A STUDY OF THE POPULATION DYNAMICS, PRODUCTION AND POTENTIAL YIELD OF THE SARDINE LIMNOTHRISSA MIODON (BOULENGER) IN LAKE KARIBA

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ABSTRACT

The limnology of Lake Kariba, especially those aspects that affect sardine biology, are described. The hydrological regime of the lake is seen as a major influence and may be one of the reasons why the fish are very much smaller in Kariba than they are in Lakes Tanganyika or Kivu. Growth was reassessed and there appeared to be a correlation between rates of growth and limnological parameters. In particular, the fish appeared to grow faster, but smaller, in the man-made lakes and this may be a consequence of food shortages brought about by their hydrological characteristics. Mortality rates were also much higher in Kariba and this tended to support the view that the lake is a relatively unsuitable habitat for the sardines. However, estimates of biomass, expressed in terms of lake volume, contradicted this as they were very similar in both Kariba and Tanganyika. The life history strategy of *Limnothrissa* in Kariba was therefore to reduce its size and increase its productivity in order to maintain the maximum possible biomass and its very high $P/\bar{B}$ ratio was probably the means by which this was achieved. In terms of lake volume the predicted yields from the pelagic communities of Kariba and Tanganyika were very similar, equivalent to about 20 000 t annually for Kariba. This is close to the yield predicted by several empirical models and the fishery now appears to be entering a phase where increases in effort will not be matched by increased yields. The mechanisms for controlling effort in the fishery appear to be inadequate and particular concern was expressed about the lack of

co-ordination between the Zimbabwean and Zambian fishery authorities in planning the development of this shared resource.

CHAPTER 1: INTRODUCTION

Lake Kariba is one of the world's largest man-made lakes and was the first of its kind to be built in Africa. At the time of its construction there had been no experience of the profound social, economic and ecological consequences of such a large reservoir and so some opportunities for detailed scientific work were lost during its early stages. Since then, however, a considerable amount of work has been done and the scope of this is indicated in the extensive bibliographies by Coche (1971), Marshall (1979a) and Ita & Petr (1983). Several studies describe the development of the ecosystem and the long-term changes that have taken place (e.g. van der Lingen 1973; McLachlan 1974; Marshall 1984a).

Much of the research has centred on the fish populations and fishing industry of the lake because Zimbabwe is a land-locked country without the lakes and large rivers characteristic of East and Central Africa. Since the country's human population is growing rapidly fish are expected to become an increasingly important source of animal protein with the man-made lakes presently being the major source (Bowmaker 1975; Kenmuir 1982). As the largest of these Kariba has attracted the most interest but its yields have not always matched up to expectations.

Early predictions were that the lake might produce as much as 31 000t per year (Maar 1959) and although catches from the inshore fishery were good at first they soon began to decline and by 1971 it was apparent that this fishery would not yield much more than 2 000t per annum (Minshull 1973). It was recognised that the major constraint to fish production in Kariba was the inability of the riverine fish species to colonise the great expanse of open water created by the new lake and, even before it was built, Jackson (1959, 1961) proposed that a pelagic planktivore should be stocked from one of the East African great lakes. Ultimately, it was the Lake Tanganyika sardine Limnothrissa miodon that was introduced in the late 1960's (Bell-Cross & Bell-Cross 1971).

The success of this introduction, the spread of the fish throughout the lake and the development of the fishery is now well documented (Junor & Begg 1971; Begg 1974a; Woodward 1974; Marshall 1979b; Junor 1982). There has been a dramatic improvement in the fish yields from the lake and in 1983 the total sardine catch was about 13 000t (Marshall & Shambare 1984; Zambian Fisheries Dept., personal communication) which is about five to six times the catch from the inshore fishery.

The basic biology of the sardine in Kariba is reasonably well known following the work of Woodward (1974), Begg (1974a, 1976) and Cochrane (1978, 1984) but there is a need for investigations into its population dynamics and potential yield. This is particularly so because of the desire by both the Zimbabwean and Zambian Governments to obtain the maximum possible yield without overfishing the resource. Such data become more important when the fact that the resource will have to be managed on an international basis is taken into account, so that some of the problems inherent in managing a "common-property" resource (Clark 1981) can be avoided.

An early attempt to estimate sardine abundance was made by Balon (1974) who counted the fish in photographs taken by skin-divers using SCUBA apparatus. This was followed by Cochrane (1978) who used commercial fishing gear, but without light attraction, to obtain an estimate of sardine biomass. Neither of these approaches were particularly successful because they were very limited in scope and duration.

Commercial catch data have been used in an effort to estimate optimum yields and levels of effort (Marshall 1981; Marshall _et al_.1982) but these were also of limited value because they were based on a relatively short time series. In addition, there is now some evidence that the early catch statistics may not be typical of the fishery as a whole (this study) and should have been excluded from the previous work.

Some of the data from the present study have been fitted to various models which require growth, mortality or biomass parameters (Marshall 1984a) but these were only preliminary values and it can now be shown that they were inaccurate and should be discounted. The data that are so far available are thus inadequate for the requirements outlined earlier and the main aim of this study is to improve their quality and provide the basic information needed to raise the management of the sardine fishery from its present "_ad hoc_" system.

This thesis is an investigation into some aspects of the life-history of _Limnothrissa_ and an assessment of the extent to which the data so obtained can be used to predict its potential yield. A striking feature of <u>Limnothrissa</u> is that it is very much smaller in reservoirs than it is in the natural lakes where it occurs. This means that it has a very much shorter life cycle and matures at an earlier age.

The hypothesis that this thesis aims to test is that this is a life-history strategy which enables the species to maximise its biomass under relatively unfavourable conditions. Furthermore, this strategy enables <u>Limnothrissa</u> to maintain its biomass and production at levels comparable to those in Lake Tanganyika (there are insufficient data from Lakes Kivu or Cahora Bassa to enable a comparison with these lakes). A consequence of this is that the potential yield is also comparable.

In order to test this hypothesis, the basic physico-chemical conditions in Kariba will be described and, when relevant, compared with those in Lake Tanganyika and elsewhere. This will be followed by a description of what is known about the biology of <u>Limnothrissa</u>, with special reference to its biology in Lake Kariba.

The next step will be a detailed examination of its growth and mortality in Kariba and its relation to the environment of the lake. This is considered to be the most crucial element of this study as the hypothesis is based on observed differences in growth, and inferred differences in mortality, in different lakes.

This is followed by an investigation of production and of potential commercial yield. These aspects are believed to be influenced by the life-history strategy of the sardine and may therefore be considered as supplementary to the main hypothesis.

Commercial catch statistics from the Kariba sardine fishery will be used throughout this thesis. If collected properly such data represent an enormous store of information and can contribute greatly to the study of a commercially-exploited species. Most African fisheries lack a sound statistical base (Willoughby 1979) and it is generally impossible to utilise many stock assessment techniques because of this. It is hoped that this study will provide an example of what can be done in an African fishery and highlight the importance of maintaining detailed, long-term records.

CHAPTER 2: LIMNOLOGICAL FEATURES OF LAKE KARIBA

INTRODUCTION

Limnological factors appear to be amongst the most important influences on the abundance, growth and life history of Limnothrissa in Lake Kariba (Marshall 1982, 1984a). It is necessary, therefore, to consider the basic limnology of the lake and especially those aspects which are most likely to influence the sardines. Several workers have investigated the lake's limnology, notably Coche (1974), but also Harding (1966), Mitchell (1970), Begg (1970, 1974b) and Bowmaker (1976), and so this section will not be a detailed review covering what they have already presented.

MORPHOLOGY AND HYDROLOGY

Lake Kariba is situated in the Middle Zambezi valley on the border between Zimbabwe and Zambia (Fig. 1). It extends from the Zambezi-Deka confluence in the west (18° 04'S: 26° 42'E) to the Kariba Gorge in the east (16° 31'S: 28° 45'E) and is about 320 km in length. It has a surface area of around 5 400 km^2 and can be divided into a number of basins bounded by island chains, narrows and belts of shallow water. Bowmaker (1973) and Coche (1974) recognise four basins but most Zimbabwean workers follow Begg (1969) and Mitchell (1970) who divide it into five. Another region from the Deka river to the eastern end of Devil's

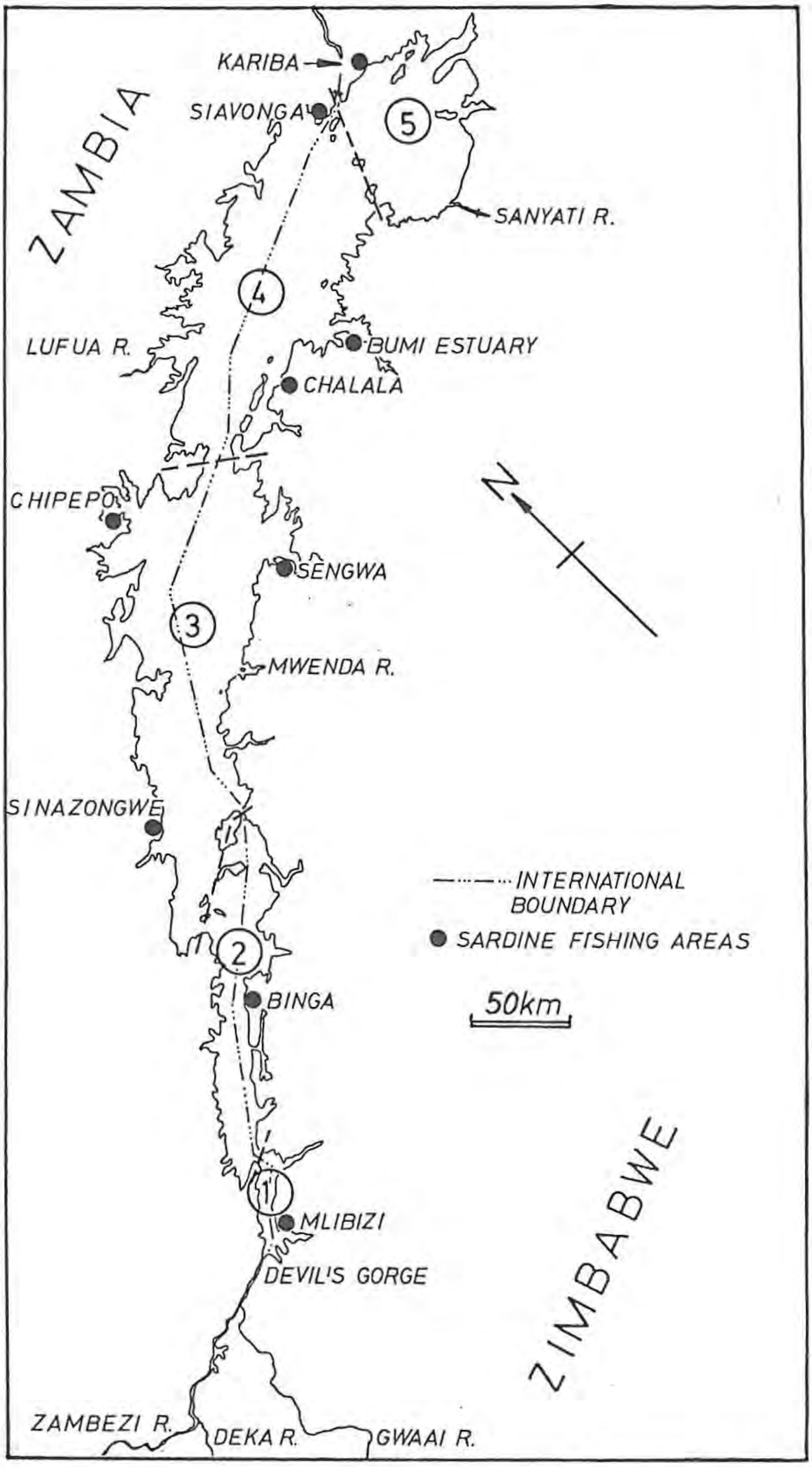


Figure1: Lake Kariba, showing places mentioned in the text. The lake basins are indicated by the encircled numbers; the Sanyati Basin is basin 5.

Gorge is essentially riverine in character and is not considered to be a lake basin.

In Africa, Lakes Volta and Nasser-Nubia now exceed Kariba in area whilst Cahora Bassa, Kossou and Kainji are smaller (Table 1) but Kariba has the greatest mean depth with over 60% of the water body being more than 20 m deep. This suggests that it might be more suitable for a pelagic species than are the others; on the other hand it may also be less productive since it has been shown that fish catches from shallow, dendritic lakes tend to be higher than those from deep ones with regular shorelines (Marshall 1984b).

Table 1: The main morphometric features of the largest African reservoirs. Data from Welcomme (1972), Coche (1974), Gliwicz (1984) and Bernacsek (1984).

	Kariba	Cahora Bassa	Nasser-Nubia	Volta	Kainji	Kossou
Length (km)	320	250	482	400	137	180
Maximum depth (m)	120	156	130	75	50	54
Mean depth (m)	29	21	25	19	12	18
Shoreline length (km)	2164	1200	8804	4828	720	3500
Shoreline Development	8.3	7.0	31.2	14.5	5.7	24.7
Area (km^2)	5400	2398	6276	8845	1280	1600
Volume (km^3)	157	70	158	165	26	30
Replacement time (years)	3	1	2	4	0.25	5
Pelagic zone (%)	62		48	36		

About 80% of Kariba's water supply comes from the Zambezi River which drains a very large area of eastern Angola and western Zambia. The main secondary rivers drain the Zimbabwean plateau to the south and the largest of these, the Sanyati, contributes about 8% of the total whilst a further 7-8% comes from direct rainfall on the lake's surface (Table 2). As in most reservoirs the outflow is very large in relation to the total volume and the replacement time is very short; about three years but rather less during periods of above-average rainfall, like the decade of the 1970's. This is in marked contrast to most natural lakes which have much longer retention times - an extreme example being Lake Tanganyika in which it is about 10 000 years (Fryer (1972). This is considered to be a significant factor in the lake's ecology, especially in regard to its nutrient dynamics (Coche 1974; Marshall & Junor 1981; Marshall 1982a, 1984a).

Lake Kariba's water level is generally very stable and rarely fluctuates by more than 2 - 3 m in a normal year (Fig. 2) but because of the 1981-82 and 1982-83 droughts it dropped continuously after mid-1981. By December 1983 it had reached 479 m above sea level, the lowest recorded since it filled in 1963. This is expected to continue into 1984 following the failure of the 1983-84 rains which led to the third consecutive drought in Southern and Central Africa.

Table 2: Mean water budgets for Lake Kariba, 1963-66 (from Coche 1974) and 1975-80 (from Central African Power Corporation).

	1963-1966		1975-1980	
	km^3	%	km^3	%
Gains:				
Rainfall on lake surface	3.5	7.0	5.0	7.6
Zambezi river (Victoria Falls)	39.0	77.2	51.7	78.4
Secondary rivers	8.0	15.8	9.2	14.0
Total	50.5		65.9	
Losses:				
Evaporation	7.2	14.3	8.6	13.2
Turbine outflow	20.5	40.6	27.6	42.3
Spillage	22.8	45.1	29.7	44.5
Total	50.5		65.9	
Replacement time (years)	3.1		2.4	

This must, of course, have significant biological consequences. Since it has been shown that sardine abundance is related to river flow (Marshall 1982a) catches might be expected to decline because the flows were so poor. On the other hand the great changes in water level will reduce the mean depth and so increase the morphoedaphic index (conductivity/ mean depth) and since increased fish yields are associated with high morphoedaphic indices (e.g. Henderson & Welcomme 1974) this will serve to maintain high fish catches from the lake. Bernacseck (1984) has suggested that this is an important factor in maintaining fish yields in the face of fluctuating lake levels. The changes in mean depth are, however, much less in a deep lake

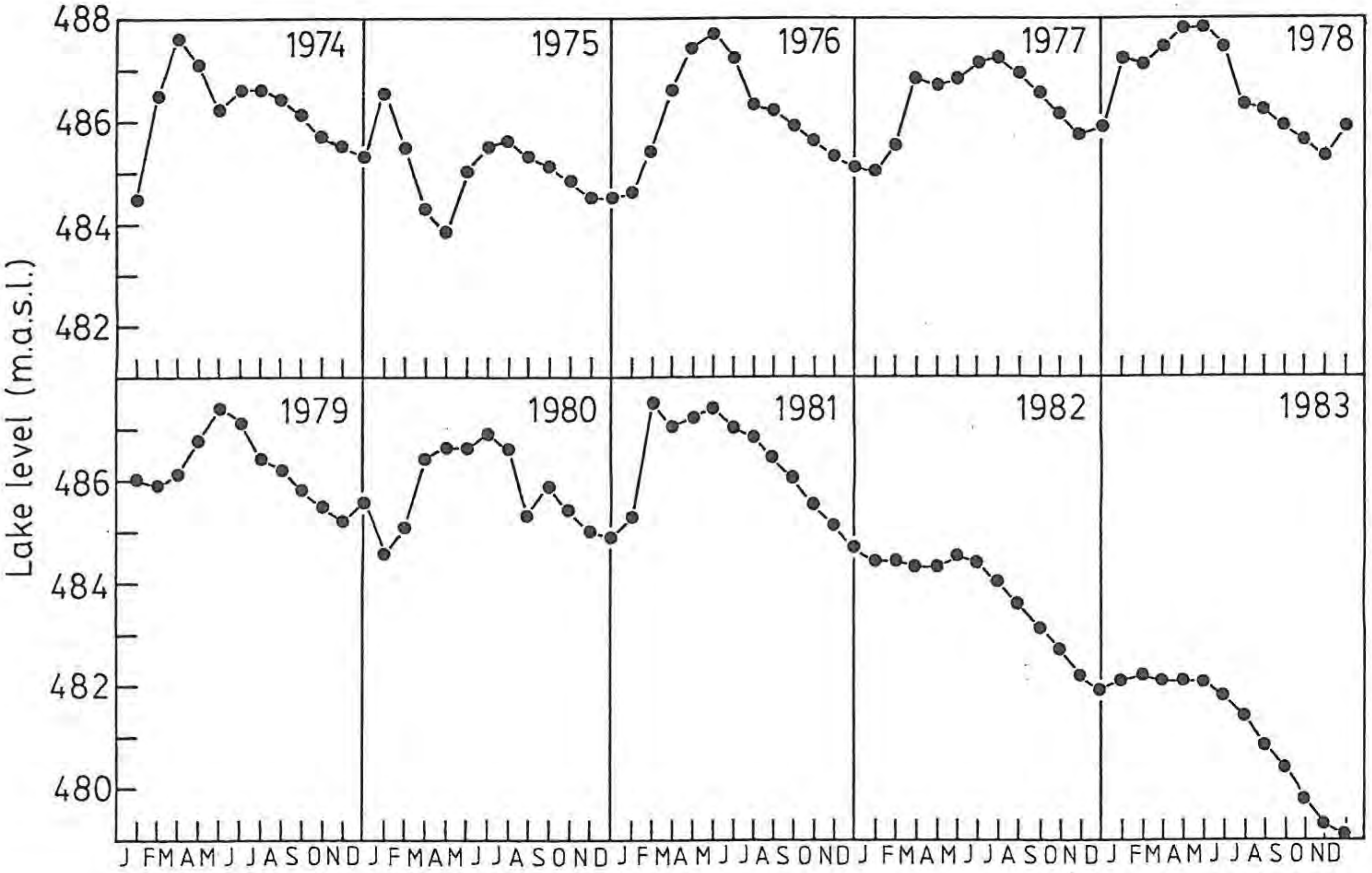


Figure 2: Lake Kariba lake levels 1974-1983. Data from Central African Power Corporation.

like Kariba than they would in a shallow one and although there is a slight increase in morphoedaphic index, and so in predicted yield per unit area, this is not enough to prevent a drop in the predicted total catch (Table 3).

Table 3: Changes in the mean lake level, area and depth of Lake Kariba, 1974-83. The morphoedaphic index (MEI) is calculated by assuming that conductivity is 85 µS cm^{-1} in all cases and yield is predicted by $Y = 23.281\ MEI^{0.4681}$ (Marshall 1984b).

	Lake level (m.a.s.l.)	Area (km^2)	Mean depth (m)	MEI	Yield (kg ha^{-1})	Total catch (t)
1974	486.27	5410	30	2.8	37.7	20395
1975	485.03	5300	29	2.9	38.3	20299
1976	486.06	5400	29	2.9	38.3	20682
1977	486.34	5415	29	2.9	38.3	20739
1978	486.65	5420	29	2.9	38.3	20759
1979	486.17	5405	29	2.9	38.3	20701
1980	485.76	5340	29	2.9	38.3	20452
1981	486.31	5412	29	2.9	38.3	20728
1982	483.65	5180	28	2.9	38.9	20150
1983	481.09	4820	27	3.1	39.5	19039

Conversely, should the lake rise rapidly in the event of good rains an increase in fish catches may be expected as a response to the release of nutrients caused by the decay of drowned vegetation and other organic matter (McLachlan, S.M. 1970). This is analagous to the eutrophic phase which occurred soon after the lake filled. A similar phenomenon may have occurred after the 2 m increase in mean lake level that took place in 1974 because inshore fish catches showed a sharp increase in 1974-75 (Marshall 1984a).

CHEMICAL STATUS AND POTENTIAL PRODUCTIVITY

Lake Kariba is considered to be oligotrophic with low potential productivity (Coche 1974) and is limited by both nitrogen and phosphorus (Thornton 1980a). The main reason for this is that the Zambezi River loses most of its nutrient load on the Barotse and Chobe floodplains upstream of Kariba (Mitchell 1973). The secondary rivers are much richer by comparison (Table 4) but as they make only a small contribution to the total water supply they do not influence the composition of the lake as a whole. They can, however, cause pronounced local effects (Mitchell 1973) and an example of this is the relationship between the abundance of *Limnothrissa* in the Sanyati Basin and the flow of the Sanyati River (Marshall 1982a).

<u>Table 4</u>: Mean water quality of some Kariba inflows and the Zambezi River below the dam, taken from Coche (1974). All data are expressed as mg l^{-1}.

	Zambezi R. above Kariba	Sanyati R.	Lufua R.	Zambezi R. below Kariba
Ca	6.6	14.9	13.9	9.7
Mg	1.9	9.0	3.8	2.2
Na	3.0	11.6	5.0	4.0
K	0.8	2.1	2.0	1.2
Total cations	12.3	36.8	24.7	17.1
$HCO_3 + CO_3$	16.7			24.9
SO_4	3.6			3.0
Cl	0.7			1.0
Total anions	21.0	57.9	37.5	28.9

Another factor is that a significant quantity of nutrients is lost through the outflow; Coche's tentative nutrient budget clearly illustrates this (Table 5). His data suggest that the lake was losing more nutrients than it was gaining but this seems unlikely in the long-term because they will be retained in sediments and by the various biological communities. One explanation for this discrepancy is that the contribution of the minor inflowing streams may not have been adequately estimated. It should be noted that the Zambezi below the dam is richer in nutrients than it is before it enters Kariba (Table 4; Hall <u>et</u> <u>al</u>. 1977) which indicates that substantial nutrient losses are occurring and that there is little likelihood of the lake becoming significantly richer in the near future (in contrast to the ideas put forward by Balon (1974, 1978)).

Table 5: Tentative nutrient budget for Lake Kariba, taken from Coche (1974). Values are the total nutrient content in t x 10^3.

IMPORTS:	Zambezi River	1695
	Secondary rivers & local runoff	419
	Rainfall on lake's surface	42
	Total Imports	2156
TOTAL EXPORTS: outflow		2346

Water chemistry alone is not always a particularly reliable indicator of potential productivity as production is a consequence of a variety of interactions between biotic and abiotic factors in the lake. A wide variety of empirical models which predict fish yields in relation to simple physical, chemical or biological data have been developed and they are perhaps a more useful means of assessing potential productivity. Four of these have been used to compare potential fish yields from Kariba with those from the other large African reservoirs (Table 6).

Table 6: Predicted fish yields (kg ha^{-1}) for the 6 large African reservoirs using various empirical models. Based on data and models in Henderson & Welcomme (1974), Melack (1976), Machena (1983), Gliwicz (1984) and Marshall (1984b). See text for an explanation of the models.

	Kariba	Cahora Bassa	Nasser-Nubia	Volta	Kainji	Kossou
Basic Parameters						
Area, A (km^2)	5400	2398	6276	8845	1280	1600
Shoreline length, L (km)	2146	1200	8804	4828	720	3500
Shoreline development, D_L	8.3	7.0	31.2	14.5	5.7	14.7
Mean depth, $\bar{z}$ (m)	29	21	25	19	12	18
Conductivity, K_L (uS cm^{-1})	80	100	230	65	73	90
Morphoedaphic index, MEI	2.8	4.8	9.2	3.4	6.1	3.0
Primary production, PG (gO_2 $m^{-2}d^{-1}$)	4.0	6.0		6.8	6.5	7.0
Empirically predicted yields:						
(a) Lake area	45	55	44	40	64	21
(b) Morphometry	29	31	62	45	37	75
(c) Morphoedaphic index	36	47	63	40	54	54
(d) Primary production	23	39		48	44	50
Mean predicted yield:	33.2	43.0	56.3	43.2	49.8	50.0

The following models were used for the comparison:

(a) Lake area:

Young and Heimbugh (1982) showed that lake area alone was a powerful predictor of fish yields in North American lakes; their approach was applied to the 17 intensively-fished African lakes and reservoirs listed in Henderson & Welcomme (1974) by Marshall (1984b). In these, total yield was predicted by the expression

$$\log_e Y_t = 3.57 + 0.76 \log_e A$$

where Y_t = total yield (t) and A = lake area (km^2). The total yield (kg) was then divided by lake area (ha) to obtain an estimate expressed in kg ha^{-1} (Table 6).

(b) Morphometry:

This model is based on the premise that shallow, dendritic lakes are more productive than deep ones with regular shorelines (Marshall 1984b). Fish yields could be predicted from

$$Y = 19.996 + 32.038\ (D_L/\bar{z})$$

where Y = yield (kg ha^{-1}), D_L = shoreline development ($D_L = L\ (2\sqrt{\pi A})^{-1}$) and $\bar{z}$ = mean depth (m).

(c) Morphoedaphic Index:

There are several versions of this widely-used model and a recent one based on data from African reservoirs (Marshall 1984b) gives

$$Y = 23.281\ MEI^{0.4681}$$

where Y = yield (kg ha^{-1}) and MEI = morphoedaphic index (i.e. conductivty/mean depth).

(d) Primary production:

Melack (1976) found that there was a relationship between fish yields and primary production which could be expressed by

$$\log Y = 0.113\ PG + 0.91$$

where Y = yield (kg ha^{-1}) and PG = gross primary production (g O_2 m^{-2} d^{-1}).

In almost every case the yields predicted for Kariba were the lowest except for the lake area model which predicted higher yields for Kariba than for three of the other lakes. This suggests that its yield should be relatively high because of its large size but that a number of other physico-chemical constraints operate to reduce this potential. They include the lake's great depth, relatively regular shoreline and low conductivity which in turn is a reflection of its poor nutrient content partly caused by the rapid through-flow of water. The models that were used are only as good as the data upon which they are based, and data from African waters are often inadequate.

THE PELAGIC ECOSYSTEM

Most biotic communities in Kariba tend to be restricted to the inshore or littoral zone. The indigenous fish species extend to about 15 m depth and are most abundant down to about 5 m (Coke 1968). Benthic mussels and rooted macrophytes are also restricted to a maximum depth of around 12 - 14 m (Kenmuir 1980; Langerman 1984). The upper limit of the thermocline is about 20 m and this depth may conveniently be regarded as the boundary between the littoral and pelagic zones. Since more than 60% of Lake Kariba is over 20 m deep and Limnothrissa is the most numerous fish species occupying that area some consideration of its main features is required.

Temperature:

Lake Kariba is warm and monomictic with a mean surface temperature of about 26°C, although it may exceed 30°C in very hot weather, whilst the minimum is about 22°C. During the period of stratification the difference between surface and bottom temperatures is rarely more than 9°C.

Stratification begins in late October when a thermocline appears at about 15 - 20 m depth. It continues until July, by which time the thermocline has dropped to about 35 m; it is at about this time that "turnover" occurs and the lake is isothermal for around 3 months until stratification begins again in October (Fig. 3). This thermal regime is similar to those in other large African reservoirs, e.g. Volta (Viner 1970), Nasser-Nubia (Latif 1984), Cahora Bassa (Gliwicz 1984) and Le Roux (Allanson & Jackson 1983).

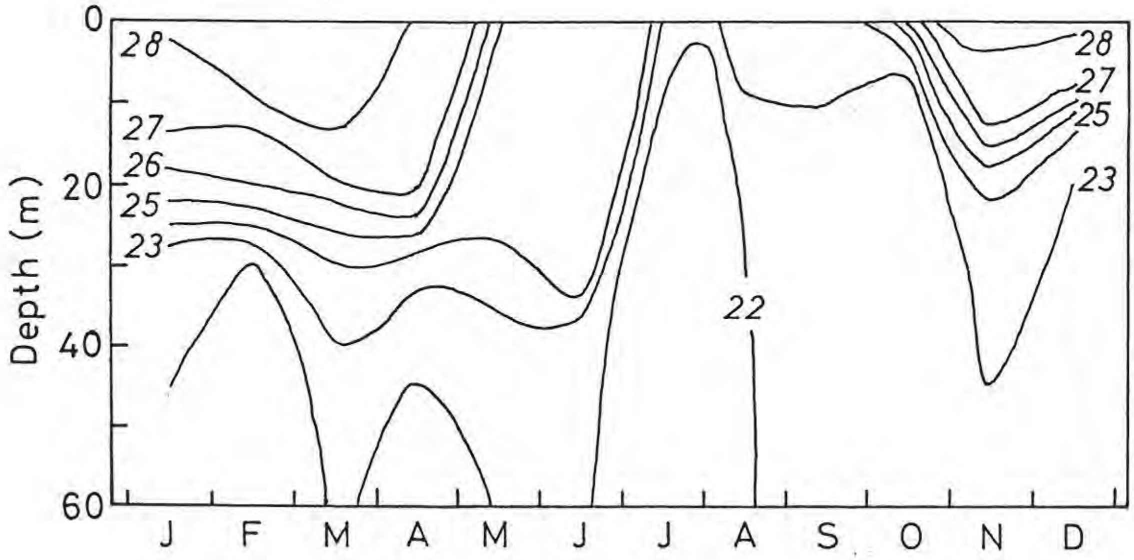


Figure 3: Temperature (^{o}C) in relation to depth in the Sanyati Basin, Lake Kariba during 1979. Redrawn from Marshall et al. (1982).

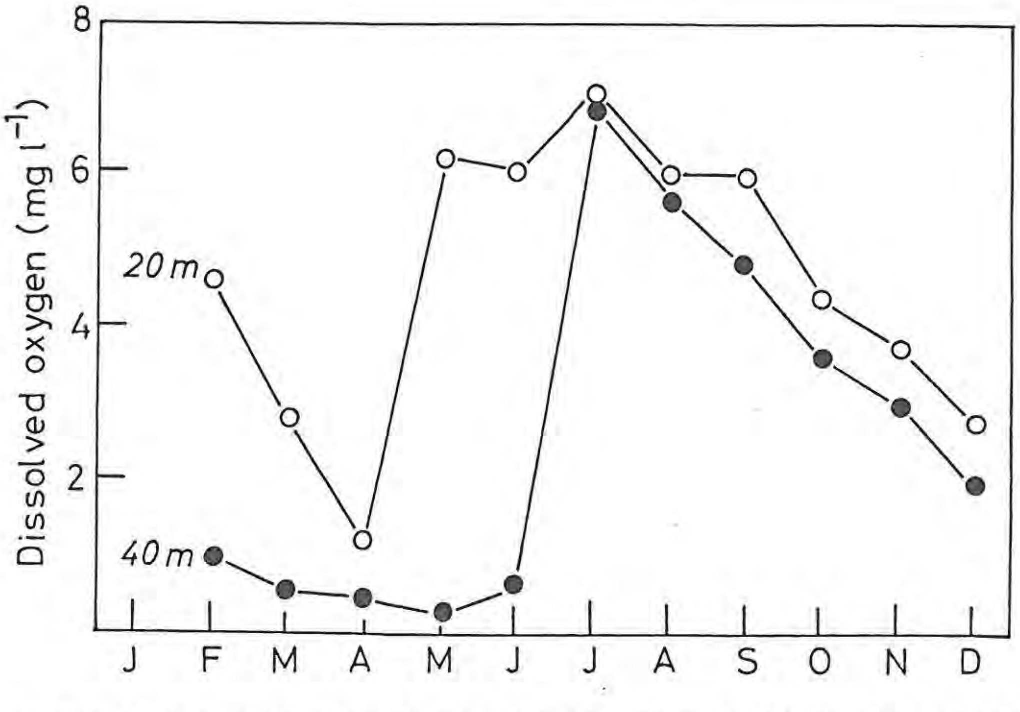


Figure 4: Dissolved oxygen at 20 m and 40 m depth in the Sanyati Basin, Lake Kariba during 1979. Redrawn from Burne (1981).

Oxygen:

In the early years of its existence Lake Kariba's hypolimnion was anaerobic because of the large quantities of organic matter flooded when the lake filled (Harding 1966). This effect decreased with time (Coche 1974) and anaerobic conditions now persist only in the deepest waters and for a relatively short period of time (Burne 1981). In the Sanyati Basin a dissolved oxygen content of less than 2 mg l^{-1} at 20 m was only once recorded and complete deoxygenation did not even occur at 40 m (Fig. 4).

This is significant as far as Limnothrissa is concerned because Cochrane (1978) suggested that it would not be able to live in water with a dissolved oxygen content of less than 2 mg l^{-1}. If this is the case then it is probably only excluded from deep water for short periods and can probably live in most areas of the lake for most of the year. Divers have, in fact, seen them at 35 - 40 m i.e. below the thermocline (A. Thomas, Zimbabwe Army Diving School) but, unfortunately, it has not been possible to get an estimate of the level of dissolved oxygen from the waters in which they were seen.

Transparency:

Water transparency is an important factor in the sardine fishery because all the fishing methods currently in use rely on light attraction and the fishermen claim that a decrease in transparency leads to reduced catches. During 1979 Secchi disc visibility in the Sanyati Basin ranged from 4.1-6.0 m with a mean of 5.1 m (Burne 1981). Visibility was lowest during the isothermal period when plankton was most abundant but the seasonal pattern was not very marked.

It is interesting to compare the Secchi Disc visibilities of the lakes in which Limnothrissa occurs because they vary considerably. Lake Tanganyika had the deepest light penetration with S.D. visibility of about 15 m (Melack 1980); this was followed by Lake Kivu with mean visibility of about 6.5 m (de Iongh et al. 1983). Visibility in Cahora Bassa was only about 1.8 m (Gliwicz 1984) which is surprising considering it is on the same river system as Kariba. This is caused by a heavy load of suspended clay which is thought to be generated from the bottom sediments by wind-induced turbulence. This must have an effect on the sardines and their biology.

The plankton cycle:

The seasonal cycle of the zooplankton has been described by Begg (1974b) and Marshall (1980) and will be discussed in greater detail in Chapter 3. Broadly-speaking the zooplankton is densest during the isothermal period after nutrients have been released from the hypolimnion at turnover. This is followed by a sharp decline in August - September as stratification is re-established. The rains bring another period of relative abundance during November - March as a response to the supply of more nutrients brought in by the inflowing rivers. Plankton abundance declines again shortly after the rains as nutrients become locked in the hypolimnion, to be released again at turnover. The rotifer Keratella tropica (Apstein) shows this pattern very clearly and can be used as an example of the typical pattern of seasonal variation in zooplankton (Fig. 5).

FISH POPULATIONS OF LAKE KARIBA

There are about 40 species of fish in Lake Kariba (Table 7) of which two, Limnothrissa miodon and Oreochromis macrochir, are known to have been introduced. Only 28 species were recorded during a brief preimpoundment study (Jackson 1961) and the discovery of another 12 species led Balon (1971, 1974a, 1974b, 1978) to postulate that they had invaded the lake from the Upper Zambezi above the Victoria Falls. It was argued that fish had always fallen over the 90 - 95 m high falls but that they had not been able to survive in the Middle Zambezi river below the falls because of the harsh ecological conditions that existed there (see Jackson 1961). These conditions changed when the lake was created and it then became possible for fish swept over the falls to become established.

Many southern African workers (Jubb 1976a, 1976b, 1977; Bowmaker et al. 1978; Marshall 1979b, 1984a; Kenmuir 1984) do not accept this view and claim that there were other ways for these fish to have found their way into Kariba. If Balon's ideas are correct then it would be neccessary to re-evaluate many of the current views about the zoogeography of southern African fish.

Before discussing Balon's claims in detail it is important to remember that the Middle Zambezi was poorly-known

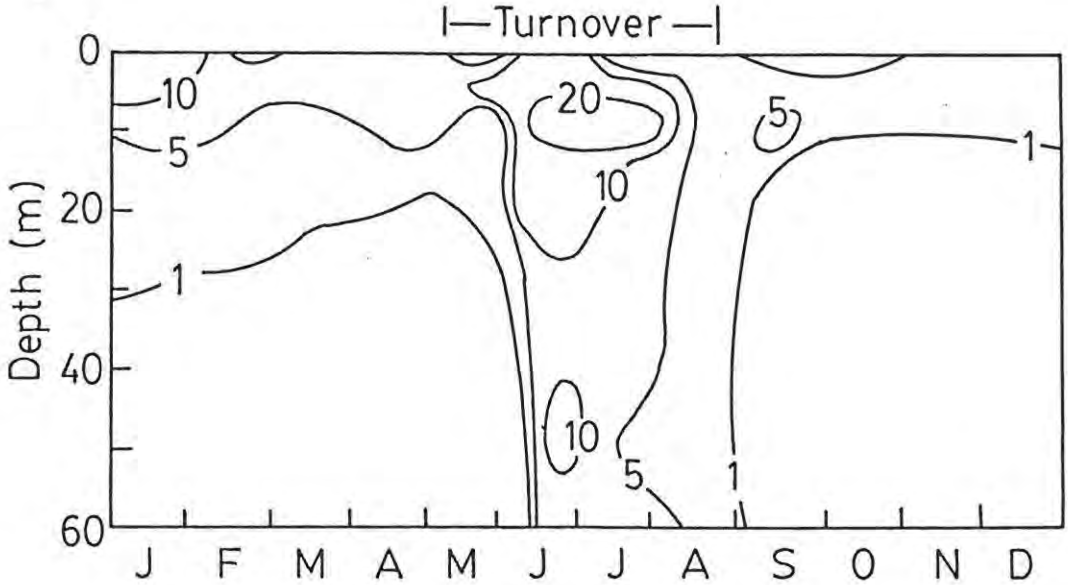


Figure 5: Seasonal abundance (no l^{-1}) in relation to depth during the day of the rotifer *Keratella tropica* in the Sanyati Basin, Lake Kariba during 1973. Redrawn from Begg (1974b).

Table 7: A list of the fish species recorded from Lake Kariba. Based on Balon (1974a) but with some names changed in accordance with recent systematic opinions (Trewavas 1981; Daget *et al*. 1984).

ANGUILLIDAE	*Anguilla bengalensis labiata* (Peters)
CLUPEIDAE	*Limnothrissa miodon* (Boulenger)*
MORMYRIDAE	*Mormyrops deliciosus* (Leach)*
	Hippopotamyrus discorhynchus (Peters)
	Marcusenius macrolepidotus (Peters)
	Mormyrus longirostris Peters*
CHARACIDAE	*Hydrocynus vittatus* Castelnau*
	Alestes lateralis (Boulenger)
	Alestes imberi Peters
	Micralestes acutidens (Peters)
DISTICHODONTIDAE	*Distichodus mossambicus* (Peters)
	Distichodus schenga Peters
CYPRINIDAE	*Barbus poechii* Steindachner
	Barbus paludinosus Peters
	Barbus unitaeniatus Gunther
	Barbus lineomaculatus Boulenger
	Barbus fasciolatus Gunther
	Barbus marequensis Smith
	Barbus radiatus Peters
	Labeo cylindricus Peters
	Labeo congoro Peters
	Labeo altivelis Peters*
	Opsaridium zambezense (Peters)
SCHILBEIDAE	*Schilbe mystus* (Linnaeus)
	Eutropius depressirostris (Peters)
CLARIIDAE	*Clarias gariepinus* (Burchell)*
	Heterobranchus longifilis Cuvier & Valenciennes
MALAPTERURIDAE	*Malapterurus electricus* (Gmelin)
MOCHOKIDAE	*Synodontus zambezensis* Peters
	Synodontus nebulosus Peters
CYPRINODONTIDAE	*Aplocheilichthyes johnstoni* (Gunther)
CICHLIDAE	*Serranochromis codringtoni* (Boulenger)*
	Serranochromis giardi (Pellegrin)
	Serranochromis carlottae (Boulenger)
	Serranochromis robustus jallae (Boulenger)
	Serranochromis macrocephalus (Boulenger)
	Pharyngochromis darlingi (Boulenger)
	Pseudocrenilabrus philander (Weber)
	Oreochromis andersoni (Castelnau)
	Oreochromis macrochir (Boulenger)
	Oreochromis mortimeri (Trewavas)*
	Tilapia rendalli (Boulenger)*

* denotes major commercial species.

ichthyologically before Kariba was built. This was acknowledged by Jackson (1961) who admitted that there was likely to be species that were overlooked during his survey and which could be expected to occur in the lake after its formation. Other species were widespread in Middle Zambezi tributaries and might have invaded the lake from them.

Balon lists 14 species which are claimed to be invaders from above the Victoria Falls. These can be grouped as follows:

(a) those which are widespread in the Middle Zambezi tributaries. There are 6 of these, namely *Marcusenius macrolepidotus*, *Labeo cylindricus*, *Barbus paludinosus*, *B. unitaeniatus*, *B. lineomaculatus* and *Pseudocrenilabrus philander*.

(b) uncommon species which had nevertheless been recorded from the Middle Zambezi or its tributaries. *Schilbe mystus* has been recorded from the Zambezi and Sanyati rivers (Jubb 1953); *Barbus poechii* was taken from the Kalomo River (upstream from Kariba) and from the Lusito River (downstream) (Balon 1974a, 1974b) and might have occurred in others; two species of *Serranochromis* (*S. robustus* and *S. macrocephalus*) were taken from small dams on the Zongwe, Chezia and Lufua Rivers which drain into Kariba from the north (JFRO 1961).

(c) some species may have been introduced. They include *Oreochromis andersoni* which was introduced into a number of tributaries on the Zimbabwean side (Toots 1970) and this species, as well as *Serranochromis giardi* and *S. carlottae*, could have been introduced unintentionally when 1.5 t of cichlid fry from the Kafue River were stocked into Kariba in 1956-1957.

The intention of this exercise was to augment stocks of *Tilapia rendalli* and to introduce *Oreochromis macrochir* but the fry were not carefully sorted and included many "wild" species (Parnell, quoted by Bowmaker *et al.*1978).

(d) the only possible invader is, therefore, *Alestes lateralis* and it is possible that it came via the Victoria Falls power station in the same way that *Limnothrissa* has passed through the turbines at Kariba (Kenmuir 1975). It has been claimed that this species is not, in fact, *A. lateralis* but another closely related to *A. humilis* (Jubb 1976b; Bowmaker *et al.* 1978) but no evidence to support this has ever been presented.

The views of the southern African workers have been dismissed as "opinions" unworthy of further comment (Balon 1977) but it is fair to point out that Balon's hypothesis is also unproven as he could not demonstrate that fish actually can survive the drop over the Victoria Falls. It seems unlikely that anyone else will be able to do so and the views of Jubb and others are the more parsimonious. Therefore, it is more likely that they are correct and Balon's hypothesis should be rejected.

A number of other changes have taken place in the fish populations of the lake since it was built and these will no doubt continue as it matures. The most obvious has been the elimination or restriction of rheophilic species whilst the cichlids have come to dominate the main lake (Begg 1974c). There have been changes within this group as well and in some areas *Oreochromis mortimeri* is apparently being replaced by *Serranochromis codringtoni* (Marshall 1984a). Another interesting cichlid is

S. macrocephalus which is increasing in numbers and spreading eastwards. It appears to have had a relatively restricted distribution in the western end of the lake but its spread may be linked to the establishment of dense beds of aquatic macrophytes as these appear to be its preferred habitat.

The effects of Limnothrissa have been most marked on the piscivorous Tigerfish Hydrocynus vittatus and this will be discussed more fully in Chapter 3. However, a number of other species, including unexpected ones like Synodontis zambezensis, prey upon sardines in shallow water and it is possible that sardine fry are taken by most species. The effects of this are unknown but it may be another factor contributing to change in the fish communities of Lake Kariba.

CHAPTER 3: A REVIEW OF LIMNOTHRISSA BIOLOGY

INTRODUCTION

Limnothrissa miodon has been studied more intensively in the lakes and reservoirs into which it has been introduced because of its actual or potential economic importance in them. Relatively little is known about it in Lake Tanganyika, its native habitat, where another sardine, *Stolothrissa tanganicae*, is more abundant and consequently of greater importance to the fishery (Coulter 1970). This chapter will be a review of what is so far known about *Limnothrissa*, especially in Lake Kariba, and will provide background information for the present study.

SYSTEMATICS

Limnothrissa is a member of the cosmopolitan and primarily marine herring family, the Clupeidae. About 20 genera and 38 species have been recorded in African freshwaters (Poll *et al.* 1984) but a number of them are estuarine with only a limited distribution in inland waters. Some 23 species occur in the rivers of West and Central Africa with the Zaire system having the most (Table 8). A few have become exclusively lacustrine and Lake Tanganyika and Lake Mweru each have two such species.

At present there are two species assigned to the genus *Limnothrissa* but Poll (1974) has indicated that the Lake

Table 8: The African freshwater clupeids, excluding estuarine species with a limited distribution in fresh waters. From Poll (1974) with the systematic arrangement from Poll *et al*. (1984).

Species	Distribution
Cynothrissa ansorgii (Boulenger)	W. Africa; Senegal-Angola
C. mento Regan	Lower Niger & lower Volta basins
Laeviscutella dekimpei Poll, Whitehead & Hopson	W. Africa; Ivory Coast-Gabon
Limnothrissa miodon (Boulenger)	Lake Tanganyika; introduced to Lakes Kivu & Kariba, invaded Lake Cahora Bassa
L. stappersi (Poll)	Lake Mweru & Zambian Zaire basin
Microthrissa minuta Poll	Lower Zaire; Dungu River
M. royauxi Boulenger	Zaire system, north of equator
Nannothrissa parva (Regan)	Zaire system; Lake Tumba, Ruki & Ubanghi Rivers
N. stewarti Poll & Roberts	Zaire system; Lake Mai-Ndombi
Odaxothrissa losera Boulenger	Central Zaire basin
O. vittata Regan	Zaire basin
Pellonula afzeliusi Johnels	W. Africa; Senegal-Zaire
P. miri (Daget)	Upper Volta, Niger & Benoue Rivers
P. vorax Günther	W. Africa; Senegal-Angola
Poecilothrissa centralis Poll	Zaire basin; Lake Tumba
P. congica Regan	Zaire basin, except Luapula & Lake Mweru
P. moeruensis Poll	Lake Mweru
Potamothrissa acutirostris (Boulenger)	Zaire basin
P. obtusirostris (Boulenger)	N.E. & E. Zaire basin
P. whiteheadi Poll	Zaire basin; Hombo River
Sierathrissa leonensis Thys van den Audeaerde	W. Africa; Senegal - Cameroon
Stolothrissa tanganicae	Lake Tanganyika
Thrattidion noctivagus Roberts	Cameroon; Sanga River

Mweru species, L. stappersi, has only been placed there provisionally. Very little is known about this fish and it may indeed by assigned to another genus once it has been better studied. This is to be expected because clupeid taxonomy is complex with meristic characters being difficult to distinguish (Otobo 1976); it is also consistent with the extensive clupeid speciation that has occurred elsewhere in the Zaire system (Poll et al. 1984).

Both of the sardines in Lake Tanganyika are slender and silvery in colour but Limnothrissa is distinguished by the possession of lingual and vomerine teeth which are absent in Stolothrissa. The latter is also more slender with a narrower head but it is not possible to distinguish between the fry of the two species (Poll 1953).

DISTRIBUTION

Limnothrissa is endemic to Lake Tanganyika but it has now been introduced into other waters and is the only African clupeid to have been translocated. It has been suggested that some of the larger riverine species might also be suitable candidates for stocking elsewhere (Marshall 1984c), but this is unlikely to happen soon when so little is known about their biology.

The possibility of introducing the Tanganyika clupeids into lakes without planktivorous fish was first considered by Belgian scientists in the 1950's. They were especially interested in Lake Kivu, a relatively young lake with fewer than 20 fish species none of which was able to utilise the abundant zooplankton that was present in the lake (Verbeke 1957). Between 1958 and 1960 large numbers of clupeid fry were taken there from Lake Tanganyika and it was hoped that Stolothrissa would become established (Collart 1960). Owing to the disruptions that followed the granting of independence to the Belgian Congo in 1960 no follow-up surveys could be done and only in 1976 was it realised that there was an abundant population of Limnothrissa in the lake (Frank 1977; Spliethoff et al. 1983).

Limnothrissa was introduced into Lake Kariba during 1967-68 and by 1970 sardines were present in all areas of the lake (Bell-Cross & Bell-Cross 1971; Junor & Begg 1971). A striking example of the speed at which this expansion took place can be seen in Kenmuir's (1971a) data on Tigerfish caught during an annual fishing tournament. In 1969 there were no sardines in their stomach contents but a year later, in 1970, they made up almost 75% of the food items recorded (Fig. 6). This meant that the sardines were able to colonise the entire Sanyati Basin and become the dominant small fish in a very short time, probably less than two years.

Some were able to survive passage through the hydroelectric turbines of the Kariba dam and live specimens were seen in the stilling-pool below it in 1970 (Junor & Begg 1971). This led to speculation that they might be able to live in the Zambezi and so colonise the Cahora Bassa dam then under construction (Junor & Begg 1971; Kenmuir 1975). This did indeed happen and

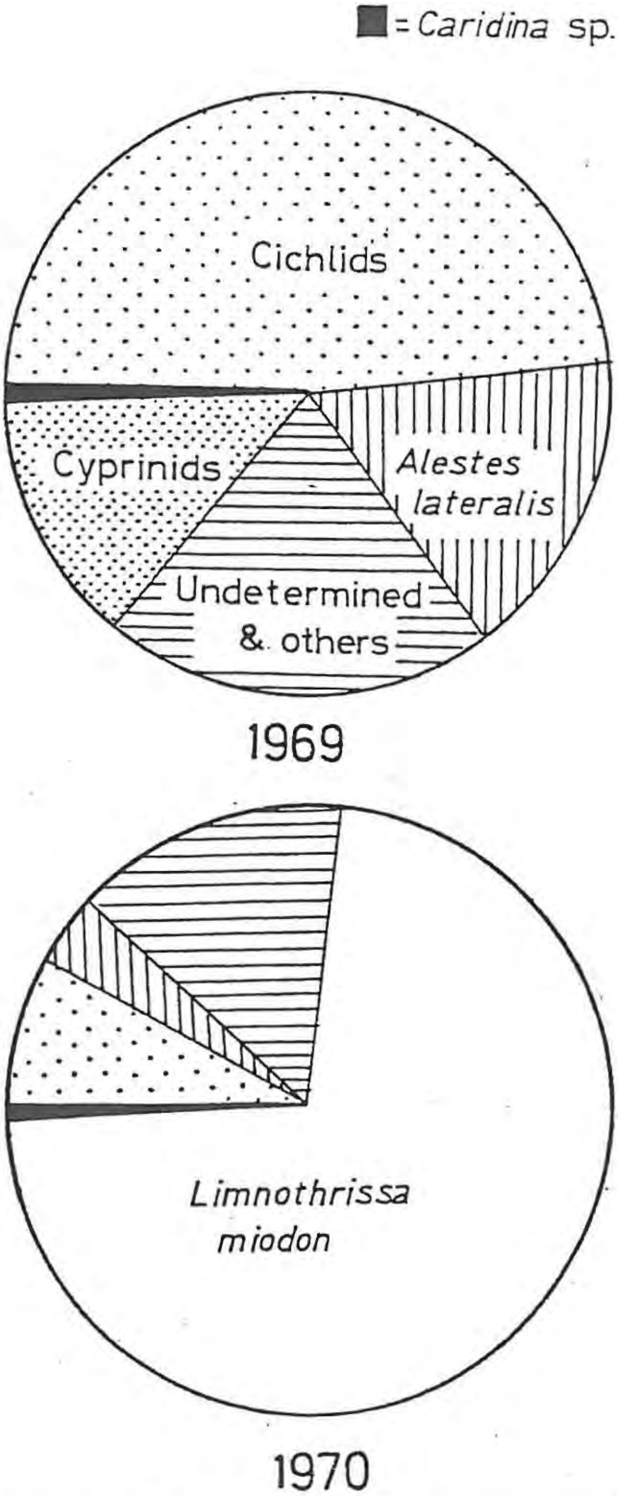


Figure 6: Stomach contents of Tigerfish caught in the Sanyati Basin during the Kariba International Tigerfish Tournament in 1969 and 1970. Redrawn from Kenmuir (1971a).

there is now a well-established population of Limnothrissa in Cahora Bassa (Bernacsek & Lopes 1984; Gliwicz 1984); in addition they have been seen in the Zambezi River (unpublished personal observations) and they could also occur in the Lower Zambezi below Cahora Bassa.

It was suggested that the introduction of sardines into Kariba was unneccessary because the characid Alestes lateralis would have become pelagic instead (Balon 1974a). There is little to support this view, however, because A. lateralis is now largely confined to the margins and the samples in which they were abundant came from shallow and not pelagic waters. Marshall (1984c) has suggested that characids are not well-adapted to pelagic conditions since they mostly take insect prey and are usually potamodromous; both factors would tend to restrict them to littoral waters. It seems almost certain that one of the river fish would eventually have become planktivorous but the length of time this might take is illustrated by Lake Kivu which was formed by a volcanic dam in the late Pleistocene but which still has no planktivore. Its depauperate fish fauna might be one reason for this but it does include representatives of the Cyprinidae, Clariidae and Cichlidae (Beadle 1974) which are families that include planktivorous (or partially planktivorous) species in other systems.

These successful introductions have led to renewed interest in stocking clupeids into other reservoirs where they do not occur such as Nasser-Nubia in Egypt/Sudan (J.M. Kapetsky, personal communication). It has also been proposed that they should be introduced into Lake Malawi in order to utilise the abundant stocks of Chaoborus larvae which occur there (Turner 1982). This action could have a profound effect on ecology of the lake as a whole and on the unique and very diverse haplochromiine fish populations in particular. Such a drastic step might be acceptable in a man-made lake, itself a major environmental disruption, but it is not in one of the African Great Lakes which require special conservation (Fryer 1972).

Other clupeids seem able to adapt to lacustrine and pelagic conditions as Lakes Kainji and Volta support abundant stocks of the riverine species that were present before they were built (Vanderpuye 1973; Otobo 1974, 1979). In this respect Limnothrissa may be closer to its ancestral river form than Stolothrissa is because it is a less specialised feeder (Matthes 1967a) and has been able to live in other lakes as well as the Zambezi River itself. Both species must have been present as fry when Lakes Kariba and Kivu were stocked but there are no records of Stolothrissa from either and it is perhaps now too specialised to be able to survive in them.

LIFE HISTORY

Reproduction

In Lake Tanganyika Limnothrissa males consistently matured at a smaller size (64 mm) than the females (75 mm) (Ellis 1971) but this was not apparent in Lake Kivu where both sexes matured at about 60 mm in length (Spliethoff et al. 1984).

The sardines hardly ever reach this size in Lakes Kariba or Cahora Bassa however (Cochrane 1984; Gliwicz 1984) and must obviously mature at a much smaller size. Begg's (1974a) data show that the smallest female with eggs was 40 mm long (Fig. 7) and he records finding mature fish of only 35 mm in length.

He also showed that they could produce up to 6 000 eggs in an 80 mm fish with the 50 mm specimens producing about 500 - 1 000. According to Matthes (1967a) large specimens (140 mm) might produce as many as 55 000 eggs. If this is the case then the Lake Tanganyika fish will be more fecund than the Kariba ones as the equation in Fig. 7 predicts that a 140 mm Kariba fish would have only 13 000 eggs; however the data are too sparse to permit many comparisons of this nature. There are also very few data on other clupeids but they generally suggest that other species are rather more fecund than Limnothrissa in Kariba. For example, Pellonula afzeliusi from two Nigerian localities appears to be almost twice as fecund (Table 9). It should also be noted that there was considerable variation in the size of maturity in Pellonula, those from the Lagos Lagoon maturing at a much larger size than those from Lake Kainji. The ability to adjust the age of maturity may therefore be a characteristic of the African clupeids.

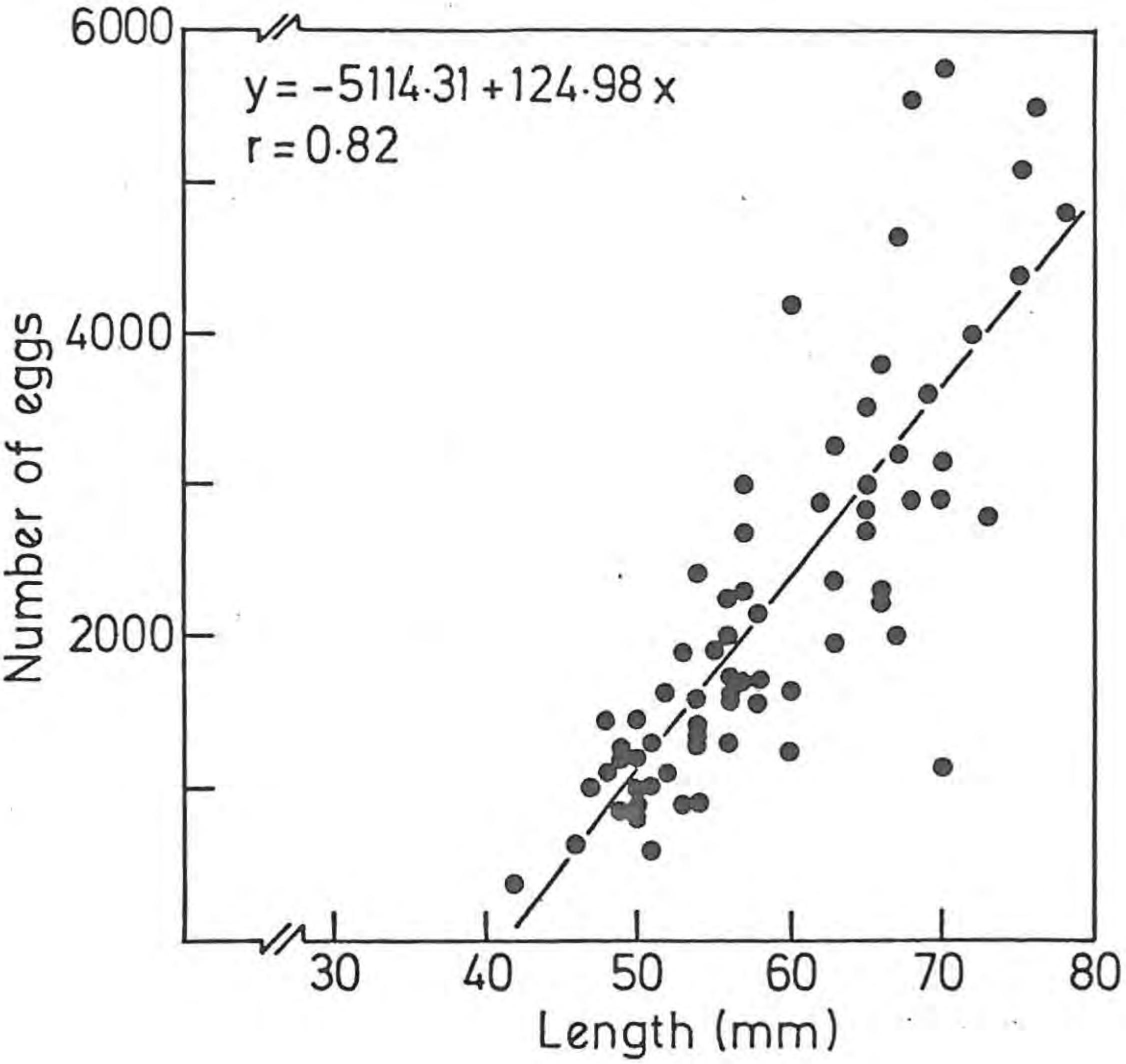


Figure 7: The fecundity of Limnothrissa in Kariba.

Redrawn from original data used in Begg (1974a).

Table 9: Predicted fecundity (no of eggs in ovaries) of Limnothrissa in Kariba and of Pellonula afzeliusi in two Nigerian localities. Data from Fig. 7, Otobo (1978) and Ikusemiju *et al.* (1983).

Length (mm)	Limnothrissa (Kariba)	Pellonula afzeliusi (Kainji)	Pellonula afzeliusi (Lagos Lagoon)
30	-	1 245	-
35	-	1 684	-
40	-	2 188	-
45	509	2 756	-
50	1 134	3 388	-
55	1 759	4 084	-
60	2 384	4 844	-
65	3 009	5 666	1 548
70	3 634	6 552	3 680
75	4 259	7 501	5 811
80	4 884	8 512	7 942

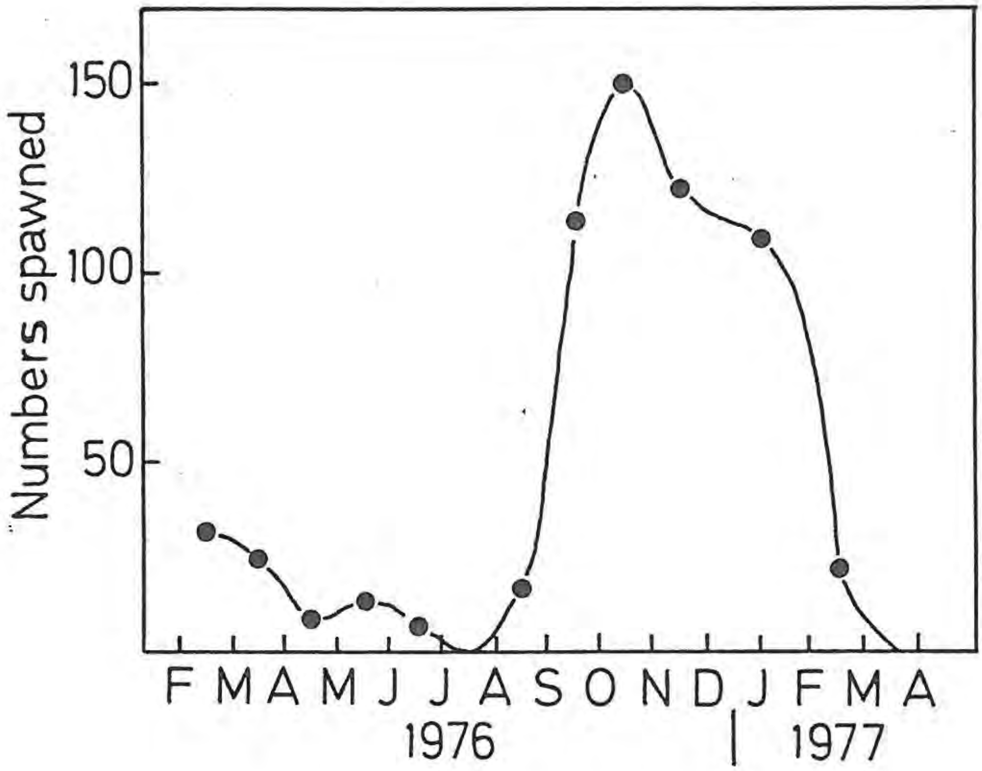
Note: Limnothrissa length is expressed as total length, the others are standard length.

Cochrane (1978) showed that in fish from Kariba the sex ratio was not significantly different from 1:1 over a 20 month period, unlike Matthes (1967a) who found that the ratio in Lake Tanganyika was highly variable and ranged from less than 1% males to a 1:1 ratio with the mean being 1:13. In Lake Kivu males were predominant amongst fish smaller than 75 mm (ratio = 1.55:1) but the larger ones were mostly females (0.35 ♂: 1♀) (de Iongh & Spliethoff, unpublished). It is likely that females grow larger than males but in Lake Kariba neither sex grows large enough to have any influence on the sex ratio. The variable figures obtained by Matthes may therefore have been artifacts caused by selective sampling or simply an inadequate sample size.

Evidence from all the lakes in which it occurs indicates that Limnothrissa breeds all year round but that there are nevertheless pronounced seasonal peaks. In Lake Tanganyika these peaks are variable; according to Coulter (1980) most spawning occurred in May-July, Matthes (1967a) noted two peaks one in May-June and the other in September-December whilst Ellis (1971) noted that December-May was the major spawning period. Ellis (1971) postulated that breeding activity was density-dependant and was related to the population structure as well as being timed to algal blooms. In Lake Kivu there was only a single major breeding period from July-November, which closely matched the plankton cycle (Spliethoff et al. 1983).

In Lake Kariba the period of greatest breeding activity was from September-March (Fig. 8) and preliminary data suggest that it is similar in Lake Cahora Bassa (Gliwicz 1984). In this case breeding did not coincide with the period of greatest plankton abundance, as it did in Lake Kivu. This suggests that breeding is not necessarily linked to plankton abundance but may support Ellis' view that breeding is density-dependant as it takes place when sardine populations are lowest.

Virtually nothing is known about the actual spawning behaviour of these fish but according to Matthes (1967a) they lay their eggs near the surface at night. He found that the



<u>Figure 8</u>: Breeding season of <u>Limnothrissa</u> in Kariba. Redrawn from Cochrane (1978) with points shown as 2-month running means.

eggs sank at about the same rate as Stolothrissa eggs ($4 - 5$ cm min^{-1}) but that Limnothrissa bred in shallower water. The eggs were thought to hatch on the bottom and some were obtained by dragging a plankton net just above the mud surface. However the eggs of the two species are indistinguishable so there may have been some confusion between them.

It seemed unlikely that the sardines would be able to breed in the open waters of Lake Kariba because their eggs would sink into the anaerobic hypolimnion. They do in fact breed in shallow waters and both Begg (1974a) and Cochrane (1978) found the fry to be abundant in these areas. In general, fry were most commonly found over rocky or sandy substrates and tended to avoid zones of submerged vegetation; recent observations, however, made during the course of a programme to sample fish with explosives, are that they occur in all habitats including vegetation (unpublished personal observations).

The clupeids are known to have extensive breeding or post-breeding migrations and those of Stolothrissa have been described in considerable detail (Roest 1978). Very little is known about Limnothrissa movements except that the fry appear to remain in shallow water and move into deeper water as they grow. This has been demonstrated in Kariba by Cochrane (1978) who found that larger fish occurred in deep water furthest from the shore (Fig. 9). Large fish presumably move back into shallow water to breed but there is no evidence to prove this.

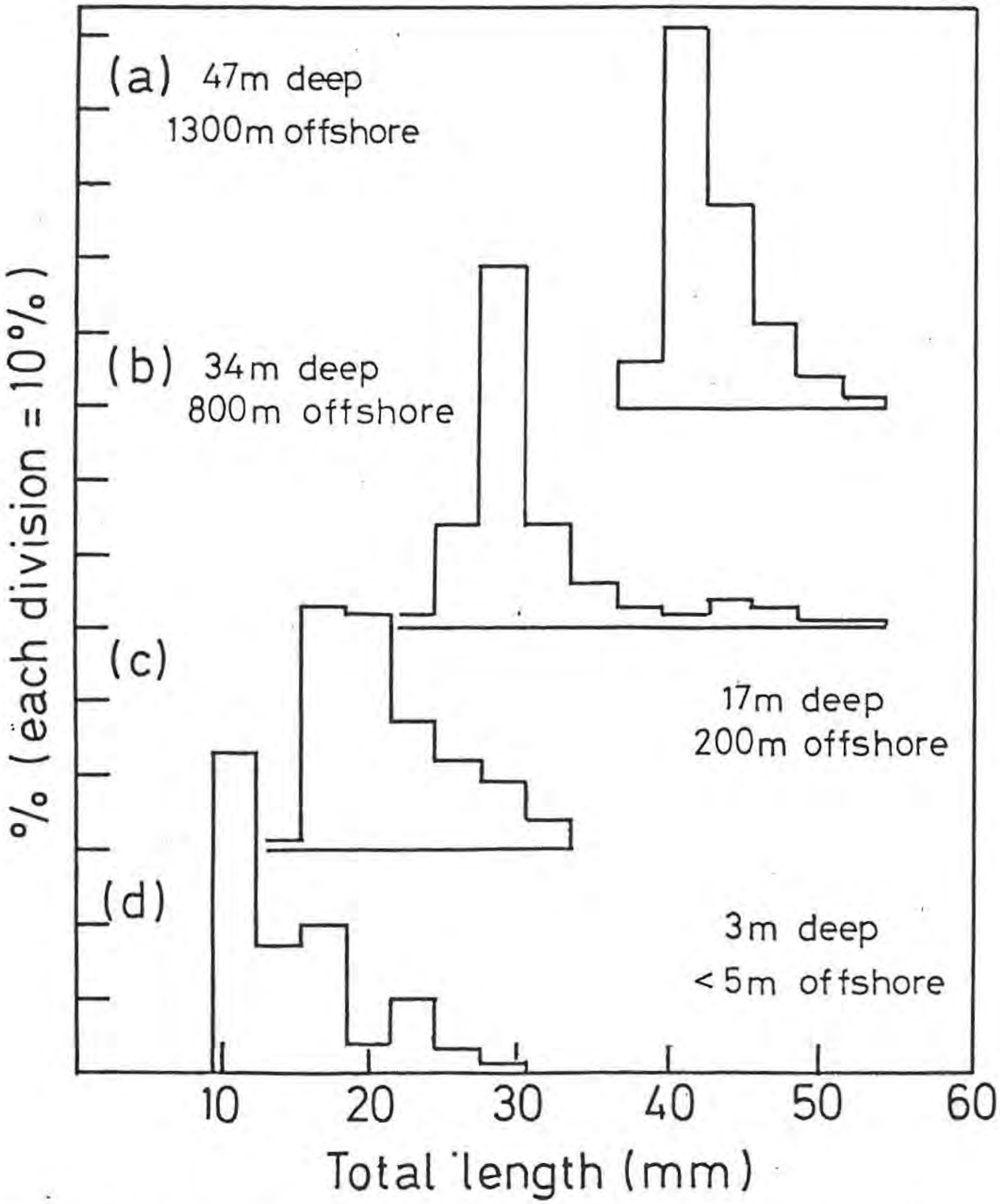


Figure 9: Length-frequencies of Limnothrissa taken from Lake Kariba in February 1976. Redrawn from Cochrane (1978).

Nothing is known about the larval or immediate post-larval phase of these fish and efforts to raise larvae from eggs at the Lake Kariba Fisheries Research Institute have not succeeded.

Feeding

Limnothrissa is generally a more catholic feeder than is Stolothrissa and Poll (1953) found that they were planktivorous when juvenile but became more omnivorous as they grew older. He showed that larger fish became predatory as well and records finding a Stolothrissa of 40 - 45 mm inside the stomach of a 120 mm long Limnothrissa. Later studies confirmed this pattern and recorded insect larvae, atyid shrimps and small clupeids as important food items (Matthes 1967a). In Lake Kivu pelagic fish were almost entirely planktivorous but littoral and inshore specimens fed on a wide variety of different items with large specimens being partly cannibalistic (Table 10).

The feeding habits of the sardines in Lake Kariba were similar and Begg (1974a) found that pelagic fish took mainly Bosmina longirostris (O.F. Muller) but also a wide variety of other organisms (Table 11). These included several relatively large crustaceans like Daphnia, Ceriodaphnia and Cypris which may subsequently have declined through size-selective predation as they were not abundant when Cochrane (1978) examined sardine stomach contents (Table 12). He found that the copepod Mesocyclops leuckarti (Claus) was the most important food item. Both authors also found that large sardines were cannibalistic and predatory; Begg caught a 64 mm sardine with a juvenile cichlid in its stomach and it was noted that large fish (> 80 mm) fed extensively on their own fry.

Table 10: Food of *Limnothrissa* in Lake Kivu. From de Iongh *et al*. (1983).

Fish length (mm)	Habitat	Food Items
65 - 90	Pelagic	*Microcystis*, nauplii, indeterminate
85 - 110	Pelagic	Copepoda
10 - 35	Littoral	Copepoda, Chrysophyta, Rotatoria, Ciliata
30 - 70	Inshore	Copepoda, *Microcystis*, Rotatoria, Chrysophyta, nauplii, insect larvae
85 - 110	Inshore	Chironomidae, juvenile clupeids, Copepoda, *Microcystis*, terrestrial insects, Trichoptera, brewery waste

Table 11: A list of food organisms utilised by *Limnothrissa* in Lake Kariba c. 1971-72. Taken from Begg (1974a).

Zooplankton	Phytoplankton	Insects
Copepod nauplii	Diatoms	Ephemeroptera
Mesocyclops	*Staurastrum*	Trichoptera
Daphnia	*Microcystis**	Chironomidae*
Ceriodaphnia	*Volvox*	Hemiptera
*Cypris**	*Eudorina*	Thysanoptera
*Bosmina**	*Pleurotaenium*	
Cyclastheria	*Ceratium*	
Trichocerca	*Spirogyra*	
Keratella		

* Most important items

Table 12: Food items found in the stomachs of 1 300 sardines from Lake Kariba during the period June 1975 to June 1976. From Cochrane (1978).

Species	No/Stomach	%	
Mesocyclops leuckarti	46.7	55.9	57.7
Tropodiaptomus kraepelini	0.6	0.7	
Copepod nauplii	0.9	1.1	
Bosmina longirostris	21.6	25.8	39.8
Ceriodaphnia dubia	10.0	12.0	
Cypris sp.	1.7	2.0	
Monostyla quadridentata	1.1	1.3	2.2
Keratella cochlearis	0.4	0.5	
K. tropica	0.2	0.4	
Other items	0.1	0.3	

Gliwicz (in preparation) has recently dismissed the importance of cannibalism on the grounds that it is only found amongst fish caught after light attraction and may only occur after the plankton has all been consumed by the abnormally dense concentrations of fish around the lights. He examined 1 058 fish taken without light attraction and found that none were cannibals. However, in Cahora Bassa, as in Kariba, the sardines were very small and it is likely that the majority were below the size at which fish-eating becomes prevalent so cannibalism would be less obvious. The inability to obtain a sufficiently large sample of bigger fish from the reservoirs means that it will not be possible to answer this question adequately for the present.

Limnothrissa is thus a predominantly planktivorous fish but is also a versatile and opportunistic species which can resort to almost any food item if necessary. In Cahora Bassa, for example, they have been recorded feeding on periphyton attached to submerged trees when plankton populations were low (G.M. Bernacsek, personal communication). In this respect it is similar to the riverine species *Pellonula afzeliusi* and *Sierrathrissa leonensis* which were able to colonise Lakes Volta and Kainji (Reynolds 1969; Otobo 1979) and rather dissimilar to *Stolothrissa* which is a more specialised planktivore (Matthes 1967a).

Growth

A striking feature of *Limnothrissa*'s biology is the difference in the size they attain in the natural lakes and reservoirs (Fig. 10). In Lake Tanganyika they reached an average maximum size of 120 mm with some of 160 - 170 mm being obtained (Poll 1953; Matthes 1967a) and they reached a similar size in Lake Kivu where Spliethoff *et al*. (1983) were able to calculate a von Bertalanffy equation with an asymptotic length of 145 mm.

In contrast, the fish from Lake Kariba were very much smaller and Cochrane (1978, 1984) estimated their asymptotic length to be only 81 mm. The average size in the commercial landings is only about 50 mm but some large individuals do occur; the record from Kariba is 155 mm. These are very rare, however, and out of approximately 80 000 fish measured during the course of this project less than 0.01% exceeded 80 mm and the longest was

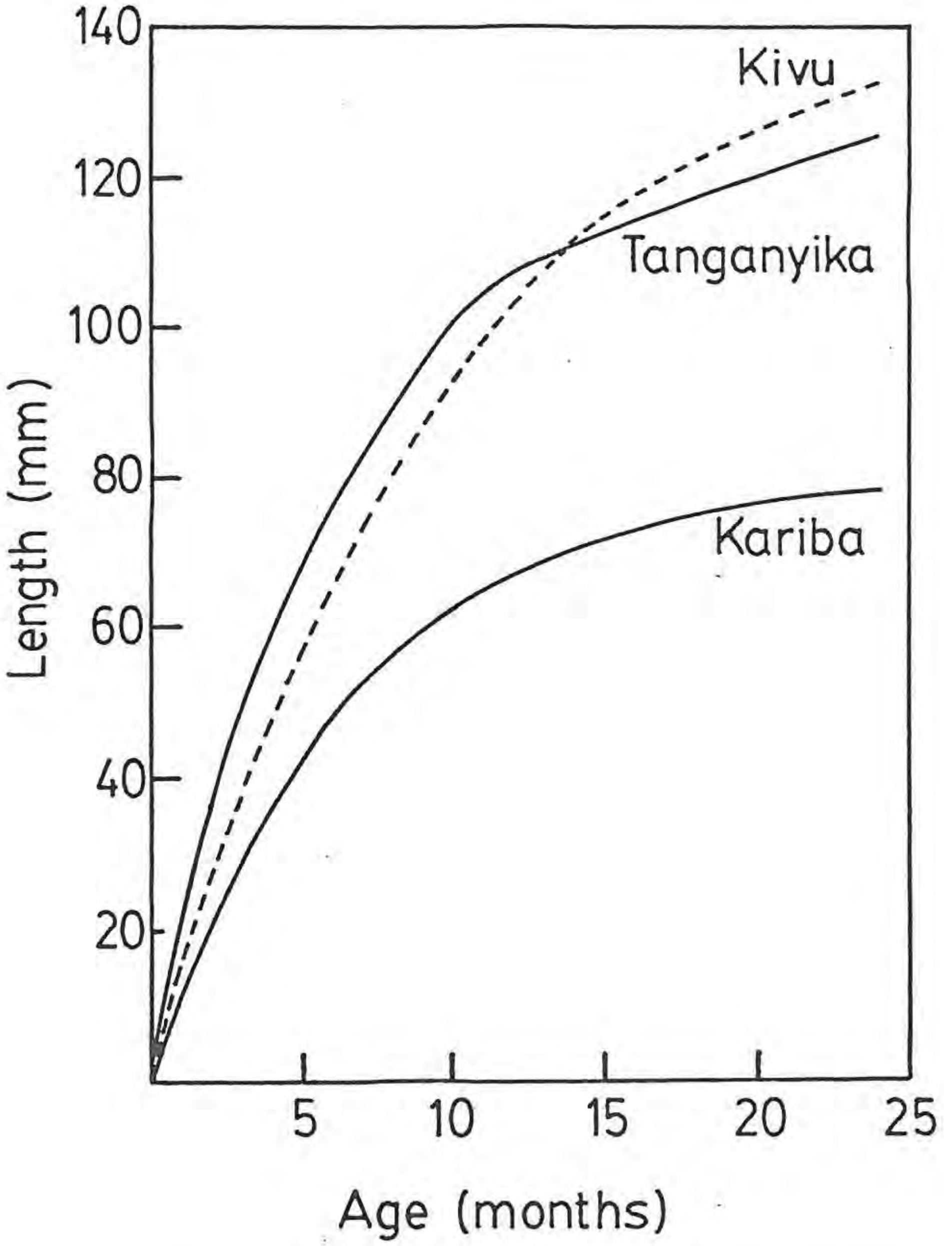


Figure 10: Growth of Limnothrissa in three African lakes. Kivu data from Spliethoff et al. (1983), Tanganyika data from Matthes (1967a) and Kariba data from Cochrane (1978, 1984).

89 mm. The sardines from Cahora Bassa are also small in size with very few exceeding 70 mm (Gliwicz 1984; Rui Silva, personal communication).

There has been considerable speculation about the reasons for these striking differences in growth. As an investigation into sardine growth forms a major aspect of this project these ideas will be discussed later.

Behaviour

Most of the work on Limnothrissa behaviour centres around its movements and distribution within the water-body. Echo-sounders provide the most practical means of following these fish and the data that are obtained will be very largely influenced by their accuracy and sensitivity.

The sardines cannot be detected in Kariba by day with the equipment that is available but they can be picked up as night falls and Begg (1976) showed that their nocturnal movements were to some extent influenced by those of the plankton. Nothing is known about their movements by day but it is assumed that they go to the bottom.

Gliwicz (1984) was able to detect them by day in Cahora Bassa and he found that the depth at which their maximum concentration occurred was related to Secchi disc visibility by

$$M_c = 3.2\ e^{0.9SD}$$

where M_c = depth of main concentration (m) and SD = Secchi disc visibility (m).

Secchi disc visibility in Cahora Bassa is generally very low (mean = 1.8 m) and the sardines were usually present at about 20 m depth. If this relationship applied in Kariba where the mean Secchi disc visibility was about 5.0 m then the maximum sardine concentrations would be expected at about 300 m depth during the day. This is clearly impossible in Kariba as the maximum depth is 120 m but it does indicate that the sardines are likely to go as deep as they can during the day. Since conditions in the hypolimnion have improved and deoxygenation is no longer so extensive they can probably go to the bottom in many areas and divers have indeed noted them below the thermocline.

They come to the surface at dawn and dusk and their habit of jumping at the surface in calm water has been noted by several authors (Junor & Begg 1971; Begg 1974a; de Iongh et al. 1983; Gliwicz 1984) but the function of this behaviour is unknown. In Lake Kivu this was the period when most feeding took place but this was not the case in Kariba where feeding appears to continue throughout the night (Begg 1974a).

Moon phase also affects their behaviour and in Kariba commercial catches are so poor during this period that most fishermen cease fishing for a few days. Echo-sounding traces show clearly that the fish are less abundant over Full Moon and it is assumed that they go to the bottom during this time. This does not appear to be an invariable habit however, as in Lake Kivu the sardines move nearer the surface during the Full Moon to a mean depth of 25 m (de Iongh et al. 1983). The reasons for this behaviour are unknown but may be connected with lunar rhythms in the zooplankton which were detected in Cahora Bassa by Gliwicz (1984).

POPULATION DYNAMICS

Very few data on the population dynamics of Limnothrissa are available and this was one of the principal objectives of the present study. Some preliminary results from this study were presented in Marshall (1984a) but the only other aspects to have received any attention are abundance and seasonal fluctuations.

Abundance

Cochrane (1978) attempted to estimate sardine abundance by using commercial purse-seiners but without light attraction; because the area enclosed by the net can be calculated it is possible to calculate biomass from his data. Estimates of 8.8 kg ha^{-1} in January 1976 and 23.1 kg ha^{-1} in April 1976 were obtained by this means. The increase of 263% was very similar to the 271% increase in the commercial catch over the same period, which indicated the potential for using commercial catches as an index of biomass. No further work was carried out unfortunately and the estimation of biomass will be a major part of this project.

The only other Limnothrissa biomass estimates were made by Lindem (1983), who used acoustical techniques to obtain a mean estimate of 8 424 fish ha^{-1} in Cahora Bassa in February 1983. If the mean weight of each fish is assumed to be 1.0 g then the mean biomass estimate is 8.4 kg ha^{-1}, which is very similar to Cochrane's figure of 8.8 kg ha^{-1} in Kariba in January.

The abundance of sardines in Kariba is largely influenced by limnological factors and variation is strongly seasonal. It has also been shown (Fig. 11) that river flow is an important long-term influence (Marshall 1982a). It appears that nutrients carried in by the rivers are retained in the hypolimnion and released at turnover, so producing the increase in plankton that typically occurs at this time (Fig. 5). If river flow is poor it is likely that fewer nutrients will be available and the abundance of sardines correspondingly reduced.

Seasonal fluctuations

The abundance of clupeids in Lake Tanganyika fluctuates considerably and is related to the seasonal pattern of the plankton (Coulter 1970). Seasonal fluctuations of *Limnothrissa* are particularly striking in Kariba and are reflected clearly in the commercial landings (Fig. 12). In general, catches were lowest in December-January and rose to a peak in August-September; there was then a rapid decline until the end of the year. Cochrane (1978) showed that this was clearly linked to the thermal regime and plankton fluctuations in the lake and the situation was examined in more detail during 1979 by the Lake Kariba Fisheries Research Institute. The following account is drawn from this work with data on chemistry from Burne (1981), on phytoplankton from Beattie (1981) and on zooplankton and sardines from Marshall (1980).

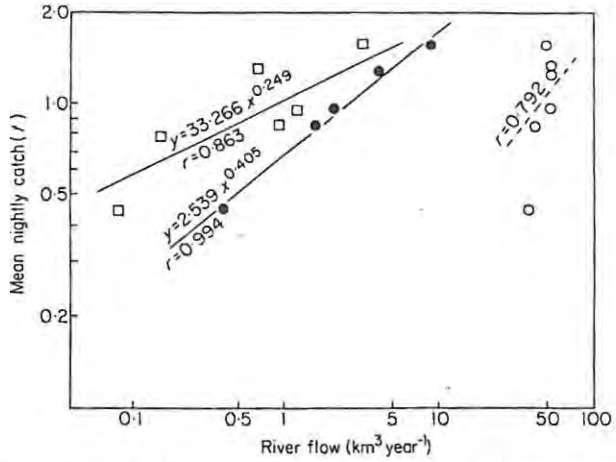


Figure 11: The relationship between sardine catches and river flow into Kariba. ● , Sanyati River; □ , Gwaai River; ○ , Zambezi River. From Marshall (1982a).

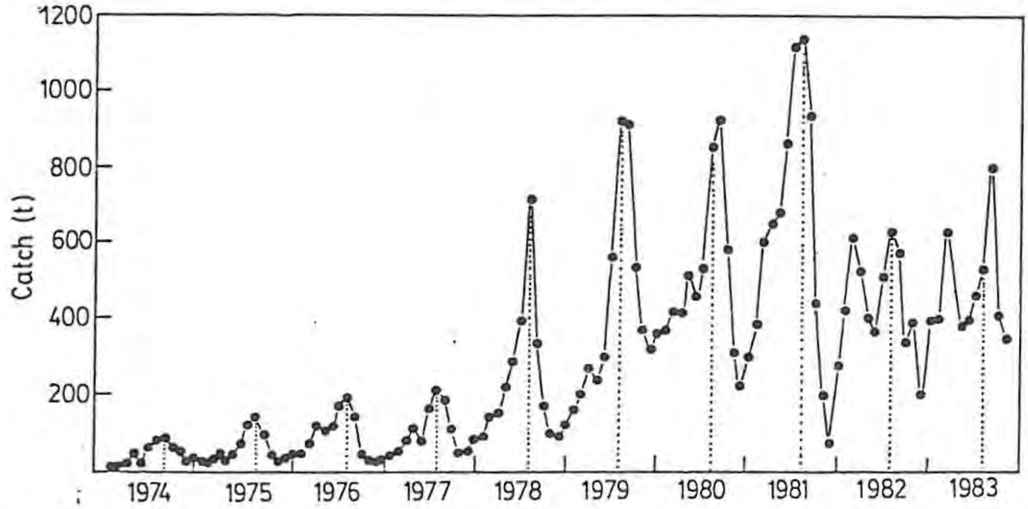


Figure 12: Monthly catches of Limnothrissa (Kariba-based vessels only). The month of August is shown for each year by the vertical dotted line.

The main physical factors which influenced the pelagic zone were river flow and water temperatures. River flow data for 1979 were not available but the mean rainfall in the Sanyati catchment can be used as an index of river flow (Fig. 13a), especially as the Sanyati River is the major influence on the eastern basin where the work was carried out. Rainfall decreased during the later part of the season and the nutrient contribution from the rivers must have decreased accordingly. The lake was also strongly stratified at this time (Fig. 13b) with an almost anaerobic hypolimnion (Fig. 13c) and it is likely that nutrient levels in the epilimnion were low. It was not possible to detect this because epilimnetic nutrient levels were low at all times during the study but an indication that this took place was the decrease in both phytoplankton (Fig. 13d) and zooplankton (Fig. 13e) that took place during this period. This was also the main breeding period for the sardines and their numbers were low (Fig. 13f).

The lake became increasingly isothermal from March onwards but turnover did not take place until the end of June when the hypolimnion rapidly became oxygenated. Nutrients must then have been released because there was a rapid increase in both phytoplankton and zooplankton. The sardine population had been increasing during this period and reached a peak in August, a month after the plankton. It is likely that these fish were produced during the breeding season at the beginning of the year and were able to move into deep water to take advantage of the high plankton population.

Figure 13: The general sequence of physico-chemical and biological events in the pelagic waters of the Sanyati Basin, Lake Kariba. From Burne (1981), Beattie (1981) and Marshall (1980).

(a) Mean rainfall in the Sanyati River catchment.

(b) Water temperatures at the surface and at 40 m depth.

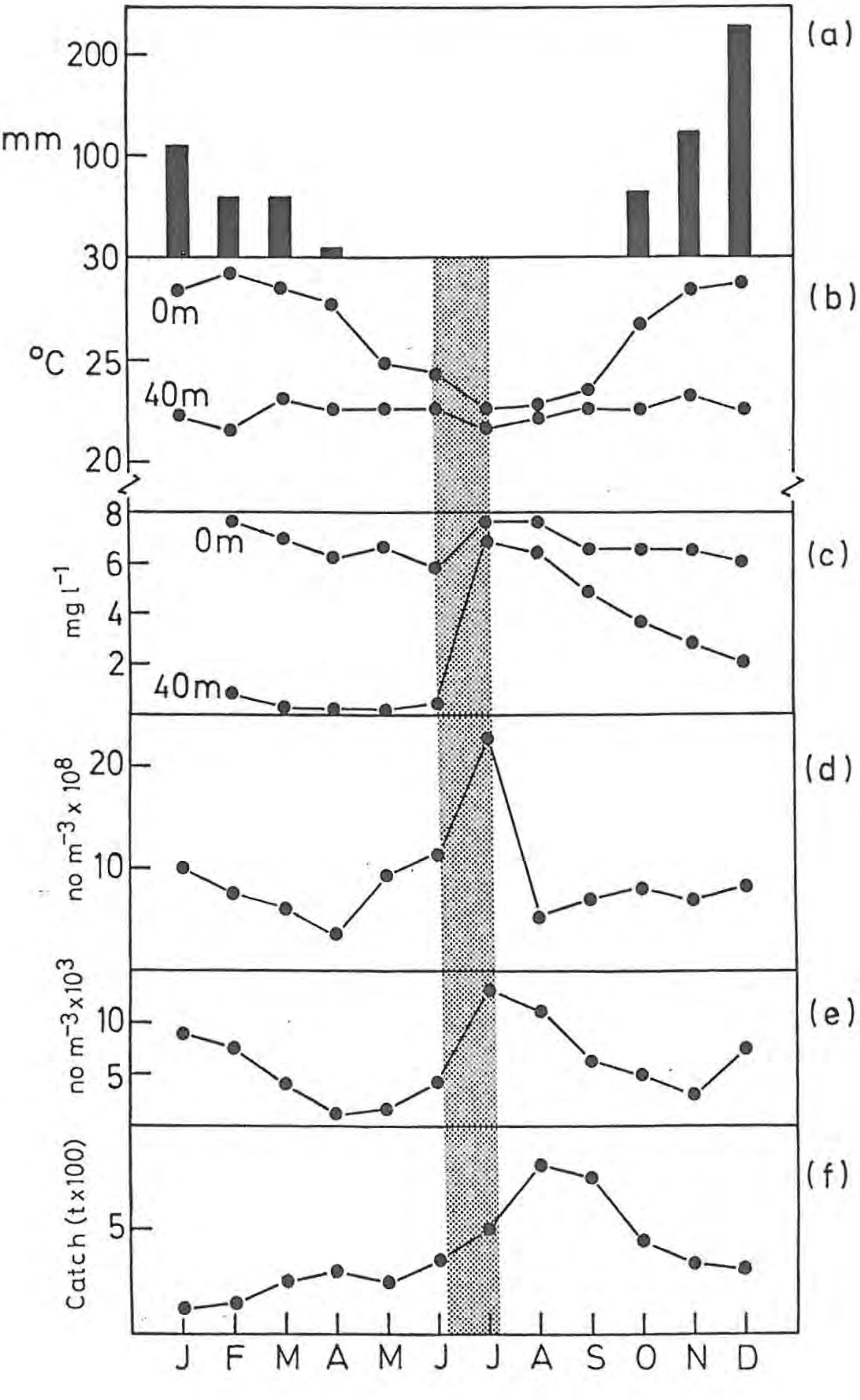
(c) Dissolved oxygen content at the surface and at 40 m depth.

(d) Mean phytoplankton abundance.

(e) Mean zooplankton abundance.

(f) Sardine landings which can be used as an index of abundance.

The shaded zone indicates the period when turnover took place.


(a)
mm
200
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30
(b)
°C
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0m
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(c)
mg l^{-1}
8
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4
2
0m
40m
(d)
no m^{-3} x 10^8
20
10
(e)
no m^{-3}x10^3
10
5
(f)
Catch (t x 100)
5
J
F
M
A
M
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J
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S
O
N
D

The third phase of this process was marked by the re-establishment of stratification and a decline in plankton as nutrients are presumably lost to the hypolimnion or through the outflow. Early rains have been shown to contribute most of the nutrients, especially phosphorus (Thornton 1980b), but this appeared to have relatively little effect on plankton abundance which increased only slightly towards the end of 1979.

The effect of this on the sardines was marked and there was a rapid decrease in their numbers from August onwards; it has been suggested that many fish die of starvation at this time (Cochrane 1978, 1984) and it is possible that many of the survivors move into shallow water to breed as the breeding season begins in September.

This appears to be the typical annual cycle in the pelagic waters of Kariba but it was disrupted in 1982 and 1983 (Fig. 12) possibly as a consequence of the 1981-82 and 1982-83 droughts.

COMMERCIAL IMPORTANCE

Lakes Tanganyika, Kivu and Cahora Bassa

Lake Tanganyika currently produces about 75 000 t yr^{-1} from its pelagic fishery (Petr & Kapetsky 1983) which consists mainly of *Stolothrissa* and *Limnothrissa*, but includes a community of four predatory *Lates* spp. (Coulter 1970, 1977, 1981). *Stolothrissa* is the most abundant species, being up to 60% of the total catch. There is some evidence, however that *Limnothrissa* can increase under exploitation (Coulter 1967).

Fisheries for Limnothrissa have not yet developed on Lakes Kivu and Cahora Bassa although experimental fishing has begun on the former (Spliethoff *et al.* 1983). There are few reliable yield estimates for these lakes but it has been suggested that the possible catch from Kivu could be as much as 30 000 t (Welcomme 1972) and from Cahora Bassa as much as 8 000 t (Bernacsek & Lopes 1984).

Lake Kariba

The fishery for sardines on Lake Kariba is presently the only one which is based entirely on Limnothrissa. Experimental fishing began in 1970 and attempts were made, on the Zambian side, to adapt traditional methods from Lake Tanganyika but with limited success (Balon 1974). It was found that inexperienced fishermen were reluctant to stay on the water at night and catches were still poor after an experienced man was brought in from Tanganyika. The traditional methods failed because the fish did not come to the surface, a phenomenon attributed to the relatively poor light penetration of the Kariba water by Woodward (1974). Begg (1974a) considered that this behaviour was possibly more typical of Stolothrissa which is the main species taken by traditional methods in Tanganyika. Lift-nets and Choromilas (a type of purse-seine (Coulter and Znamensky 1971)) were also used but with poor results and there seemed to be no prospects for establishing a successful fishery for the sardine (Balon 1974).

Experimental fishing continued on the Zimbabwean side, however, and a variety of methods were attempted (Begg 1974a). Purse-seines, with light attraction, were found to be the most successful and the first commercial unit was established in 1973. Since then a variety of lift-nets have been devised and these are now more common that the purse-seines in the fishery; the various types and the way they operate have been described by Cochrane (1978), Langerman (1979) and Marshall *et al.* (1982).

The fishery developed slowly at first and there were only 10 boats operating by 1977 but rapid expansion took place after this so that there were 100 boats on the Zimbabwean side by 1980 (Junor 1982). Expansion was then restricted so that only 120 boats were in use on the southern shore at the end of 1983. The Zambian fishery began in 1981, using Zimbabwean fishing methods, and has expanded rapidly with 110 boats being in operation by the end of 1983 (S.P. Subramaniam, Zambian Fisheries Dept., personal communication).

The total catch followed this trend and rose to a peak of 12 000 t in 1981. Since then Zimbabwean catches have declined but there has been a steady increase in Zambian catches so that the total catch in 1983 was over 13 000 t (Fig. 14).

ECOLOGICAL IMPACT OF THE SARDINES ON LAKE KARIBA

Any introduced species is likely to affect its new environment once it becomes established and this may often be deleterious; a Zimbabwean example is the destruction of aquatic

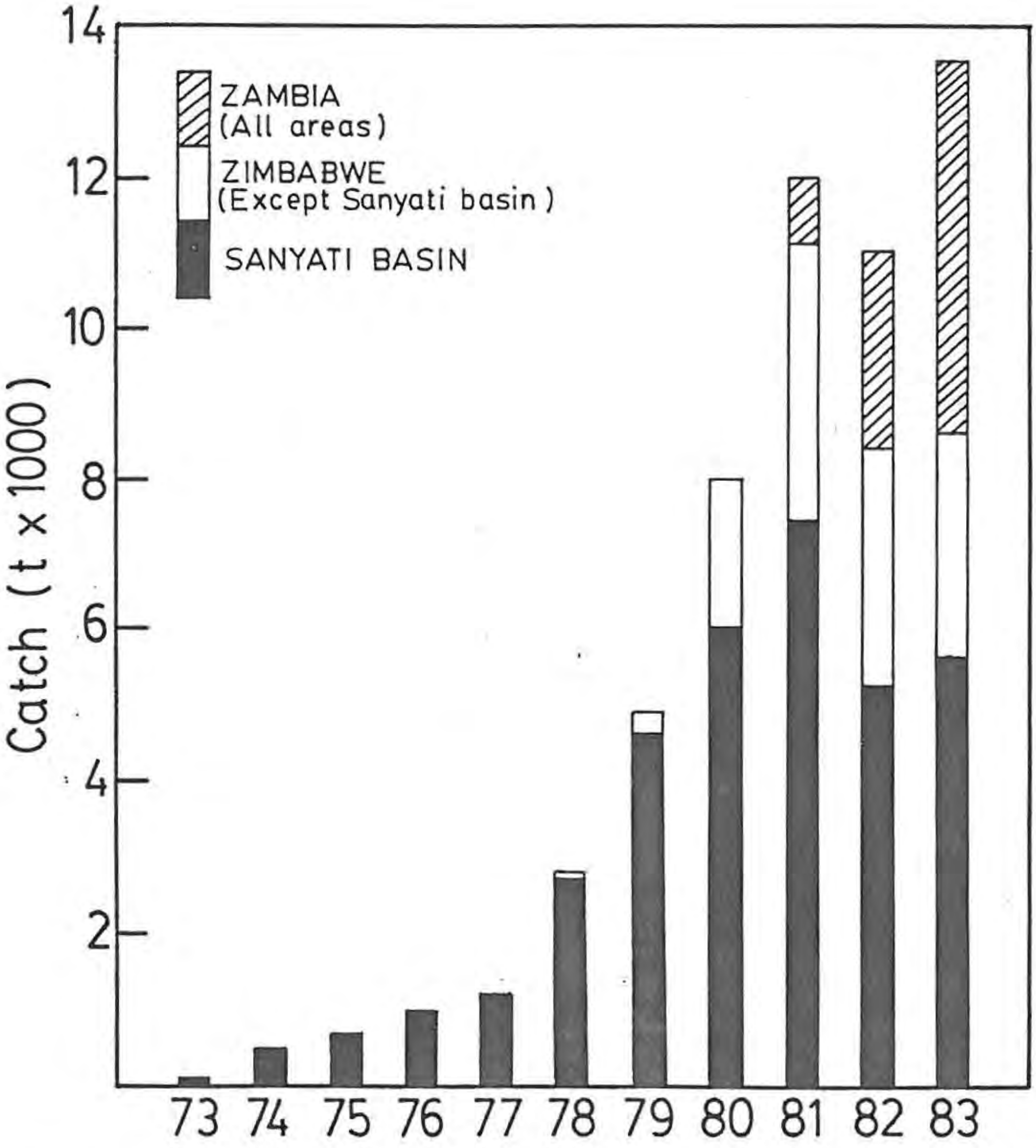


Figure 14: Total catch of Limnothrissa from Lake Kariba, 1973-1983. Zimbabwe data from Lake Kariba Fisheries Research Institute records, Zambian data from the Department of Fisheries, Chilanga, Zambia.

macrophytes by Tilapia rendalli and the consequent elimination of waterfowl and other species (Junor 1969). Limnothrissa has had a clear and significant impact on the commercial fishery but its other ecological effects are less obvious.

Once the sardines had invaded the Sanyati Basin and become the main prey of the Tigerfish there was speculation that the predator's population dynamics would change (Kenmuir 1971b). Changes in the abundance of the Tigerfish have indeed taken place and it is an interesting example of the response of a predator to an increase in the abundance of its prey as well as to commercial fishing and unregulated exploitation.

Prior to the introduction of Limnothrissa the Tigerfish made up about 5% of the total inshore gill-net catch but this rose to about 10% after the arrival of the sardine. It also became semi-pelagic with a considerable number being taken by the sardine fishermen as a by-catch (Cochrane 1976; Junor & Marshall 1979). It soon became less important, however, and the decline was attributed to fishing pressure in open water by the sardine fishermen and in the breeding areas by unlicensed fishermen (Marshall et al. 1982; Langerman 1984).

Since Hydrocynus is an important component of all the different fisheries on Kariba it is useful to examine the changes that have taken place in its population, using data from four different fisheries. Each fishery is of a different intensity, but as they take fish of different age groups they offer a means of following changes within the population.

These fisheries are:

(a) research nets set by the Lake Kariba Fisheries Reseach Institute. They consist of a fleet ranging from a mesh size of 37 mm ($1\frac{1}{2}$") to 175 mm (7"), increasing by 12 mm ($\frac{1}{2}$") increments. Over 80% of the Tigerfish caught in these nets were less than one year old (Langerman 1984) and data from this source give a good index of relative abundance of young of the year.

(b) the pelagic fishery which includes Tigerfish as a by-catch. Most of those taken by this fishery were around 2 years old (Langerman 1984).

(c) the commercial gill-net fishery is restricted to nets with a minimum mesh size of 100 mm and the mean age of the Tigerfish taken by it is about 3 years (Langerman 1984). The catch statistics from fishing area C.1 which lies between the Gache Gache and Naodza Rivers (see Fig. 16) have been selected in preference to those from area C.2 which lies between the Sanyati and Gache Gache Rivers. This is because the latter include many fish from the Sanyati River itself which have been caught there illegaly. As the Sanyati is a major breeding area for Tigerfish (Kenmuir 1973; Langerman 1984) many of the fish taken are older breeding females. The statistics from this area are not therefore considered to be typical of the lake as a whole.

(d) the Kariba International Tigerfish Tournament (KITFT) is an annual fishing competition that takes place entirely within the Sanyati Basin. Whilst it is not as intensive a fishery as the other three it provides a sample of 1 500 - 2 000 fish is made available in the space of only 3 days. As fish weighing more than 1 kg are the only ones accepted this is an unusual opportunity to sample the older fish in the stock. The age range is more variable than it is in the other fisheries but most of the fish are four to five years old (Langerman 1984).

The relative abundance of Tigerfish in each of these fisheries is shown in Fig. 15. Following the establishment of sardines in the Sanyati Basin in 1970, there was a rapid increase in the number of young Tigerfish (Fig. 15a) and strong year-classes persisted until about 1975. Numbers declined sharply after that time and appear now to have stabilised at a relatively low level. The cause of this decline is not known.

This pattern was reflected, but about 2 years later, in the pelagic catches (Fig. 15b). The sharp drop in catches of pelagic Tigerfish was at first attributed to the effects of increasing fishing effort (Marshall et al. 1982; Langerman 1984) but this view now appears to be incorrect. It seems more likely that it was brought about by a lack of recruits to the fishery following the decrease in the abundance of young fish.

The same situation also occurred in the gill-net fishery, but again, another 2 years later (Fig. 15c). There was, however, an earlier increase in the abundance of the fish from these nets which reached a peak in 1974-1975. It is possible that these fish were responsible for the strong year classes of 1970-1975.

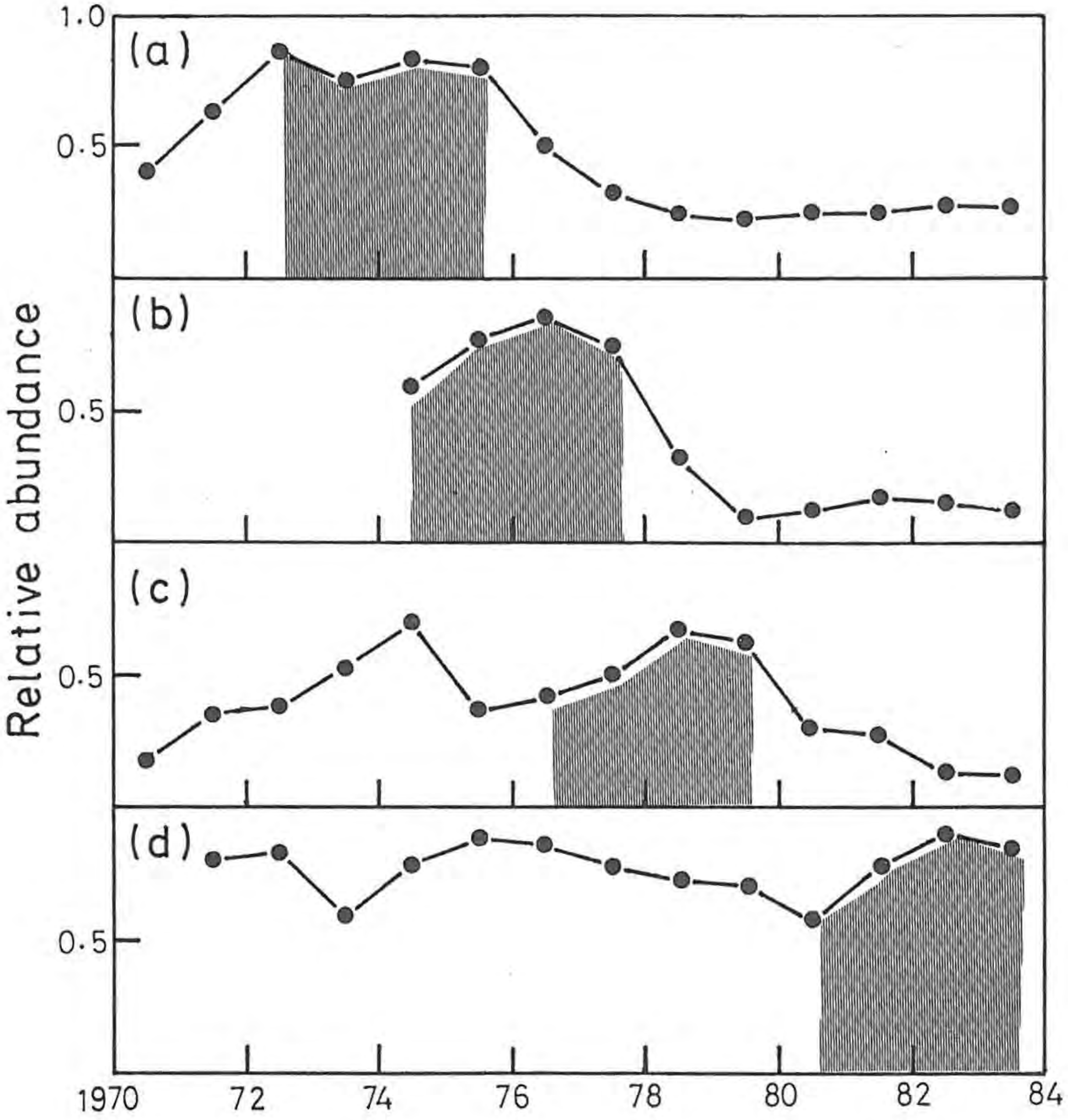


Figure 15: The relative abundance of Tigerfish in four different fisheries on Lake Kariba, 1970-1984.
(a) LKFRI research nets; (b) pelagic fishery; (c) commercial gill-net fishery; (d) KITFT angling returns.
Data points are shown as 2-year running means, the shaded area indicates some of the strong year-classes that followed the sardine invasion in 1969-1970.

Finally, the KITFT catches seem to follow this pattern (Fig. 15d) and the relatively good catches of recent years may represent the survivors of the strong year-classes that followed the sardine invasion of 1969-70. Improved catches at the KITFT also followed the earlier increase recorded in the catches from the gill-net fishery.

The decrease in young Tigerfish is a matter of concern especially as there is no obvious explanation for it. Catches from the pelagic and gill-net fisheries have already dropped to very low levels and those from the KITFT may do so in due course. If this does happen then it would indicate that breeding stocks of Tigerfish have decreased and a further decline in the catch of young fish could be expected.

Limnothrissa may have initially been responsible for an increase in the Tigerfish population but the predator's abundance is not simply related to that of its prey but may be affected by a complex interaction of other factors, most of which have not yet been identified. The situation appears to be quite different from that in Lake Tanganyika, where a decrease in the predatory Lates community was clearly linked to an increase in fishing activity (Coulter 1970).

In Lake Tanganyika the decrease in predators led to an increase in the sardine community but it is not clear if such an interaction has occurred in Lake Kariba.

Other fish species also prey on the sardines and Eels Anguilla nebulosa labiata, Butter Catfish Eutropius depressirostris and Squeakers Synodontis sp. are frequently taken in sardine fishing nets, especially in the western areas of the lake (unpublished observations). It is not known if this has had any effect on the abundance of these species.

Some birds have also benefitted from the sardines, especially the White-winged Black Tern Chlidonias leucoptera (Temmink) which feeds extensively on them (Begg 1973). It has recently begun feeding around fishing vessels at night, taking dead fish floating away from them (Marshall 1984d). Another behavioural change was noted in the Pied Kingfisher Ceryle rudis (L.) where birds were seen flying several kilometres from shore to catch sardines and then flying back to eat them; presumably the ease of catching them justified the extra energy expenditure (Junor 1972).

Brooks & Dodson (1965) and many others since, have shown that planktivorous fish can change the nature of a zooplankton community through size-selective predation. This is a widespread phenomenon (Zaret 1980) and it must have occurred in Kariba following the introduction of Limnothrissa. Unfortunately, there are virtually no data on the lake's plankton before this took place except for some early work by Begg (c. 1968). Bowmaker (1973) made some observations in the Mwenda estuary in 1967-68 whilst Mitchell (1975) studied Chaoborus there in 1969-70, shortly after the sardines had become established.

The available data suggest that the larger planktonic forms such as Ceriodaphnia, Daphnia, Diaphanosoma and the larger copepods have declined and the plankton is now dominated by smaller forms such as Bosmina and Mesocyclops (Begg 1974b, 1976; Marshall 1980). The status of Chaoborus at the present time is of interest as it may have been eliminated by the sardines. Turner (1982) has suggested that sardine predation has led to the elimination of Chaoborus from Lake Tanganyika and this has formed the basis of his controversial proposal to stock Limnothrissa into Lake Malawi where there is a large population of Chaoborus. Unfortunately, Mitchell's work has never been repeated and the situation of this species in Kariba is unknown at present.

A final impact of the sardine on Lake Kariba may be its influence on the nutrient dynamics of the lake. It has, for example, been suggested that they may have contributed to the decline of the floating fern Salvinia molesta Mitchell by utiising nutrients that were formerly available to the plant (Marshall & Junor 1981). Although this seems very likely the evidence is largely circumstantial and this subject requires further investigation.

CHAPTER 4: DATA COLLECTION AND FIELD SAMPLING

The principal sources of data used in this project were the fishing returns submitted by the commercial fishermen, samples taken from the commercial catches and samples obtained from two transects carried out in the Sanyati Basin. They are described in this chapter in order to avoid repetition in subsequent ones which will only include descriptions of the methods used to estimate the particular aspects under discussion.

FISHING RETURNS

All sardine fishermen on the Zimbabwean side of Lake Kariba are required to submit a monthly return giving details of the weight of fish caught each night by each vessel. There are heavy penalties for failing to submit returns but these have rarely been imposed and efforts to convince the fishermen of their value have been preferred. A report by Marshall (1981) was circulated and gave examples of the way in which the data could be used thus stimulating a great deal of interest amongst the fishermen. These returns are now considered to be as accurate as any obtained from a commercial fishery and are a comprehensive and valuable source of information.

The method for collecting sardine statistics in Zambia is not known but it is apparently similar to the Zimbabwean system. Catch statistics have been supplied by the Zambian Fisheries Department and as they appear to be close to the comparable Zimbabwean figures they have been accepted without qualification and are incorporated into this project. They are almost certainly more accurate than most African statistics as they are collected from literate fishermen operating from a few well-defined areas, factors which do not usually apply to fisheries elsewhere on the continent.

SAMPLING

Samples from commercial landings

Samples were taken every month from commercial catches at Kariba from 1978 - 1983. A handful of fish were taken directly from the fish containers aboard vessels of several different companies on the same day. They were pooled to make up a sample of 1 000 - 2 000 fish. The tendency to select fish was strongly resisted and and it was hoped that representative samples were obtained.

Regular samples were also obtained from a fisherman based in the Bumi River mouth during 1980 -1982. These were used as a comparison with those taken from the pelagic waters of the Sanyati Basin.

The fish in these samples were all measured to the nearest millimetre (total length) but no attempt was made to weigh them because they were usually soaked in brine, refrigerated or physically damaged in other ways.

Sanyati Basin transects

Two transects were established within the Sanyati Basin and monthly samples were taken from July 1981 to July 1983; it was hoped that this programme would begin in January 1981 but this was not possible because of a lengthy breakdown of the Research Vessel "Pelican". The first transect began at the mouth of the Sanyati Gorge (Station 1) whence the lights of Kariba town were visible 33 km away to the north (Fig. 16). The second transect began in the Gache-Gache Bay (Station 6) and proceeded northwest towards the lights of Siavonga in Zambia.

Since all the sampling was carried out at night the choice of transects was governed by two factors. Firstly, the "Pelican" had no operational compass or radar and without these navigational aids landmarks such as town lights had to be clearly visible at all times. Secondly, care had to be taken to ensure that areas of emergent or just submerged trees were avoided as these were a hazard to the vessel and the sampling gear. This problem became increasingly severe during the course of the project as the falling lake level exposed more and more trees and made large areas of the basin very hazardous to a vessel at night.

Because of the lack of navigational aids it was impossible to locate each station with any precision. The initial station was fixed just before dusk and sampling did not begin until well after dark. As the total travelling time for each transect was about two hours, the boat was stopped every 30 minutes so that each transect consisted of 5 stations each in the same general area. One transect could be completed in a night

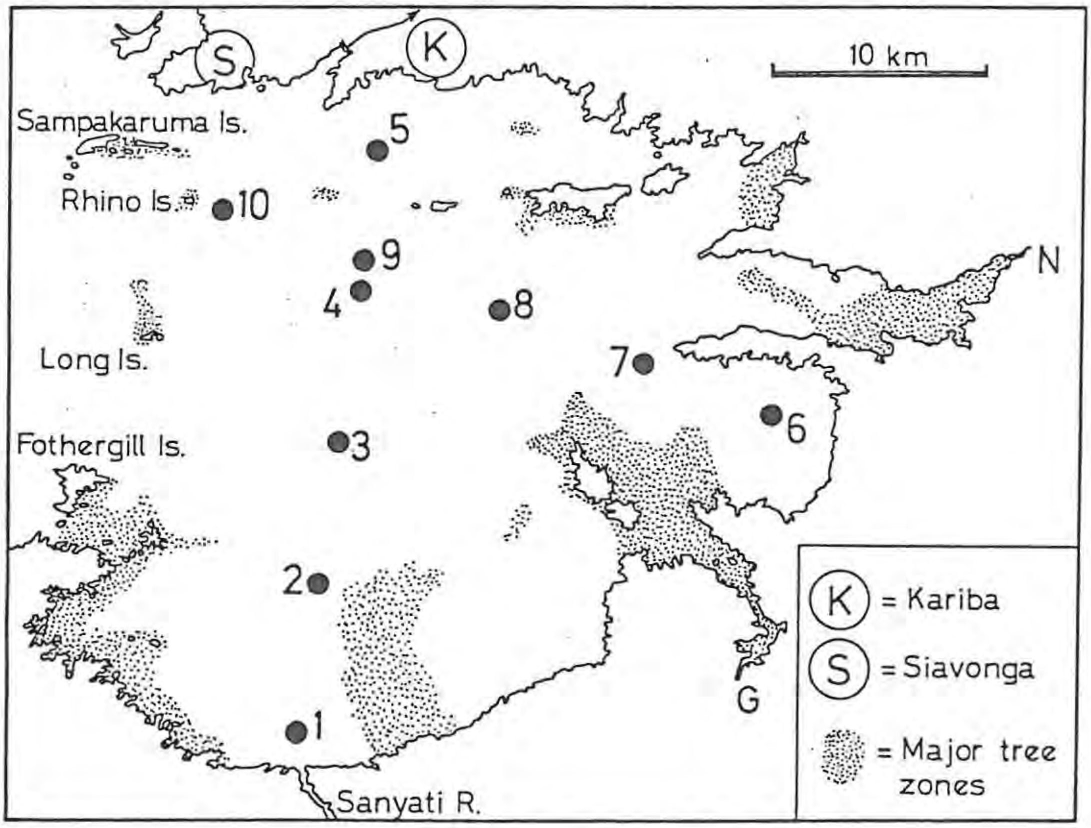


Figure 16: The Sanyati Basin, Lake Kariba, showing the two transects and the approximate location of the 10 sampling stations. The letters N and G indicate the location of the Naodza and Gache Gache Rivers.

(weather permitting) and it was felt that the basin had been sampled reasonably well and without endangering vessel or crew.

Most stations were necessarily sited in deep water to avoid submerged trees but station 6 was in a bush-cleared area in water only 10 m deep where the sampling gear could be safely lowered to the bottom.

Samples were taken with a smaller version of the commercial dip-net in use on Kariba. It consisted of a conical net 3 m in diameter at the mouth and 7 m deep; it was made of the 8 mm mesh nylon netting used commercially but the lower half was lined with mosquito gauze so that very small fish could be retained. It was mounted on a boom and pulley over the stern of "Pelican" and operated by a hydraulic winch.

Wherever possible it was lowered to a depth of 30 m (at its mouth) so that it was below the main concentration of sardines, characteristically located between 10 and 20 m in depth (Fig. 17). This was impossible on some occasions because of the submerged trees and there were times when the net became entangled and brought tree-branches to the surface. Samples were abandoned when this happened.

The hydraulic winch was operated at full speed (c. 20 m min^{-1}) as catches appeared to be rather lower at half-speed (Table 13). This was especially so at Full Moon and it was possible that the fish were able to see and avoid the net more easily. There was relatively little variation between catches at New Moon and First Quarter but catches were seriously reduced at Full Moon (Table 13) which is a phenomenon that is

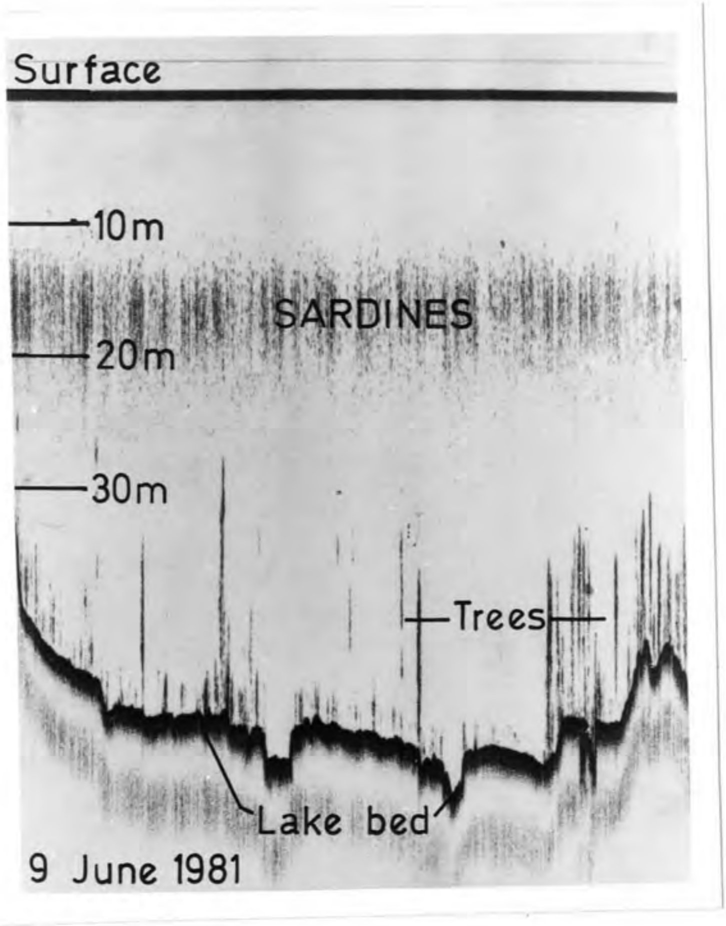


Figure 17: An echosounder trace from Lake Kariba, showing the typical distribution of sardines at night. Note the echoes from submerged trees on the lake bed.

readily apparent in the commercial catches. Accordingly the transect samples were taken as close to New Moon as possible in order to minimise this effect.

Table 13: The effect of winch speed and moon phase on Limnothrissa catches, using the experimental sampling gear without light attraction. All samples were taken between 1930 and 2130 hrs. and the data shown are the means of 6 hauls.

	Date	15 June 1981	22 June 1981	29 June 1981
	Moon Phase	Full Moon	First ¼	New Moon
Full speed (c.20 m min^{-1})	No./haul	2.7	32.0	20.0
	g/haul	3.8	51.1	36.6
Half speed (c.10 m min^{-1})	No./haul	0.2	23.5	18.0
	g/haul	0.3	37.5	32.9

Five samples were taken at each station with the net being hauled vertically to the surface and the fish being removed from the bottom of the cone. Since the refrigeration facilities on the "Pelican" were unreliable the samples were preserved in 10% formalin. The fish were removed the following morning and washed, their total weight was determined and each fish measured to the nearest millimetre (total length). The mean individual weight was then estimated by dividing the total by the number of fish in the sample.

The effect of formalin on the weight of the sardines was examined by preserving 20 samples of 5 fish in the preservative. They were weighed fresh and then 1, 2 and 6 days after being placed in formalin. There was an overall increase in weight of from 5 - 10 % (mean = 8 %) after 1 day but no change on the second (Fig. 18). There was a slight decrease in weight by the 6th day but this could have been a result of the loss of body fluids caused by physical damage to the fish during handling.

The effect of formalin on the length of the fish was not determined as it has been shown that these changes are insignificant (Parker 1963).

Balon (1974c) noted the effect of formalin on the weights of several species of Kariba fish and found that weight both increased and decreased by as much as 20 %. He concluded that the effect of formalin on fish weight was highly variable and should be determined separately in each new study.

A number of people were responsible for taking the length measurements of the sardines and the effect of individual biases had to be taken into account. A common practice was the tendency to round off to the nearest 5 mm and an extreme example of this is shown in Fig. 19, where clear peaks at exactly 5 mm intervals are evident. Such a length-frequency pattern is unlikely to occur naturally and once this problem was pointed out to staff it did not occur again. Balon (1974c) also noted the effect of individual bias and found that measurements made by others differed by anything from -5% to +11 % from those made by himself. Once again, such errors need to be assessed each time a new study is begun.

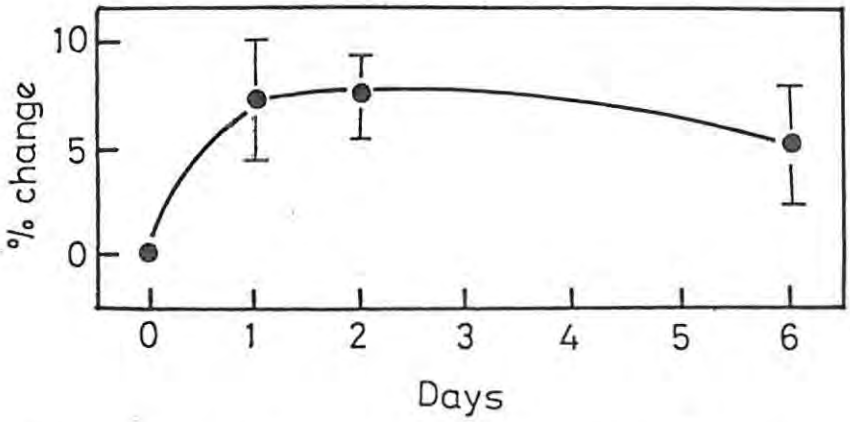


Figure 18: The change in weight of sardine samples preserved in 10% formalin for 1, 2 and 6 days. The points are means and the vertical bars represent ± 2 x standard error.

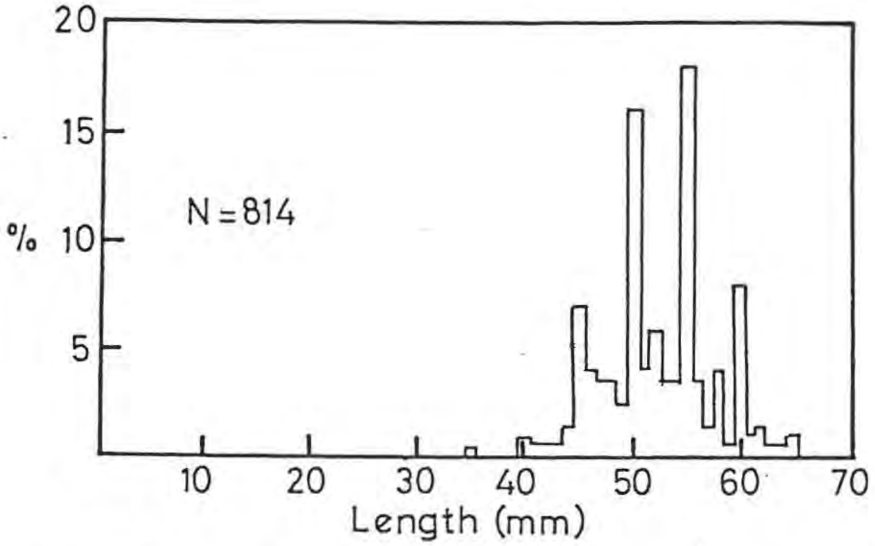


Figure 19: The length-frequency distribution of a sample of *Limnothrissa* collected in May 1982 to show the effect of personal bias in making measurements. Note the peaks at 5 mm intervals.

CHAPTER 5: EFFORT AND CATCH IN THE COMMERCIAL FISHERY

INTRODUCTION

Fishing is one of the major influences exerted by humans on the fish populations and its effect may be reflected in changes in the catch per unit effort (CPUE). Catch and effort are therefore fundamental data required for the management of any fishery and without this information it becomes very difficult to make any predictions about the potential yield. The statistics from the Kariba sardine fishery are very detailed and are thus of critical importance to this project which is an attempt to improve the predictions of potential yield for management purposes.

The way these statistics were collected has already been described (ch. 4). This chapter will present the data and they will later be used in the surplus yield models (Schaefer 1957; Fox 1970) to enable predictions of maximum sustainable yield and optimum effort to be made (ch. 10).

EFFORT

The methods used to catch sardines on Kariba have been described elsewhere (Begg 1974a; Cochrane 1978; Anon. 1978; Langerman 1979) and need not be considered in detail. A brief description is necessary, however, because the use of different methods on the Zimbabwean side has made the calculation of effort rather more complex than it would have been if only one type was in use as it is in Zambia.

The nets in use were divided into three categories, as follows:

Category A: in which the net is less than 30 m in circumference. These are all the "dip-net" type, which is a conical net suspended over the side or stern of the boat and hauled vertically to the surface. All gear in use on the Zambian side is equivalent to this category.

Category B: in which the net is 30 - 100 m in circumference (for a lift-net) or length (for a purse-seine). This category includes the larger lift-nets and chiromila purse-seines (see Coulter and Znamensky 1971).

Category C: which are large purse-seines with a length of more than 100 m but less than 200 m.

For the purpose of estimating effort, A category nets were regarded as 1 unit of effort, B category as 1.5 units and C category as 2 units. This was based on the ratio of the B and C catches to those from the A category nets (Table 14) and appears to have been fairly consistent since 1978 when A nets were first introduced. The mean C category ratio of 2.34 appears to be exceptionally high but it has been inflated by the ratio of 3.89 recorded in 1978. This was probably abnormal because there were very few A category boats in operation at that time and they were probably not numerous enough to affect the catches of the C category nets. If the 1978 data are excluded the ratio becomes 2.03 which is close to the figure that has been adopted.

Table 14: The total effort, mean nightly catch and ratio of catches for the 3 gear categories in use on Lake Kariba, 1978-1983. The data include Zambian vessels which are all equivalent to the Zimbabwean A category.

	Boat-nights			Boat-nights (%)			Mean nightly catch (t)*			Catch ratio		
	A	B	C	A	B	C	A	B	C	A	B	C
1978	905	4 260	898	14.9	70.3	14.8	0.28	0.61	1.09	1.00	2.18	3.89
1979	4 877	5 607	1 111	42.0	48.4	9.6	0.30	0.49	0.77	1.00	1.63	2.57
1980	17 649	7 795	1 227	66.2	29.2	4.6	0.23	0.37	0.50	1.00	1.61	2.17
1981	28 113	6 997	807	78.3	19.5	2.2	0.29	0.38	0.61	1.00	1.31	2.10
1982	43 127	2 879	940	91.9	6.1	2.0	0.22	0.26	0.41	1.00	1.18	1.86
1983	55 100	2 256	879	94.8	3.9	1.3	0.22	0.23	0.32	1.00	1.04	1.45
									Mean	1.00	1.49	2.34

*Based on Kariba-based vessels only as all boats from Kariba fish in the same areas and B and C category gear is not used elsewhere.

There has been a steady shift from the larger gear types and the A category boats now account for nearly 95% of the total effort. Linked with this is a steady decline in the efficiency of the other two types and the catch ratios in 1983 were reduced to 1A: 1.04B:1.45C and the original classification of effort into 1A:1.5B:2.0C may well become redundant. One of the reasons for this is that the owners of A category nets have been able to reduce their labour requirements by developing hydraulic and electrical winches for hauling their nets. This has enabled them to increase the number of hauls they can make per night and so improve their efficiency. By contrast the purse-seines are brought in by hand and the number of hauls they can make in a night has not been increased. In addition the purse-seines are 35 m deep and so they are limited in the areas they can fish; this problem has become especially serious as the lake level has dropped because of the increased danger of snagging the nets in trees.

Because of this it was decided to retain the 1:1.5:2 ratio as it could be restored if mechanical hauling of purse-seines could be introduced or if the lake level rises. B and C category nets are now such a small proportion of the total effort that final estimates are unlikely to be significantly biased.

Total effort in the fishery is therefore expressed as "unit-nights" with 1 unit-night being the actual night fished but multiplied by a correction factor of 1.5 for B nets and 2.0 for C nets. By 1983 the total effort had reached 60 000 unit-nights (Table 15) of which about 39 000 were on the Zimbabwean side.

Table 15: Fishing effort (unit-nights) from various areas of Lake Kariba, 1974-1983 (Zimbabwean data from L.K.F.R.I. records; Zambian data from Department of Fisheries, Chilanga).

Area	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Kariba	616	1 297	1 833	3 113	8 995	14 404	22 818	24 393	23 578	24 481
Bumi						195	789	1 670	1 459	1 036
Chalala						43	6 052	9 953	10 560	11 645
Sengwa					96	319	586	668	539	565
Binga-Mlibizi						548	1 550	1 188	1 291	1 063
Total (Zimbabwe)	616	1 297	1 833	3 113	9 091	15 509	31 795	37 872	37 427	38 790
Siavonga								2 057	8 798	13 449
Chipepo								268	1 781	3 421
Sinazongwe								26	1 347	4 402
Total (Zambia)								2 351	11 926	21 272
TOTAL	616	1 297	1 833	3 113	9 091	15 509	31 795	40 223	49 353	60 062

This total was allowed to rise rapidly on the Zimbabwean side from 1978-1980 but has increased very slowly since then, whilst the Zambian fishery began in 1981 and has increased steadily ever since. It is not known what is the present maximum effort the Zambians will permit and the lack of co-ordination between the two authorities is a matter for concern.

CATCH

The total sardine catch rose from 487 t in 1974 to 13 573 t in 1983 (Fig. 14) of which 8 603 was taken in Zimbabwe and 4 970 in Zambia. The most important area on the Zimbabwe side is Kariba itself and vessels based there all fish within the Sanyati Basin. The other important areas were Chalala, and Siavonga in Zambia and these three areas between them produced about 78% of the total catch (Table 16). If catch is expressed as in terms of area it can be seen that the lake yielded 28.16 kg ha^{-1} in 1983 (Table 17) which is the highest yet recorded; if the yield was expressed in terms of the "standard" lake level of 5 400 km^2 then the 1983 yield is reduced to 25.13 kg ha^{-1} but it still remains the highest recorded figure.

Table 16: Total catch of *Limnothrissa* (t) from various areas of Lake Kariba, 1974-1983.

	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Kariba	487	654	1 050	1 171	2 737	4 554	5 957	7 408	5 249	5 590
Bumi						78	172	284	232	171
Chalala						8	1 259	2 878	2 486	2 567
Sengwa					35	83	116	171	112	98
Binga-Mlibizi						151	484	390	309	177
Total, Zimbabwe	487	654	1 050	1 171	2 772	4 874	7 988	11 131	8 388	8 603
Siavonga								738	1 817	2 545
Chipepo								124	378	851
Sinazongwe								10	468	1 574
Total, Zambia								872	2 663	4 970
TOTAL	487	654	1 050	1 171	2 772	4 874	7 988	12 003	11 051	13 573

Table 17: Sardine yield from Lake Kariba in relation to lake area.

	Mean lake level (m.a.s.l.)	Mean lake area (km^2)	Yield (t)	Yield ($kg\ ha^{-1}$)
1974	486.27	5410	487	0.90
1975	485.03	5300	654	1.23
1976	486.06	5400	1 050	1.94
1977	486.34	5415	1 171	2.16
1978	486.65	5420	2 772	5.11
1979	485.17	5405	4 874	9.02
1980	485.76	5340	7 988	14.96
1981	486.31	5412	12 003	22.18
1982	483.65	5180	11 051	21.33
1983	481.09	4820	13 573	28.16

If approximately 2 000 t of inshore fish are added to this total the yield from Kariba becomes 32.31 kg ha^{-1} which is very close to the predicted yield in Table 6. However, it is still below the yield from the other large reservoirs such as Volta which produced 57 kg ha^{-1} in 1979 (Vanderpuye 1984) or Nasser-Nubia which yielded 76 kg ha^{-1} in 1981 (Latif 1984). In both cases this came from gillnet fisheries alone and there is little doubt that Volta's yield would be greatly increased if its clupeid stocks were utilised.

CATCH PER UNIT EFFORT

As in any other fishery CPUE of Kariba sardines decreased as the fishing effort increased and by 1983 the CPUE was only 0.23 t unit-night^{-1} (Table 18). This trend was consistent in all areas of the fishery with the exception of Sinazongwe and Chipepe in Zambia. Effort in these areas was relatively low (Table 15) and may not have had any effect on the stock there although this is to be expected as effort is increased. CPUE generally showed an increase in 1981 which was an exceptionally good year for most fishermen and possibly atypical.

DISCUSSION

The catch data make it possible to give accurate estimates of effort, yield and CPUE for the Kariba sardine fishery. A striking feature was the sharp decline that took place in 1982 and 1983, especially in the Sanyati Basin. As it had been suggested that poor river flow might affect catches (Marshall 1982a) it is worth examining this aspect in more detail.

Sanyati Basin catches dropped from 11 000 t in 1981 to 8 400 t in 1982 and 8 600 t in 1983. There was a breakdown in the normal seasonal pattern with the August-September peaks being greatly reduced (Fig. 12). Overall CPUE dropped from 0.26 t in 1980 to 0.22 t in 1982 even though effort had not changed significantly; this can be shown clearly by plotting total yield against total effort (Fig. 20).

There are two possible explanations for this. The first is that the increase in the numbers of fishermen at Siavonga led to competition with the Kariba-based boats although they tend not to fish in the same areas and the Zambian vessels do not fish

Table 18: CPUE (t unit-night^{-1}) from various areas of Lake Kariba, 1974-1983.

	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Kariba	0.79	0.50	0.57	0.38	0.30	0.32	0.26	0.30	0.22	0.23
Bumi						0.40	0.22	0.17	0.16	0.17
Chalala						0.19	0.21	0.29	0.24	0.22
Sengwa					0.36	0.26	0.20	0.26	0.21	0.17
Binga-Mlibizi						0.28	0.31	0.33	0.24	0.17
Zimbabwe mean	0.79	0.50	0.57	0.38	0.30	0.31	0.25	0.29	0.22	0.22
Siavonga								0.36	0.21	0.19
Chipepo								0.46	0.21	0.25
Sinazongwe								0.38	0.35	0.36
Zambia mean								0.37	0.22	0.23
Mean, all areas	0.79	0.50	0.57	0.38	0.30	0.31	0.25	0.30	0.22	0.23

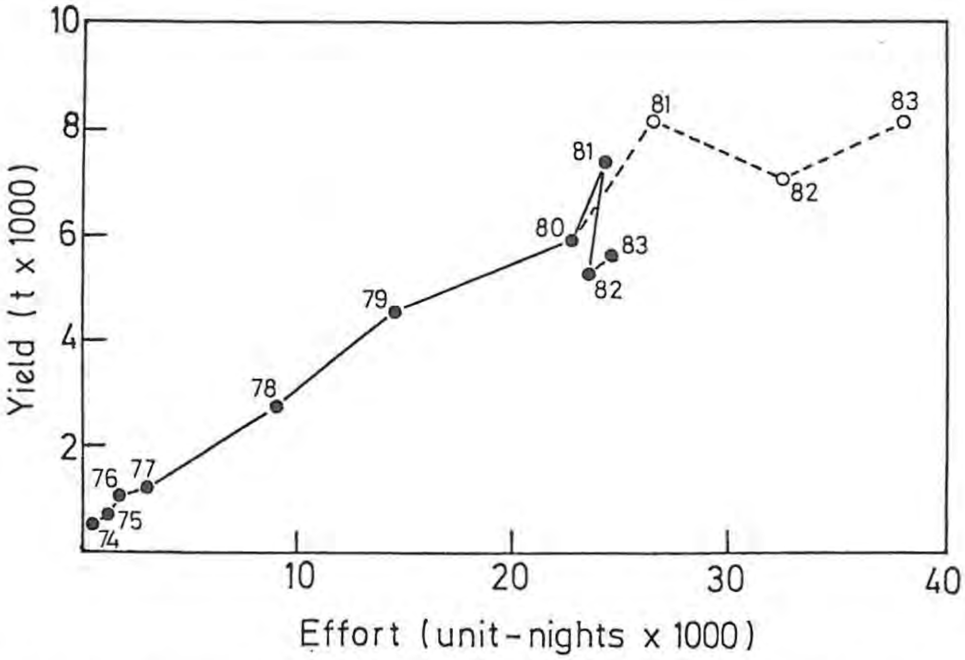


Figure 20: The relationship between effort and yield for Kariba-based vessels (solid line) and combined Kariba and Siavonga-based vessels (broken line).

in the Sanyati Basin itself. This may indeed be a factor but the combined data from Kariba and Siavonga show that there was an overall decline in 1982 but that the general trend appeared to be re-establishing itself (Fig. 20). The CPUE at Siavonga dropped in 1983 but it increased slightly at Kariba where fishermen put a great deal of effort into improving their fishing efficiency. This was reflected by a slightly increased catch but the normal seasonal pattern was not restored and this suggests that a basic biological factor was responsible for the low catches.

It has already been shown that fish catches in the Sanyati Basin are influenced by the flow of the Sanyati River (Fig. 11) and since the flow of the river was extremely poor in 1981-82 and 1982-83 this might be the reason why the catches were reduced. Flow data for the Sanyati are not, unfortunately, available for the last few years but some indication of flow can be obtained from the estimates of mean rainfall in the catchment area (Zimbabwe Meteorological Dept. 1980, 1982a,b) which was as follows:

1979-80 :751.0 mm, leading to "normal" flow in 1980.
1980-81 :988.1 mm, leading to "good" flow in 1981.
1981-82 :408.1 mm, leading to "poor" flow in 1982.

Examination of the catch data for these three years reveals that they were much the same for the early part of the year i.e. from January-April (Fig. 21). From then on they were considerably different. In all three years there was a drop in the catch in May but in 1980 and 1981 there was a rapid recovery to a peak in August or September. As shown earlier (Fig. 13),

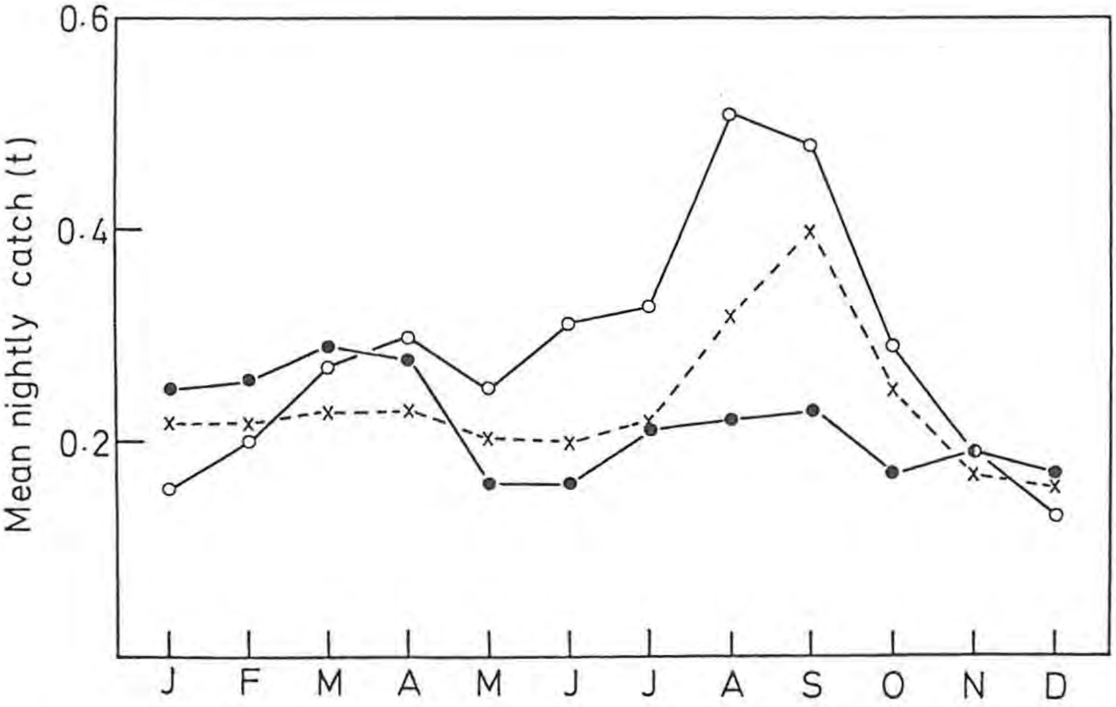


Figure 21: The mean nightly catches recorded by Kariba-based "A" category vessels. X , 1980: ○ , 1981: ● , 1982.

this peak follows the plankton peak that results from the release of hypolimnetic nutrients at turnover. These nutrients are brought in by the rivers and so if river flow is poor, nutrient supplies will be reduced and a low catch is likely during August or September. This was indeed the case during 1982 when catches were very low and did not even equal those recorded during the early part of the year. This supports the suggestion that river flow is a major influence on sardine abundance and it will be interesting to see what follows from a year of good rainfall.

There remains the possibility that these fluctuations are within the range of normal variability and that there is no single extrinsic factor responsible for them. The data series is still too short to show whether this is the case but it is hoped that they will eventually be explained satisfactorily because of their economic consequences for the fishery.

CHAPTER 6: GROWTH AND MORTALITY

INTRODUCTION

Growth and mortality parameters are probably the most important data needed for any fish stock assessment as they are used in almost all the deterministic models (e.g. see Beverton & Holt 1957; Ricker 1975; Gulland 1983). The growth of Limnothrissa has been investigated in Lake Kariba (Cochrane 1978, 1984) but there are no data on mortality except for some preliminary results from this project (Marshall 1984a). It is necessary, therefore, to re-examine growth so that mortality can be estimated.

The differences in growth of Limnothrissa in lakes and reservoirs has already been described (ch. 3) and it is clear that changes in growth rate are an important aspect of the sardine's response to its environment. This question will be explored further in this chapter.

METHODS

Growth

Methods for determining fish growth have been reviewed by many authors and can be divided into 3 basic categories (Jearld 1983);

(i) an empirical approach based on direct observation of fish held in captivity or marked and recaptured. This method could not be used with Limnothrissa because the sardines were very delicate and any handling invariably resulted in the death of the fish. They can only be handled as very small fry (Matthes 1967b) when, of course, they cannot be marked. Some fry were raised in an aquarium at Lake Kariba Fisheries Research Institute but their growth rate was only about half that noted by Cochrane (1978) and the experiment was considered a failure (J.D. Langerman, personal communication).

(ii) an anatomical approach based on aging individual fish from scales, bones or other structures. Since Limnothrissa is a small fish with a short life-cycle clear marks were not apparent on most hard body structures. Begg (1974a) found marks on the scales of large (> 70 mm) sardines which might have been annual marks, but he was unable to verify this. A difficulty with using sardine scales is that they are nearly all shed when the fish are caught and it is thus impossible to obtain a standard sample. It is also difficult to tell if a scale found on a fish belonged to that fish or whether it was a detached scale from another.

The presence of diurnal rings on fish otoliths has also been used as an aging criterion (Pannella 1971) and applied to the larvae of Engraulicypris sardella (Günther) in Lake Malawi (van Lissa 1982). The method is extremely time-consuming, however, and as suitable microscope facilities were not available at Kariba no attempt was made to use it.

(iii) the final approach is a statistical one based on the analysis of length-frequency distributions. This was the method that was ultimately adopted; as it contains a high degree of subjectivity it was necessary to use various methods to separate the individual modes from the polymodal distributions. They included using probability paper (Cassie 1954), semi-logarithmic plotting plus fitting parabolas to the plot (Tanaka 1962) and plotting natural logarithms of the frequencies, then fitting a straight line to the significant differences (Bhattacharya 1967). The latter was generally the most satisfactory method and was therefore used most often.

Growth can be expressed in mathematical terms; the von Bertalanffy equation is the most frequently-used model and Pauly (1981) has shown that its application to fish is realistic on physiological grounds. Beverton & Holt (1957), Ricker (1975) and Gulland (1983) should be referred to for the derivation and methods of fitting the equation and the following account is drawn from these sources.

The von Bertalanffy equation for growth in length is

$$l_t = L_\infty \left[1 - e^{-K(t - t_o)} \right]$$

where l_t = length at time t (mm), L_∞ = the asymptotic length or the length the fish would reach if it were to grow indefinitely, K = a growth constant and is the rate at which the fishes' length approaches L_∞ and t_o the "age" at which the fish would have a length of zero.

Once the length modes were identified a Ford-Walford plot (Gulland 1983) was constructed. In this length

$(l_t + 1)$ is plotted against length one month earlier (l_t), and a line of equality drawn in. A regression line was then fitted to the data points and the intersect of this line with the line of equality provides a visual estimate of L_∞ . If the slope of the regression line is steep the visual estimate may be unreliable and L_∞ can be fixed with greater precision by

$$L_\infty = \frac{a}{1 - b}$$

where a and b are the regression constants.

The slope of the regression (b) is equal to e^{-K} and so the growth constant $K = -\log_e b$.

The final parameter of the von Bertalanffy equation, t_o, is more difficult to estimate, especially when fish of known age and length are unavailable. The parameter t_o is calculated by plotting $\log_e((L_\infty - l_t)/L_\infty)$ against time t. This gives a straight line with the slope = -K and the intercept on the t axis = t_o. Known-age Limnothrissa were not available so estimates of length at age (l_t) were made from growth curves fitted to the length-frequency distributions.

Some recent papers (Pauly & Martosubrato 1980; Petrere 1983) have used Pauly's empirical equation, based on 153 sets of t_o, L_∞ and K, to estimate t_o. In this

$$\log(-t_o) = -0.3922 - 0.2752 \log L_\infty \quad -1.038 \log K$$

where L_∞ is in cm (total length) and K is expressed on an annual basis. An estimate of t_o was obtained with this expression and compared with the figure obtained graphically.

Growth in weight was estimated from the length-weight relationship

$$w = a\ l^b$$

in which w = weight (g), l = length (mm) and a and b are the regression constants derived from the expression $\log w = a+b \log l$ (note that a is the antilog in the final equation).

The instantaneous growth coefficient, G, is used in production studies and is calculated from

$$G = \frac{(\log_e \bar{w}_2 - \log_e \bar{w}_1)}{\Delta t}$$

where G = instantaneous growth coefficient, $\bar{w}_1$ and $\bar{w}_2$ = the mean weights at times t_1 and t_2 and Δt is the difference in time between t_1 and t_2 (Chapman 1968).

Once the growth equation was calculated it was possible to estimate the age of a fish from its length by the equation

$$t = \frac{1}{K} \log_e \frac{L_\infty}{(L_\infty - l_t)} + t_o$$

where K, L_∞ , t_o are parameters of the von Bertalanffy equation and l_t = length at time t (Gulland 1983). This expression was used to construct a table of length at age for Limnothrissa and so made it possible to convert length-frequency distributions into age-frequency.

The previous parameters have all related to the growth of individual fish but the rate of growth of the population as a whole is of interest because of its application to certain yield prediction models. The rate at which a population would grow until the carrying capacity of the environment had been reached is referred to as the intrinsic rate of population growth

(r_m) (Andrewartha & Birch 1954). It is implicit in the surplus yield or "Schaefer" model (Pauly 1982) but is, unfortunately, rather difficult to estimate. Pauly (1982) showed that the relation between r_m and mean body weight obtained by Blueweiss <u>et al</u>. (1978) for a wide range of animals was applicable to fish in general. The estimate of r_m was obtained from the expression

$$r_m = 0.025\ \bar{w}^{-0.26}$$

where r_m is expressed on a daily basis and $\bar{w}$ = mean weight (g), and applied to various production models (ch. 10).

Mortality

Mortality is most usefully expressed as the decrease of an age group of fish with time by the expression

$$N_t = N_o e^{-Zt}$$

where N_o = initial number of fish at time t = o, N_t = the number of fish remaining at the end of time t, and Z = instantaneous rate of mortality (Pauly 1983). Since

$$Z = M + F$$

where M = instantaneous rate of natural mortality and F = the instantaneous rate of fishing mortality, it is possible to seperate mortality rate into that caused by fishing from that from other causes.

The samples taken from the commercial catches between 1978 and 1983 were aged and catch curves constructed for each year in order to calculate mortality. A catch curve is the natural logarithm of the number of fish in each age class ($\log_e N$) plotted against age (Ricker 1975). A regression can then be fitted to the right hand or descending curve so that

$$\log_e N = a - bt$$

and b, with the sign changed, gives an estimate of Z. The regression is fitted only to the descending arm of the curve because these are the fish that are fully vulnerable to the fishing gear.

Pauly (1983) has pointed out that when a length-frequency sample is converted to an age distribution the effect of non-linear growth is to distort the catch curve for older fish. This is because a size interval of larger fish will contain a wider range of age groups than the same size interval of smaller ones. He proposed a solution to this problem by rewriting the catch curve so that

$$\log_e(N/\Delta t) = a - bt$$

where Δt = the difference between the age at the upper and lower limits of the size class, t = the age at the midpoint of that size class and N = the number of fish in the size class. This procedure was used to estimate *Limnothrissa* mortality from commercial samples collected at Kariba and Bumi.

Catch curves give an estimate of Z or total mortality. In order to estimate natural mortality (M) the estimates of Z from Kariba and Bumi were plotted against the relative fishing effort (f) in each area. The lowest fishing effort at Bumi was regarded as $f = 1.0$ and the other effort values were converted to multiples of this. A regression was then fitted so that

$$Z = a + bf$$

where the intercept a = M (since f=0, F=0 and therefore M = Z).

The Kariba fishery is unusual in Africa because fishing effort is accurately known and so the method outlined can be used. For situations where effort is not known an empirical method of obtaining M from growth parameters and water temperatures has been developed (Pauly 1983). This method was employed as a comparison with the previous one, and uses the expressions

$$\log M = 0.0066 - 0.279 \log L_{\infty} + 0.654 \log K + 0.4634 \log T$$

and

$$\log M = 0.2107 - 0.0824 \log W_{\infty} + 0.6757 \log K \; 0.4687 \log T$$

where M = natural mortality (annual rate), L_{∞} and W_{∞} = asymptotic total length (cm) and weight (g), K = growth coefficient and T = mean water temperature (°C).

RESULTS

Growth

A comparison of the mean lengths and weights of sardines from two transect stations (Station 6, inshore and Station 4, pelagic) gave a useful indication of the general pattern of growth. Mean sardine lengths at Station 6 declined from about August 1981 onwards, suggesting that smaller fish were beginning to appear in the inshore areas (Fig. 22a). The smallest mean length occurred, however, in January 1982 indicating that this was the peak breeding period when the greatest number of small fish were present and from then on the mean length increased steadily, to a maximum of 55 mm in November. The pattern repeated itself in 1982-83 but the smallest mean length was recorded in February-

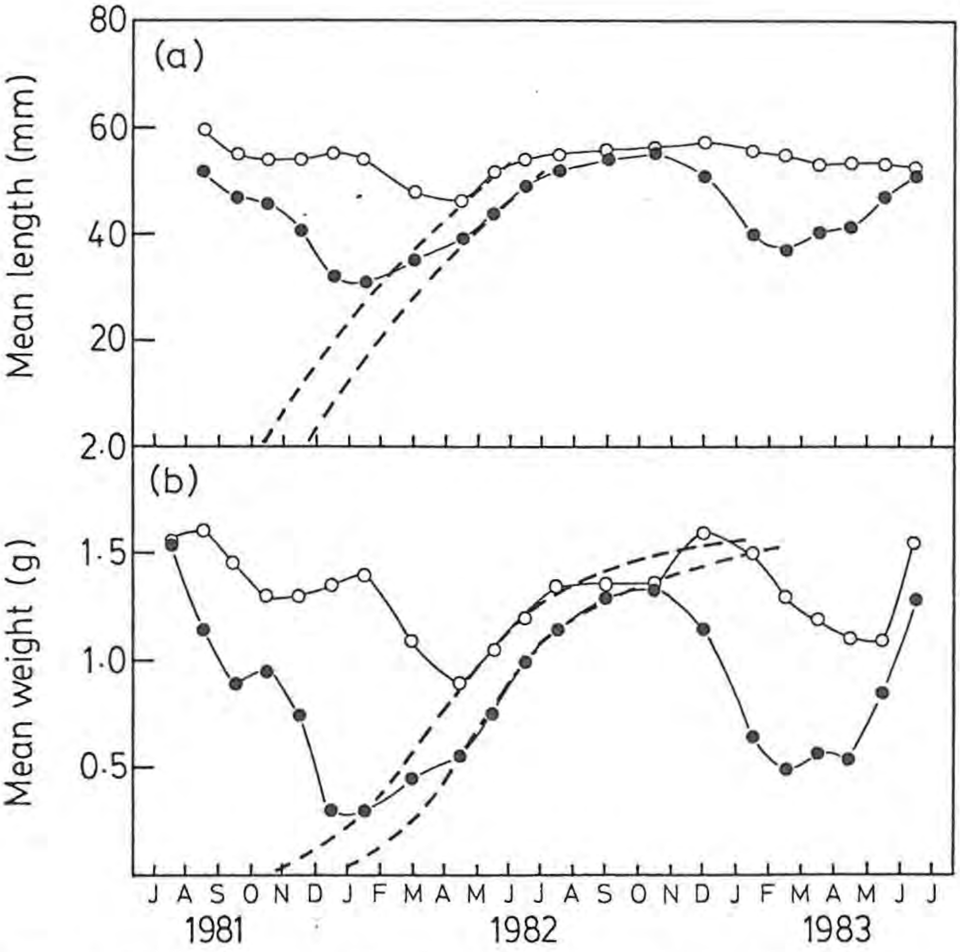


Figure 22(a) The mean lengths of fish taken at an inshore station, Station 6 (●), and a pelagic station, Station 4 (○).

(b) The mean weights of the same fish.

The data have been smoothed by plotting 2-month running means and the heavy broken lines indicate the general pattern of growth.

March and so the main breeding period was probably later than it had been the year before.

The mean lengths at Station 4 followed the same broad pattern but the fish were never as small as they were inshore and the smallest mean size was recorded about 3 months later. This can be attributed to the fact that the sardines breed in shallow water and move offshore as they grow larger (Fig. 9) and so relatively few small fish occur in pelagic waters.

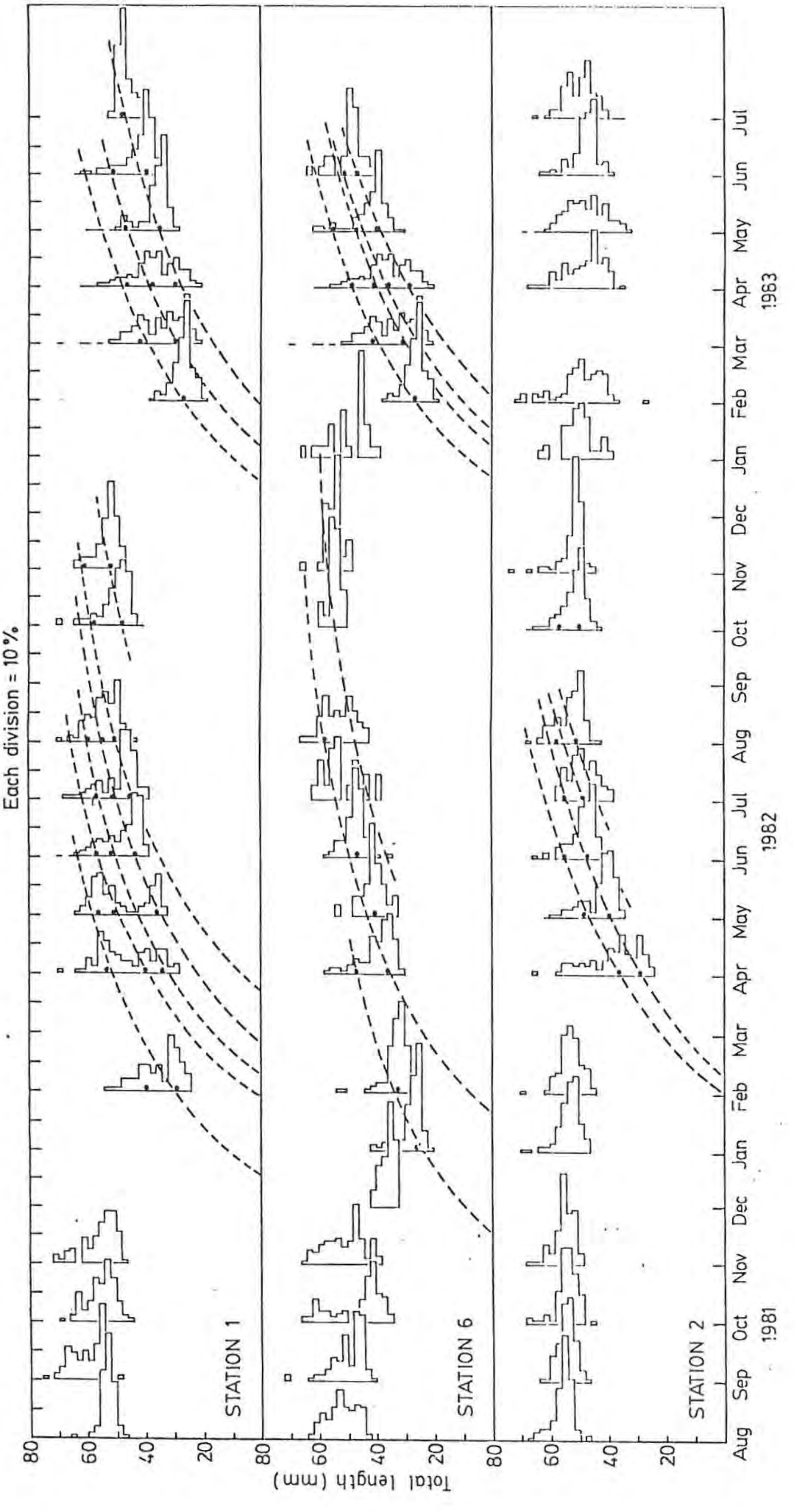
This pattern was shown even more clearly by the mean weights of the fish at the two stations (Fig. 22b). The typical S-shaped curve of weight growth is evident and the times when fish were spawned appear to be November-January in 1981-82 and January-March in 1982-83.

The general pattern therefore indicates that the sardines can grow to about 55 mm in length and 1.5 g in weight in a 12 month period. However, as their length distributions were usually strongly polymodal these data are likely to be biased and cannot be used to construct a growth equation.

This was done using data from Stations 1 and 6 i.e. those nearest the shore where the length modes were most clearly discernable. Length modes were not easily distinguished in the samples from pelagic stations except for Station 2 where a growth curve could be detected in 1982, but not in 1983 (Fig. 23).

Once the main length modes had been identified it was possible to fit them to a Ford-Walford plot (Fig. 24). The slope of the regression line through the points was 0.776 and so $K = 0.254$ and $L_{\infty} = 74.2$ mm, by calculation.

Figure 23: Length-frequency distributions of *Limnothrissa* from three Sanyati Basin transect stations. The points show some of the modes used in the Ford-Walford plot whilst the broken lines represent approximate growth curves.


Each division = 10%
STATION 1
STATION 6
STATION 2
Total length (mm)
80
60
40
20
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
1981
1982
1983

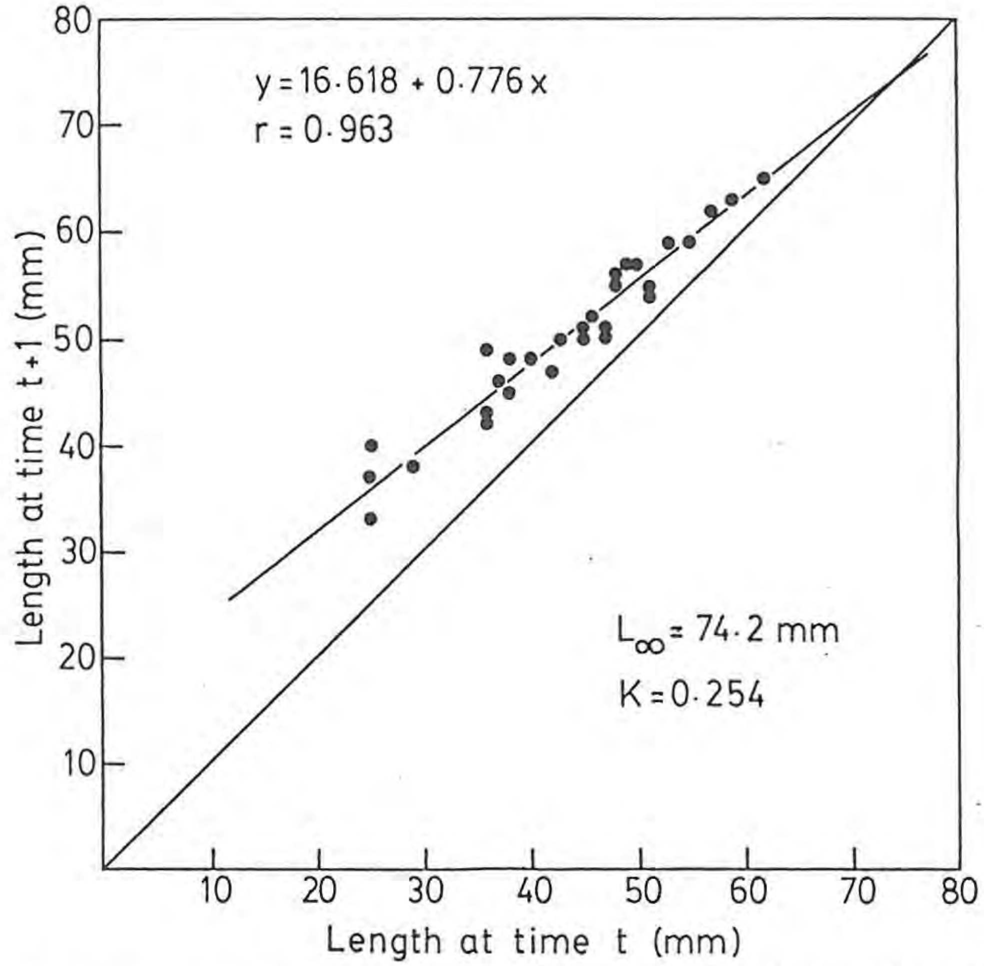


Figure 24: A Ford-Walford plot of sardine length-modes; data from Sanyati Basin Samples.

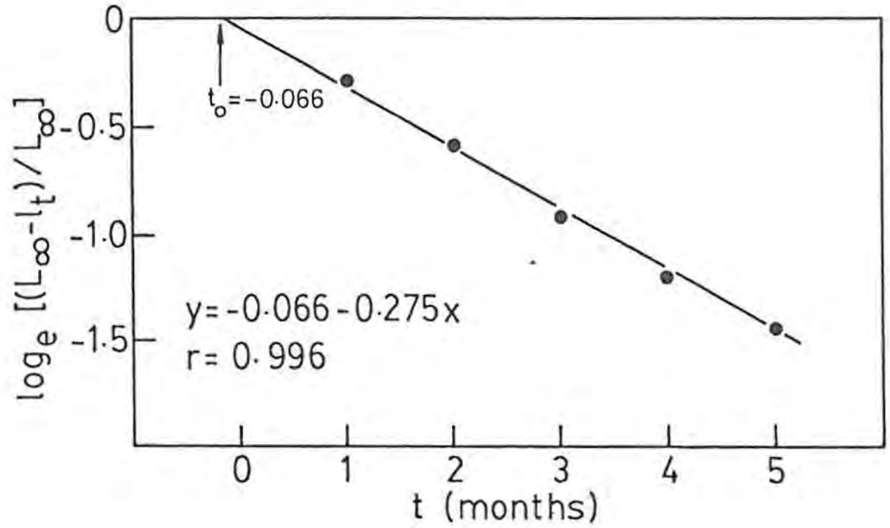


Figure 25: The estimation of t_o with length at age estimated from the growth curves shown in Fig. 23.

By plotting $\log_e((L_\infty - l_t)/L_\infty)$, where l_t was taken as the mean from the curves shown in Fig. 23, against t an estimate of $t_o = -0.066$ was obtained (Fig. 25). An estimate of $t_o = -0.07$ was obtained from Pauly's equation.

The growth of Limnothrissa can therefore be expressed by the following von Bertalanffy equation:

$$l_t = 74.2 \left[1 - e^{-0.254(t + 0.066)} \right].$$

In order to check that the Sanyati Basin samples were representative of the lake as a whole some samples were taken from shallow water (c. 20 m deep) in the Mwenda estuary in 1982. Several different cohorts appeared between January and June and the fish did not remain in the estuary much after they reached 40 mm (Fig. 26). A Ford-Walford plot drawn from these data gave $K = 0.219$ and $L_\infty = 71.8$ mm which is not significantly different from the estimates obtained from the Sanyati Basin samples.

The length-weight relationship, determined from a sample of 500 freshly-caught sardines, was

$$W = 0.000012\ l^{2.863} \qquad \text{(Fig. 27)}.$$

From this it was possible to construct a growth curve for weight and the curves for length and weight are shown in Fig. 28. The asymptotic weight (i.e. the weight of the fish at its asymptotic length) was $W_\infty = 2.72$ kg.

Instantaneous growth coefficients were calculated at monthly intervals for each age up to 12 months (Table 19). The coefficients were high at first but decreased exponentially and the mean was $G = 0.37$. The same mean could be obtained by calculation, using the mean weights at $t = 1$ and $t = 12$ months,

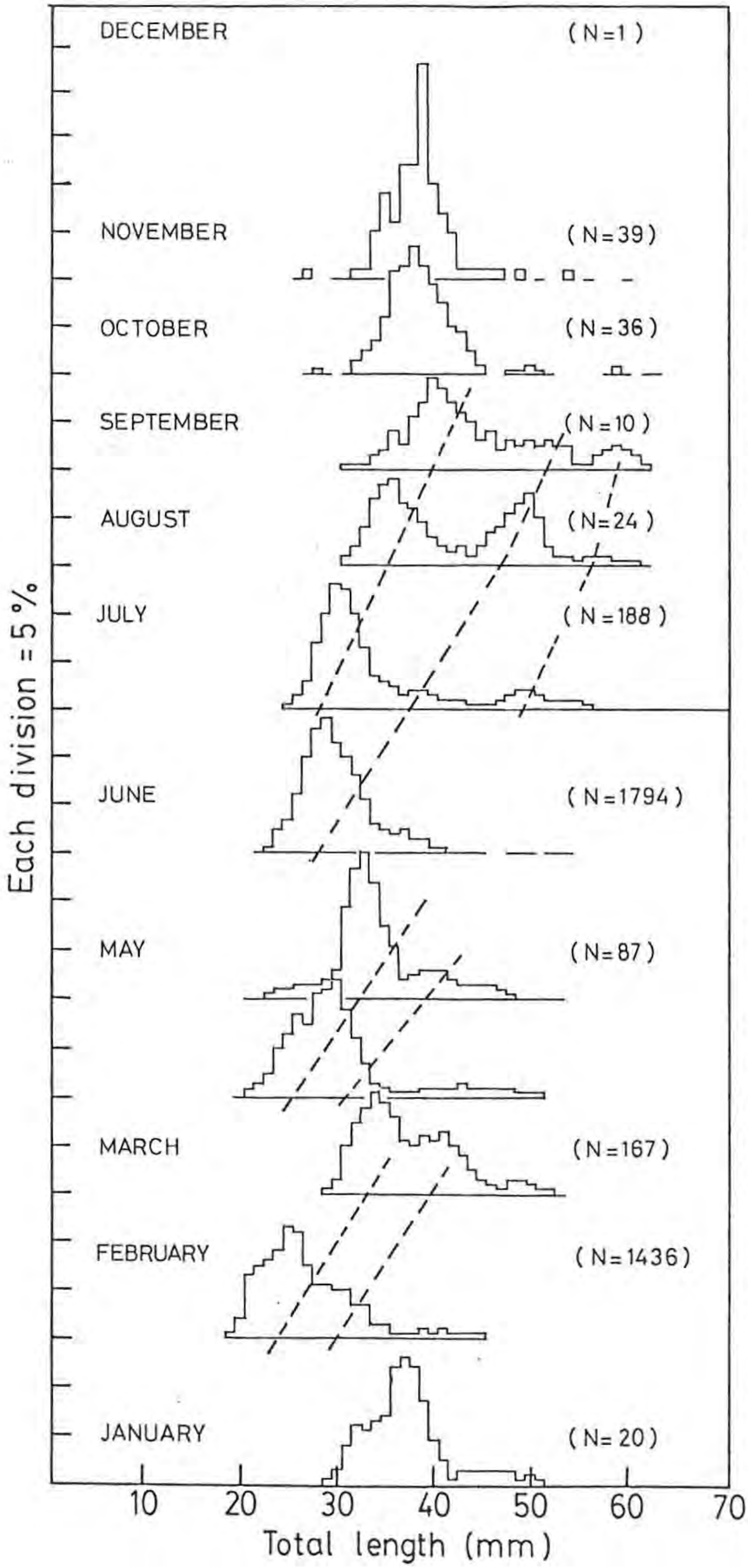
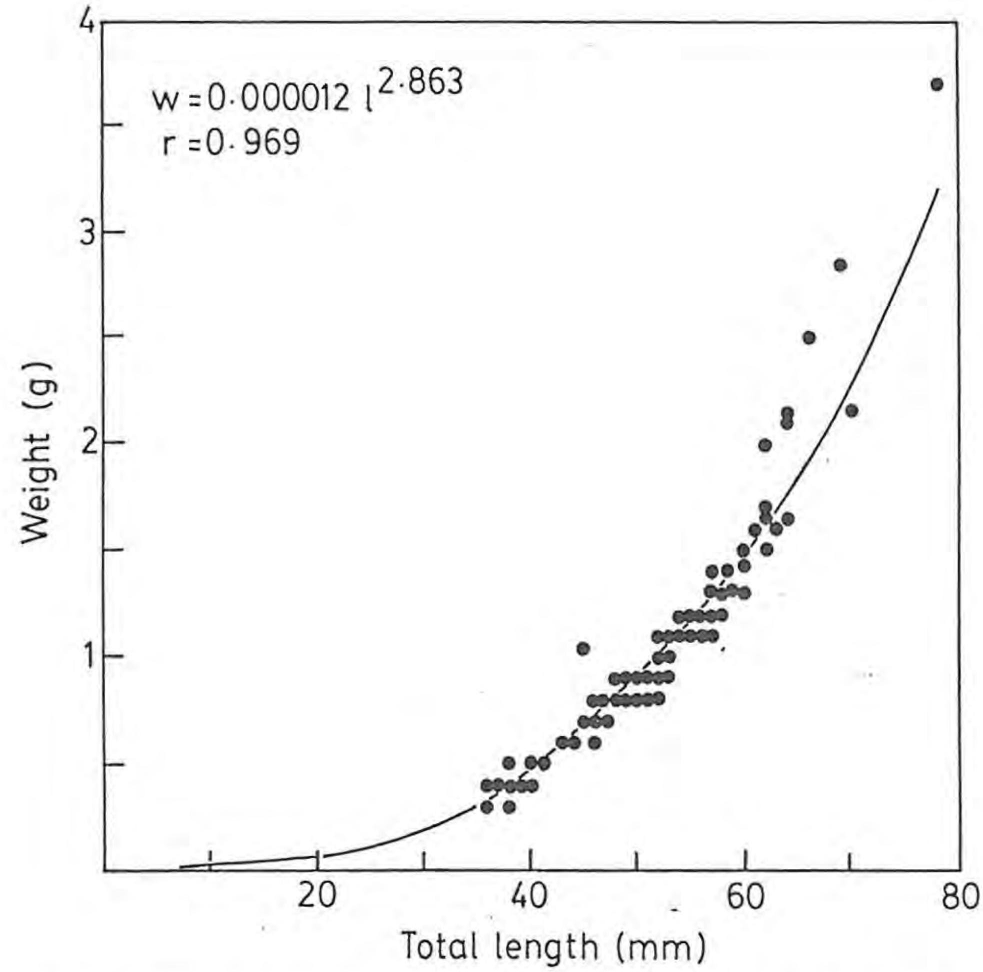


Figure 26: The length-frequency distributions of samples taken in the Mwenda estuary during 1982. The numbers in brackets are the number of fish taken per haul and the broken lines indicate the progression of the length modes.



<u>Figure 27</u>: Length-weight relationship of 500 freshly weighed <u>Limnothrissa</u> from Lake Kariba. Each point may represent several values.

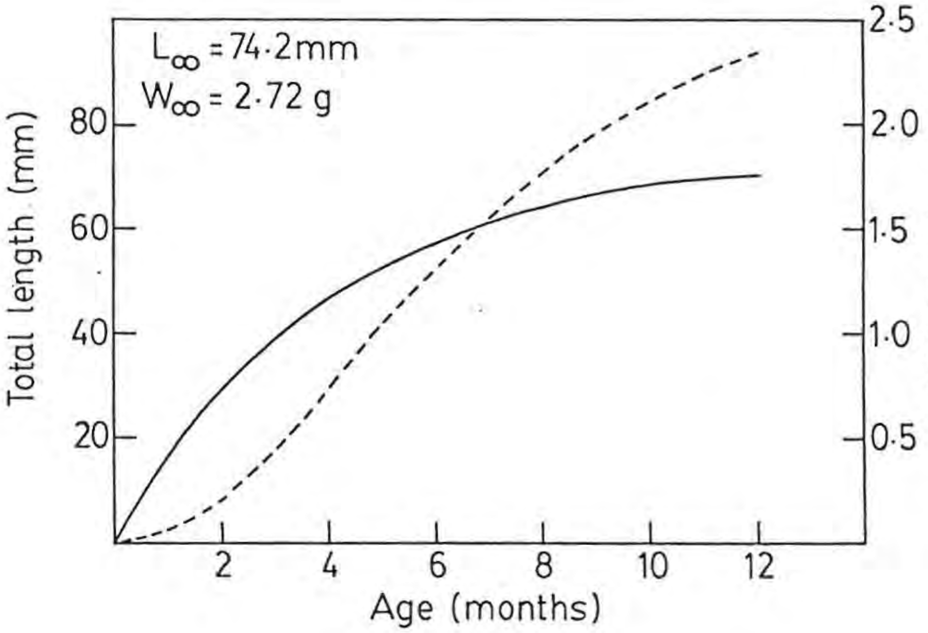


Figure 28: Growth curves for length (solid line) and weight (broken line) fitted with the von Bertalanffy equation for *Limnothrissa* from Kariba.

thus

$$G = \frac{(\log_e 2.37 - \log_e 0.04)}{11} = 0.37$$

Table 19: The growth coefficient (G) for sardines in Kariba, calculated at monthly intervals.

t (months)	l_t (mm)	$\bar{w}$ (g)	G
1	17.6	0.04	1.66
2	30.3	0.21	0.81
3	40.1	0.47	0.49
4	47.8	0.77	0.34
5	53.7	1.08	0.23
6	58.3	1.36	0.17
7	61.9	1.62	0.12
8	64.6	1.83	0.09
9	66.8	2.01	0.07
10	68.4	2.15	0.05
11	69.7	2.27	0.04
12	70.7	2.37	
		Mean	0.37

The mean lengths at each age were then estimated (Table 20). Accurate ages could only be assigned to fish up to 12 months old or about 74 mm in length because after that the growth increments were too small to be distinguished.

Table 20: Conversion of length to age for Limnothrissa in Lake Kariba.

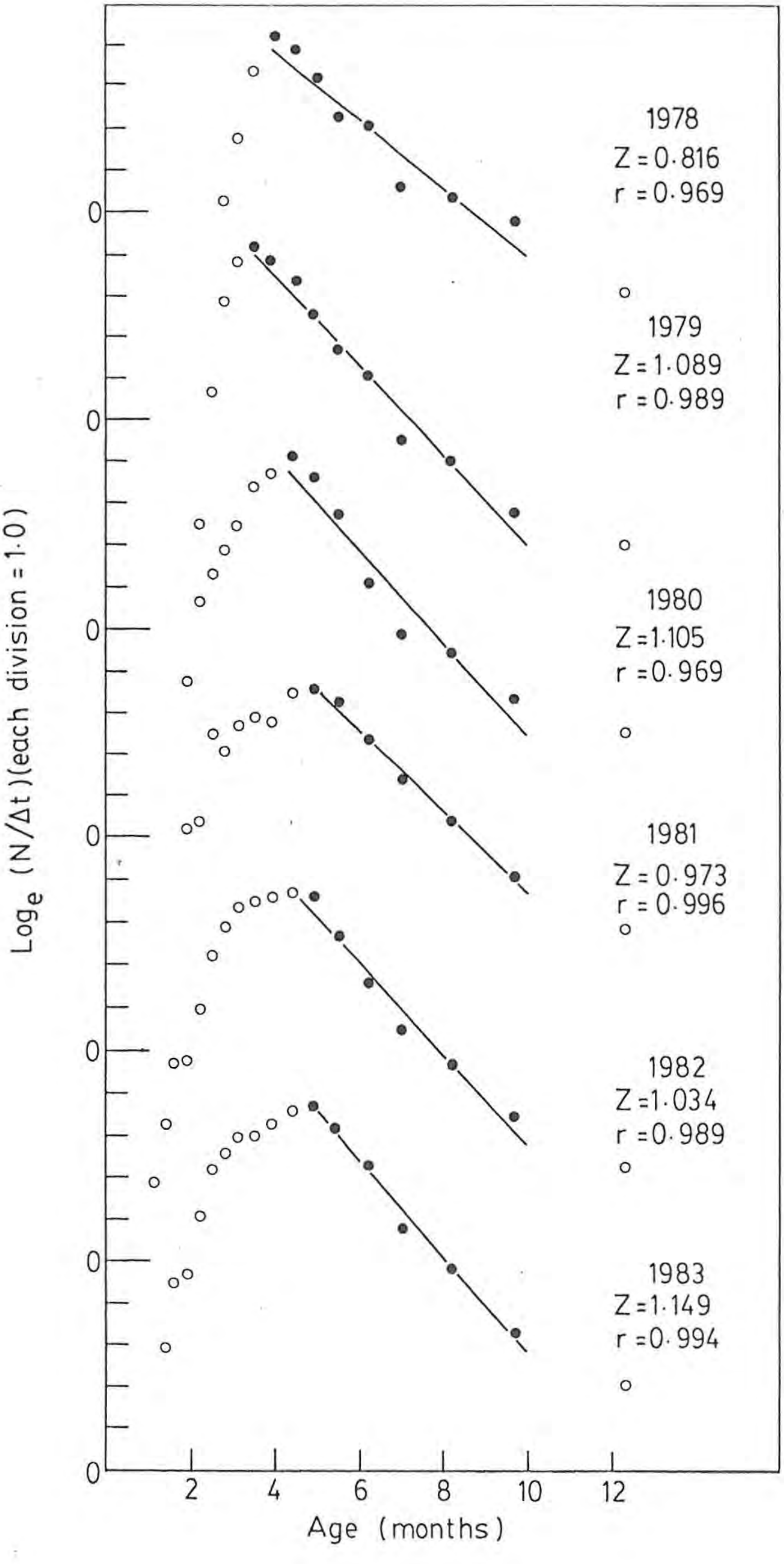
Length range (mm)	Age (months)	
	Range	Midpoint
10-24	0.51 - 1.50	1.0
25-35	1.51 - 2.50	2.0
36-44	2.51 - 3.50	3.0
45-50	3.51 - 4.50	4.0
51-56	4.51 - 5.50	5.0
57-60	5.51 - 6.50	6.0
61-63	6.51 - 7.50	7.0
64-65	7.51 - 8.50	8.0
66-67	8.51 - 9.50	9.0
68-69	9.51 -10.50	10.0
70	-	11.0
71	-	12.0
72	-	14.0
73	-	16.0
74	-	23.0

The last growth parameter to be estimated was the intrinsic rate of growth (r_m). The mean length of 30 000 fish taken from the commercial catches was 50.61 mm and so the mean weight, calculated from the length-weight relationship, was 0.91 g. From this, $r_m = 0.026$ (daily rate) and $r_m = 9.490$ (annual rate).

Mortality

Catch curves for the Sanyati Basin fish show that total mortality was very high and the monthly rates ranged from 0.816 in 1978 to 1.149 in 1983 (Fig. 29). The rates were lower

Figure 29: Catch curves for *Limnothrissa* taken from the Sanyati Basin, 1979-1983. The open circles represent younger age classes which were not fully selected and have therefore been excluded from the regressions used to calculate Z.


Loge (N/Δt) (each division = 1·0)
0
0
0
0
0
0
0
2
4
6
8
10
12
Age (months)
1978
Z = 0·816
r = 0·969
1979
Z = 1·089
r = 0·989
1980
Z = 1·105
r = 0·969
1981
Z = 0·973
r = 0·996
1982
Z = 1·034
r = 0·989
1983
Z = 1·149
r = 0·994

for fish taken in the Bumi estuary, ranging from 0.695 to 0.718 (or approximately 0.7 in each case) (Fig. 30).

This suggests that the Bumi fish were a separate stock and not influenced by fishing in the Sanyati Basin. For this reason the Bumi and Sanyati data could be used to obtain an estimate of natural mortality (M), by plotting Z against relative fishing effort (Fig. 31). The intercept of the regression through the points on to the x axis is equivalent to M and so M = 0.731. Two of the estimates for Z at Bumi are rather lower than this but if all the figures are rounded off to one decimal place they all become 0.7 and it would appear that the low levels of fishing effort at Bumi have not significantly increased the mortality rate.

A final estimate of mortality can be obtained from Pauly's equation, and they were

(i) from L_∞ : 5.28 (annual rate) = 0.44 (monthly rate).

(ii) from W_∞ : 5.54 (annual rate) = 0.46 (monthly rate).

DISCUSSION

The general pattern of growth revealed that there were several cohorts produced during an extensive breeding season and in this respect Limnothrissa is similar to the other clupeids (Roest 1978; Chapman & van Well 1978). Breeding appeared to take place rather later in 1982-83 than it had a year previously but the reasons for this are not apparent.

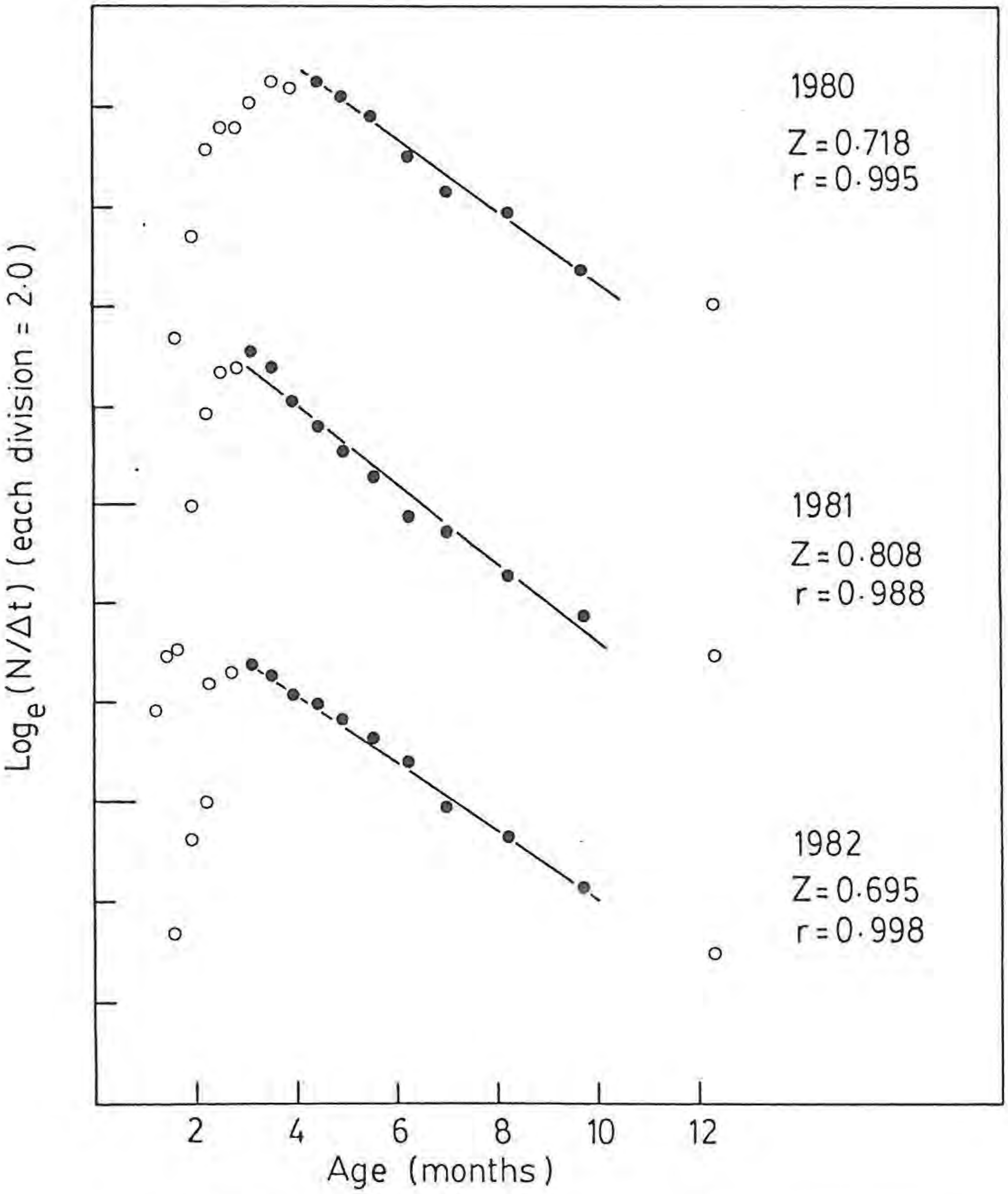


Figure 30: Catch curves for Limnothrissa taken from the Bumi estuary from 1980-1982. As in Fig. 29 the open circles represent inadequately selected age classes and have not been used for the estimation of Z.

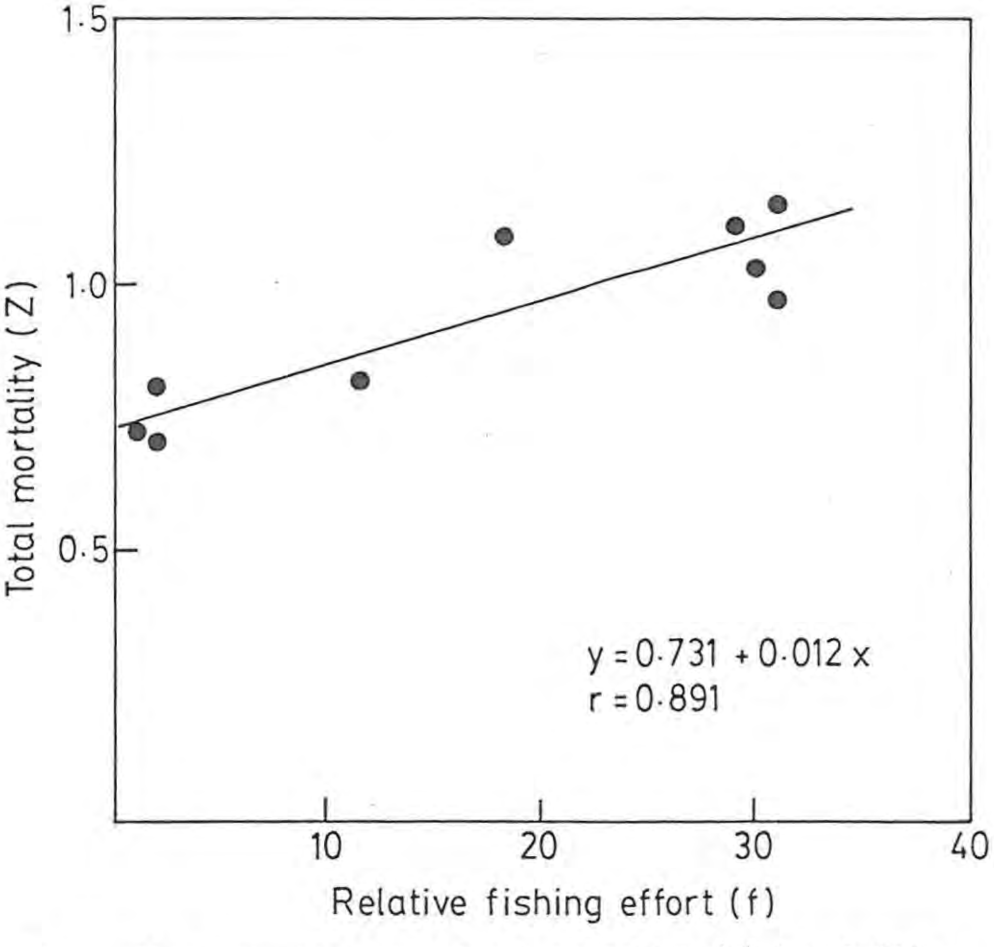


Figure 31: Estimation of natural mortality (M) by plotting Z against relative fishing effort (f) for samples taken from the Sanyati Basin and Bumi estuaries.

The discussion that follows is based on the assumption that the von Bertalanffy equation is a realistic description of fish growth. It is used very widely and is an essential requirement for the dynamic-pool models of Beverton & Holt (1957) which form the basis of many subsequent concepts in fish population dynamics. Some authors have argued that this general acceptance has obscured some basic defects in the equation.

Paloheimo & Dickie (1965) suggest that growth does not have a theoretical asymptote, which is a basic assumption of the von Bertalanffy equation. They point out that, because it is frequently applied to samples of younger fish well below their theoretical maximum size it only accurately describes early growth. Knight (1968) took this argument further and gave examples of linear growth as well as ones where maximum size actually decreased with increasing age (this example was of humans, not fish, however). He also (Knight 1969) proposed a modification of the equation to allow for linear growth.

Another critic of the von Bertalanffy equation was Roff (1980) who proposed "a motion for its retirement" on the grounds that it had outlived its usefulness. He suggested that other curves, especially the parabola, might be more acceptable descriptions of fish growth but he gave few examples and his arguments were not clearly supported and seem to have gained no general support.

In a detailed re-examination of the von Bertalanffy growth equation Pauly (1981) showed that the physiological relationships on which it was based are valid, at least for fish.

He showed that growth in fishes was limited by the allometric growth of the absorptive surfaces (i.e. the gills) and because of this growth conformed to the "2/3 rule" which was used by von Bertalanffy in the original derivation of his equation.

Pauly also pointed out the generalisation that $L_\infty \approx L_{max}/0.95$ where L_{max} = the maximum size of the fish and noted that L_∞ calculated from the von Bertalanffy equation was often very much greater than L_{max}. He modified the equation, by including factors to take account of anabolism and catabolism, to overcome this problem and lead to closer agreement between L_∞ and L_{max}. This he referred to as the generalised von Bertalanffy growth formula whilst the usual expression was termed the special von Bertalanffy growth formula.

In reality these equations are probably two ways of saying the same thing and in deciding which one to use Knight's (1969) view that the parameters of the growth curve should be a direct description of the graphical appearance of the data should be taken into account. In this study, the growth of Limnothrissa shows a clear trend towards an asymptote (see Figs. 22 and 23) and since an insignificant number of fish exceeded the calculated asymptotic length (< 0.01 %) the value calculated for L_∞ seems realistic.

The von Bertalanffy equation therefore appears to be an accurate description of the growth of Limnothrissa in Kariba and its use is justified. The growth of sardines in Kariba was previously described by Cochrane (1978, 1984) but the description obtained during the course of this study was considerably different from the one he calculated, in which

$$l_t = 81 (1 - e^{-0.14t}).$$

The figure for L_∞ was not significantly different and certainly within the range that might be expected from a fish with plastic growth rates. Cochrane also considered that $t_o = 0$ and this is probably a valid assumption because this parameter was found to be so small in this study.

The main difference lies in the value of K, the growth constant, which was only 0.14 in Cochrane's work but 0.254 in this study. This was almost certainly a consequence of the short data series that he used and also because he included data from commercial catches. The data from Station 2 show that length modes are not clearly defined in pelagic catches (Fig. 23) and attemps to estimate growth from commercial catch samples during this study suggested that the value of K would be underestimated; this is shown in the growth data given in Marshall (1984a).

The striking differences in growth of Limnothrissa in lakes and reservoirs has already been shown (Fig. 10) and this is clearly an important factor in the ecology of this fish. Cochrane (1978) considered that a lack of atyid shrimps was responsible for this because the larger fish required a larger prey, but this seems unlikely because these shrimps are not a major food source in Lake Tanganyika (Hecky et al. 1981) or in Lake Kivu (de Iongh et al. 1983), both lakes where the sardine grows to a large size.

In his later paper Cochrane (1984) merely attributes the differences in growth to a food shortage and this is perhaps the more likely explanation. Spliethoff et al. (1983), working in Kivu, also considered this to be the case and used the exponent, b, from the length-weight relationship as an index of food availability. They considered that Lake Tanganyika had the greatest food abundance as b = 2.981, followed by Kivu (b = 2.7) and then Kariba (b = 2.368 (from Cochrane 1978)). However, in this study b = 2.863 and the differences between it and the figures from Tanganyika and Kivu are possibly too small to be significant.

Marshall (1984a) postulated that the hydrological conditions in the reservoirs were responsible for the low food availability because of nutrient losses resulting from their rapid water turnover. Unfortunately, there are insufficient data on the plankton populations and their production rates from the various water-bodies to enable this to be verified, but some information can be obtained from their morpho-edaphic indices.

The morpho-edaphic index (ch. 2) is a rough indicator of lake fertility which can be used to predict fish yields (e.g. Henderson & Welcomme 1975; Schlesinger & Regier 1982; Marshall 1984b) and can therefore be taken as a rough indication of the food available in a pelagic ecosystem. Meaningless morpho-edaphic indices are obtained from very deep lakes, like Tanganyika ($\bar{z}$ = 700 m) and Kivu ($\bar{z}$ = 240 m), and it has been suggested that mean depths exceeding 25 m have no influence on the MEI (Oglesby 1977; Schlesinger & Regier 1982). A more realistic MEI value is thus obtained if the mean depth is reduced to 25 m in deep lakes and this figure, referred to as the MEI_{25}, has been used in an attempt to demonstrate the effect of limnological factors on sardine growth patterns (Table 21).

Table 21: The relationship between Limnothrissa growth parameters and the MEI_{25} in four African waters.

	MEI_{25}	L_∞	K	Source
Kariba	3.2	74.2	0.25	1
Cahora Bassa	4.8	c.70	c.0.45	2
Tanganyika	20.0	c.115	c.0.18	3
Kivu	48.0	145	0.10	4

Sources: 1. This study.
2. Estimated from data in Gliwicz (1984).
3. Estimated from data in Matthes (1967a).
4. Spliethoff et al. (1983).

The data from Tanganyika and Cahora Bassa are only approximations but it seems clear that in the more fertile lakes the sardines grow to a larger size but at a slower rate. Although Cahora Bassa has a higher MEI_{25} than Kariba it is possibly a less suitable sardine habitat because of its high turbidity and correspondingly low Secchi Disc readings. However, work in Lake le Roux, South Africa has demonstrated that both zooplankton abundance and fish growth were depressed by high turbidity (Allanson & Jackson 1983) so this hypothesis requires more data before it can be accepted.

The same study also demonstrated that the growth of some cyprinid fish is related to zooplankton abundance and this supports the view that the differences in *Limnothrissa* growth rates are a result of differences in food availability. The work of Blaber *et al*. (1981), who showed that the morphology of the estuarine clupeid *Gilchristella aestuarius* (Gilchrist) was influenced by its zooplankton food resources, is more evidence for this view. *Pellonula afzeliusi* is another example of a clupeid with apparently different growth rates in different environments. In Lake Kainji females of 65 mm were recorded (Otobo 1978) but in the Lagos lagoon they reached 90 mm (Ikusemiju *et al*. 1983). The estuarine situation almost certainly provided more food than the reservoir and this was further reflected in their reproductive biology because the estuarine fish matured at a greater size and were more fecund than the ones from Lake Kainji. This is comparable to the situation of *Limnothrissa* in Lake Tanganyika compared to Lake Kariba.

It is interesting to speculate on the role of predation, including fishing which can be considered as a specialised form of predation, on growth rates. It is known that fishing can reduce the mean size of a species, for example *Oreochromis niloticus* (Linnaeus) in Lake George, Uganda (Gwahaba 1973), but there are few data to show if this also affects the growth rate. In Lake Kivu, where the fishery is poorly-developed and there is no piscivorous predator, the growth rate of *Limnothrissa* is low in contrast to Lake Kariba, with a well-developed fishery and an abundant piscivorous predator, where it is high. In Lake Tanganyika, Stolothrissa is the most heavily preyed upon species, as it makes up the bulk of the commercial catch and is also taken by the four pelagic Lates spp. as well as by Limnothrissa itself (Poll 1953; Matthes 1967a; Coulter 1970). Its growth rate is comparable to Limnothrissa's in Kariba (K = 0.277 (Chapman & van Well 1978) and K = 0.224 (Roest 1978)) and apparently higher than that species' growth rate in Tanganyika. Unfortunately this must remain as speculation until more data are available.

The mortality rates found in this study were extremely high but there is very little information on mortality of other small species with which to compare them. In Pauly's (1980) list of natural mortality rates for 175 fish stocks there are only 14 where $L_\infty < 10$ cm and in these M varies from 0.73 to 5.2 (annual rate) which is considerably lower than the annual rate of 8.4 for the Kariba sardines. Natural mortality rates are clearly very variable and the value obtained in this study is probably realistic, especially as mortality may also be related to environmental factors in the same way that growth seems to be.

The only estimates of African freshwater clupeid mortality are for Stolothrissa in Lake Tanganyika where M = 2.77 and Z = 5.48 (Roest 1978) or Z = 5.16 (Chapman & van Well 1978). These annual rates are very much lower than those in Kariba where M = 8.4 and Z = 8.4-13.8, and this may be a consequence of the relatively adverse conditions that appear to exist in Lake Kariba. It should be noted that the lower preliminary mortality data given in Marshall (1984a) are considered to be underestimates because the original information came only from samples taken from commercial catches.

Finally, mortality rates can be used to indicate the state of the stock sice, generally-speaking, sustainable yield can be optimised when $F \approx M$ (Pauly 1983). In the Sanyati Basin during 1983 the annual rate of total mortality was $Z = 13.78$ which means that $F = 5.38$, assuming that $M = 8.4$ (annual rates). Fishing mortality was thus well below natural mortality which suggests that the Limnothrissa stock could sustain a considerably higher fishing effort. An estimate of the relative fishing effort needed to raise F to 8.4 can be obtained from Fig. 31. By extrapolating the regression and converting to monthly values a relative fishing effort (f) of 55.7 would be needed to give optimum sustained yield. This implies that the present fishing effort could be increased by by another 47 %.

The mortality rates obtained from Pauly's empirical equations were very much lower than those derived from the catch curves. Pauly considered that his method would overestimate the mortality of strongly-schooling pelagic fish but this does not seem to be the case in Kariba. Whilst his method may be a useful one for obtaining an approximate value it is not a substitute for detailed biological information.

The discussion may be concluded by briefly considering the possible causes of this very high mortality. The Tigerfish would appear to be a very important cause as they prey on the sardines in open water. However, it appears that the number of Tigerfish in the pelagic region of the lake has decreased (Fig. 15) and their effect on Limnothrissa may have declined accordingly.

Cochrane (1978, 1984) presented some evidence to show that starvation was a major cause of mortality, especially after the winter isothermal period when plankton abundance decreased rapidly. The marked seasonal changes in plankton abundance draw attention to the relative instability of the pelagic ecosystem of the lake. The high mortality rates can be viewed as a consequence of this factor.

CHAPTER 7: BIOMASS

INTRODUCTION

The estimation of fish biomass in a large body of water may be technically very difficult and biomass data are often inferred from experimental or commercial catch statistics or other such data. In spite of this, they are very important for any stock assessment and an objective of this study was to obtain estimates of Limnothrissa biomass in Lake Kariba.

Previous attempts to do this were very limited and the data that were obtained cannot be used in this study. Balon (1974a) carried out an acoustic survey in February 1971 and attempted to use underwater photographs to estimate sardine densities. He gives only one density value (8 fish m^{-3}) but this is of doubtful value because the methods employed to obtain it are very superficially described. The author claims that the underwater photographs could be used to estimate density because the angle of the camera lens was known, but none of this information is given in Balon (1974a) and so this claim must be rejected until such data are made available.

Cochrane (1978) was able to use a commercial purse-seiner for one night in February 1976 and another in April. He sampled at 8 stations, without using light attraction, and obtained mean values of 2.8 and 7.4 kg per haul respectively. He made no further use of these data but it is possible to convert them to g m^{-2} because he gives the dimensions of the net that was used.

Commercial catch statistics provide a valuable means for monitoring long-term changes in a fish population and Marshall (1982a) used them to show the effect of river flow on sardine abundance. If commercial catches could be related to biomass it would be possible to use them to check on changes in biomass or as a predictive tool. Such relationships have been determined for the sardine fishery on Lake Tanganyika (Herman 1978; Roest 1978) and an objective of this section was to investigate if such a relationship existed in the Kariba fishery. If it did, then it would be possible to convert earlier catch statistics to a measure of biomass and so assess changes which may have taken place in previous years.

METHODS

All biomass values were computed from the samples taken during the Sanyati Basin transects (ch. 4). The area of the net mouth was known and it was assumed that this was the area sampled in each vertical haul. Biomass was then calculated by the expression $B = (w \times 0.92)/(n \times 7.1)$, where B = biomass ($g\ m^{-2}$), w = weight of catch (g) which is adjusted to take account of the 8 % reduction in weight caused by preservation in formalin (Fig. 18), n = number of hauls and 7.1 = the area of the net mouth (m^2).

A direct estimate of biomass cannot always be obtained and it is possible to calculate it from fishing mortality and yield (Pauly 1983) since $Y = F.B$ and so $B = Y/F$, where

B = biomass, F = fishing mortality and Y = yield. Since both yield and fishing mortality are known (chs. 5 & 6) this method was used to provide an independent estimate of biomass.

The biomass estimates obtained from the transect samples were compared with the commercial catches taken by the A category nets operating in the Sanyati Basin on the same nights that the samples were taken. The total biomass in the Basin was also estimated by multiplying the biomass (kg ha^{-1}) by the approximate area of the Basin at the time, which varied according to lake level fluctuation. The Basin areas were calculated from the tables in Coche (1974) which give the percentage reduction in the various lake basins in relation to the drop in lake level. An attempt was also made to relate commercial catches to the total biomass.

Variablity between stations and between biomass and the commercial catches was assessed by means of analysis of variance (Sokal & Rohlf 1981).

RESULTS

Estimates from sampling:

The biomass estimates from the Sanyati Basin showed an extremely high degree of variability from one station to another (Table 22). The fish were clearly very patchily distributed and there was no clear pattern except that biomass was frequently high at Station 1 which was located just off the mouth of the Sanyati Gorge.

Table 22: The biomass (kg ha^{-1}) of Limnothrissa at the 10 Sanyati Basin stations. Dashes indicate that no samples were taken, in March and December 1982 bad weather prevented any sampling whilst in September 1982 the "Pelican" was engaged in a prolonged search for an aeroplane which crashed in the lake.

Station	1	2	3	4	5	6	7	8	9	10	Mean
July 1981	326	17	134	79	199	14	97	94	110	93	116.3
August	723	144	244	111	43	28	90	68	106	53	161.0
September	244	31	94	16	35	48	38	14	58	29	60.7
October	60	49	26	109	28	63	97	65	72	57	62.6
November	70	132	58	24	10	32	52	70	70	-	57.6
December	-	-	-	104	39	29	63	26	-	-	52.2
January 1982	28	225	129	32	28	47	64	57	95	38	75.3
February	125	117	84	39	45	20	22	22	38	-	56.9
March	-	-	-	-	-	-	-	-	-	-	-
April	41	95	34	266	113	15	116	97	94	-	96.8
May	16	129	52	6	22	5	44	48	12	-	37.1
June	52	112	54	12	11	31	17	140	50	-	53.2
July	208	15	67	71	17	6	61	46	8	6	50.5
August	52	29	56	32	11	14	-	-	-	-	32.3
September	-	-	-	-	-	-	-	-	-	-	-
October	74	63	45	6	14	8	5	44	-	-	32.4
November	34	52	11	44	19	13	29	59	40	6	30.7
December	-	-	-	-	-	-	-	-	-	-	-
January 1983*	3	14	19	4	5	6	1	1	1	1	5.5*
February	36	36	10	1	26	2	22	41	23	2	19.9
March	20	8	32	21	17	17	70	74	8	31	29.8
April	144	130	29	-	42	24	13	78	29	-	61.1
May	32	125	31	7	20	23	13	8	9	1	26.9
June	107	75	13	12	4	8	12	110	143	-	53.8
July	10	68	147	142	26	2	2	29	22	52	51.2

*This is almost certainly an underestimate as sampling was unavoidably carried out during Full Moon.

The one -way analysis of variation, carried out on the log-transformed data, was as follows:

Source of variation	Degrees of freedom	Sums of squares	Means of squares	F ratio	F probability
Between samples	21	22.206	1.057	5.569	0.000
Within samples	179	33.990	0.190		
Total	200	56.197			

From this it can be seen that there is a very high unexplained (residual) variation and that the location of the sampling station is an insignificant cause of variability. The analysis of variance requires the following assumptions; the samples are independently drawn from a normally-distributed population; the parent populations have the same variance; the components of variance must be additive (Elliott 1977). It is clear that none of these assumptions hold for the Limnothrissa stock in Lake Kariba.

In addition to being highly variable spatially, the biomass also varied according to season and the mean biomass in the four six-month periods (excluding January 1983) was:

July - December 1981	85.07 kg ha^{-1}
January - June 1982	63.86 kg ha^{-1}
July - December 1982	36.48 kg ha^{-1}
February - July 1983	40.45 kg ha^{-1}

The decline in biomass during 1982 and the early part of 1983 corresponds to the trend in the commercial catches which showed

Table 23: The mean biomass of Limnothrissa in the Sanyati Basin (kg ha^{-1}) and the extrapolated total biomass (t) for the basin and the whole lake. Areas are given as km^2.

	Mean	Sanyati Basin		Lake Kariba	
	biomass	Area	Biomass	Area	Biomass
July 1981	116.3	876	10 188	5 440	63 267
August	161.0	871	14 023	5 420	87 262
September	60.7	863	5 238	5 390	32 717
October	62.6	859	5 377	5 335	33 397
November	57.6	850	4 896	5 305	30 557
December	52.2	846	4 416	5 270	27 509
January 1982	75.3	842	6 340	5 245	39 494
February	56.9	842	4 791	5 245	29 884
March	-	-	-	-	-
April	96.8	842	8 151	5 245	50 772
May	37.1	842	3 142	5 260	19 515
June	53.2	842	4 479	5 245	27 903
July	50.5	837	4 227	5 210	26 310
August	32.3	833	2 691	5 165	16 683
September	-	-	-	-	-
October	32.4	820	2 657	5 050	16 362
November	30.7	808	2 481	4 970	15 258
December	-	-	-	-	-
January 1983*	5.5	808	444	4 970	2 734
February	19.9	808	1 608	4 990	9 930
March	29.8	807	2 405	4 960	14 787
April	61.1	807	4 931	4 960	30 305
May	26.9	806	2 168	4 950	13 315
June	53.8	803	4 320	4 925	26 497
July	51.2	799	4 090	4 865	24 909

* The January 1983 sample was taken at Full Moon and is therefore almost certainly too low.

a similar decline during 1982 and 1983 (ch. 5).

The mean biomass in the Sanyati Basin ranged from a maximum of 14 023 t in August 1981 to a minimum of 1 608 t in February 1983 (the estimate for January 1983 is not included as it was taken during the Full Moon). The mean for the whole sampling period was 4 886 t or 58.01 kg ha^{-1}.

These values have been extrapolated to the lake as a whole and they give total biomass estimates ranging from 87 262 t to 9 930t. The mean for the whole sampling period is 30 315 t.

Relationship between biomass and commercial catches:

There was a relationship between the mean nightly catch and the biomass (Fig. 32a) but it was only just significant and would be of little value for predictive purposes. A much closer relationship is evident when the mean nightly catch is plotted against the total biomass (Fig. 32b). This suggests that it is possible to predict the total biomass in the Sanyati Basin, at least, from the mean commercial catches.

Commercial catches may be used to give an indication of the biomass in the whole lake. In Table 24, the mean catch for A category vessels based at Kariba (i.e. those fishing in the Sanyati Basin) for the years 1978-1983 is given and the total biomass in the basin estimated from the relationship in Fig. 32b. The mean area of the lake during each year is known and as the Sanyati Basin makes up 15.8 % of the lake, its mean surface area can then be estimated. The total biomass can then be converted to an

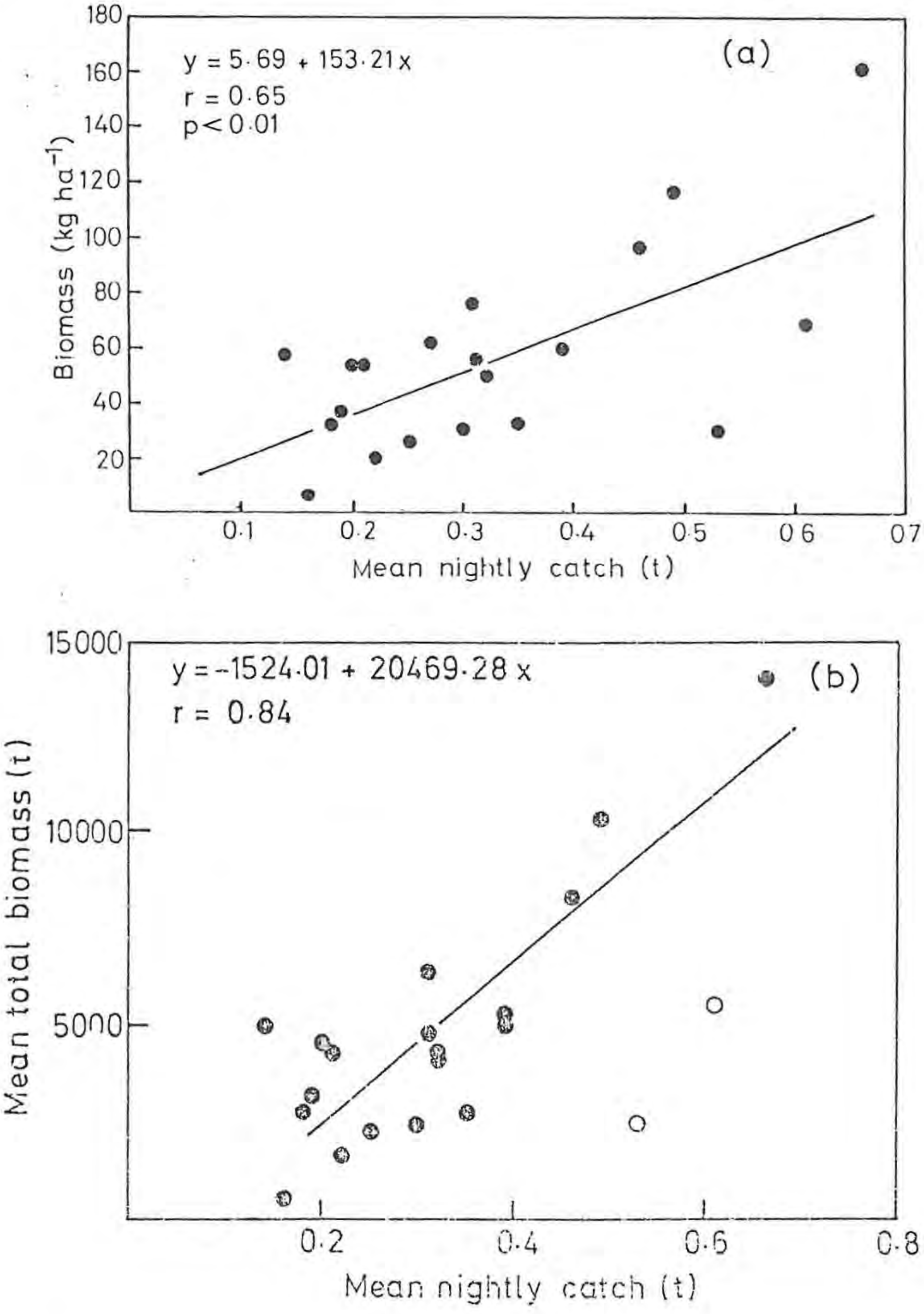


Figure 32: The relationship between commercial catches and (a) mean biomass, (b) mean total biomass. The two outlying data points in (b), indicated by open circles have been ommitted from the regression.

Table 24: The mean values for catches by A category vessels (t night^{-1}) fishing in the Sanyati Basin and the calculated total biomass (t) for 1978-1983. The mean area of the basin (km^2) and the derived biomass (kg ha^{-1}) is also given. The mean area of the whole lake (km^2) is also given and from this the total biomass (t) has been estimated.

	Sanyati Basin				Lake Kariba	
	Mean catch	Biomass	Area	Biomass (kg ha^{-1})	Area	Biomass
1978	0.28	4 207	856	49.14	5 420	26 633
1979	0.30	4 617	854	54.06	5 405	29 219
1980	0.23	3 184	844	37.73	5 340	20 147
1981	0.29	4 412	855	51.60	5 412	27 926
1982	0.22	2 979	818	36.42	5 180	18 866
1983	0.22	2 979	766	38.89	4 820	18 745
Mean	0.26	3 798	832	45.65	5 262	24 021

estimate in kg ha^{-1} and from this a value for the entire lake can be obtained. The mean biomass for the six-year period was 45.65 kg ha^{-1} and the mean total biomass was 24 021 t. This was substantially lower than the mean biomass values obtained from the Sanyati Basin transects but the mean for these was probably increased by the very high values obtained in July and August 1981, which was a year in which biomass appeared to be high and commercial catches were large.

Estimates by calculation

Biomass estimates made from fishing mortality and yield were considerably lower than those made from the sampling programme (Table 25). Once again 1981 proved to be an exceptional year with a high biomass and low fishing mortality.

Table 25: Mean monthly biomass of Limnothrissa in the Sanyati Basin, calculated from yield and fishing mortality (F).

	Y (t/month)	F*	B (tonnes)	B (kg ha^{-1})
1978	228.1	0.116	1966.4	23.1
1979	279.5	0.389	975.6	11.5
1980	496.4	0.405	1225.7	14.4
1981	617.3	0.273	2261.2	26.6
1982	437.4	0.334	1309.6	15.4
1983	465.8	0.449	1037.4	12.2

*Estimated from Z values in Fig. 29 minus M = 0.7.

DISCUSSION

The extremely patchy distribution of Limnothrissa in Lake Kariba appears to be similar to the distribution of other pelagic species such as the clupeids in Lake Tanganyika (Johanesson 1974 ; Chapman 1976) or Engraulicypris in Lake Malawi (Rufli & Vitullo 1982). Zooplankton in Lake Kariba is known to be very patchy (Marshall 1980; Magadza 1980) and this may contribute to the uneven sardine distribution. The factors that cause this are poorly known but it does appear to be linked to some extent to the influence of the inflowing rivers.

Magadza (1980) showed that the Sanyati River itself was the main influence on zooplankton abundance in the Sanyati Basin which may explain why the fish biomass was generally highest at Station 1, located just off the mouth of the Sanyati Gorge. This tends to support the hypothesis that sardine abundance is affected by the flow of tributary rivers (Marshall 1982a). It may also be reflected by the drop in biomass that took place in 1982 and 1983 following two drought years when river flows were poor.

Biomass values for the Sanyati Basin were extrapolated to the whole lake on the grounds that as the basin represents about 16 % of the lake's surface, a large enough area was sampled. Furthermore, the commercial catches from other areas were similar to those from the basin (see Table 18) suggesting that they were made from a stock with a similar density. Despite this, the extrapolation of these data to the whole lake should be regarded with caution as the relationship between biomass and commercial catches may be significantly different in other parts of the lake.

The fact that there was only a weak relationship between commercial catches and biomass, when expressed in terms of a unit of area, but a much better one when biomass was expressed as the total stock seems to be contradictory. However, fish catches perhaps depend more on the total stock than they do on its areal density, especially when the lake level is taken into account. Another factor to take into account is the potential effects of light attraction as it seems likely that a large number of boats using this method of fishing will disrupt the pattern of fish distribution. This fishing method makes it possible to draw fish from the entire population and so the estimate of total stock will be more important than its areal density.

There are few biomass estimates from other lakes with which to compare the Kariba data. Estimates from Lake Tanganyika vary considerably and acoustic surveys suggest that the biomass may be as high as 500 kg ha^{-1} (Herman 1978). Other workers have made lower estimates and Coulter (1981) considered the biomass of clupeids in the lake to be about 230 kg ha^{-1}. Since the acoustic estimates include the predatory species the true value may lie somewhere in between. The Tanganyika value is very much higher than the ones for Kariba but this is to be expected if the view (already discussed in regard to growth) that the former is a much more suitable sardine habitat is correct.

Clupeid biomass in Lake Kainji ranged from 1 569-3 138 t which is equivalent to about 12 - 24 kg ha^{-1} (Otobo 1979). This is substantially lower than the Kariba values and it may be that it is the least suitable for sardines. It is relatively shallow, has a short retention time and low conductivity (see Table 1) and so may be most suitable for inshore species of which it now yields about 35 kg ha^{-1} (Ita 1984).

Finally, some preliminary data are available from Cahora Bassa where an acoustic survey gave estimates of 3 557 - 14 413 individuals per hectare with a mean of 8 424 (Lindem 1983). If the average weight of these fish is assumed to be 1.0 g then biomass ranged from 3.6 - 14.4 kg ha^{-1} (mean = 8.4 kg ha^{-1}). This is very much lower than the Kariba values but as the survey was only carried out in one month (February 1983) and in a restricted area of the lake, it might not truly reflect the situation there.

The Kariba biomass estimates were higher when obtained from direct sampling than when they were calculated from catch and mortality data. It is possible that the estimates of fishing mortality were too high and if they were lower the biomass estimate would be incresed. The mean biomass value from the sampling (58 kg ha^{-1}) was also higher than all of those estimated from the commercial catch/total biomass relationship (Table 24). The explanation for this may lie in deficiencies in this relationship and emphasises the need to treat this with caution.

The sardine biomass appeared to be very much lower than the biomass of the inshore species. Balon (1973) and Mitchell (1976) made estimates of around 500 kg ha^{-1} from blocked-off coves which were poisoned with rotenone. Langerman (1984) used explosives to sample a much wider range of habitats and found that biomass was much lower in rocky, poorly-vegetated areas; his mean biomass estimate was about 325 kg ha^{-1}. This difference is to be expected because of the greater diversity of both habitats and species in the littoral areas but it suggests that a mean value of 58 kg ha^{-1} for sardines is not unrealistically large.

Biomass of any fish species, but more especially a pelagic one, is perhaps better expressed in terms of the volume of the water body and not its area. There are obvious difficulties, especially when considering rivers or floodplains and it is hard to make comparisons as data from almost all waters is expressed in terms of area. However, an attempt was made to compare the biomass of clupeids from three African lakes, in terms of volume rather than area, and some interesting conclusions emerged (Table 26).

The biomass in Kariba and Tanganyika now become very similar, but in Kainji it remains much lower. The biomass data tend to contradict the growth and mortality data which suggest that Kariba is less suitable for sardines than Tanganyika. It appears, however, that both lakes are supporting their maximum possible biomass which is comparable in both. In Lake Kariba, Limnothrissa appears to have been able to maximise its biomass by remaining much smaller. Thus it matures and breeds earlier and has a smaller life-span and has a much greater production/biomass ratio (ch. 9).

As discussed earlier, Lake Kainji seems to be the least suitable for sardines and their biomass is much lower. Very little information about the biology of these fish is available but there is some evidence to suggest that they have

Table 26: The biomass of clupeids in three African lakes expressed in terms of their volume.

	Kariba	Tanganyika	Kainji
Surface area (km^2)	5 400	32 900	1 280
Inhabited depth (m)	30(1)	150(2)	
Inhabited volume (km^3)	117(3)	4 935(4)	26(5)
Biomass (kg ha^{-1})	44(6)	365(7)	12 - 24(8)
Biomass (t)	24 000	1 200 850	1 500 - 3 000
Biomass (t km^3)	205	243	58 - 115

Notes: (1) This depth was the limit of the epilimnion and is probably a mean value for any year.

(2) Taken from means of the data in Kufferath (1953) and Coulter (1963). Also from Coulter (pers. comm.)

(3) Estimated from the capacity curve (Zimbabwe 1978).

(4) Because of its steep sides the area of Lake Tanganyika at 200 m depth was assumed to be similar to its surface area.

(5) Because it is shallow and has a considerable drawdown it was assumed that the entire volume of Lake Kainji is habitable.

(6) This study.

(7) This value is the average of those given by Herman (1978) and Coulter (1981).

(8) From Otobo (1979).

attempted to adapt to an unstable environment in much the same way as <u>Limnothrissa</u> has adapted to Kariba. In Lake Kainji <u>Pellonula afzeliusi</u> were sexually mature at 30 mm in length (Otobo 1978), whilst in the Lagos Lagoon, where conditions were presumably less variable and food more abundant, they did not do so until they were 65 mm long. Despite this it would seem that conditions in Kainji were possibly too extreme to enable them to establish a large biomass. Another factor may be that both <u>Pellonula</u> and <u>Sierrathrissa</u> are riverine forms and therefore perhaps less able to adapt to alcustrine environment.

CHAPTER 8 : SELECTION

INTRODUCTION

Fishing nets, of almost any kind, will be highly selective in the types and sizes of fish that they take and so influence the population dynamics of the affected species. The age at which fish become vulnerable to a particular fishing gear and when they become fully selected are important in some of the deterministic models for yield prediction, especially the yield per recruit model of Beverton & Holt (1957). Since these will be used in a subsequent chapter the selection characteristics of the sardine fishing gear in use on Kariba need to be examined.

METHODS

Net selectivity was determined from the length and age structure of samples taken from commercial catches during the period 1978-1983. Recruitment begins at time t_r or length l_r which is the age or length at which fish first appear in the catch (Fig. 33). Net selection then becomes increasingly effective to the point where the age or length group is fully selected by the gear i.e. all individuals are vulnerable and any fish longer or older than these will be equally vulnerable. In a typical age- or length-frequency distribution this will be all the fish represented by the right-hand or descending arm of the curve. Finally, the age or length of "first capture" (t_c; l_c)

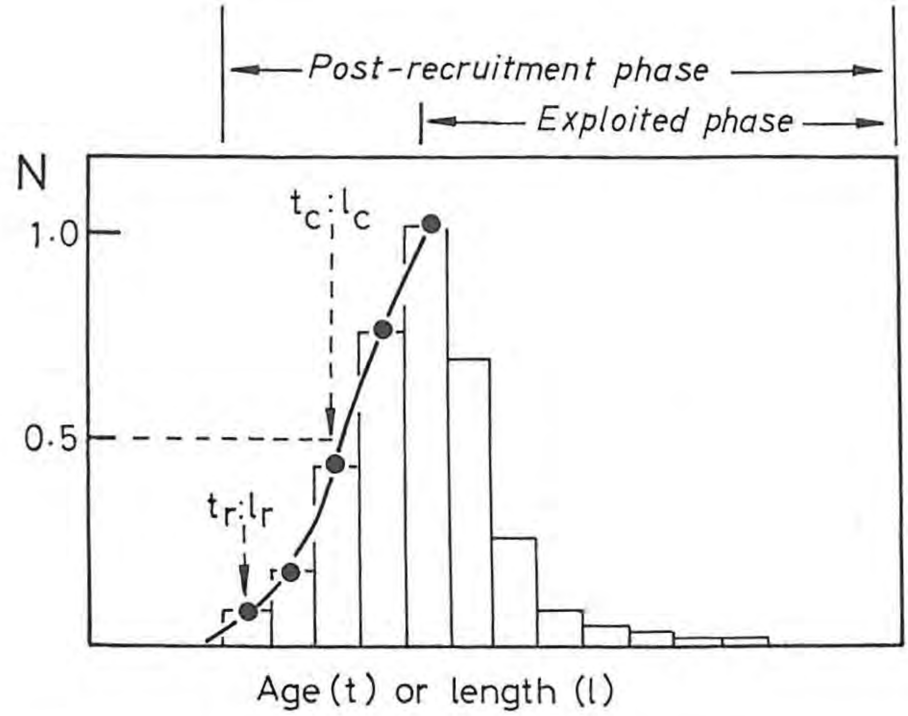


Figure 33: A hypothetical length or age-frequency distribution, with a net selection curve superimposed, to illustrate the terms used in this chapter. Taken in part from Beverton & Holt (1957).

is conveniently the point where 50% of the fish are fully selected (Pauly 1983).

RESULTS

Length-frequency distributions of samples from the Sanyati Basin (Fig. 34) show that the sardines were fully selected at about 47-49 mm in length, except that in 1979 they were about 45 mm in length and in 1981 they were considerably larger (54mm). Length at first capture (l_c) was usually about 41-46 mm except in 1981 when it was 49 mm.

Until 1982 the age of recruitment (t_r) was 2 months but this was reduced to 1.5 months in 1982 and 1983 (Fig. 35). The time of first capture (t_c) was variable and ranged from 2.5 months in 1979 to 4.0 months in 1981.

Samples taken in the Bumi estuary show the effect of fishing in estuarine stocks. The fish were smaller, being fully selected at 40 mm compared to 45-50 mm in open water (Fig. 36). The length of recruitment was never less than 20mm whilst the length of first capture ranged from 43 mm in 1980 to 40 mm in 1982, which is again generally smaller than in open water. The selection for age characteristics in these samples was as follows

1980 : $t_c = 3.34$ $t_r = 1.63$ months
1981 : $t_c = 2.25$ $t_r = 1.17$ months
1982 : $t_c = 2.34$ $t_r = 1.55$ months.

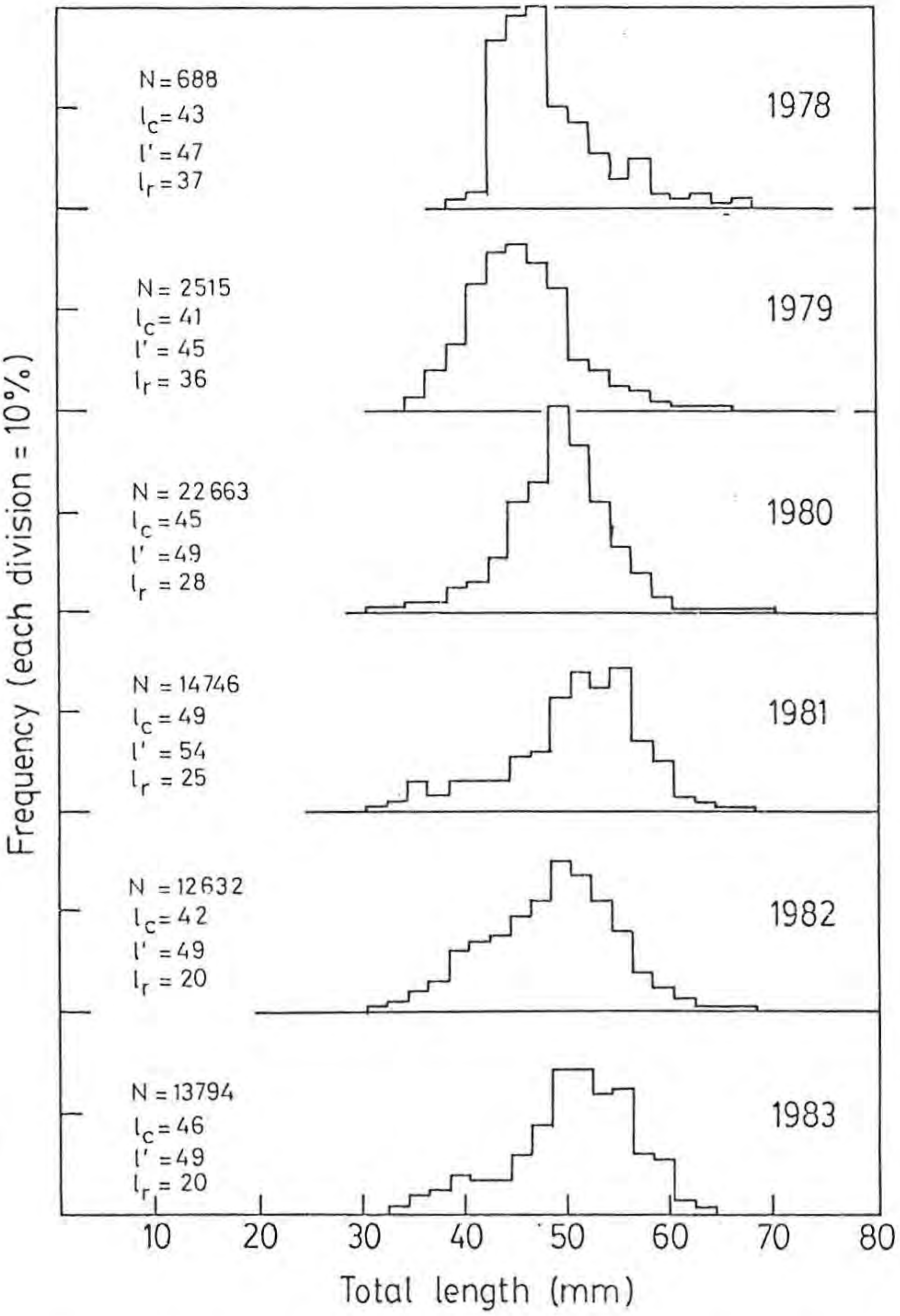


Figure 34: Length-frequency distributions of samples taken from Sanyati Basin commercial catches, 1978-1983.

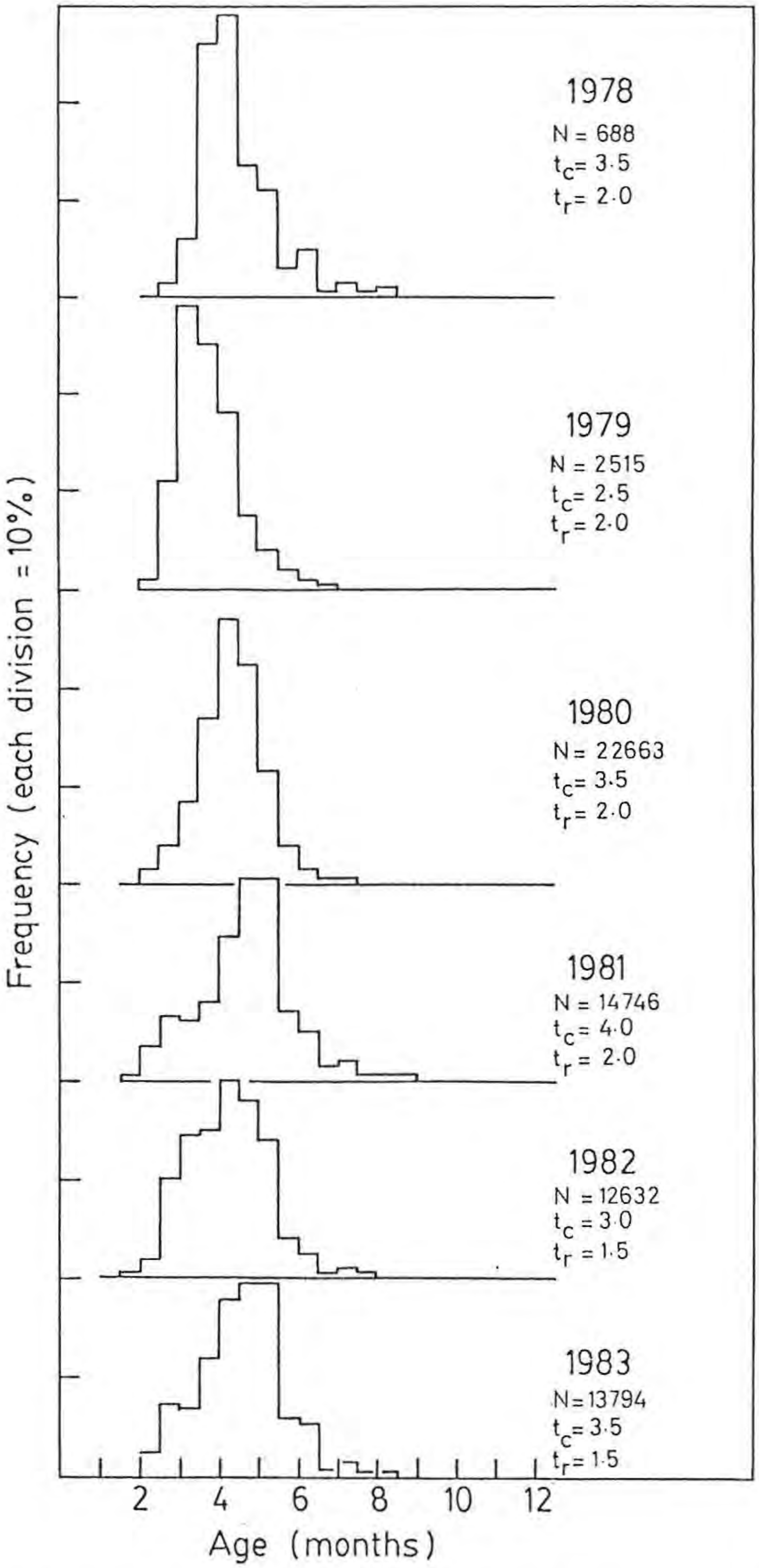


Figure 35: Age-frequency distributions of samples taken from Sanyati Basin commercial catches, 1978-1983.

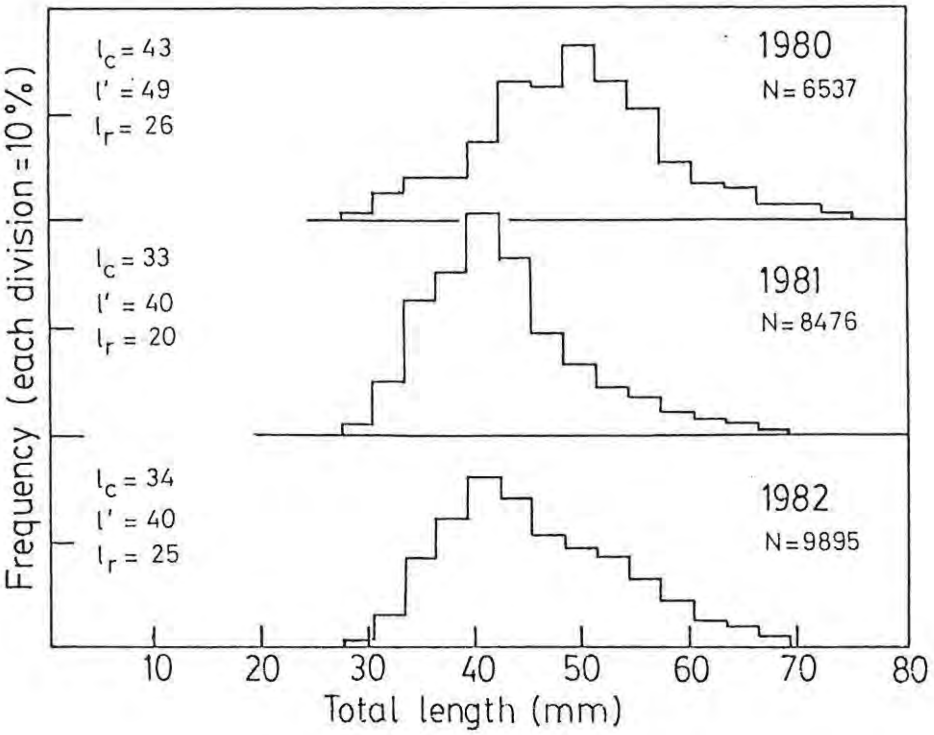


Figure 36: Length-frequency distribution of samples taken from the Bumi estuary commercial fishery, 1980-1982.

DISCUSSION

The minimum size of sardine that can be taken by the gear currently in use is about 20 mm (or about 1.5 months old) but very few fish of this size are actually taken because the small fish tend to remain in very shallow water where the fishermen cannot operate. This was demonstrated in the Sanyati Basin transects with small fish only being taken at Station 6 (an inshore station) and also by the smaller size of fish taken in the Bumi estuary. This has important management consequences because it emphasises the importance of controlling fishing in very shallow water. Fortunately, most of the shallow areas of Kariba are protected by submerged trees.

CHAPTER 9: PRODUCTION

INTRODUCTION

Relatively few production studies have been made in African freshwaters and production studies have not in general been applied to the management of commercial fisheries. The basic parameters required to estimate production, abundance, growth rate and mortality rate, have now been estimated and it is therefore possible to assess the production of *Limnothrissa* in Lake Kariba.

The most detailed study from any African lake to date is that carried out in Lake George, Uganda where production was determined at all levels of the ecosystem (Burgis & Dunn 1978). A major study of fish production was carried out by Balon (1974a) in Lake Kariba. The methodology in this study had to be reconsidered (Mahon & Balon 1977) which meant that some of the results were changed; nevertheless this remains one of the only investigations of production in a complex community of African fishes.

The investigation did not include *Limnothrissa*, however, and so the data in this chapter can be regarded as being complementary to the earlier work. The only study of production in pelagic species is Coulter (1981) who examined production and potential yield in the pelagic community of Lake Tanganyika. This work related particularly to *Stolothrissa* which is the most abundant species in that community.

METHODS

Production is defined in this study as "the total elaboration of new tissue by a species or population during a given period of time" (Chapman 1968, 1978). In his study on Lake Kariba, Balon (1974a) devised a number of terms for different types of production. These include "total production" which appears to be synonymous with the definition of production given earlier. It is also the same as "ecological production" and both terms are used by Balon. Further subdivisions include "availablable production" which is the total surviving tissue elaborated at the end of an interval of time; "final production" which is the same as available production in an exploited population and includes the amount removed by the fishery; finally, "yield" was referred to as the harvestable part of production. These terms have not been adopted for this study as they seem to be poorly defined and it is not always clear from the data given by Balon what is being referred to.

In this section production will be estimated by the Instantaneous growth rate method, derived from the work of Ricker and Allen and discussed in detail by many subsequent authors (e.g. Chapman 1968, 1978; Waters 1977). In this method production is estimated as the product of the mean biomass and the instantaneous growth rate, so that

$$P = G.\bar{B}$$

where P = production (kg ha^{-1}), G = instantaneous growth coefficient (rate) and $\bar{B}$ = mean biomass (kg ha^{-1}); all of these terms apply during a given period of time.

This method is generally most successful for a species which reproduces in distinct cohorts. This limits its applicability to Limnothrissa in Kariba where the population is made up of several cohorts which appear in a very short time period and which cannot be readily separated. This problem was overcome by using a hypothetical cohort of 10 000 fish at time $t = 1$ month and their numbers in subsequent months were estimated by assuming a natural mortality rate, $M = 0.7$ per month and fitting the expression $\log_e N_{t+1} = \log_e N - 0.7$, where N = the number of fish at time t and t+1.

The mean weights of the fish at each age were estimated (Table 20) and the biomass calculated as the product of numbers and mean weight. The instantaneous growth rates for each age interval are known (Table 19) and these were used to calculate production at monthly intervals by multiplying the instantaneous growth rate by the mean biomass during the month.

An indication of what proportion of this production might be available to fisherman was obtained by repeating this procedure, but with a mortality rate of 1.4. This relies on the assumption that, at optimal exploitation, $F \approx M$ and so a fishing mortality equal to natural mortality has been included. This mortality rate was applied to fish aged 3 months and older since they are the ones that are vulnerable to the fishing gear currently in use. The difference between the two estimates can be interpreted as the proportion of the total production that could be converted into commercial yield.

The production estimates obtained by this method are of limited value because they are not expressed in terms of a unit of area. This problem was dealt with by using the production to biomass ratio ($P/\overline{B}$) since the mean biomass was known.

RESULTS

Production from the entire cohort, with natural mortality only, was about 3 100 g in 12 months (Table 27) and the $P/\overline{B}$ ratio was 6.90. Production from fish of 3 months and older was about 1 000 g yr^{-1} whilst the $P/\overline{B}$ ratio was only 2.91.

Production from the cohort with fishing mortality of 0.7 included was reduced to 2 700 g for the entire cohort and 626 g for the 3 month old and older fish (Table 28). If this was the optimum fishing effort then the commercial yield would be about 51 % of the total production.

The situation in the Sanyati Basin in 1983 was that $Z = 1.15$, $t_c = 3.5$ months and the total yield was 5.590t. The difference in production between a hypothetical 10 000 fish cohort with these mortality rates and the one with no fishing mortality was 337.75 g. If each group of 10 000 fish at $t = 1$ produced 337.75 g in commercial yield then the total number of recruits to this fishery was 1.66×10^{11} fish. This reasoning can be applied to all Sanyati Basin catches from 1978 - 1983 (Table 29) to give an indication of the number of recruits that were needed to support the fishery.

Table 27: Production from a hypothetical *Limnothrissa* cohort with natural mortality (M) = 0.7. t = age (months), N = numbers, $\bar{w}$ = mean weight (g), B = biomass (g), $\bar{B}$ = mean biomass (g), G = instantaneous growth coefficient, P = production = $G\bar{B}$ (g).

t	N	$\bar{w}$	B	$\bar{B}$	G	P
1	10 000	0.04	400.00			
				721.43	1.66	1 197.57
2	4 966	0.21	1 042.86			
				1 100.94	0.81	891.76
3	2 466	0.47	1 159.02			
				1 051.14	0.49	515.06
4	1 225	0.77	943.25			
				799.95	0.34	271.98
5	608	1.08	656.64			
				533.68	0.23	122.75
6	302	1.36	410.72			
				326.86	0.17	55.57
7	150	1.62	243.00			
				189.21	0.12	22.71
8	74	1.83	135.42			
				104.90	0.09	9.44
9	37	2.01	74.37			
				56.54	0.07	3.96
10	18	2.15	38.70			
				29.57	0.05	1.48
11	9	2.27	20.43			
				14.96	0.04	0.60
12	4	2.37	9.48			

	Entire cohort	Fish $\geqslant$ 3 months
Production (P)	3 092.88 g	1 003.55 g
Mean biomass ($\bar{B}$)	448.11 g	345.20 g
P/$\bar{B}$ ratio	6.90	2.91

Table 28: Production from a hypothetical Limnothrissa cohort with natural mortality (M) = 0.7 and, from the age of 3 months, fishing mortality (F) = 0.7 so that total mortality (Z = F + M) = 1.4. Column headings are the same as Table 27.

t	N	$\bar{w}$	B	$\bar{B}$	G	P
1	10 000	0.04	400.00			
				721.43	1.66	1 197.57
2	4 966	0.21	1 042.86			
				1 100.94	0.81	891.76
3	2 466	0.47	1 159.02			
				895.60	0.49	438.84
4	821	0.77	632.17			
				425.17	0.34	144.56
5	202	1.08	218.16			
				143.08	0.23	32.91
6	50	1.36	68.00			
				43.72	0.17	7.43
7	12	1.62	19.44			
				12.47	0.12	1.50
8	3	1.83	5.49			
				3.45	0.09	0.31
9	0.7	2.01	1.41			
				0.92	0.07	0.06
10	0.2	2.15	0.43			
				0.54	0.05	0.03
11	0.05	2.27	0.11			
				0.07	0.04	0.003
12	0.01	2.37	0.02			

	Entire cohort	Fish ≥ 3 months
Production (P)	2 714.97 g	625.64 g
Mean biomass ($\bar{B}$)	304.31 g	169.45 g
P/$\bar{B}$ ratio	8.92	3.69

Table 29: Total recruitment to the Sanyati Basin fishery, estimated from yield, mortality and production data.

	$Z^{(1)}$	$P\ (g)^{(2)}$	$Y\ (g)^{(3)}$	Commercial Catch (t)	No. of fish at start
1978	0.816	873.33	130.22	2 737	2.10×10^{11}
1979	1.089	671.07	332.48	4 554	1.37×10^{11}
1980	1.105	662.55	341.00	5 957	1.74×10^{11}
1981	0.973	743.41	260.14	7 408	2.85×10^{11}
1982	1.034	703.46	300.09	5 249	1.75×10^{11}
1983	1.149	639.42	364.13	5 590	1.54×10^{11}

(1) From Fig. 29.

(2) Calculated from a hypothetical cohort using data from Fig. 29.

(3) Estimated by subtracting P from 1 003.55 g which is production when $F = 0$, $M = Z = 0.7$ (Table 27).

If this reasoning can be extended to the whole lake, assuming that the mortality and selection parameters apply universally, the 1983 yield of 13 573 t would have come from 4.02×10^{11} recruits.

The $P/\bar{B}$ ratio was very high for the unexploited cohort but this conforms to the general pattern that small, short-lived fish have high ratios. <u>Limnothrissa</u> appears to fit the pattern of $P/\bar{B}$ ratios in relation to maximum body size shown by the inshore species of Lake Kariba (Fig. 37).

The $P/\bar{B}$ ratio of the exploited stocks in the Sanyati Basin during the study period was about 2.9 and the mean biomass was about 58 kg ha^{-1}. Thus production in the basin was about 168 kg ha^{-1} which, since the average area of the

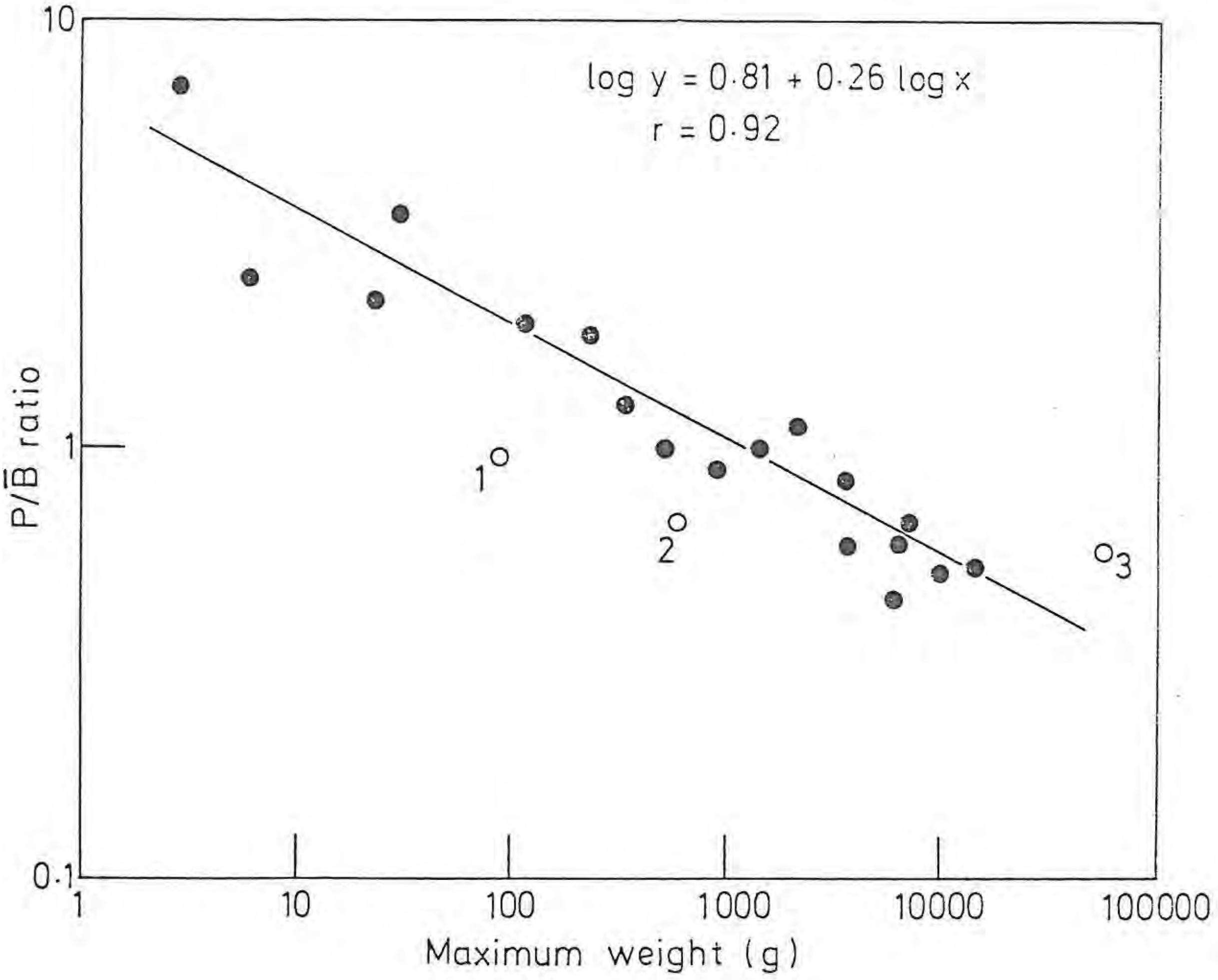


Figure 37: The relationship between maximum body weight and the P/B̄ ratio for Lake Kariba fish. The values for *Synodontis nebulosus* (1), *Schilbe mystus* (2) and *Heterobranchus longifilis* (3) have not been included in the regression as the samples from which they were calculated were too small to be representative. Data from Mahon & Balon (1977) and Kenmuir (1983).

basin was about 840 km^2, amounted to about 14 112 t. Assuming that this applies to the entire lake production during the study period would be about 88 200 t annually. If the assumption that commercial yield could be as much as 51 % of the total then a yield of 45 000 t may be possible.

DISCUSSION

The production rates for Limnothrissa are relatively low when compared to some other species. In Lake Kariba some species had rates which were very much higher e.g. Alestes lateralis which produced about 366.9 kg ha^{-1} yr^{-1} whilst the inshore community as a whole produced about 1 223.9 kg ha^{-1} yr^{-1} (Mahon & Balon 1977). This is to be expected, however, in a complex multi-species community occupying a variety of ecological niches.

The inshore fish community is, however, restricted to water of about 15 m depth (Coke 1968) and so inhabits only about 30 % of the lake. Total production from this community is thus around 19 800 t yr^{-1}. The sardines, by contrast, can utilise the entire lake and, assuming a production of 168 kg $ha^{-1}yr^{-1}$, the total production would amount to 90 720 t yr^{-1}. This is considerably greater than the total from the inshore community and emphasises the importance of the sardines from an economic point of view.

The $P/\bar{B}$ ratios are perhaps the most useful aspects of production studies as they can be compared with those from other species or other systems. Leveque *et al.* (1977) have shown that the ratio is related to mortality and longevity and is highest in small, short-lived species. The ratio for *Limnothrissa* is well within the limits predicted for a species of its size and longevity and is also higher than the ratio of 4.7 (over 15 months) calculated for *Stolothrissa* in Lake Tanganyika (Coulter 1981). In this fish the mortality rate was lower and after 12 months 2.5 % of the original cohort still survived; by contrast, only 0.05 % of *Limnothrissa* survived in Lake Kariba.

A clear relationship between maximum size (and presumably longevity and mortality rates) and $P/\bar{B}$ ratio was shown by all Kariba fish, including the sardines. This is to be expected since both the pelagic and inshore communities are subject to the same physico-chemical limiting factors.

The mean total production of 168 kg ha^{-1} was very much lower than the value of 560 kg ha^{-1} given for the pelagic community in Lake Tanganyika (Coulter 1981). However, as discussed earlier with regard to biomass, production would also be more appropriately discussed in terms of lake volume rather than area. Using the data in Table 26, production can be recalculated in volumetric terms as follows:

Lake Kariba: 775 t km^{-3}
Lake Tanganyika: 373 t km^{-3}.

In volumetric terms, therefore, production in Kariba appears to be about twice as high as it is in Tanganyika. This is apparently anomalous as the biomass is about the same in the two lakes (Table 26) but it is accounted for by the fact that in Kariba the fish are much smaller and have a greater $P/\overline{B}$ ratio. Lake Kariba seems to a relatively adverse habitat for the sardines and the reduction in their size, together with a high $P/\overline{B}$ ratio appears to be a means of maintaining a high biomass (this aspect is discussed in greater detail in chapter 11).

In Lake George, Uganda the production of *Oreochromis niloticus* was estimated to be 5 500 t yr^{-1} or 220 kg $ha^{-1}yr^{-1}$ (Burgis & Dunn 1978). This is only slightly higher than the estimate for the pelagic community of Lake Kariba and very much lower than that for Lake Tanganyika. It seems very low, considering that Lake George is highly eutrophic with dense blooms of *Microcystis aeruginosa* Kutz. which can be utilised by *O. niloticus* (Moriarty 1973; Moriarty *et al.* 1973). Lake George has a volume of only 0.5 km^3, all of which is habitable by fish, and so production can be recalculated to become 2 750 t km^{-3}. This is an extremely large value and clearly illustrates how much more productive this lake is when compared to Kariba or Tanganyika. The production data now appear to reflect the trophic status of the lakes more realistically when expressed in volumetric terms.

Production data may be a useful method for estimating fish yields from tropical waters because production proceeds at a higher and more continuous rate than it does in temperate ones (Coulter 1981). This implies that a species like *Limnothrissa* could sustain an annual harvest greater than its mean biomass because of its short life and high productivity.

CHAPTER 10: ON THE POTENTIAL YIELD OF THE SARDINE FISHERY

INTRODUCTION

The ability to predict the potential yield of a fishery is clearly a desirable objective, especially in one like the Kariba sardine fishery which is intensively developed but apparently not yet at its maximum. In this chapter, therefore, some approaches to estimating the yield will be described and applied. They fall into three broad groups, which are more or less sequential and show a gradation of increasing accuracy.

The first group consists of a series of empirical models which attempt to predict yield from a variety of environmental parameters. This approach is generally most suitable as a guide to the minimum yield that might be expected from a potential fishery that is presently undeveloped. They have nevertheless been applied to the sardine fishery in order to assess their value, to see if their predictions are at all close to reality and to show if there is likely to be room for further expansion of the fishery.

The next group of models are based on limited biological data of the type which might be assembled following a biological survey or during the early stages of a fishery. The predictions made by them are, like those from the preceding group, approximations but one might expect them to be more accurate because they are based on characteristics of the stock under investigation and not a series of variable and possibly inadequately determined environmental parameters.

The last group consists of two of the most widely-used models for estimating maximum sustainable yield; the surplus yield model (Schaefer 1954, 1957) and the yield per recruit model (Beverton & Holt 1957). Neither can be applied until the fishery has been in operation for some time and the response of the stock to fishing pressure has been evaluated. Schaefer's model is empirical in that it is based on the observed relationship between yield and effort. It requires a reasonably long series of catch statistics and can give estimates of the maximum sustainable yield and the optimum level of fishing effort.

By contrast, Beverton & Holt's model is deterministic in that it uses the characteristics of the stock which will determine the yield. The model allows for the manipulation of population parameters so that the maximum yield can be determined in relation to fishing effort, the age of first capture or the age of recruitment. Although it does not predict yield in terms of weight it allows an assessment of how far the fishery is from, or beyond, maximum sustainable yield - provided that recruitment patterns do not change. The way in which the fishery operates can then be varied by, for example, changing the fishing gear so that a different age group is selected.

METHODS

Empirical models

Some empirical models were used earlier to relate Kariba's potential productivity to other African reservoirs (Table 6); whilst they were useful for comparative purposes, several included data from Kariba in their formulations. Consequently the predictions will tend to be close to reality in any event and so it was necessary in this section to use empirical models which did not include data from Kariba.

The first used air temperature as a predictor (Schlesinger & Regier 1982) and fish yields could be predicted by

$$\log Y = 0.061T + 0.043$$

where Y = yield (kg ha^{-1}) and T = mean air temperature (^{o}C).

The next two models use the morphoedaphic index (conductivity/mean depth). In a study of 17 intensively-fished African lakes Henderson & Welcomme (1974) were able to predict yield by the expression

$$\log Y = 1.1557 + 0.4681 \log MEI$$

where MEI = the morphoedaphic index. This equation was modified by Toews & Griffith (1979) who introduced lake area as a predictive parameter; their equation was

$$\log Y = 1.4071 + 0.3697 \log MEI - 0.00005465 A$$

where A = lake area.

In a study of North American lakes Young & Heimbugh (1982) were able to demonstrate that lake area alone was a powerful predictor of fish yield. Marshall (1984b) adapted this approach to the 17 intensively-fished lakes of Henderson & Welcomme (1974) and found that fish yield was related to area by

$$\log_e Y = 3.57 + 0.76 \log_e A$$

and it should be noted that Y = total yield (t). For comparative purposes yield was then expressed in kg ha^{-1} which was obtained by simple division.

Schlesinger & Regier (1982) proposed a modification of the MEI by including temperature and obtained two relationships

(i) $\log Y = 0.050T + 0.280 \log MEI + 0.236$

(ii) $\log Y = 0.044T + 0.482 \log MEI_{25} + 0.021$

where MEI = the morphoedaphic index (Total Dissolved Solids/mean depth) and MEI_{25} = morphoedaphic index with the mean depth reduced to 25 m for those lakes where it exceeds this.

The two final models that were used are based on primary production. Melack (1976) found that

$\log Y = 0.91 + 0.113\ PG$

where PG = primary productivity ($g\ O_2\ m^{-2}\ day^{-1}$). Oglesby (1977) predicted fish yield in $g\ C\ m^{-2}\ yr^{-1}$ and to convert this to $kg\ ha^{-1}$ it was necessary to multiply by 100; the adjusted predictive equation was

$\log Y = -4.00 + 2.00 \log PP$

where PP = primary productivity ($g\ C\ m^{-2}\ yr^{-1}$).

Limited biological data

The yield from a more or less unfished stock can be predicted if an estimate of natural mortality and biomass is available by

$Y = 0.5\ M\ B_v$

where 0.5 = a mean figure for the proportion of the stock that can be taken, M = natural mortality (annual rate) and B_v = unfished biomass (Gulland 1971).

If the intrinsic rate of population growth (r_m) is known then there are two equations that can be used to predict yield. The first is from Ricker's (1975) derivation of the simple Schaefer (parabolic) model which gives

$$Y = \frac{r_m B_v}{4}$$

where B_v is taken to be the same as B_∞, the carrying capacity of the environment for the stock. The second approach is from Pauly (1982) who combined the previous expression with the equation for estimating r_m of Blueweiss et al. (1978) which is

$$r_m = 0.025\ \bar{w}^{-0.26}$$

where $\bar{w}$ = the mean individual weight (g) of the fish being studied. Yield was then expressed on an annual basis by

$$Y = 2.3\ \bar{w}^{-0.26}\ B_v\ .$$

Two models given by Csirke & Caddy (1983) were also used. The first was

$$Y = \frac{r_m \bar{B}\ (B_v - \bar{B})}{B_v}$$

where $\bar{B}$ = the mean biomass of the stock. Their other model did not indicate potential yield but instead gave the optimal levels of total and fishing mortality at which maximum sustainable yield could be attained. These were calculated as follows

$$Z_{msy} = 0.5\ r_m + M$$

and

$$F_{msy} = 0.5\ r_m$$

where Z_{msy} and F_{msy} = optimum levels of total and fishing mortality and M = natural mortality.

The Schaefer (surplus-yield) model

In its simplest form this model assumes that catch per unit effort (CPUE) will decrease linearly as effort increases such that

$$\bar{U} = a - bX$$

where $\bar{U}$ = CPUE, X = fishing effort and a, b are regression constants. From this, equilibrium yield is estimated by

$$YE = aX - bX^2.$$

It has been argued, however, that this is not a linear but an exponential relationship (Fox 1970) in which case

$$\log_e \bar{U} = a - bX$$

which can be transformed to

$$\bar{U} = U_{max} e^{-bX}$$

where U_{max} = the maximum CPUE. Equilibrium yield then becomes

$$YE = U_{max} X \, e^{-bX}.$$

Both approaches were used with data on effort and CPUE coming from ch. 5.

The linear model gives a parabolic curve of equilibrium yield which eventually reaches zero. The optimum yield is at the top of the parabola and the optimum effort can be estimated by inspection. In the exponential model equilibrium yield reaches a peak and then decreases towards, but never reaches, zero. Maximum equilibrium yield and optimum effort are less easily determined by inspection, but can be calculated from

$$E_{opt} = \frac{1}{b}$$

and

$$YE_{max} = \frac{U_{max}}{be}$$

where b = regression constant, e = the base of natural logarithms, E_{opt} = optimum effort and YE_{max} = maximum equilibrium yield.

Yield per recruit

The data on growth and mortality (ch. 5) and the selection characteristics of the fishing gear (ch. 7) were fitted to Beverton & Holt's (1957) yield equation which is

$$Y/R = F\,W_{\infty}\,e^{-M(t_c - t_r)}\left[\frac{1}{Z} - \frac{3e^{-K(t_c - t_o)}}{Z + K} + \frac{3e^{-2K(t_c - t_o)}}{Z + 2K} - \frac{e^{-3K(t_c - t_o)}}{Z + 3K}\right]$$

where F, M and Z = the rates of fishing, natural and total mortality respectively (monthly values); t_c = age of first capture and t_r = the age of recruitment; t_o, K and W_{∞} = parameters of the von Bertalanffy growth equation.

The model was first applied to the sardine fishery with t_c varying and then with M varying and all other parameters constant. Yield per recruit was then calculated for the years 1978-83 using the data in chs. 5 and 7. From this it was then possible to obtain the relation between the stock, estimated from Table 24, and the number of recruits. A stock-recruit curve was then plotted by the method in Gulland (1983), which, with the notation slightly changed, is

$$R = C\,B\,e^{-DB}$$

where R = recruits, B = the mean biomass and C and D are constants. The expression was then fitted by plotting

$$\log_e \frac{R}{B} = \log_e C - DB$$

which becomes

$$\frac{R}{B} = C\ e^{-DB}.$$

RESULTS

Empirical models

The parameters that were fitted to the models were; air temperature = 25.9°C (Meteorological Department); MEI = 2.8 based on conductivity = 80 μS cm^{-1} and mean depth = 29.2 m; lake area = 5400 km^2 (a "standard" mean value); MEI = 2.24 and MEI_{25} = 2.62 based on TDS = 65.4 mg l^{-1} (Coche 1974); PG = 6.4 g O_2 m^{-2} day^{-1} and PP = 620.5 g C m^{-2} yr^{-1} (Machena 1983). The predicted yields (kg ha^{-1}) were as follows

Air temperature model:	41.96
MEI model:	23.17
MEI + lake area model:	18.94
Lake area model:	45.15
MEI + air temperature model:	23.03
Primary production (PG) model:	26.90
Primary production (PP) model:	38.50

The range was 19-45 kg ha^{-1} which is equivalent to an annual yield of 10000-24300 t.

Limited biological data

A reliable estimate of B_v was difficult to obtain because there are no data from the period before the fishery began but reference to ch. 7 suggests that 60 kg ha^{-1} would be a realistic value. The annual rate of natural mortality was 8.4 (ch. 6) and by using these values in Gulland's equation yield was estimated at 252 kg ha^{-1}.

The rate of population growth was determined from Blueweiss _et_ _al_. (1978) (ch. 6) to be 9.490 and so the yield estimated from Ricker's equation was 142.35 kg ha^{-1} and from Pauly's expression it was 141.43 kg ha^{-1}.

The mean sardine biomass was estimated to be 44 kg ha^{-1} (ch. 7) and consequently Csirke & Caddy's method predicted a yield of 109.72 kg ha^{-1}. The optimum annual mortality rates were $Z_{msy} = 13.08$ and $F_{msy} = 4.68$.

The Schaefer (surplus yield) model

The linear version of this model gave an estimate of maximum equilibrium yield of 14 600 t and optimal effort of 86000 unit-nights (Fig. 38). The exponential version gave rather higher values; maximum yield was 16821 t and optimum effort was 129900 unit-nights (Fig. 39).

Yield per recruit

The yields per recruit with the age of first capture varying from $t_c = 3$ to $t_c = 7$ months are shown in Fig. 40. At the present level of fishing where F 0.5 and $t_c = 3$ months the yield from 100 recruits is about 20 g but was considerably reduced with increasing t_c. If this present level of fishing was doubled so that F = 1.0 the yield would only increase to 25 g and it it was doubled again so that F = 2.0 yield would

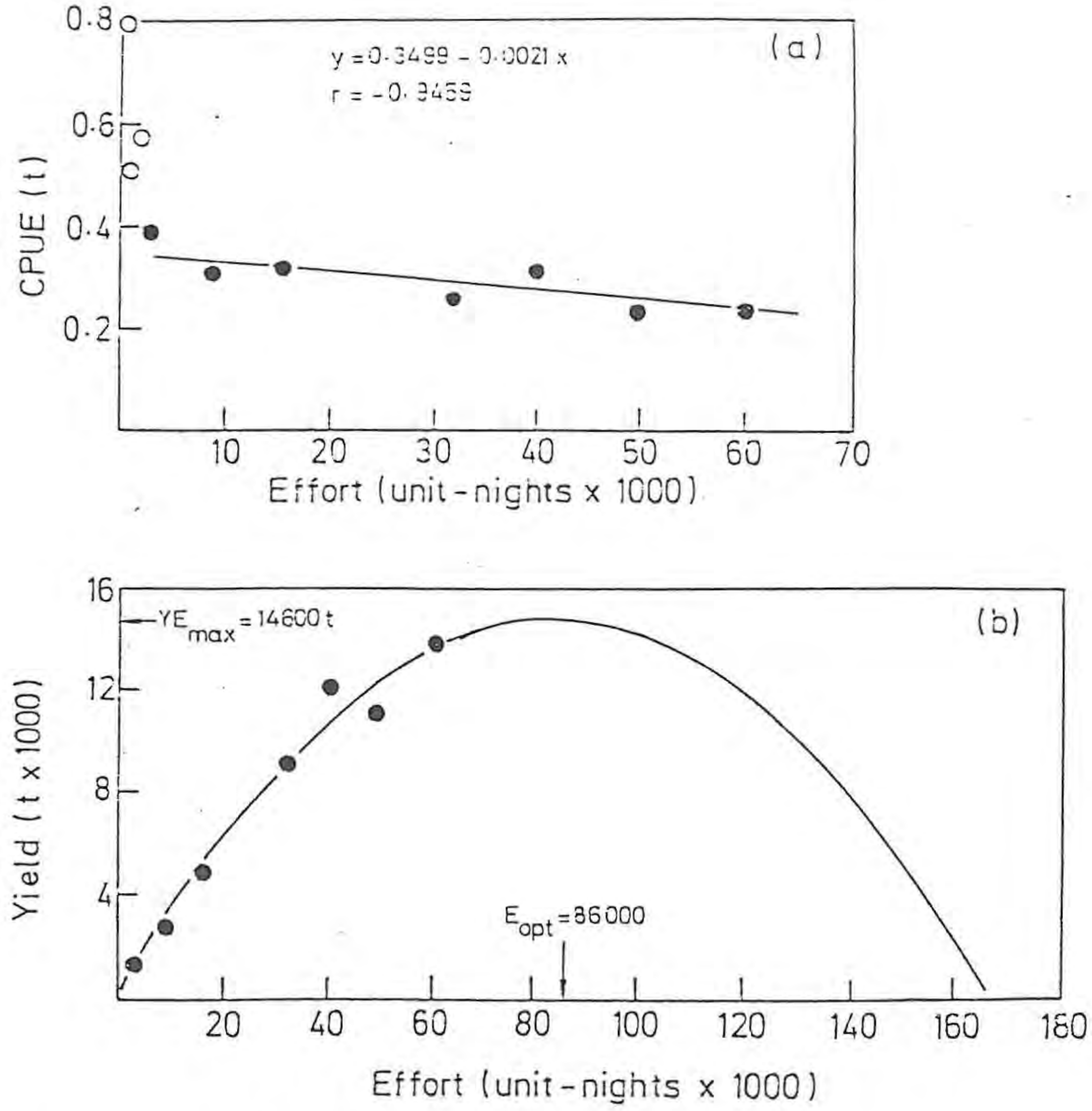


Figure 38: (a) The linear relationship between effort and catch per unit effort CPUE (Schaefer 1954, 1957). The first 3 years data (open circles) have been excluded.

(b) Estimation of maximum equilibrium yield and optimum effort from the linear relationship.

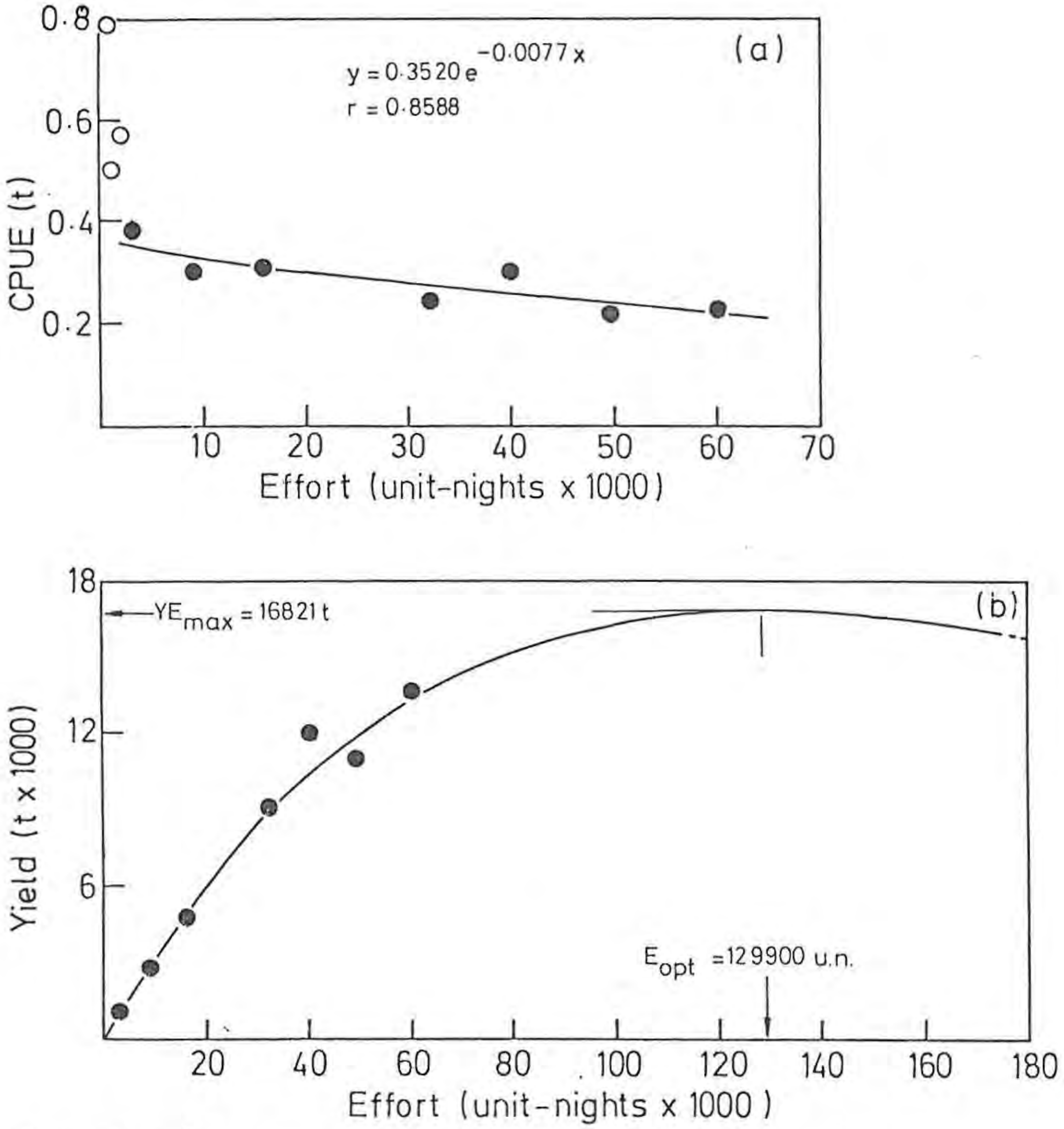


Figure 39: (a) The exponential relationship between effort and catch per unit effort, CPUE. (Fox 1970). The first 3 years' data (open circles) have been excluded.

(b) Estimation of maximum equilibrium yield and optimum effort from the exponential relationship.

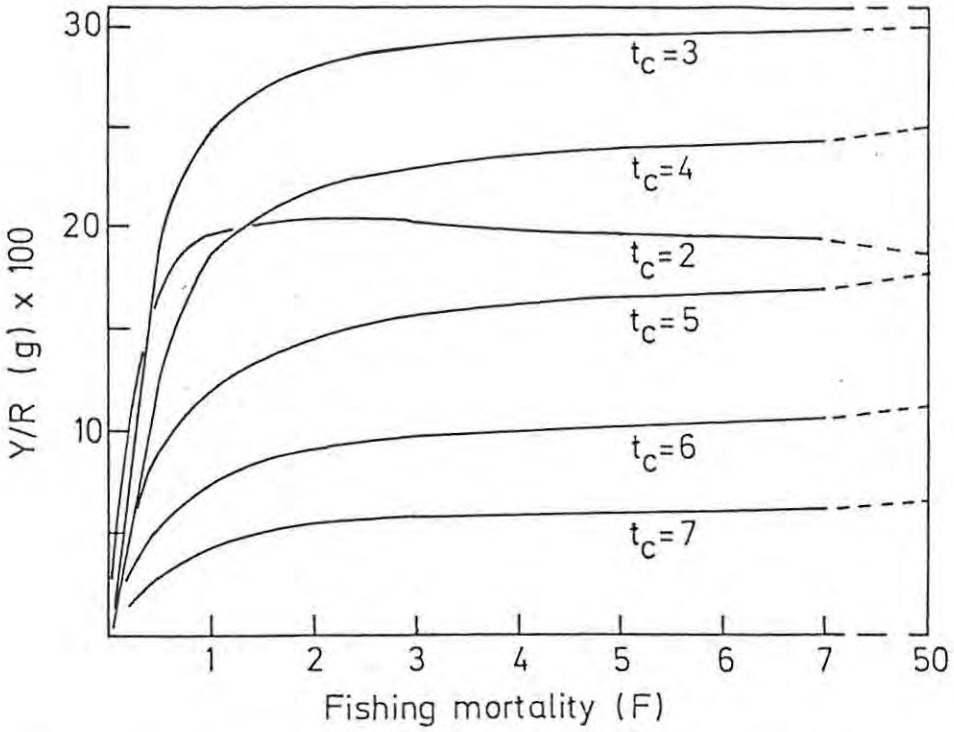


Figure 40: The yield per recruit (x 100) with variable fishing mortality and t_c ranging from 2 - 7 months. Constants are: W = 2.72 g, $M = 0.7$, $K = 0.254$, $t_o = -0.066$, $t_r = 2.5$.

only reach about 28 g. There would then be a steady increase in yield as effort increased but this is so slight that even when $F = 50.0$ the yield per 100 recruits would only be 30 g.

The yield per recruit when natural mortality varies is shown in Fig. 41. The current level of natural mortality is estimated to be 0.7 (monthly) but it could presumably vary from 0.6 - 0.8, which would have a considerable effect on the yield.

The yields per recruit from 1978-83 combined with the total catch from the fishery make it possible to estimate the number of recruits (Table 30). The table also shows the mean stock in the lake and the relationship between stock and recruits as shown in Fig. 42 .

Table 30: The yields per recruit from the sardine fishery, 1978-83 with the estimated number of recruits and the mean stock during each year. The constants used in the Y/R estimations were $M = 0.7$, $K = 0.254$, $W \ = 2.72$ g, $t_o = -0.066$.

	F	t_c	t_r	Y/R x100	Yield (t)	Recruits	Stock (t)
1978	0.12	3.5	2.0	4.77	2772	5.81×10^{10}	28728
1979	0.39	2.5	2.0	14.03	4874	3.47×10^{10}	27864
1980	0.41	3.5	2.0	10.91	7988	7.32×10^{10}	21276
1981	0.27	4.0	2.0	7.05	12003	1.70×10^{11}	23760
1982	0.33	3.0	1.5	8.02	11051	1.38×10^{11}	20466
1983	0.45	3.5	1.5	8.57	13573	1.58×10^{11}	18792

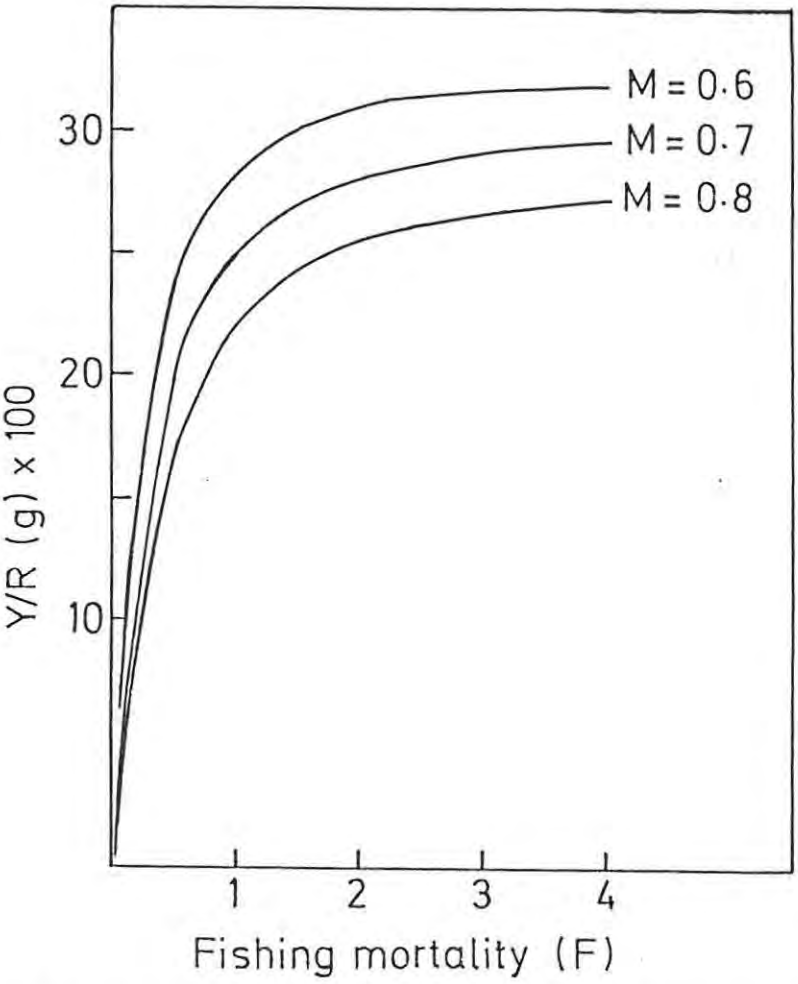


Figure 41: The yield per recruit (x 100) with F varying from 1 to 4 and M varying from 0.6 to 0.8. Constants are W = 2.72 g, K= 0.254, t_o = -0.066, t_r = 2.5, t_c = 3.

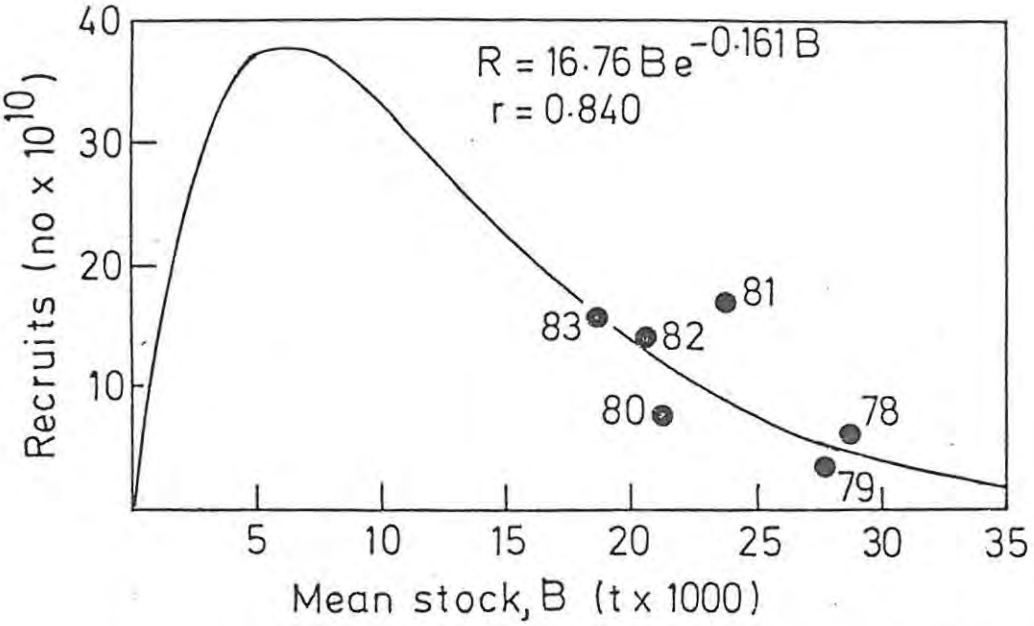


Figure 42: The stock-recruitment relationship for Limnothrissa in Kariba, 1978 - 1983.

DISCUSSION

The yields predicted by the empirical models were highly variable and this is probably a reflection of inadequacies in the original data. The models of Schlesinger & Regier (1982) and Oglesby (1977) were based on a considerable number of lakes from various latitudes, but with very few tropical or sub-tropical examples. Henderson & Welcomme's data must have reflected the general inaccuracy of fishery statistics in African inland waters and this will consequently have influenced Toews & Griffith's model. Primary production estimates from African lakes are often based on spot samples or very short data series (Melack 1976) and this means that predictive models based on this parameter should be used with care. The Kariba data are certainly limited in this way as the project from which they came only lasted about 6 months and samples were only taken at 3 stations (Machena 1983), so they may not be truly representative of the lake as a whole.

The total fish yield from Kariba is presently about 16000 t (or 29.63 kg ha^{-1}) of which about 13000 t (or 24.07 kg ha^{-1}) is of Limnothrissa. The empirical models will estimate yield from the lake as a whole and it can be seen that 4 of the 8 models give predictions that are already below the current yield. The mean of the remaining 4 models is 42.05 kg ha^{-1} and this is perhaps a reasonable figure to use for predictive purposes. At this yield the total production from the lake would be 22707 t and since the inshore fishery is unlikely to exceed its present production of 3000 t yr^{-1} (Marshall 1982b; Marshall et al. 1982) a sardine yield of around 19700 t seems likely.

Using empirical models in this way, after an intensive fishery has already been established, is not what they were designed for. There is certainly a temptation to select those models which will give predictions that are closest to the situation in existence and care should be taken to avoid this. These models are most useful before a fishery has been established and can act as a guide to what might be expected and probably to the minimum that might be produced. None would have been very useful in Kariba if Limnothrissa had not been introduced to occupy the pelagic zone as inshore catches alone do not indicate the lake's potential. This emphasises the need for detailed biological knowledge to be used in conjunction with these models.

The yields predicted by the models which included limited biological data were very much higher than those predicted by the empirical ones. The highest prediction was from Gulland's equation and at 252 kg ha^{-1} the total catch would reach 136000 t yr^{-1}. Ricker's and Pauly's equations give similar estimates, as they should since the equations are basically identical (the slight difference is caused by rounding off at various stages), and at 140 kg ha^{-1} the total yield would be 75600 t yr^{-1}. Csirke & Caddy's method gave a rather lower estimate of 110 kg ha^{-1} which would result in a total catch of 59400 t.

The differences between these predictions and those from the empirical models is striking. It should be remembered, though, that these expressions are only approximations and they should be treated with a great deal of caution. In particular, it is possible that they are completely unsuited to a species like Limnothrissa which has an extremely unusual life history for a commercially-exploited species.

The estimates of potential yield so far suggest that there is room for a considerable expansion of the fishery. The estimated optimum mortality rates indicate the opposite for they are lower than those prevailing in the fishery at present (in 1983, $Z = 13.788$ and $F = 5.388$). In the case of a Limnothrissa fishery, on Kariba or any other lake, it seems that mortality might be a better means of estimating the yield and managing the fishery than are the biomass models.

In any event these models, like the empirical ones, are most suited to a situation where a fishery has yet to begin and serve mainly as a guide to what should be possible (empirical) and what might be possible (limited biological data). The next two approaches are based on the performance of the fishery itself and the characteristics of the species concerned and are thus likely to be most reliable.

The Schaefer model tends to reflect the history of the fishery and is consequently of relatively limited predictive value (Clay 1984). However, in a situation like the Kariba sardine fishery which has been operating for several years but has clearly not reached its peak this may not apply. Both the linear and the exponential models indicate that the fishery could be increased but that the extra effort needed would not produce a corresponding increase in catch. If the linear model is correct then the present level of effort (60000 unit-nights in

1983) could be increased by 43% but this would only improve the yield by 12%. If the exponential model is more realistic then effort could be raised by 116% for a yield increment of 25%. The yield/effort increase ratio is very similar for both models (0.21 and 0.28 respectively).

This indicates that the fishery is now beginning to reach a stage where economic factors will begin to affect its production. Further expansion could be discouraged by the increased costs of catching the fish. It can be argued that the relationship between CPUE and effort will change as the data series becomes longer and this would seem to be the case as the first attempt to use this model on the Limnothrissa fishery gave very much lower estimates after 7 years of data (Marshall et al. 1982). However, they included data from 1974-76 which appear to be anomalous and have been ommitted in the present study. There is no clear reason why these catches should be so different and declined more rapidly but it is possible the effort has not been calculated accurately for the early years when only 2 purse-seiners were fishing during this period.

As more data are assembled the predictions from this model will change but it seems unlikely that the potential yield will be much above those predicted at present. It is interesting to note that the mean empirical yield is predicted to be about 23000 t which is much closer to the maximum predicted by the Schaefer models than to the ones based on the limited biological data.

The yield per recruit model tends to support these conclusions, that the total yield can be increased but this will not be proportionate to the amount of effort needed to bring it about. Thus if fishing effort was doubled so that $F = 1.0$ the yield from 100 recruits would rise from 20 to 25 g only; a 100% increase in effort would bring about a 20% increase in yield. If the fishing effort was doubled again so that $F = 2.0$ the yield would increase only to about 27.5 g per 100 recruits. It seems therefore that the opportunity for greatly increased expansion of the sardine fishery without greatly increasing its operating cost no longer exists.

Nor would reducing the mesh size so that younger fish were caught be a solution because the yield per recruit is very much lower when $t_c = 2$ months (Fig. 40). It seems that the fishing gear currently in use gives the best possible yield and that there is nothing to be gained by changing it.

The stock-recruit relationship appears to follow the pattern of the typical "Ricker" curve although the data series is rather short and it could change once more are available. The shape of this curve is very similar to the one obtained by Roest (1978) for Stolothrissa and is an example of the phenomenon of compensation (Cushing 1968) in which there is high recruitment at low stock levels and low recruitment at high stock levels. It was not possible, or advisable, to take this model further because of the limited data but it seems likely that the "dome" of the curve represents the recruitment at maximum fishing intensity (i.e. greatest reduction of stock). This appears to be about half of what it is at present which again supports the view that there is limited scope for expansion of the fishery. It must be emphasised, however, that this relationship is largely speculative as it is based on the most preliminary of data and should therefore be treated with caution. It is presented here because this is the first time this has been attempted for any fish species in Lake Kariba and to draw attention to the possibilities this method offers in the hope that future workers will consider its application and collect data accordingly.

In conclusion, it seems that yield from the Kariba fishery may be unlikely to exceed 20 000t annually (37 kg ha^{-1}) and that anything beyond this will be uneconomical, requiring a disproportionately large increase in fishing effort. The only lake pelagic community for which yield predictions have been made is that in Lake Tanganyika (Coulter 1977, 1981) and it is interesting to compare the predictions from the two lakes.

The present yield from Tanganyika is about 22 kg ha^{-1} which is lower than Kariba's, but it could be raised, at least in the northern end, to theoretically as much as 350 kg ha^{-1} (Coulter 1981). If a rather more conservative value of 250 kg ha^{-1} is applied to the whole lake (and this is 10 times the present yield) then, on a volumetric basis the yield from Tanganyika becomes about 167t km^{-3}. This compares to a yield of 171 t km^{-3} from Kariba and once again emphasises the view that sardine biomass is similar in the two lakes and at its maximum in each.

CHAPTER 11: CONCLUDING DISCUSSION

Life history

There appear to be significant differences between the environments of reservoirs (Kariba, Cahora Bassa) and natural lakes (Tanganyika, Kivu) which have resulted in the "stunting" of Limnothrissa in the former. The phenomenon of stunting is known from many fish species and is especially common in culture systems where it is usually attributed to overcrowding and a shortage of food. It can be overcome in these situations by changing the environment or reducing the population (Fryer & Iles 1972; Burrough & Kennedy 1979; Dadzie & Wangila 1980; Murnyak et al. 1984).

The reasons for stunting are rather more complex amongst natural populations. In Lake Sibaya, South Africa, for example, it was found that both Oreochromis mossambicus (Peters) and Clarias gariepinus showed good growth and maintained condition whilst feeding in inshore areas as juveniles but slow growth and poor condition when living in offshore areas as adults. This was caused by a deterioration in the quality rather than the quantity of the food that they utilised in this environment (Bruton 1979). In this case stunting was brought about by a variety of biotic and abiotic factors. In another example, the growth of C. gariepinus was generally least in environments where large individuals were unable to feed on fish (Bruton 1976) and again it was the quality of food which appeared to affect the fish's growth.

In Maine, U.S.A. Walton (1983) showed that alewives Alosa pseudharengus were stunted following a change in life history pattern. The stocks he examined were intermediate between fully landlocked and typically anadromous forms and it was postulated that dwarfing (stunting) and associated changes in larval development and early ontogeny may have been the basis for the development of fully landlocked stocks. Food may also have been limiting in the system where the fish were stunted but this could not be clearly demonstrated.

Hydrological, geological and morphoedaphic differences between them support the view that food is likely to be limiting in man-made lakes compared to natural ones but there is very little direct evidence to support this. Indeed, primary productivity in Lake Tanganyika is low in comparison to many other tropical lakes (Hecky et al. 1981) and the mean value of 0.8 g C m^{-2} day^{-1} is considerably lower than the mean of 1.7 g C m^{-2} day^{-1} recorded in Kariba (Machena 1983). In addition to this the two lakes appear to support very similar pelagic biomasses and there would thus seem to be no obvious reason why the sardines should not be the same size in each lake.

Noakes & Balon (1982), discussing the question of stunting in cichlids, have suggested that the adoption of an "altrical" life style i.e. with a short period of somatic growth (judged by body size) and the early onset of breeding might be an adaptation enabling these fish to occupy floodplain pools or new habitats. The object of this strategy is to produce as many individuals as possible in a relatively unstable or short-lived environment and this may be the explanation for the stunting of Limnothrissa in Kariba.

It is almost certainly a more variable environment than Lake Tanganyika. The hydrological regime results in a rapid water turnover and, at times, marked fluctuations in lake level, which in turn will influence the nutrient supply. Nutrient dynamics are also affected by the seasonal cycle of stratification and by river flows. Because of its large volume with small inflow and outflow these aspects are less important in Lake Tanganyika and although there are variations in the upper watercolumn (Coulter 1963, 1967) these are unlikely to have the pronounced effect that they do in Kariba. In order to maintain a high biomass in Kariba the sardines have had to become mature at an early age, grow to a smaller size and withstand a high mortality rate. This life history strategy can be considered in terms of the r- and K-selection concept (Pianka 1970, 1972).

These terms are derived from the widely-used logistic growth curve where r is the slope or growth rate of the population and K is the upper asymptote or carrying capacity of the environment (Noakes & Balon 1982). An r-selected species is one in which population growth is paramount and they are characterised by being small, with a short life cycle and early reproduction, and they tend to inhabit unpredictable or variable environments. In contrast, a K-selected species will tend to be large, with a longer life cycle and inhabit a more stable environment. Pianka considers that no species is likely to be completely r- or K-selected and must reach a compromise between the two extremes.

This implies that a species could show a greater degree of *r*- or *K*-selection if it were placed in a new environment. *Limnothrissa* must be more strongly *r*-selected in Kariba than it is in Tanganyika and as the optimal strategy of an *r*-selected species is "to channel all possible matter and energy into reproduction with the smallest practicable amount into each individual offspring" (Pianka 1970) this has enabled it to maintain a high biomass in the lake. The end result of an *r*-selected strategy is high productivity and *Limnothrissa* in Kariba were found to have an extremely high $P/\bar{B}$ ratio which, again, can be seen as a means of maintaining a large biomass in the face of very high mortality rates.

The stunting of *Limnothrissa* in Kariba may not therefore be simply a response to food shortage but part of a life history strategy designed to permit the establishment of the maximum biomass in the face of a relatively unstable and variable environment. The data obtained in this study highlight the importance of expressing fish biomass in terms of volume rather than area, even though they are imprecise at present and there are few others that can be used for comparative purposes.

The data also imply that a pelagic system might support the same biomass of pelagic species by means of that species adopting a different life history strategy. This conclusion should not be reached too readily as some species may be better adapted to pelagic systems than others and so may be able to maintain a high biomass in very variable systems. The cyprinid Engraulicypris sardella of Lake Malawi is considered to be a poorly-adapted pelagic species (Turner 1982) and the biomass can be estimated to be 145 000 t (Rufli & Vitullo 1982). As the lake has a surface area of 30 800 km^2 and is anoxic from 200 m the habitable volume will be around 5 000 km^3. This gives a biomass estimate of 29 t km^{-3} which is well below the estimate from Kariba or Tanganyika. Since the average rate of primary productivity (0.74 g C m^{-2} day^{-1}) (Degnbol & Mapila 1982) is comparable to Tanganyika's such a large difference is unexpected. This supports the view that the cyprinid is a less efficient planktivore than are the clupeids and it is possible that the large biomass of Chaoborus that occurs in Lake Malawi makes up the difference.

It is equally possible that the heterotrophic bacterial production that Hecky et al. (1981) have postulated as a mechanism for increasing fish productivity in Lake Tanganyika does not operate, or operate as efficiently, in Lake Malwai. Until more is known about this system in both lakes Turner's (1982) proposal to introduce the sardine into Lake Malawi should be treated with caution.

Ecological effects

The ecological effects of Limnothrissa in Lake Kariba have been discussed (ch. 3) but some further consideration can be given to its role in the nutrient dynamics of the lake. Marshall & Junor (1981) discussed this in relation to the decline in abundance of Salvinia molesta but did not at that time have a reasonable estimate of sardine biomass.

The sardines contain about 2.5% nitrogen and 0.6% phosphorus (wet weight) (Chemistry & Soil Science Institute, Ministry of Agriculture) and so a biomass of 44 kg ha^{-1} or 24000 t would retain 600 t of nitrogen and 137 t of phosphorus. Biomass may, of course be much higher at certain times of the year and estimates of 60000 t were obtained during this project; this would mean that much higher levels of these nutrients would be retained. These values are lower than the quantities retained by Salvinia at its peak in 1962; then the weed mat of 1000 km^2 retained about 7925 t of nitrogen and about 417 t of phosphorus (Mitchell 1973). The lake was, of course, still eutrophic in 1962 (Coche 1974) and nutrient levels are now very much lower so it is likely that the sardines do in fact act as a nutrient reservoir and may have contributed to the decline of Salvinia.

It is also possible that the removal of large numbers of sardines from the lake could lead to the loss of significant quantities of limiting nutrients. A yield of 20000 t would result in the loss of 500 t of nitrogen and 120 t of phosphorus which is almost as much as the amount retained in the mean biomass. It would certainly seem that it should have an effect but more data are needed before this can be substantiated. It is interesting to speculate on the possibility that the fishery could be limited through a loss of nutrients brought about by fish removal.

Potential yield

A variety of models to predict yield were used and they gave widely varying predictions. The Schaefer (Fox version) and Beverton & Holt models were probably the most reliable because they were based on the actual performance of the fishery or the response of the population to fishing pressure. Silliman (1971) has discussed the problems associated with the use of the Schaefer-type models and concluded that they fitted best to fish recruited at an early age. They would thus appear to be most suitable for a species like Limnothrissa which was recruited at an age of 2-3 months.

The main conclusion was that the fishery is now apparently entering a phase where increased fishing effort will not result in a proportionate increase in yield. The maximum sardine yield from Kariba appears to be about 20000 t annually and, in terms of volume, this was very similar to the predicted yield from Lake Tanganyika. This is, of course, to be expected in view of the similarity in biomass between the two lakes.

If the arguments concerning the life history strategy of Limnothrissa in different lakes is correct it might be possible to predict yields from Lake Kivu and Lake Cahora Bassa, assuming that the optimum yield will be around 170 t km^{-3}. Lake Kivu has a surface area of 2699 km^2 and the water is anoxic from 70 m in depth (Beadle 1974); it thus has a volume habitable by sardines of around 189 km^3 and the yield might therefore by 32130 t annually. This is close to the yield of 30000 t suggested by Welcomme (1972) and well above the experimental yield of 42 kg ha^{-1} (extrapolated to 13500 t) which was attained by Spliethoff et al. (1983).

Cahora Bassa is a completely different type of water body and is likely to be the most variable of any that Limnothrissa inhabits. It has a surface area of 2398 km^2 but its water level changes by as much as 10 m annually which means that total area fluctuates as much as 20% each year (Bernacsek 1984; Bernacsek & Lopes 1984). Thermal stratification is limited to a relatively small area of deep water and this breaks down during the isothermal period each year. It is extremely difficult, therefore, to obtain an estimate of the habitable volume of water in this lake and an arbitary figure will have to be used. The mean depth (at full capacity) is about 21 m; if a depth of 15 m and a surface area 10% less than the full one is adopted then habitable volume might be 36 km^3. Yield could then reach 6120 t which is rather less than the 8000 t predicted by Bernacsek & Lopes (1984).

This discussion is, of course, highly speculative, especially in the case of Cahora Bassa where the estimation of volume is especially difficult. The method does seem feasible, however, because primary production data suggest that both lakes are similar in potential to Kariba and Tanganyika (Kivu primary production = 0.66 - 1.48 g C m^{-2} day^{-1} (Spliethoff et al. 1982) and Cahora Bassa = 0.38 - 4.68 g C m^{-2} day^{-1} (Gliwicz 1984)). Further data are needed before this concept can be fully utilised, but it may be a useful means of assessing yield of pelagic clupeids and might be extended to other waters with different species, such as Volta and Kainji Lakes in West Africa.

The success of the sardine fishery on Kariba has led to increased interest in the exploitation of clupeids, either naturally occurring or introduced, in other lakes. As discussed earlier (ch. 3) Kariba is the only man-made lake supporting such a fishery and although clupeid potential has been recognised in both Volta and Kainji no fishery has yet developed on these lakes. Proposals have been made for the introduction of *Limnothrissa* into Lake Nasser (J.M. Kapetsky, personal communication) but nothing has been done so far. Nor have natural populations been fully exploited, except in some traditional fisheries such as the Atalla fisheries on the lower Niger (Awachie & Walson 1978). A pilot project to utilise *Poecilothrissa moeruensis* has begun on Lake Mweru in Zambia (Zambian Fisheries Department, personal communication) and there may be a potential for such species as *Nannothrissa stewarti* in Lake Mai-Ndombi or *Poecilothrissa centralis* in Lake Tumba provided they occur in sufficient numbers. There is clearly a need for further investigations into this group of fish and their true potential in African waters is far from being realised.

Management aspects

The aim of this project was not to provide a detailed management plan for the Kariba sardine fishery but to give some basic data which could be used to prepare such a plan. There are, however, some aspects of management that require discussion.

The sardine resource is of course shared between Zimbabwe and Zambia with both countries ultimately being entitled to an equal share. The stock is a common-property resource with no value until it is landed and this introduces a number of management problems. In particular there is the question of the "fisherman's dilemma" (Clark 1981), i.e. what is the best strategy to adopt to ensure the best yield in the face of the strategy adopted by the other fishermen?

Clark's example can be used, with two fishermen, A and B, exploiting the same resource. If both A and B fish to conserve the resource then it could yield an arbitrary catch of 6 units, with A and B taking 3 each. This is the optimum strategy, but, if A fishes to deplete the resource it might only yield 5 units in total with 4 going to A and only one to B. If A and B both fish to deplete the stock would only yield 4 units but both fishermen would take 2 each. The dilemma then is that, assuming no cooperation between the exploiters, the best strategy from B's point of view is to fish to depletion although both fishermen will ultimately be losers after the stock has declined.

This analogy can very easily be extended to the Kariba sardine stock where Zimbabwe and Zambia represent the two fishermen and the two countries might adopt very different management strategies which could lead to a disastrous competition. What is particularly disturbing is that there is still no formal body, with representatives from both countries, having power to set a management policy for the stock as a whole. Although informal contacts exist these are inadequate and, in general, Zimbabwean and Zambian fishery authorities are planning the sardine fishery in almost total ignorance of the other side's views and intentions.

This is an especially serious problem when it comes to the control of fishing effort which Gulland (1978) considers to be the most significant factor in the collapse of numerous fisheries. Several marine clupeid fisheries have collapsed, largely through uncontrolled effort aggravated by political, economic or climatic factors (e.g. Murphy 1977; Radovich 1981; Cram 1981). The most dramatic example of all was the Peruvian anchoveta where yield dropped from 12 million tons in 1970 to less than 2 million tons in 1973. The effect of the high level of effort did not become obvious until after the "El Nino" of 1972, a periodic climatic event which resulted in the incursion of warm water into the cold waters off Peru. This caused a decline of the anchoveta stocks from which they have never recovered; in 1978 the catch was only 0.5 million tons (Glantz 1979; Clark 1981).

Significantly, steps to control effort were only made after catches had begun to decline and this is when these steps are particularly difficult to enforce because of their effect on the fishermen themselves. If catches are so low that it becomes necessary to reduce effort a fisherman will be reluctant to sell vessels as their value (in terms of potential catch) will have declined and he may be unable to recoup their original cost. Furthermore, he is likely to want to increase his fishing effort in an attempt to cover his costs, repay his debts or recover his capital. The burden of salvaging the fisherman might then fall on the state.

It could be argued that such a scenario is unlikely on Kariba because it is unlikely that the sardine stocks could be overfished to the point that there would be insufficient breeding stock to maintain catches in the next season. It is true indeed that the whole lake stock became established within 2-3 years from only about 300 000 fry (Bell-Cross & Bell-Cross 1971) and that many of the breeding areas are protected by submerged trees. Nevertheless it could be possible to raise fishing effort to such a level that the stock might not be able to recover from some environmental stress, such as a drought; the drought of 1981-82, for example, may have been responsible for a drop in the yields of 1982. With a very much increased level of effort these yields may have become too low to be economical causing fishermen to be forced out of the fishery and resulting in instability in the industry.

The example of the small goby Mistichthyes luzonensis of the Philippines is perhaps a warning in this regard. This minute fish (at 25 mm length it is the smallest commercially-exploited species) was extremely abundant in Lake Buhi where it supported a flourishing traditional fishery. The introduction of motorised fishing vessels led to great increase in fishing capacity (= effort), aggravated by the establishment of two alien species (tilapia and freshwater prawns), and caused the collapse of the traditional fishery (Gindelberger 1981). This very small fish presumably had life history characteristics similar to those of Limnothrissa but it was not able to withstand the effects of high fishing effort and an external stress. In this case the stress was the exotic species and although there is no evidence of any exotic likely to affect sardines in Kariba the possibility that this could happen should not be ignored.

The social effects of instability in the Kariba sardine fishery are likely to be severe as it is one of the main employers along the lake shore (Marshall et al. 1982). The Sebungwe region i.e. the districts bordering the southern shore of Kariba, have a limited resource base and rapid population growth (ARDA 1982; Taylor 1982) and fish production from Kariba plays an important part in the economy of the region (Marshall 1982b). Any reduction in yields could lead to severe social problems especially as Lake Kariba is located in an endemic famine area (Scudder 1972).

The only management recommendation that will be made in this study is that a joint Zimbabwe/Zambian planning authority be established formally to control the Kariba sardine fishery. In particular its terms of reference should include the control of effort before it begins to affect the fishery. This requires the establishment of a sound statistical and biological data base and it is hoped that this project will have contributed to this.

In Chapter 1 the current management of the sardine fishery was described as being "ad hoc" which implies that it is presently likely to be able to react to events only after they have occurred. The establishment of a cooperative management programme would be a step towards removing the management policies from a reactive to a predictive phase where events could be known in advance and problems solved before they have become acute.

Conclusion

Before this study was undertaken the small size of Limnothrissa in Kariba was an attribute that had given rise to considerable speculation. Begg (1974a) suggested that it may have been a result of a general shortage of food compared to Lake Tanganyika. Cochrane (1978) considered that the lack of atyid shrimps (which he supposed were abundant in Lake Tanganyika) meant that fish over 65 mm in length could not grow to the next stage, at about 80 mm in length, where they became cannibalistic. He assumed that once they became cannibals they could grow to a large size.

These explanations seemed unsatisfactory as the idea that prey size limited predator size does not seem valid in an aquatic system. The view that prey abundance would limit the size of a fish predator appears more realistic and the question was whether the available prey were utilised more effectively by a large number of small fish or a small number of large ones?

Thus the basic hypothesis of this thesis was derived i.e. that the small size of Limnothrissa in Lake Kariba was a life-history adaptation to enable it to maximise its biomass in relatively unfavourable conditions. The data assembled in this thesis support this hypothesis and indicate that the actual biomass in Lakes Kariba and Tanganyika is very similar.

The abundance of these fish in the two lakes has also been a matter of some discussion as the primary productivity is very similar in each. There seemed no reason why the sardines should be so much more numerous in Tanganyika than they were in Kariba. The idea that fish abundance should be expressed in terms of volume rather than area has made it possible to make a more accurate assessment of sardine biomass in the two lakes. That this idea has not been employed before, to any significant extent reflects the difficulty of acquiring the neccessary data. Very few biomass estimates are available from African lakes and the calculation of volume, or habitable volume, is also made difficult by the lack of information. Nevertheless, it is likely that volume will prove to be a more significant parameter by which to measure biomass, at least for lacustrine fish populations. This is indicated by the conclusions of this study i.e. that Lakes Tanganyika and Kariba support a similar pelagic biomass; such a conclusion was not certain when the project was begun even though it was thought that the Limnothrissa were small in Kariba in order to utilise the available food resources effectively. It is clear that they do this and, by means of high production and a high P/$\bar{B}$ ratio, maintain a large biomass as a result.

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APPENDIX A: PUBLISHED PAPERS

Some papers dealing with the ecology of Lake Kariba or aspects of sardine biology were published during the course of this project. Copies of these papers are included for reference and they are numbered as follows:

1. 1979. Fish populations and the fisheries potential of Lake Kariba. S. Afr. J. Sci. 75: 485-488.
2. 1981. (with F.J.R. Junor) The decline of *Salvinia molesta* on Lake Kariba. Hydrobiologia 83: 477-484.
3. 1982. The influence of river flow on pelagic sardine catches in Lake Kariba. J. Fish Biol. 20: 465-469.
4. 1982. (with F.J.R. Junor & J.D. Langerman) Fisheries and fish production on the Zimbabwean side of Lake Kariba. Kariba Studies (10): 175-231.
5. 1982. Fish production potential of Lake Kariba. Zimbabwe Agric. J. 79: 173-177.
6. 1984. Small pelagic fish and fisheries in African inland waters. CIFA Tech. Pap. (14): 25p. Rome; FAO.

APPENDIX B: THE EFFECT OF A REDEFINED ESTIMATION OF EFFORT ON THE SURPLUS YIELD MODELS.

INTRODUCTION

The estimation of fishing effort gave rise to a number of difficulties in this study, notably in the relationship of the various gear types to each other. When these were first used in the sardine fishery their catches were sufficiently distinct to enable them to be classified according to the ratio 1A: 1.5B: 2C, and this ratio was used to calculate effort.

However, in recent years this ratio appears to be changing and the catches from the various nets are becoming closer to each other. This raises the possibility that the B or C nets might be a more realistic standard by which to calculate effort, and this, of course, would have an effect on the surplus yield predictions and consequently on the management options available.

A drawback to this is that the B and C nets have steadily decreased in importance and in 1983 they made up only 5 % of the total fishing effort on the lake. As the fishery expands they are likely to become even less important as all the new vessels that are being introduced can be placed into the A category.

In reality, every vessel is different from the others and a solution to this problem might be to regard each one as a single unit of effort without considering the type of net that might be mounted on it. Effort would thus be measured by simply multiplying the number of boats by the number of nights they fished. The purpose of this appendix is to examine the effect of doing this on the surplus yield models and the predictions that can be made from them.

METHODS

Effort was calculated from the data set out in chapter 5, with additional information from unpublished data held at the Lake Kariba Fisheries Research Institute. The methods of fitting the surplus yield models are described in chapter 10.

RESULTS

The revised effort estimates, the total catch and the catch per unit effort (CPUE) are shown in the following table:

	Effort (Boat-nights)	Catch (t)	CPUE (t boat-night^{-1})
1974	313	487	1.56
1975	720	654	0.91
1976	1 018	1 050	1.03
1977	1 890	1 171	0.62
1978	6 063	2 772	0.46
1979	11 595	4 874	0.42
1980	26 671	7 988	0.30
1981	35 917	12 003	0.33
1982	46 946	11 051	0.24
1983	58 235	13 573	0.23

The effect of this is to bring about a reduction in the estimates for total effort, especially in the earlier years when the B and C category nets made up a much greater proportion of the fishing effort. As a result, the corresponding values for CPUE have been increased. As in the main thesis it is clear that the relationship between CPUE and effort was significantly different in the earlier years (1974-1976) from what it became later (Fig. 1a).

The equilibrium yield curves (Fig. 1b) indicate that the optimum levels of effort and the maximum equilibrium yields are considerably lower than those predicted in chapter 10. This is illustrated in the following table:

	A	B
Linear model: Optimum effort	45 000	86 000
Maximum yield	11 750	14 600
Exponential model: Optimum effort	62 500	129 900
Maximum yield	12 370	16 821

Note; A = revised estimate of effort (each boat = 1 unit)

B = standard estimate of effort (1A = 1.5B = 2C)

DISCUSSION

There is a significant and striking difference in the parameters obtained with the revised and standard methods of estimating effort. If the revised estimate was accepted it would be concluded that the fishery has already reached its limit and

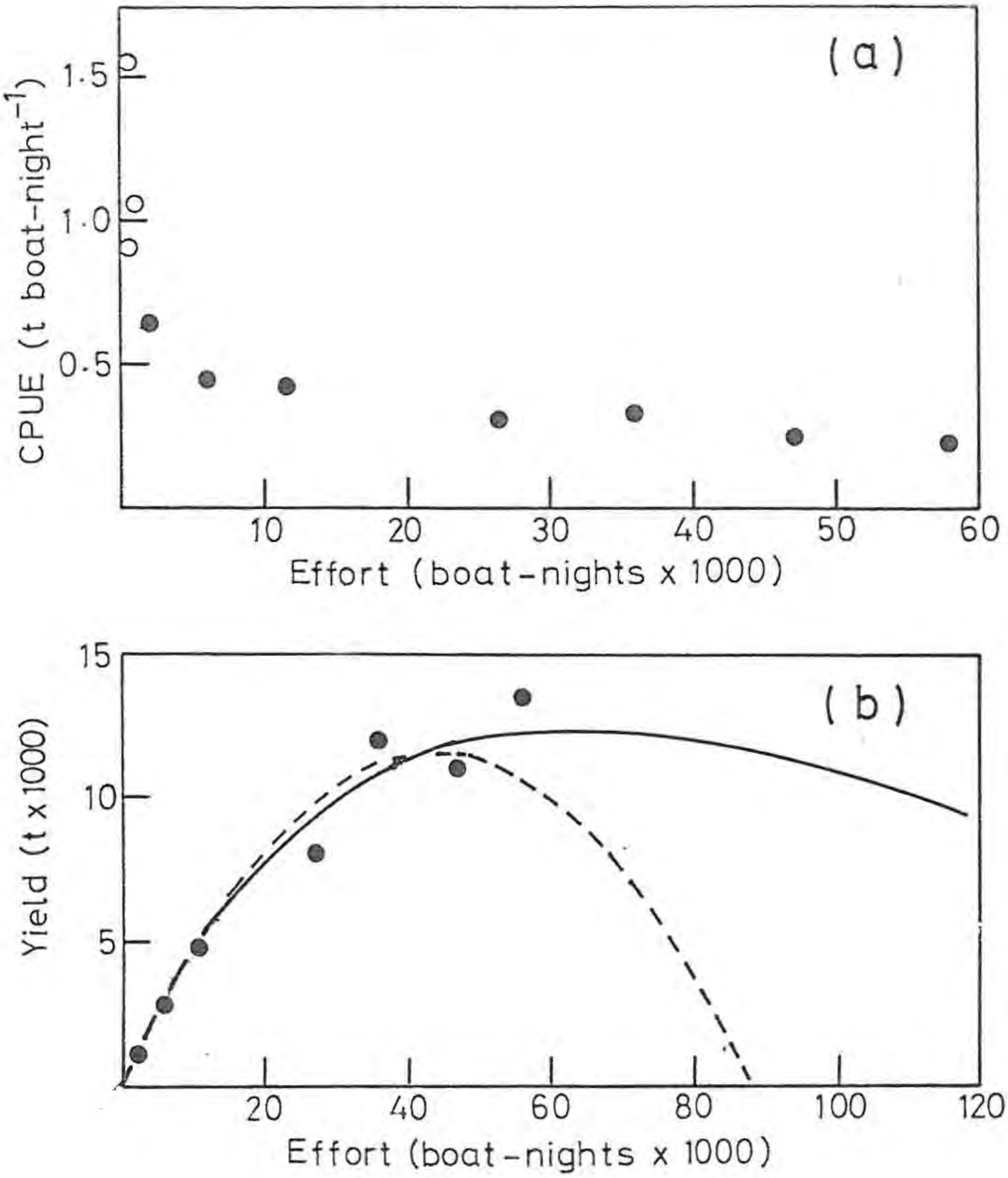

Figure 1: (a) The relationship between effort (revised) and CPUE. The data for 1974-76 (open circles) have been omitted from the regressions, which are $y = 0.53 - 0.006x$; $r = 0.91$ (linear model) and $y = 0.54\ e^{-0.016x}$; $r = 0.95$ (exponential model).

(b) Equilibrium yield curves calculated from the data in (a). The linear model is shown as a broken line, the exponential as a solid one and the points represent the data for 1977-83.

that further expansion of the fishery could cause a decline in catches. This is in contrast to the conclusions of chapter 10 where it was shown that the fishery could still be expanded but that any increase in effort was not likely to bring about a corresponding increase in yield.

One reason for these differences may be that, by regarding all vessels as being equal, major differences between them are overlooked. By lowering the effort value attached to the B and C boats we may be overemphasising the decrease in CPUE that comes with increased effort, and this will lead to lower predictions.

This highlights the importance, and the difficulty, of obtaining a realistic measure of effort in the Kariba sardine fishery. As discussed in chapter 11, uncontrolled increases in fishing effort may be the most important factor causing collapses in fisheries but effort cannot be controlled unless it can be accurately measured. As the fishery progresses and the B and C boats decrease in importance (assuming that this trend continues) effort should become easier to assess and the data from earlier years will become less important and can be ignored.