempered by the knowledge that later populations will probably be of much lower biomass and projected plans must be based on this assumption. In Lake Kariba expectations of a continuing highly productive fishery were soon disappointed, leading to an exodus of many fishermen from the lake to seek alternative employment.

Clupeids seem to thrive in large man-made impoundments from early on and where no natural stocks exist in new lakes deliberate or accidental introductions are likely to be successful (e.g. Kariba and Cabora Bassa). However, as indicated, some consideration of their likely impact on the aquatic environment is required before deliberate introductions are contemplated in any water-body.

The early fish population of a new lake is likely to differ appreciably from the later population and fishing methods should be improvised and adapted to take advantage of all segments of the fish community over a period of time. For example, in the early years of Kariba long lines and small-meshed nets could have been used to tap the *C. gariepinus* and *A. imberi* populations, respectively. In Lake Robertson the *Clarias* population was tapped very effectively by long lines in the first few years of its existence (Bowmaker, pers. comm.; McIlwaine Research Centre Records).

Population strengths may vary from year to year with some species if their success or otherwise is dependent on forces or events not within their control. For example, the success of *A. imberi* may depend on whether or not lake level rise coincides with their breeding season. This offers some scope for manipulating the environment for the benefit of certain species if their life histories are known, e.g. not lowering the lake level if marginal breeding is taking place.

In the absence of human interference the evolutionary process in a large man-made lake is a fairly lengthy process and relative stability is likely to be reached only one to two decades after closure. Since the success of some species depends on the development of suitable substrate conditions once lake level stabilizes then the longer the filling phase, the longer the evolutionary process is likely to take. Fishery planners should take this into account.

Human interferences, e.g. fish introductions, will probably cause further changes which are likely to prolong the evolutionary process. The increase of *H. vittatus* in Lake Kariba following the sardine introduction is an example. Constant monitoring of fish populations is thus necessary to detect possible changes, particularly if these can be exploited beneficially. The increase of tigerfish in Lake Kariba following the sardine introduction led to the establishment of a successful canning industry at Kariba.

Introductions might be immediately successful, as in the case of the sardines, or only moderately successful and only evident after many years, as in the case of *O. macrochir*. Some species will disappear completely from the new environment and others less completely (i.e. remnants or relict populations may occur). Other species not hitherto recorded in the area are likely to appear and increase the complement or diversity of fish species present. Their origin might be from one or more of a number of possible sources.

Acknowledgements

I would like to thank Mr F.J.R. Junor, formerly Officer-in-Charge of the Lake Kariba Fisheries Research Institute, Mr J.L. Minshull, of the Ichthyology Section, National Museum, Bulawayo, Dr R.A. Jubb, formerly of the Ichthyology Section, Albany Museum, Grahamstown, and Mr P.B.N. Jackson of the J.L.B. Smith Institute of Ichthyology, Grahamstown, for commenting on various drafts of this paper. Mrs M. Kenmuir did the typing and the final copies of the illustrations. Published with the approval of the Director of National Parks and Wildlife Management.

References

BALINSKY, B.I. & JAMES, G.V. 1960. Explosive reproduction of organisms in the Kariba Lake. *S. Afr. J. Sci.* 56: 101 – 104.

BALON, E.K. 1971a. First catches of Lake Tanganyika clupeids (Kapenta – *Limnothrissa miodon*) in Lake Kariba. *Fish. Res. Bull. Zambia* 5: 175 – 186.

BALON, E.K. 1971b. 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. 1972. Possible fish stock size assessment and available production survey as developed on Lake Kariba. *Afr. J. Trop. Hydrobiol. Fish* 2: 45 – 73.

BALON, E.K. 1973. Results of fish population size assessment in Lake Kariba coves (Zambia), a decade after their creation. In: Man-made lakes: their problems and environmental effects. (Eds.) Ackerman, W C., White, G.F. & Worthington, E.B. pp.149 – 158. Geophysical Monograph Series Vol. 17. American Geophysical Union, Washington.

BALON, E.K. 1974a. Fishes of Lake Kariba, Africa. T.F.H. Publications.

BALON, E.K. 1974b. The relationship of Lake Kariba to the Victoria Falls. In: Lake Kariba — a man-made tropical ecosystem in Central Africa (Eds.) Balon, E.K. & Coche, A.G. Monogr. Biol. 24. Dr W. Junk, The Hague.

BALON, E.K. 1974c. Fishes from the edge of Victoria Falls, Africa: demise of a physical barrier for downstream invasions. *Copeia* 3: 643 – 660.

BEADLE, L.C. 1974. The Inland Waters of Tropical Africa. Longman, London.

BEGG, G.W. 1968. Notes on the molluscan constituents of the benthos of Lake Kariba. *Lake Kariba Fish. Res. Inst. Proj. Rept.* 3 (cyclostyled).

BEGG, G.W. 1974. The distribution of fishes of riverine origin in relation to the limnological characteristics of the five basins of Lake Kariba. *Hydrobiologia* 44: 272 – 285.

BELL-CROSS, G. 1968. The distribution of fishes in Central Africa. *Fish. Res. Bull. Zambia* 40: 3 – 20.

BELL-CROSS, G. 1972. The fish fauna of the Zambezi River System. *Arnoldia, Rhod.* 5(29): 1 – 19.

BELL-CROSS, G. 1976. The distribution of fishes in Rhodesian river systems. Information Circular 5. Queen Victoria Museum, Salisbury.

BELL-CROSS, G. & BELL-CROSS, B. 1971. Introduction of *Limnothrissa miodon* and *Limnocaridina tanganicae* from Lake Tanganyika into Lake Kariba. *Fish. Res. Bull. Zambia* 5: 207 – 214.

BLAKE, B.F. 1977. Lake Kainji, Nigeria. A summary of the changes within the fish populations since the impoundment of the Niger in 1968. *Hydrobiologia* 53: 131 – 137.

BOUGHEY, A.S. 1963. The explosive development of a floating weed vegetation on Lake Kariba. *Adansonia* 3: 49 – 61.

BOWMAKER, A.P. 1973. Potamodromesis in the Mwenda River, Lake Kariba. In: Man-made lakes: their problems and environmental effects. (Eds) Ackermann, W.C., White, G.F. & Worthington, E.B. pp.159 – 164. Geophysical Monograph Series Vol 17. American Geophysical Union, Washington, D.C.

BOWMAKER, A.P. 1975. Fisheries productivity of Lake Kariba. *Tobacco Forum* 2: 17 – 25.

BOWMAKER, A.P., JACKSON, P.B.N. & JUBB, R.A. 1978. Freshwater Fishes. In: Biogeography and ecology of Southern Africa. (Ed.) Werger, M.J.A. pp.1 181 – 1 230. Monogr. Biol. 31. Dr W. Junk, The Hague.

BRUTON, M.N., JACKSON, P.B.N. & SKELTON, P.H. 1982. Pocket guide to the freshwater fishes of Southern Africa. Centaur Publishers, Cape Town.

BURNE, R.H. 1977. An investigation of the possibility of future exploitation of the estuarine areas of Lake Kariba by the gill-net fisheries. *Lake Kariba Fish. Res. Inst. Proj. Rept.* 27 (cyclostyled).

CAULTON, M.S. 1977. A quantitative assessment of the daily ingestion of *Panicum repens* by *Tilapia rendalli* Boulenger (Cichlidae) in Lake Kariba. *Trans. Rhod. Sci. Assoc.* 58: 38 – 42.

COCHRANE, K.L. 1976. Catches of *Hydrocynus vittatus* Castelnau during sardine fishing operations in Lake Kariba. *Kariba Studies* (7): 98 – 108. National Museums and Monuments of Rhodesia, Salisbury.

COCHRANE, K.L. 1978. Seasonal fluctuations in the catches of *Limnothrissa miodon* (Boulenger) in Lake Kariba. *Lake Kariba Fish. Res. Inst. Proj. Rept.* 29: 1 – 163 (cyclostyled).

DONNELLY, B.G. 1971. The fish population changes on Lake Kariba between 1960 and 1968. Part 1 Cichlidae. Part 2 Characidae and Citharinidae. *Lake Kariba Fish. Res. Inst. Proj. Rept.* (cyclostyled).

HAMMAN, K.C.D. 1980. Post-impoundment trends in the fish populations of the Hendrik Verwoerd Dam, South Africa. *J. Limnol. Soc. sthn. Afr.* 6: 101 – 108.

HARDING, D. 1966. Lake Kariba, The hydrology and development of fisheries. In: Man-made Lakes (Ed.) Lowe-McConnell, R.H. Academic Press, London.

HATTINGH, E.H. 1961. The problem of *Salvinia auriculata* and associated aquatic weeds on Kariba Lake. *Weed Res.* 1: 303 – 306.

JACKSON, P.B.N. 1960. The ecological effects of flooding by the Kariba Dam upon Middle Zambezi fishes. *Proc. 1st. Fed. Sci. Congress 1960*, Salisbury, Rhodesia.

JACKSON, P.B.N. 1961. Ichthyology. The fish of the Middle Zambezi. *Kariba Studies.* (1): 1 – 36. National Museums of Southern Rhodesia.

JACKSON, P.B.N. & ROGERS, K.H. 1976. Cabora Bassa fish populations before and during the first filling phase. *Zool. afr.* 11: 373 – 397.

JUBB, R.A. 1961. An illustrated guide to the freshwater fishes of the Zambezi River, Lake Kariba, Pungwe, Sabi, Lundi and Limpopo Rivers. Stuart Manning, Bulawayo.

JUBB, R.A. 1964. Some fishes of the Victoria Falls region. In: The Victoria Falls. (Ed.) Fagan, B.M. *Comm. Press. Nat. Hist. Mon. & Rel.*, Northern Rhodesia.

JUBB, R.A. 1976a. Letter to the Editor. *J. Limnol. Soc. sthn Afr.* 2: 35 – 36.

JUBB, R.A. 1976b. Unintentional introductions of fishes via hydroelectric power-stations and centrifugal pumps. *J. Limnol. Soc. sthn Afr.* 2: 29 – 30.

JOUBERT, C.S.W. 1975. The food and feeding habits of *Mormyrops deliciosus* (Leach) 1818 and *Mormyrus longirostris* Peters 1852 (Pisces: Mormyridae) in Lake Kariba, Rhodesia. *Kariba Studies* (5): 68 – 85. National Museums and Monuments of Rhodesia, Salisbury.

JUNOR, F.J.R. & BEGG, G.W. 1971. A note on the successful introduction of *Limnothrissa miodon* Boulenger, the 'Lake Tanganyika Sardine' to Lake Kariba. *Newsl. Limnol. Soc. sthn Afr.* 16: 8 – 14.

KENMUIR, D.H.S. 1971a. An analysis of data on the tigerfish *Hydrocynus vittatus* Castelnau obtained from Kariba International Tigerfish Tournaments 1969 & 1970. *Newsl. Limnol. Soc. sthn Afr.* 17: 13 – 21.

KENMUIR, D.H.S. 1971b. An introduction to the biology of *Labeo altivelis* Peters in the Sanyati Basin, Lake Kariba. *Lake Kariba Fish. Res. Inst. Proj. Rept.* 6 (cyclostyled).

KENMUIR, D.H.S. 1971c. An investigation into the decline of the *Labeo congoro* stocks in the Sanyati Basin of Lake Kariba. *Lake Kariba Fish. Res. Inst. Proj. Rept.* 7 (cyclostyled).

KENMUIR, D.H.S. 1973a. The ecology of the tigerfish *Hydrocynus vittatus* Castelnau, in Lake Kariba. *Occ. Pap. Natn. Mus. Rhod.* B5(3): 115 – 170.

KENMUIR, D.H.S. 1973b. Observations on a breeding pair of *Tilapia rendalli rendalli* Boulenger in an experimental tank at Lake Kariba Fisheries Research Institute. *Hydrobiologia* 43: 365 – 370.

KENMUIR, D.H.S. 1975. Sardines in Cobara Bassa Lake? *New Scientist* 65: 379 – 380.

KENMUIR, D.H.S. 1976. Fish spawning under artificial flood conditions on the Mana Flood-plain, Zambezi River. *Kariba Studies* (6): 86 – 97. National Museums and Monuments of Rhodesia, Salisbury.

KENMUIR, D.H.S. 1977. Fish population changes in Lake Kariba, Rhodesia. *Lake Kariba Fish. Res. Inst. Proj. Rept.* (cyclostyled).

KENMUIR, D.H.S. 1978. A Wilderness Called Kariba. 140 pp.

Wilderness Publications, Salisbury.
KENMUIR, D.H.S. 1980a. Aspects of the biology and population dynamics of freshwater mussels in Lake Kariba and Lake McIlwaine. *Lake Kariba Fish. Res. Inst. Proj. Rept.* 36, and Ph.D. thesis (Univ. of Natal).
KENMUIR, D.H.S. 1980b. The mussel resources of Lake Kariba. *Trans. Zimb. Scient. Assoc.* 60(2): 7 – 10.
KENMUIR, D.H.S. 1981. The evolution of a lake. *In Flight.* 1(2): 14 – 19.
KENMUIR, D.H.S. 1982a. Fish production prospects in Zimbabwe. *Zimbabwe Agric. J.* 79: 11 – 17.
KENMUIR, D.H.S. 1982b. How landlocked Zimbabwe has developed its fishing industry. *Fishing News International* 21: 16 – 19.
KENMUIR, D.H.S. 1983. Fishes of Kariba, Wilderness Publications, Harare 131pp.
LANGERMAN, J.D. 1979. Sardine fishing methods used on Lake Kariba. *Rhod. Sci. News.* 3: 108 – 110.
LELEK, A. 1973. Sequence of changes in fish populations of the new tropical man-made lake, Kainji, Nigeria, West Africa. *Arch. Hydrobiol.* 71: 381 – 420.
LEWIS, D.S.C. 1974. The effect of the formation of Lake Kainji, (Nigeria) upon the indigenous fish population. *Hydrobiologia* 45: 281 – 301.
LOWE-McCONNELL, R.H. 1975. Fish communities in tropical fresh waters. Longman, London & New York.
MABAYE, A.B.E. 1980. The biology of *Haplochromis codringtoni* in Lake Kariba. Univ. of Zimbabwe Report (cyclostyled), Salisbury.
MARSHALL, B.E. 1979. Fish populations and the fisheries potential of Lake Kariba. *S. Afr. J. Sci.* 75: 485 – 488.
MARSHALL, B.E. & JUNOR, F.J.R. 1981. The decline of *Salvinia molesta* on Lake Kariba. *Hydrobiologia* 83: 477 – 484.
MARSHALL, B.E., JUNOR, F.J.R. & LANGERMAN, J.D. 1982. Fisheries and fish production on the Zimbabwean side of Lake Kariba. *Kariba studies* (10): 175 – 231.
MARSHALL, B.E. & LANGERMAN, J.D. 1979. The Tanganyika sardine in Lake Kariba. *Rhod. Sci. News.* 13: 104 – 105.
MARSHALL, B.E. & VAN DER HEIDEN, J.T. 1977. The biology of *Alestes imberi* Peters (Pisces: Characidae) in Lake McIlwaine, Rhodesia. *Zool. Afr.* 12: 329 – 346.
MATTHES, H. 1968. The food and feeding habits of the tigerfish, *Hydrocynus vittatus* (Cast. 1861) in Lake Kariba. *Beaufortia* 15: 143 – 153.
McLACHLAN, A.J. 1969. The effect of aquatic macrophytes on the variety and abundance of benthic fauna in a newly created lake in the tropics. *Arch. Hydrobiol.* 66: 212 – 231.
McLACHLAN, A.J. 1974. Development of some lake ecosystems in Tropical Africa with special reference to the invertebrates. *Biol. Rev.* 49: 365 – 397.
MINSHULL, J.L. 1973. The establishment of a fishery among the resettled Batonka people at Lake Kariba, Rhodesia. *Proc. 11th Congr. Int. Comm. Large Dams,* 413 – 419.
MITCHELL, D.S. 1969. The ecology of vascular hydrophytes on Lake Kariba. *Hydrobiologia* 34: 448 – 464.
MITCHELL, D.S. & ROSE, D.J.W. 1979. Factors affecting fluctuations in extent of *Salvinia molesta* on Lake Kariba. *PANS* 251: 171 – 177.
MITCHELL, S.A. 1976. The marginal fish fauna of Lake Kariba. *Kariba Studies* (8): 109 – 162. National Museums & Monuments of Rhodesia, Salisbury.
MITCHELL, S.A. 1978. The diurnal activity patterns and depth zonation of marginal fish as shown by gill-netting in Lake Kariba. *Kariba Studies* (9): 163 – 173. National Museums & Monuments of Rhodesia, Salisbury.
PARNELL, F.I. 1960. Chapter III, Fisheries: Stocking of Lake Kariba. In: *Ann. Rep. Dept. Game and Fisheries,* 1959. Gvt Printer, Lusaka.
PARNELL, F.I. 1961 Chapter III, Fisheries: Lake Kariba Fisheries. In: *Ann. Rep. Dept. Game and Fisheries* 1960. Gvt Printer, Lusaka.
PETR, T. 1967. Fish population changes in the Volta Lake in Ghana during its first sixteen months. *Hydrobiologia* 30: 193 – 220.
PETR, T. 1968. The establishment of a lacustrine fish population in the Volta Lake in Ghana during 1964 – 1966. *Bull. de l'IFAN* 30 (Ser. A, 1): 257 – 269.
PETR, T. 1971. Lake Volta — a progress report. *New Scientist* 49: 178 – 180.
RZOSKA, J. 1966. The biology of reservoirs in the U.S.S.R. In: Man-made Lakes (Ed.) Lowe-McConnell, R.M. Academic Press, London.
SOULSBY, J.J. 1963. Fishing survey at Kariba. *Rhod. Agric. J.* 60(5): 135 – 138.
TOOTS, M. 1970. Exotic fishes in Rhodesia. *Rhod. Agric. J.* 67(4): 1 – 6.
VAN DER LINGEN, M.I. 1973. Lake Kariba: early history and south shore. In: Man-made lakes: their problems and environmental effects. (Eds.) Ackermann, W.C., White, G.F. & Worthington, E.B. pp.132 – 142. Geophysical Monograph Series Vol 17. American Geophysical Union, Washington, D.C.
WESSELS, C.L., TANNOCK, J., BLAKE, D. & PHELPS, R.J. 1980. Chlorinated hydrocarbon insecticide residues in *Crocodilus niloticus* Laurentius eggs from Lake Kariba. *Trans. Zimb. Scient. Assoc.* 60(3): 11 – 17.
WHITWELL, A.C., PHELPS, R.J. & THOMSON, W.R. 1974. Further records of chlorinated hydrocarbon pesticide residues in Rhodesia. *Arnoldia, Rhod.* 6(37): 1 – 7.