A contribution to the biology of *Tilapia mossambica* Peters in Lake Sibaya, South Africa.

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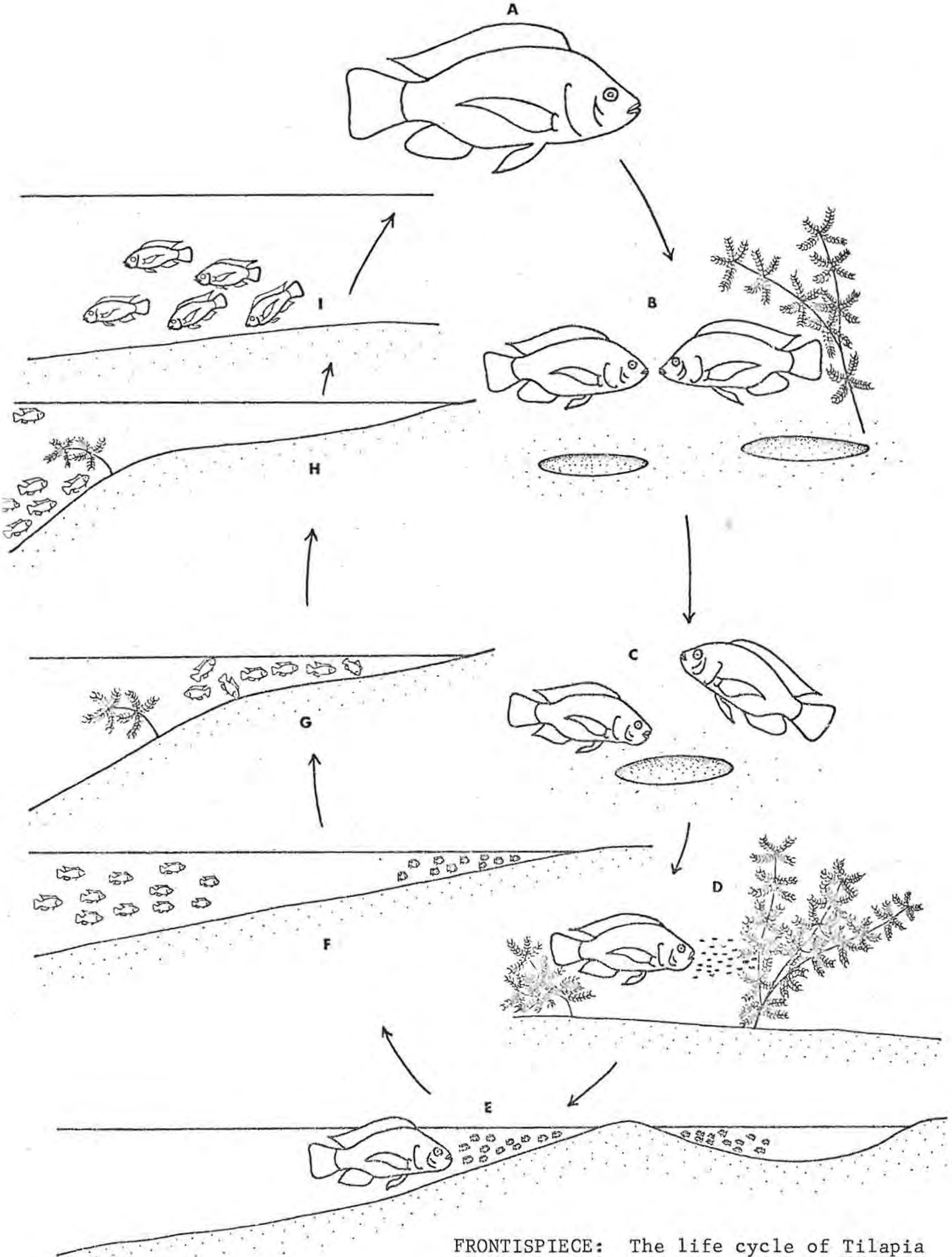

FRONTISPIECE: The life cycle of Tilapia mossambica in Lake Sibaya.

Adult fishes (A) move into shallow water in the warm season where males establish territories and construct nests (B). Females visit the nesting grounds and courtship and spawning takes place (C). The females carry the young to sheltered areas where they are brooded (D) but return to shallow water to release the fry (E). The fry live in very shallow water but occupy deeper and deeper water as they grow larger (F), remaining on the terrace during the day (G) but moving onto the slope at night (H). Small adults live in deeper water beyond the slope (I).

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RESUMÉ

An account is given of some aspects of the biology of Tilapia mossambica Peters in Lake Sibaya, South Africa.

Previous work on Tilapia in Lake Sibaya is reviewed. Apart from brief gillnet surveys, which recorded the species' presence, no research on T. mossambica had been performed at Lake Sibaya before the two-year study of Minshull who collected data on food preferences, depth distribution of juveniles and breeding biology of adults.

The main physiographical features of the lake are outlined. Lake Sibaya is a warm shallow coastal lake with extensive shallow terraces in the littoral which shelve abruptly into underwater valleys. The substrate is predominantly sandy. Aquatic macrophytes are generally restricted to water 1-7 m deep. Adult fishes (over 8 cm SL) are usually absent from water deeper than 12 m and shallower than 0.5 m, whereas juveniles may occur at all depths, and fry only in very shallow water.

T. mossambica inhabits the littoral in the warm and transition periods (August to April) but moves into deep water in the cool season (May to July). Exposed and sheltered shallow areas are utilised for different purposes by adult fishes, the former for nesting, and the latter for feeding and mouth-brooding. Habitat selection by males was governed by nest site selection. Nests were most common in sheltered, sparsely vegetated littoral and sub-littoral areas, but also present in well-vegetated sheltered areas. Breeding females preferred sheltered littoral areas but ventured onto the terrace to release the young. Juvenile and fry T. mossambica inhabited shallow exposed shores with a temperature gradient which reversed diurnally.

The breeding, shoaling and feeding behaviour of T. mossambica is described, and integrated with data on T. mossambica from other systems. The breeding season spans seven months. Shoaling takes place in shallow water probably as a means of protection. T. mossambica is an omnivorous feeder relying largely on diatoms.

The main predator is probably the barbel Clarias gariepinus, but avian predators may be more important.

A method whereby the time of formation of rings on the scales of T. mossambica is described. The fishes were found to reach maturity after one year at a length of about 8 cm in females, and after two years at 10 cm in males. The breeding population had a standard length mode of 14 cm (females) and 17 cm (males). The maximum final size was about 24 cm SL.

An estimate of the standing crop for fishes in the littoral and sublittoral areas of the eastern and southern shores of the south basin is given. The data were derived from a mark and recapture technique.

The biology of T. mossambica in Lake Sibaya as revealed by the present study is discussed with reference to data on the same and similar species in other systems. The utilisation of the available resources in the lake by T. mossambica is commented upon, and reference is made to the significance of stunting, and the importance of the retention of generalised characters for the successful habitation of the cyclically-renewed habitat of the littoral. Precocious breeding in T. mossambica is regarded as a functional adaptation which increases the proportion of fishes small enough to utilise the rich food resources in shallow water.

INTRODUCTION

The biology of many Tilapia species in natural systems is well documented. These studies include those of Lowe (1952, 1953) on various Tilapia species in Lake Malawi, Lowe-McConnell (1956, 1956A, 1957 and 1958) on various species in East African lakes, Fryer (1959) on various species in Lake Malawi, Fryer (1961) on T. variabilis in Lake Victoria, Garrod (1959, 1963) on T. esculenta in Lake Victoria, Mortimer (1960) on T. andersonii in 'Northern Rhodesia' (= Zambia), Welcomme (1964) on various species in Lake Victoria, and Coe (1966) on T. grahami in Lake Magadi.

The natural history of T. mossambica is less well-known and, although there have been extensive studies on aspects of the species' biology in artificial impoundments and in the laboratory, its biology in a natural lake system is unknown. The purpose of this investigation has been to examine some of the facets of T. mossambica's biology in Lake Sibaya. The presence of large populations in this coastal lake is to be expected from what we know of its distribution in south and east Africa. The species occurs in most eastward-flowing rivers and coastal lakes from the lower Zambezi southwards to the Bushmans river near Port Elizabeth.

While I have remarked on the paucity of information on this species from natural systems, we cannot overlook the works of Whitehead (1962) and Trewavas (1966) on T. mossambica and other species in the eastward-flowing rivers of East Africa. Their work was however mainly related to classification. Brief comments on the natural history and distribution of T. mossambica are also available in Jubb (1966, 1967) and Crass (1964).

Turning to the extensive studies on the species in artificial impoundments, the work of Vaas and Hofstede (1952) and Pannikar and Tampi (1954) contribute significantly to the general biology of T. mossambica in ponds. Koura and el Bolock (1958) record growth and survival in Egyptian ponds and Le Roux (1961) on growth in various Transvaal impoundments. The species has been introduced into artificial impoundments in Africa, Asia, Europe and America for cultivation, and has been the subject of numerous brief reports, e.g. Hickling (1970).

Laboratory studies are very numerous and include those of Baerends and Baerends van Roon (1950) and Seitz (1948) on behaviour, Neil (1964) on colour changes and social behaviour, Rodman (1966) on sound production, Neil (1966) on T. mossambica's behaviour in Hawaiian ponds, Potts et al (1967) on water balance, and Pandion and Raghuramon (1972) on food conversion efficiency. Several studies on temperature preferences and the effects of low or high water temperatures have also been carried out, including Long et al (1961); Allanson, Ernst and Noble (1962); Allanson and Noble (1964); Allanson (1966); Kemp (1966); Badenhuizen (1967); Dharmamba et al (1967); Minshull (1967); Bok (1968); Solomon and Allanson (1968); Job (1969A, 1969B); Donnelly (1969B); Allanson and Cross (1970); Allanson, Bok and van Wyk (1971) and Josman (1971).

As a result of these studies, many aspects of T. mossambica's success as a culture fish are well-documented, as also is its tolerance of environmental extremes.

While this rich background of data has proved of immense value in the investigation of the biology of T. mossambica in Lake Sibaya, I hope to be able to integrate new data into this background so as to provide a more critical appraisal of the biology of this important cichlid species.

Lake Sibaya has proved to be ideal for such a study on the species. The lake is small (65 sq km), closed, unpolluted, and has not been fished to any large extent by the local Africans or at all by a commercial organisation. The lake has a simple cichlid community consisting of three Tilapia species (mossambica Peters, sparrmanii A. Smith, rendalli (Boulenger) and one other cichlid, Hemihaplochromis philander (M. Weber). No Tilapia species have been artificially introduced into the lake as far as can be ascertained. The primary importance of the present study is that it is the first comprehensive investigation of the biology of T. mossambica in a completely natural environment.

A further area of interest stems from the analyses of Fryer (1960) and Fryer and Iles (1969, 1972), where it was pointed out that two important African Cichlid groups, Tilapia and the Haplochromis flocks, have differed in their evolutionary paths; the Haplochromis flocks of the great lakes towards super-specialisation, and the genus Tilapia towards the retention of more generalised characters. Retention of generalised characters they note, has allowed many Tilapia species to colonise new, or cyclically renewed, habitats. It is hoped that the data to be presented will add further knowledge of the way in which a generalised Tilapia species has utilised a new environment, in this case a relatively young natural lake.

The foundation of this study was laid by Minshull (1968, 1969, 1970) who investigated some aspects of the species' biology in Lake Sibaya in 1968 and 1969. Most of Minshull's work was carried out in the main basin of Lake Sibaya. Using gill-nets and home-made fishtraps, he collected data on fish distribution and movements, gut contents and breeding condition. As with Minshull's work my studies were carried out with the assistance of one unskilled African, and it soon became apparent that a comprehensive study of the whole lake, or even the main basin, was impracticable with the limited personnel available. For this reason, the present work, which was carried out from 1970, through to 1972, was confined largely to the south basin after May, 1970. The smaller area of the south basin made mark, release and recapture methods more feasible, and an investigation of T. mossambica's biology as a whole more manageable, for a two-man team. The south basin exhibited the same major topographical features as the main basin, i.e. shallow marginal terraces, steep-sloping western and eastern shores, gently sloping northern and southern shores, and deep underwater canyons converging on a deep point. The assumption was made that the south basin population was representative of the *T. mossambica* population of the whole lake.

A note on Taxonomy:

T. mossambica from Natal have previously been referred to as *T. natalensis* (e.g. Baerends and Baerends-van Roon, 1950); *T. rendalli* as *T. melanopleura* (e.g. Crass, 1964); and *T. mortimeri* from Kariba as *T. mossambica* (e.g. Coke, 1967). According to Jubb (pers. comm.), studies on the status of these species have shown that *T. natalensis* is synonymous with *T. mossambica* Peters, and that *T. melanopleura* Dumeril should be referred to as *T. rendalli* (Boulenger). Fishes from Kariba previously known as *T. mossambica* are *T. mortimeri* Trewavas. *T. mossambica* from the lower Zambesi (Kaborabassa to the Zambesi delta), and from the Limpopo system remain as such.

Because of the paucity of information on *T. mossambica* in a natural system, the data here are sometimes compared with data on closely related species, such as *T. mortimeri*. Though specific differences obviously do exist between these two species, it was thought that the comparison of two such similar species would assist in describing the characteristics of the *T. mossambica* population from Lake Sibaya.

ACKNOWLEDGEMENTS

The author wishes to express his sincere thanks to Professor B.R. Allanson who, as founder of the Lake Sibaya Research Station and chief supervisor of the research programmes, generously gave of his time to supervise the project even when on sabbatical leave. Dr R.E. Boltt is thanked for his meticulous supervision during the latter part of the study. The solid work of my African assistant, Mr Nelson Mdletshe, is sincerely appreciated. Thanks are also due to Dr B.J. Hill for training me in SCUBA techniques; to Mrs P. Eva for her enduring patience and for typing the manuscript; to Rob and Rey Hart who helped me solve many problems, and to Mr A.T. Forbes and Mr A. Ribbink, who acted as diving partners. My wife, Carolynn, was a source of help and encouragement at all times.

Financial assistance was received from the Research Committee of Rhodes University and the South African Council for Scientific and Industrial Research. I would like to express my gratitude to these organisations for their considerable help.

The material assistance of the Department of Bantu Affairs is sincerely appreciated. It is hoped that the information contained within these pages will be of assistance in the planning of the overall development of the Sibaya area for the long term benefit of the African inhabitants.

PREVIOUS WORK ON THE *TILAPIA* OF LAKE SIBAYA

Professor Warren of the Department of Zoology of the University College of Natal visited Lake Sibaya in 1914 and collected specimens of *T. rendalli* which he sent to the British Museum.

Tinley (1958) conducted a survey on the ecology of Lake Sibaya with special reference to the hippopotamus. He recorded the presence of *T. mossambica* in the main lake, and *T. sparrmanii* in both the main lake and the adjacent pans. Tinley reported that some *T. mossambica* are harvested by the local natives in summer, being caught either in 'umono' traps in the lake, or in very shallow water in the marginal areas after heavy rains.

Tinley (1964) further noted that *T. mossambica* may be harvested at Lake Sibaya using fish spears, locally made gill-nets, and unbaited valve baskets, the latter being set singly or in association with barriers. Fishing devices were found to be less common at Lake Sibaya than in most other areas of Tongaland.

In two unpublished reports to Natal Parks, Game and Fish Preservation Board, Pike (1968a and b) outlined the results of brief surveys on the fishes of Sibaya carried out in 1966, 1967 and 1968, using gill-nets. The average condition factor (CF, calculated from total lengths) for T. mossambica was found to be 56, very low compared with the CF of 72 for fishes of the same species in the same weight range from the Pongola Floodplain pans, 70 km to the west. The CF of T. rendalli from Sibaya (63) was found to approximate the general average for the species in Natal (70).

Minshull (1968, 1969) examined the stomach and rectal contents of 130 T. mossambica from Sibaya and found that diatoms were the chief constituent of the food. This assessment was made after it had been noted that 'Diatoms are found with chloroplasts intact in the stomach of the fish, but the rectum contains only the siliceous skeletons of diatoms'. In T. sparrmanii (17 fish examined) diatoms were reported to be digested to a lesser extent than in T. mossambica, but aquatic macrophytes appeared to be utilized to a greater extent, especially in the larger fish. T. rendalli (25 fish) utilized aquatic macrophytes, epiphytic algae and insects. T. mossambica and T. sparrmanii, he reports, appeared to be competitive feeders, with the latter utilizing an additional source of food in the form of aquatic macrophytes.

Pike (1969) carried out a series of gillnet surveys and expressed the opinion that the T. mossambica population at Sibaya was not an economically exploitable population.

A series of papers on various aspects of the ecology of Lake Sibaya was published in the Transactions of the Royal Society of South Africa, volume 38, part 3, 1969. Boltt, Hill and Forbes (1969) carried out a preliminary investigation of the distribution of submerged macrophytes and fish in Sibaya using diving techniques. They found that T. mossambica nested either in association with submerged

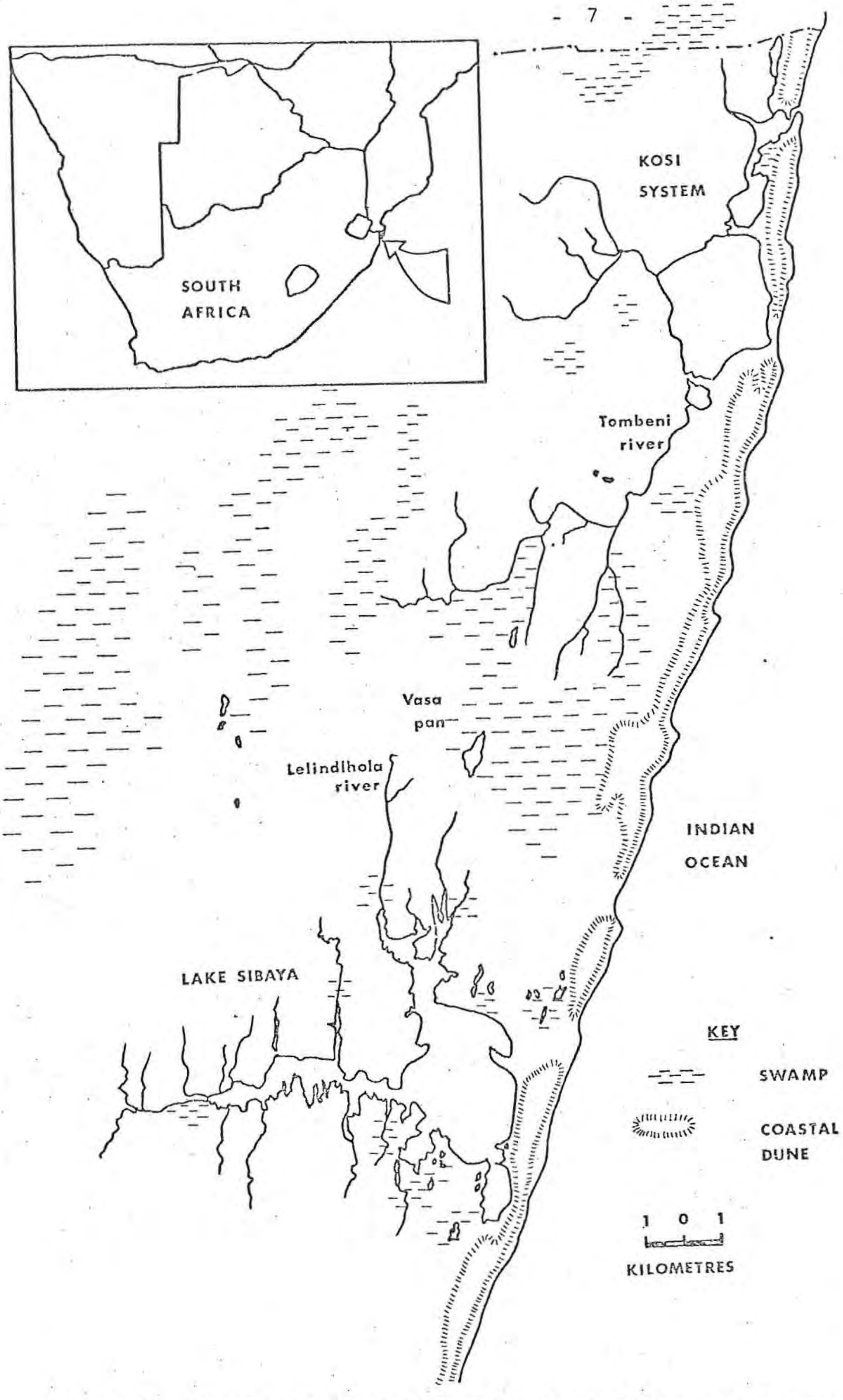


Figure 1: Map of the coast of Kwazulu, South Africa, indicating the position of Lake Sibaya in relation to the sea and the Kosi lake system.

macrophytes, or in very shallow water (less than one metre). The diameter of the nests was found to vary from 0.5 to 1.5 m, with the mean diameter at one metre. T. mossambica and T. sparrmanii were positively identified in shallow water, and shoals of small T. mossambica were tentatively identified at 20 m several kilometres from the shore.

Minshull (1970), sampling with 0.24 m^3 gauze traps, reported T. mossambica to be the most abundant fish species on the exposed terrace, and showed a depth zonation whereby smaller fish were more common in shallower water. A diurnal horizontal migration was noted and the suggestion made that these movements were governed by fluctuations in water temperature and light intensity. The breeding season of T. mossambica, T. rendalli and T. sparrmanii was found to extend from early October to May in the summer of 1968/1969.

LAKE SIBAYA - THE HABITAT

Lake Sibaya (32°40' E, 27°25 S) is a land-locked freshwater lake, the surface of which varies around 20 metres above mean sea-level. The lake, 65 sq km in area, is situated on a coastal plain which consists of Recent and Tertiary sands overlying Cretaceous beds (Hill, 1969), in KwaZulu, South Africa (Figure 1). The shore of the lake is sandy with no rock apart from a small outcrop of lateritic ironstone on the north-eastern shore of Etsheni Bay (Figure 2, a foldout under the back cover). The lake is made up of a main basin 8.5 km long and 6 km wide, into which open two smaller basins in the south, and two large arms, one in the north and one in the west. The profile and bathymetry of the whole lake and of the south basin (from Hill, pers. comm. 1971) are shown in Figures 2 and 3 respectively (foldouts under the back cover). The maximum depth is 40 m, and the mean depth 13 m (Hill, 1969). A shallow tombola is situated between the main and the south basin. The numerous arms and bays, at least in the western and northern areas of the lake, result in a well-developed shore-line

Figure 4: View across the south-eastern shore of the main basin in November 1971 showing wide, scoured beaches, and a shallow terrace, with a sudden descent into deep water.

Figure 5: View westwards from the eastern shore of the main basin in November 1970 showing the shallow pools in the eulittoral.

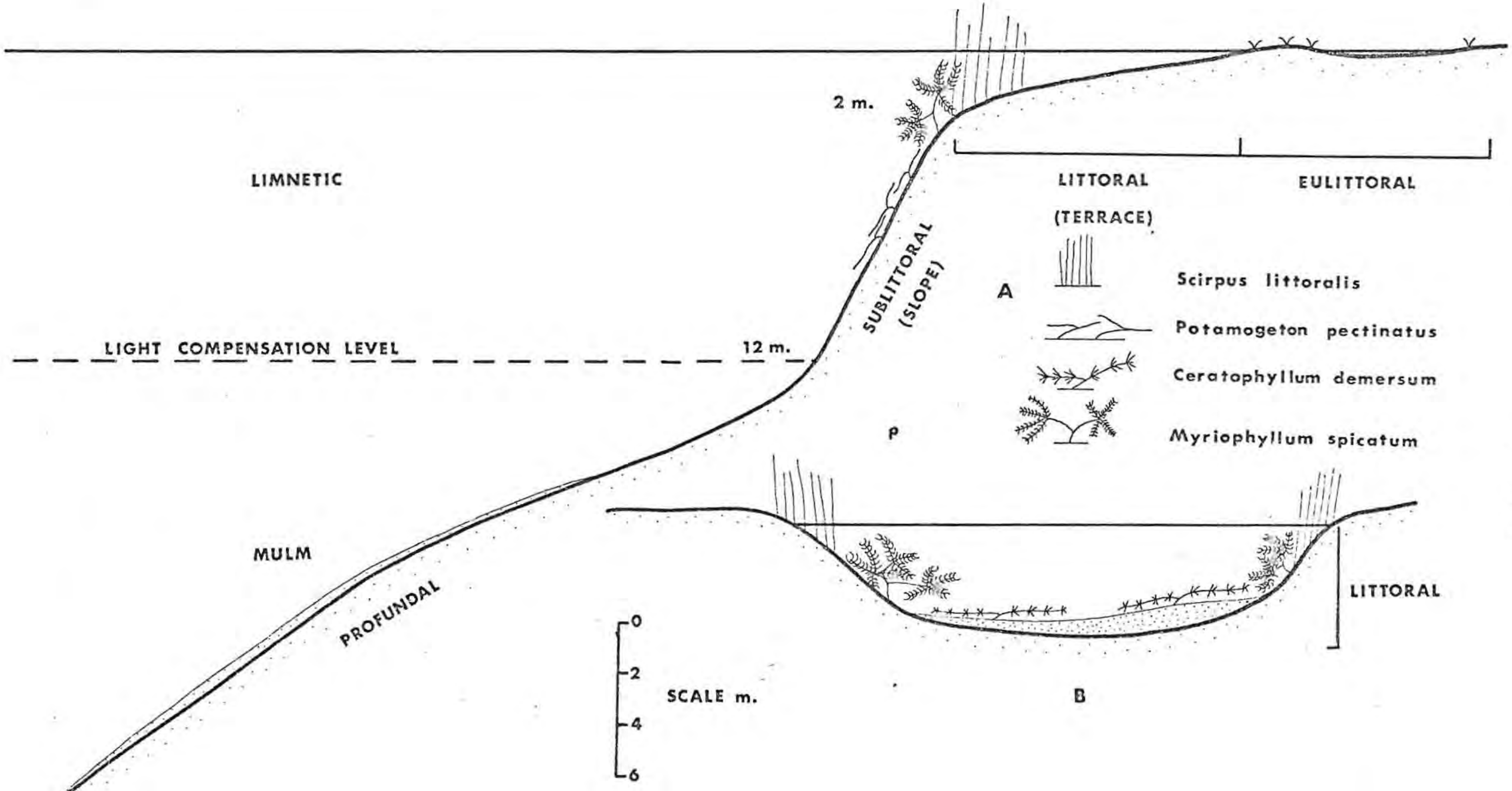


Figure 6: Diagram of an exposed eastern shore (A) and a sheltered bay (B). The topographical nomenclature used in the text is shown in the figures.

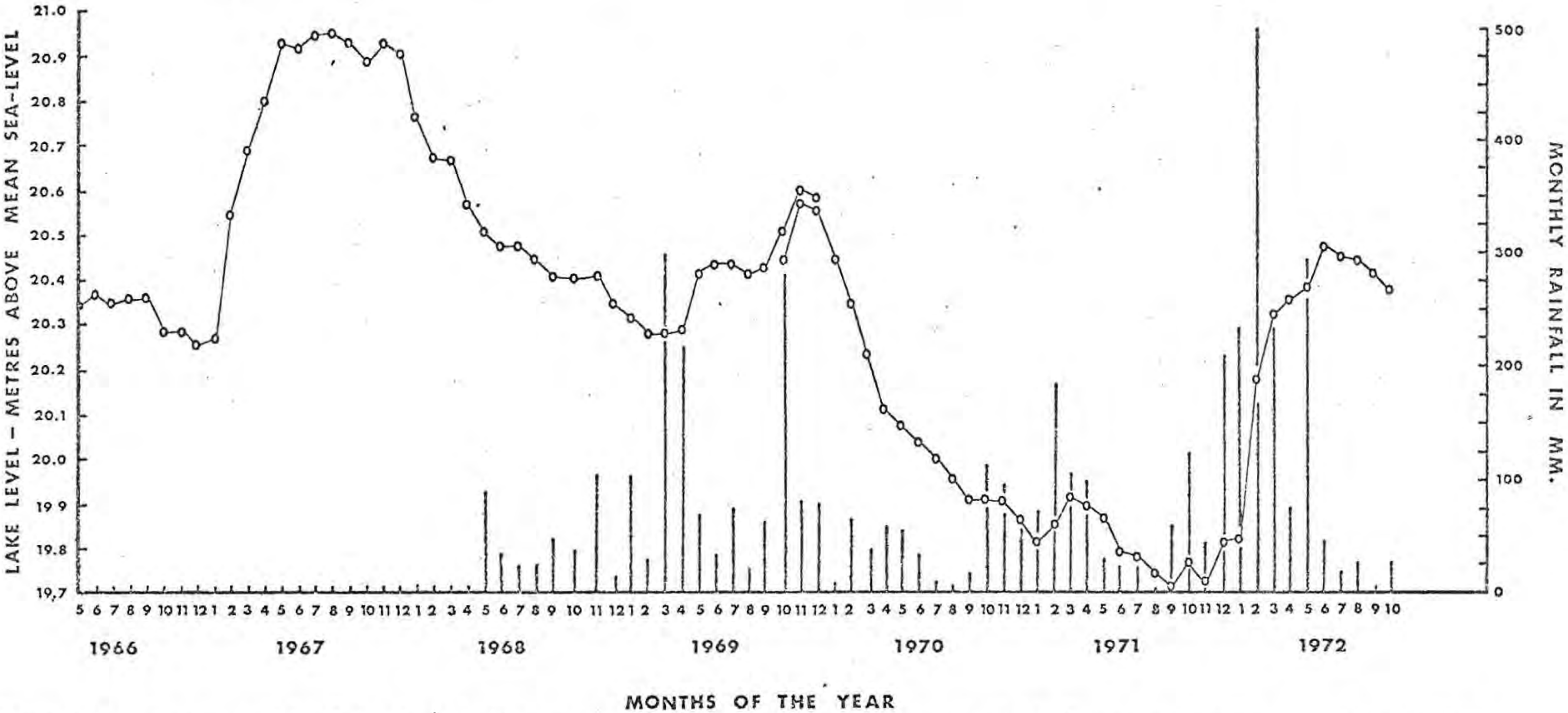


Figure 7: Mean monthly lake level (linear graph) and mean monthly rainfall (histograms) measured at Lake Sibaya. Lake level data were obtained from Department of Water Affairs "Ott" recorders at Banda Banda Bay (May 1966 to December 1969) and at the Research Station (October 1969 to October 1972). The two level recorders are calibrated to slightly different heights above mean sea level which explains the discrepancy in October, November, December 1969. Rainfall was recorded by means of a standard rain guage at the Research Station (Fig. 2).

with a shore length of 144 km and a shore development of 4.96.

The northern and south-western shores of Lake Sibaya shelve gently into the deeper water (Fig. 2). These shores are exposed to heavy wave action from the prevailing northerly and southerly winds. On the western, eastern and south-eastern shores, deep water often occurs close inshore, and there is a shallow terrace (Figs 2, 4, 5 and 6) with a maximum depth of about 2 m ending abruptly in a steep declivity with a slope of 25 to 30^{o} from the horizontal (Boltt, Hill and Forbes, 1969). Extensive shallow pools often form in the eulittoral zone after heavy rain (Fig. 5). Diagrammatic profiles of the lake floor are given in Figs 6A and B.

The deep underwater valleys (Fig. 2) suggest that Lake Sibaya was formed at a time when a change in sea-level of at least 20 m occurred. The numerous lakes along the coast of Zululand and southern Mocambique, e.g. Sibaya, St Lucia, Kosi system, Piti, were probably formed at the same time. Evidence from Lake St Lucia suggests that the lake floors were cut over 6000 years ago, but became isolated from the sea between 6000 and 3000 years ago, due to a sharp fall in sea-level (Hill, pers. comm., December 1972). Lake Sibaya is land-locked, but lakes St Lucia, Kosi and Piti retain a connection with the sea.

The lake is separated from the sea by a range of forest-covered sand-dunes in the east, and surrounded to the north, south and west by undulating grasslands interspersed with marshes, pans and stands of indigenous woodland and forest. The lake is fed by numerous, short, perennial and seasonal streams, of which the Lelindlhola in the north-west is the largest (Fig. 1).

The lake level is subject to considerable fluctuations dependent on rainfall (Fig. 7). For example, the level rose 76 cm between December 1971 and May 1972 following 1577.6 mm of rainfall. Water is added by direct precipitation, runoff and underground

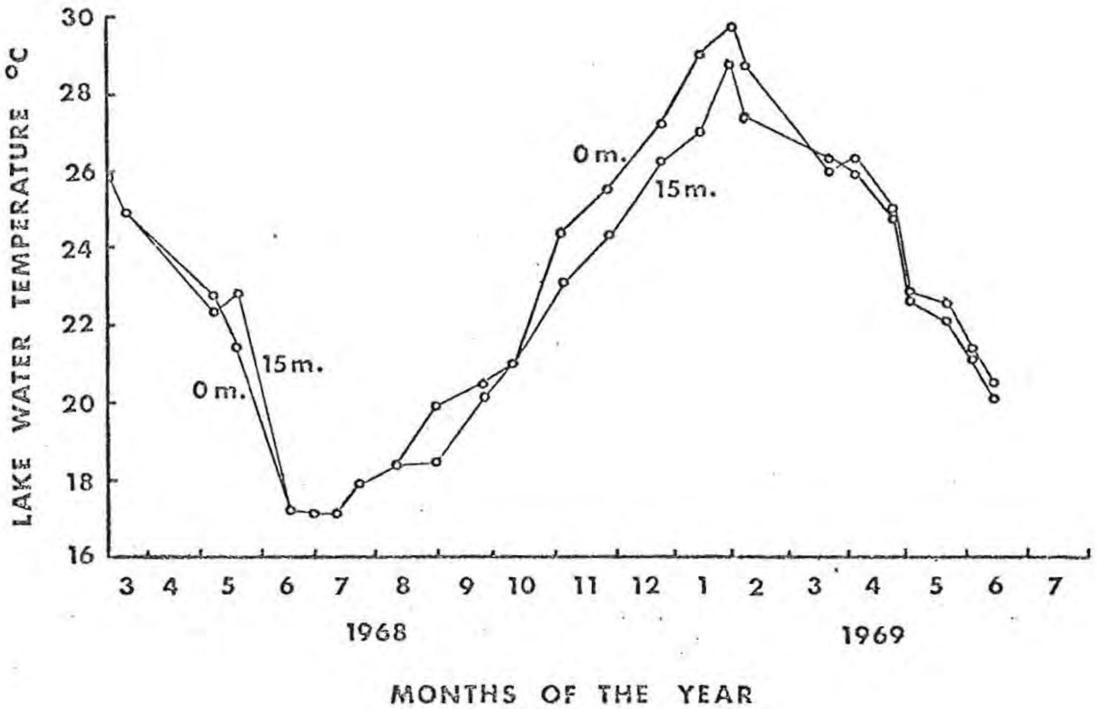


Figure 8: Lake water temperatures measured by means of a bathythermograph at south basin buoy (Fig. 3) at the surface and at 15 m. Data from unpublished field notes of Minshull.

seepage from the catchment; and lost by evaporation and seepage to the sea. Seepage appears to take place under the coastal dunes, and outflows can be seen at low Spring tide on the marine shore (Fig. 2). Although the amount of water lost by seepage to the sea is unknown, some measure of the importance of this form of outflow can be gained when it is realised that despite the inflow of stream water with a relatively high chloride content (2.651 meq/l, Allanson and van Wyk, 1969) and considerable evaporation, relatively constant chloride values (3.704 meq/l) are maintained in the main water body.

The average annual rainfall is 1000 mm on the eastern shore, and 800 mm on the western shore (Dept. Water Affairs, 1966), but is subject to marked fluctuations. Thus the annual rainfall measured at the research station in 1969 and 1970 differed by 820 mm. Highest monthly rainfalls were recorded in late summer, and lowest monthly rainfall in the period June to September.

Lake Sibaya is warm and variably homothermal, with a complex and unstable pattern of thermal stratification in summer (Allanson and van Wyk, 1969). Lake water temperatures at south basin buoy showed a seasonal variation of 12.8^{o}C in 1968 and 1969 reaching a maximum in January and a minimum in June and July (Fig. 8, data from unpublished field notes, Minshull, 1969). Measurement of oxygen indicated that no departure of more than 6% from saturation occurred during winter months, but that the percentage saturation may decrease to 68% at 38 m in midsummer (Allanson and van Wyk, 1969). Chloride concentrations are high for freshwater (135 mg/l). Secchi disc measurements averaged 3.0 m in July, 1965 (Allanson and van Wyk, 1969), and 1% of subsurface illumination occurred at 12 m in January, 1967.

Two major substrate types are found in the lake-sand and mud (Boltt, 1969). The substrate is predominantly sandy. Sandy substrates, except in wave-washed areas, are sometimes covered by a 1-3 cm layer of fine flocculent detritus, containing large quantities

Figure 9: A sheltered well-vegetated shore with macrophyte growth to the water edge. November, 1971. (Banda Banda Bay, south basin, see Figure 3).

Figure 10: An exposed barren shore showing a wide shallow terrace and extensive beach. November 1971. (South-west shore, main basin).

of blue-green algae, green filamentous and unicellular algae, detritus and protozoa. This detritus layer will be referred to as "mulm", a term borrowed from aquarists. Muddy substrates were found mainly in submerged valleys, though not necessarily in the deepest water. The muddy substrates may be described as highly degraded, oxidised organic mud, and will be referred to as gyttja.

Submerged aquatic macrophytes are mostly absent from water shallower than 1.5 m on the exposed shores. Potamogeton pectinatus L. and P. schweinfurthii A. Benn are the dominant species at depths of 1.5 to 4 m. Below 4 m, Myriophyllum spicatum L. is dominant except in very sheltered areas, where Ceratophyllum demersum L. is more common. Emergent macrophytes include Scirpus littoralis Schrad., Typha latifolia L. ssp. capensis Rohrb., Juncus krausii Hochst., Cyperus papyrus L. and Phragmites mauritianus Kunth. In sheltered bays, semi-emergent species, such as Nymphea capensis Thunb., and floating species, such as Pistia stratiotes L., are found. Sheltered and exposed shores are illustrated in Figures 9 and 10. Macrophytes are absent from water deeper than 7 m, probably due to reduced light intensities (Boltt, Hill and Forbes, 1968).

The standing crop of plankton is low. According to Hart (pers. comm., 1972) the phytoplankton density, measured as chlorophyll 'a', averaged less than 2 micrograms per litre throughout the year. The calanoid copepod Pseudodiaptomus hessei, the dominant zooplankton in terms of biomass, averaged less than 2 individuals per litre.

The fauna of the lake is derived from both freshwater and estuarine components. Of the 16 species of fish recorded (Appendix 1), four (Glossogobius giurus (Hamilton and Buchanan), Gilchristella aestuarius (Gilchrist and Thompson) and Atherina breviceps Valenciennes, in Cuvier and Valenciennes, are reported normally from estuaries, and of these, only G. giurus has been consistently reported from inland waters (Jubb, 1967). Silhouettea sibayi Farquharson is only known from Lake Sibaya (Farquharson, 1970) and Croilia mossambica J.L.B. Smith only from a few coastal lakes in the region, Poelela, Nhlange and Sibaya. Besides the four cichlids, the freshwater fishes include a mormyrid recorded only from sheltered bays, two small Barbus species, two species of Clarias and two small species of Aplocheilichthys. Similarly, the invertebrate fauna has freshwater and estuarine components (Allanson, Hill, Boltt and Schultz, 1966; Boltt, 1969). The lake is inhabited by 72 hippopotami (November, 1972), about 80 nile crocodiles, Crocodilus niloticus, and a moderate variety of aquatic birds.

The vicinity of Lake Sibaya is populated by primitive farming Africans of the Thonga tribe.

In general the south basin of the lake was found to exhibit the same physical and biotic features as the main basin and was thought to be representative of the lake as a whole.

METHODS

SAMPLING EQUIPMENT AND METHODS

Sampling methods, and the design of the sampling equipment, were determined largely by the physical characteristics of the lake shore. Two seine nets were designed for the present study, the first to be pulled into shore up the steep slope and over the lip of the terrace (slope seine), and the second to be pulled along the shallow terrace parallel to the shore (terrace seine). Over 80% of the Tilapia mossambica sampled in the present study were caught by means of the seine nets. In addition gillnets and specially designed fish-traps were used for sampling fishes in deep water and in well-vegetated areas. Other methods of fish collection or recording included rod and line, various small seine nets, trawl nets and an echosounder. The sampling methods and equipment are discussed in detail below:

Slope seine: The characteristics of the slope seine, and the other sampling equipment, are given in Table 1. The slope seine is

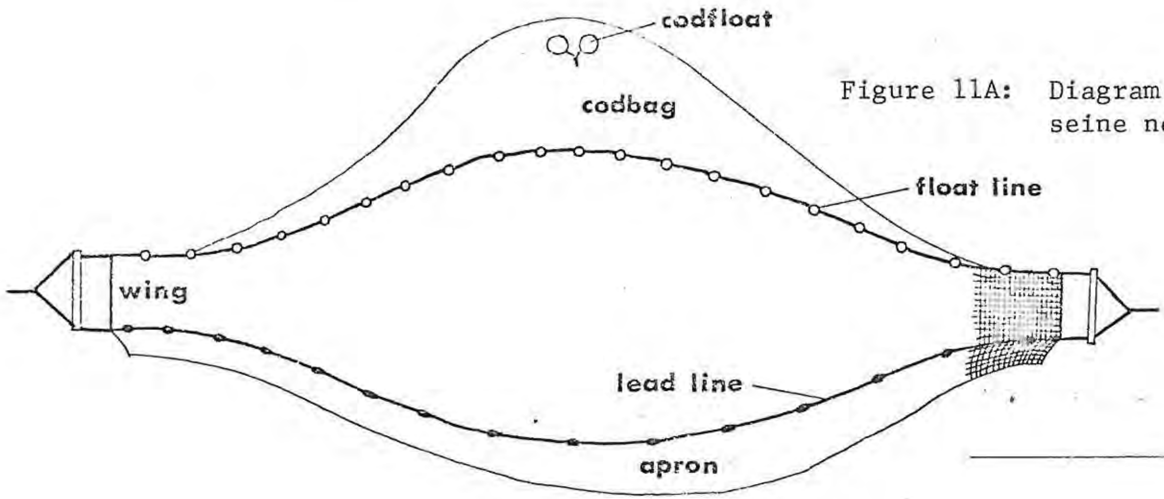


Figure 11A: Diagram of the modified slope seine net.

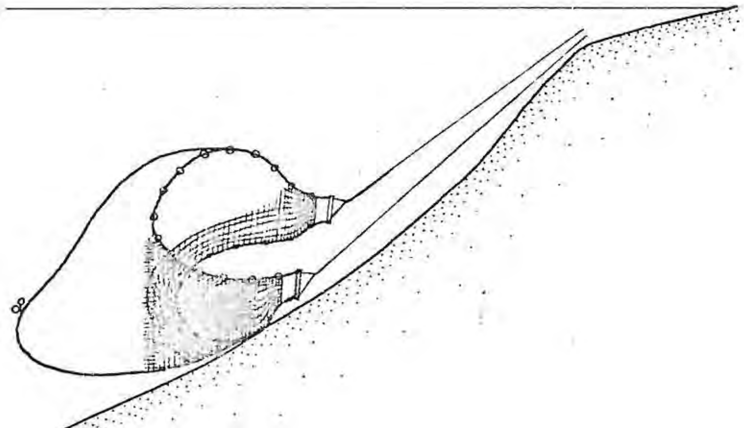


Figure 11B: Diagram showing the shape of the slope seine when pulled up the slope as observed underwater using diving equipment.

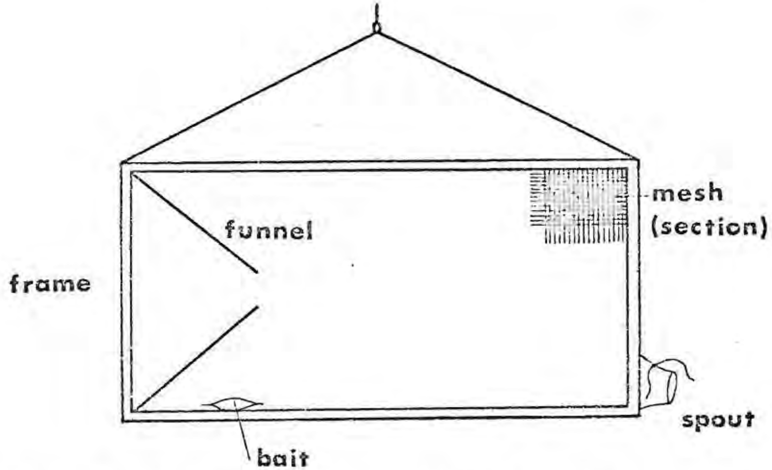


Figure 11C: Diagram of a fishtrap (Types 1 and 2) viewed from the side. The frame and funnel are covered by mesh.

Pulling the slope seine

The net is pulled out from the shore by boat (Fig. 12), towed round in an arc (Fig. 13), and then pulled up the slope by hand (Fig. 14).

Photographs by Biccard-Jeppe, 1971.

Figure 12

Figure 13

Figure 14

illustrated in Figure 11A. This net, a large-bagged negatively-buoyant seine, was laid over water about 15 m deep from an outboard powered boat by pulling the net straight out from the shore until the landward rope attached to a pole on shore became taut (Fig. 12). The rope attached to the boat was then towed back to shore in an arc so that the two ropes were about 17 m apart (Fig. 13). After allowing the net to sink, the ropes (each 45 m long) were pulled in by hand at a rate of about 15 m per minute, and the net landed on the shore (Figs 14 and 11B).

TABLE 1

Characteristics of the fish sampling equipment giving the dimensions, mesh size and selectivity of the seine-, gill- and trawl-nets, and the fish-traps. The selectivity of the equipment is expressed as the size range of fishes which were caught in the various nets and traps.

SAMPLING EQUIPMENT	TOTAL WIDTH	EFFECTIVE WIDTH	LENGTH	DEPTH	BAR MESH	SELECTIVITY *T. MOSSAMBICA*
Slope seine	15 m	10 m	5 m	4 m	1.27 cm	4 cm SL +
Terrace seine	28 m	18 m	3.7 m	1.5 m	1.27 cm	4 cm SL +
Fry seine	6 m	4 m	0.3 m	0.5 m	0.1 cm	1-4 cm SL
Gillnet	30 m	-	-	1.5 m	2.5 cm	13-16 cm SL
Gillnet	30 m	-	-	1.5 m	1.9 cm	12-15 cm SL
Beam trawl	2.4 m	-	11 m	2.4 m	1.27 cm	not determined
Otter trawl	7.3 m	5.5 m	3 m	2.0 m	1.27 cm	4 cm SL +
Fishtrap Type 1	1 m	-	0.4 m	0.4 m	0.1 cm	1 cm SL +
Type 2	1.3 m	-	0.6 m	0.6 m	1.27 cm	4 cm SL

SL = Standard length

A weighted apron was attached to the lead line of the slope seine after underwater observations using Self-contained Underwater Breathing Apparatus (SCUBA) had indicated that the lead line was lifting off the substrate when the net was pulled up the slope. The lead line remained on or very close to the substrate on subsequent pulls, as indicated by diving observations and by the fact that increased catches of the bottom-living fishes Glossogobius giurus and Clarias gariepinus were made. Direct observations during diving showed that the flight reaction of T. mossambica (and T. sparrmanii) when enclosed in a net was invariably to attempt to escape underneath the net. Thus it is more important to ensure that the lead line does not lift above the substrate than it is to ensure that the float line reaches the surface. On the other hand T. rendalli was noted to escape over the top of the net, and was rarely caught in the slope seine. Two small floats were attached to the end of the codbag of the slope seine to lift the codbag off the substrate.

The slope seine was found to be efficient for sampling adult and juvenile T. mossambica to a depth of 10 m on the slope and on the terrace.

Terrace seine: This long-winged shallow seine net was only effective in areas with low macrophyte cover. The net was pulled parallel to the shore along the terrace by means of a 19 m rope attached to a Land-Rover on the shore and a 44 m rope attached to a launch beyond the slope. After sampling an area of shore, the boat was landed and the net closed by hand. Water one to three metres deep was netted.

Fry seine: A hand-pulled 0.1 cm bar mesh nylon gauze net was used for catching fry and juvenile Tilapia in very shallow water.

Gillnets: 2.5 and 1.9 cm bar mesh multifilament nylon gillnets were surface, middle and bottom set over deep water and in shallow well-vegetated areas in the conventional manner. The gillnets were usually serviced after 18 to 24 hours. Use of a spatulate, blunted strip of metal facilitated removal of fishes from the gillnets without damage to the fishes.

Fishtraps: Two types of fishtraps, designated Types 1 and 2 in Table 1, were used. Both traps were designed along the lines of the

Figure 15: Front view of a type 2 fishtrap showing the funnel in the foreground, with a 1.27 cm bar nylon stretched across the frame of the trap (cf Fig. 11C).

native 'Umono' fish traps. A rectangular frame with an invaginated funnel at one end was covered with mesh, either 0.1 cm bar nylon gauze (Type 1 fishtrap) or 1.27 cm bar nylon thread (Type 2) (Figs 11C and 15). An opening at the opposite end to the funnel was provided for the removal of fish. The traps were baited with bread placed inside a 0.1 cm bar gauze bag inside the trap. Type 1 traps had a volume of 0.24 cu m and Type 2 traps a volume of 0.448 cu m.

The fishtraps were laid on the lake floor, suspended in mid-water or at the surface attached to buoys and anchored by heavy weights. The traps were laid in various habitats and in deep and shallow water. Sampling time usually varied between 18 and 48 hours. The depth of deep-set traps was measured by means of a maximum-recording depth gauge which was lowered onto the trap immediately before recovery. Two or three traps were usually laid at one setting at increasing depths and distances from the shore. The fishtraps usually yielded large numbers of fishes, as well as crustaceans and molluscs, in good condition.

Type 1 traps were used from January 1970 until September 1971, and Type 2 traps for the remainder of the study period.

The effectiveness of fishtraps as indicators of fish distribution was tested. Underwater observations, and trapping in the experimental pools, indicated that the catchability of the fishtraps was high in the warm season (99% of pool fish sampled), but decreased in the cool season. Thus with the pool fish population remaining constant, the catch per unit effort in the cool season was 60% of that in the warm season. Lower activity levels in the cool season probably brought about this lower catchability.

<u>Beam trawl</u>: This deep-bagged trawl net was fitted with a ventral hydroplane at an angle of 30° from the horizontal to provide lift, and hollow aluminium mouth struts. The net was pulled by means of two 80 m long ropes attached to one or two launches. The top speed reached was only 2-3 knots with the net no deeper than 4 metres as indicated on

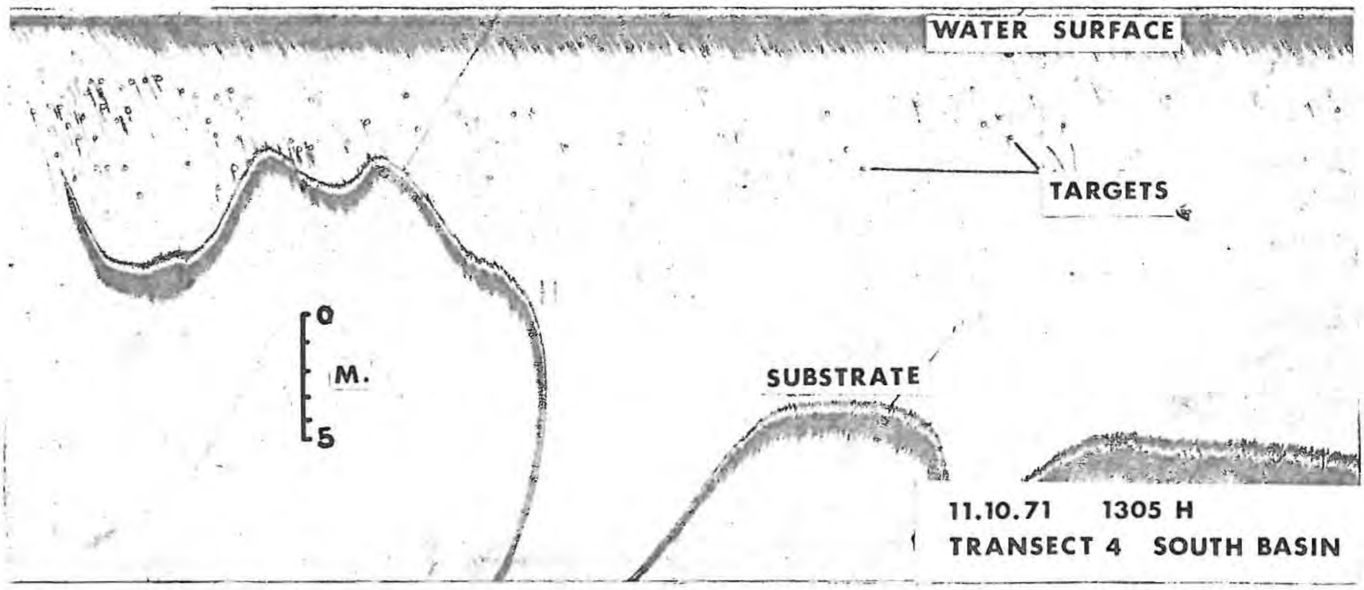


Figure 16: Reproduction of an echotrace showing the upper horizontal line at the water surface which denotes the transducer position, the solid line formed as a result of total beam deflection from the substrate, and distinct dots in mid-water forming targets. The transect number refers to the number given in Figure 17.

echo-sounding traces. The net proved to have too high a resistance to be pulled by the boat and engine available.

Otter trawl: A positively-buoyant shallow bagged trawl net with lateral otter boards was used to sample fishes in the surface water over dense vegetation. The net, pulled by two boats, was landed inboard. The otter trawl proved to be effective for catching juvenile *Tilapia* but was rarely used as two launches were not usually available for netting.

Rod and Line: Pre-reproductive (i.e. territory-seeking but not territory-guarding) male *T. mossambica* were readily caught using rod and line. Damage to the fish was minimal.

Other methods: SCUBA was used for underwater observations on fish distribution and behaviour, plant cover, *Tilapia* nest distribution, and substrate types.

Data from fish caught by Africans were also collected.

Echosounding: A recording white-line echosounder was used to study the distribution of fishes in open water in Lake Sibaya. A battery-powered 12 volt Seascribe echosounder mounted on a 4.8 m aluminium outboard-powered launch was used. The echosounder had a chart range of 0-21 metres with increments of 18.6 m to a maximum of 113.2 m. Transducer transmitting angle was 45^{o}, with an ovoid sound beam. Echoes were not recorded within 1.8 m of the transducer which was mounted 15 cm below the water surface. The echotrace was made on electro-sensitive paper 7.62 cm wide. The upper horizontal line on the echotrace (Fig. 16) denotes the transducer position. The "white line" mode was used so as to aid in distinguishing between the bottom and fish very near the bottom.

The majority of the echosounding transects were carried out in the south basin. Six lines of transect were chosen according to the following criteria:

(1) the lines should traverse as many different habitats as possible,

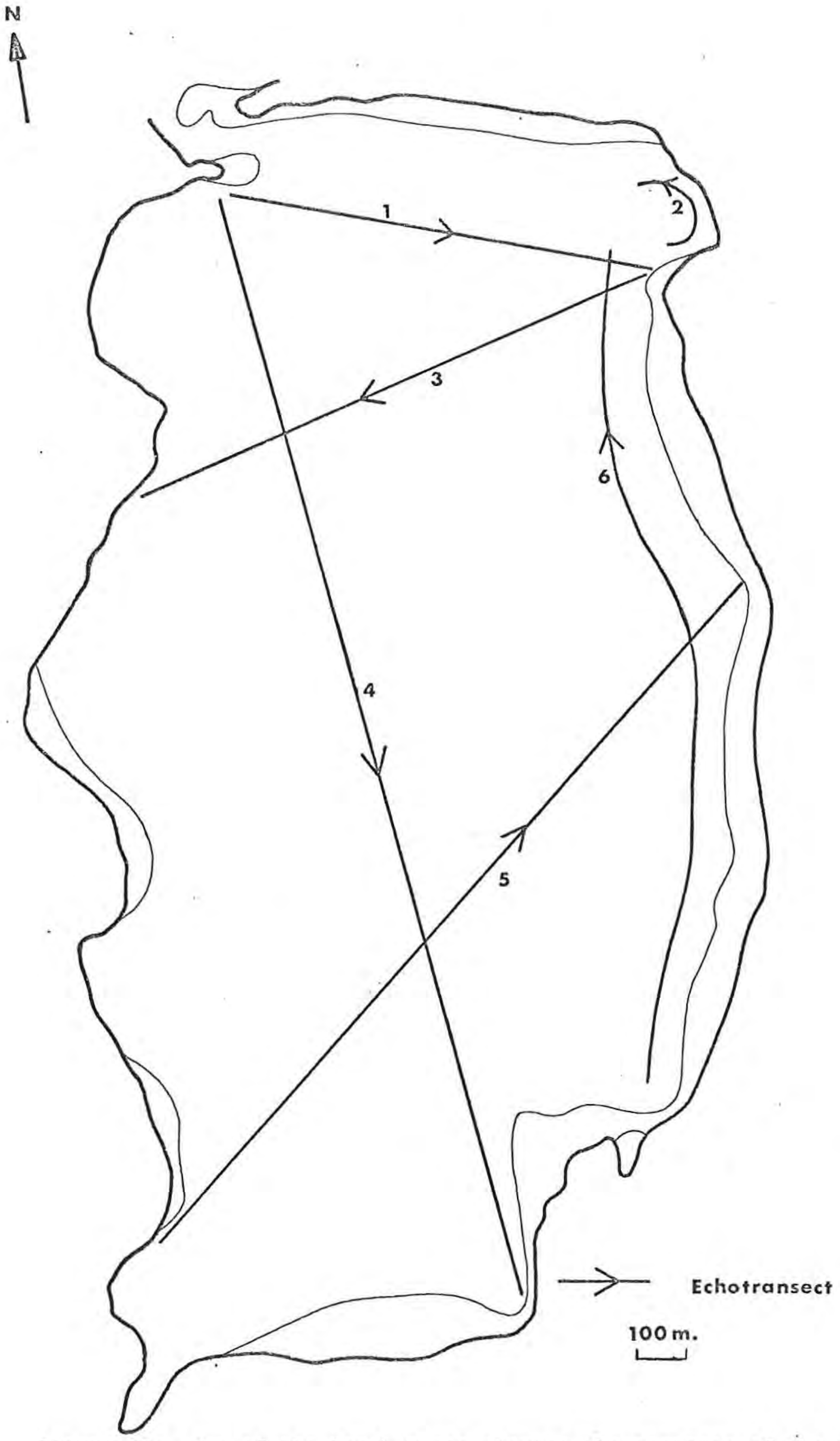


Figure 17: Map of the South Basin showing the position of the 6 echosounding transects referred to in the text. The arrows indicate the direction of movement of the boat while echosounding, and the numbers of the transect numbers given on the echotraces reproduced as Figure 16. The narrow black lines denote the edge of the terrace.

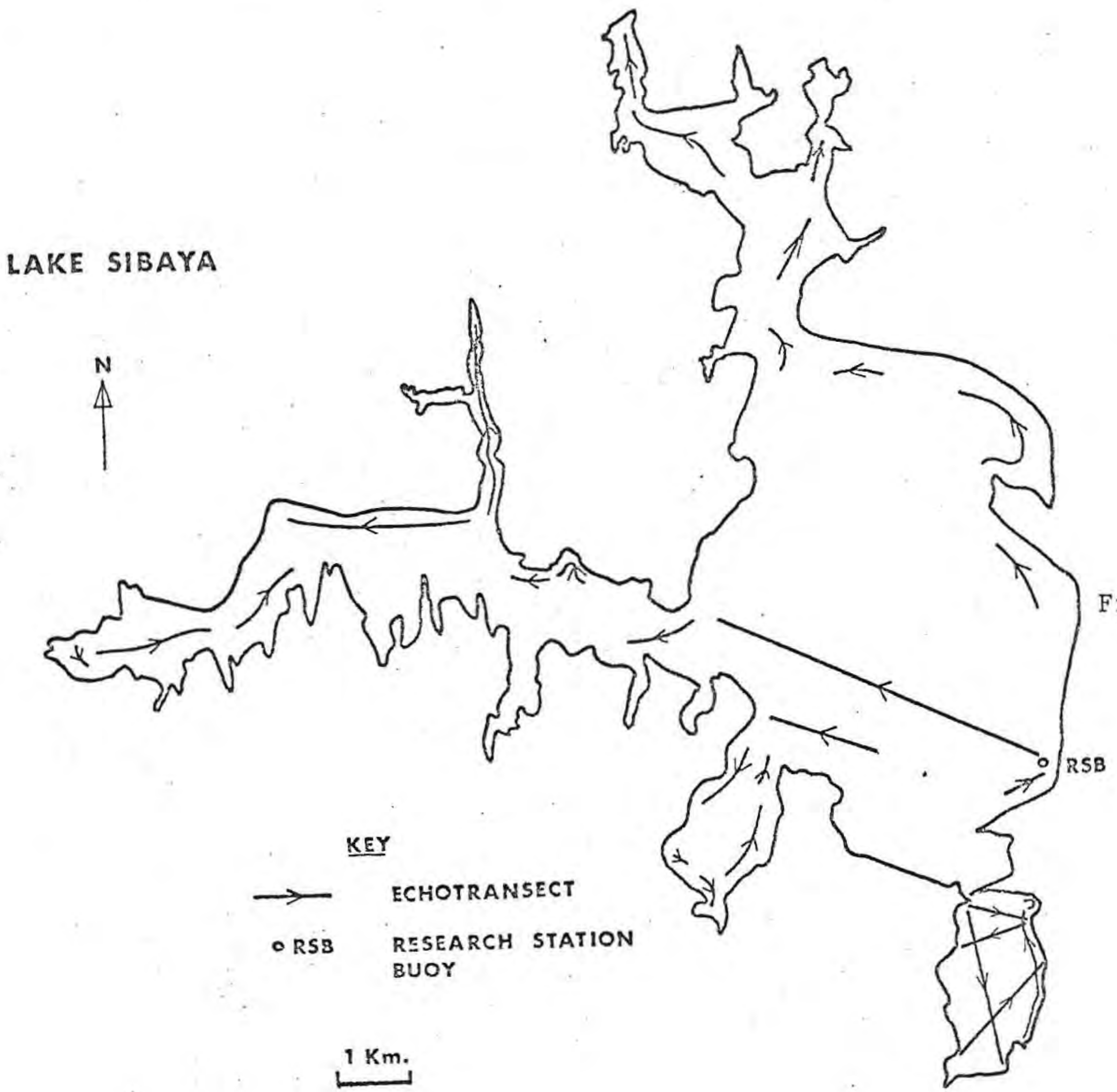


Figure 18: Map of Lake Sibaya showing the position and direction of the various echotransects in different parts of the lake.

e.g. weeded, barren, gently sloping, steeply sloping, level, deep, shallow, with soft and hard substrate;
(2) prominent landmarks, visible by day and night, should be present at either end of each transect line so that near identical transects could be followed each time. The six transect lines chosen are shown in Figure 17.

Echosounding along the six basic lines of transect in the south basin was carried out on eleven occasions (13.6.70, 7.9.70, 5-6.10.70, 2.2.71, 18.3.71, 7.4.71, 26.4.71, 12.9.71, 11.10.71, 17.11.71) starting at approximately 1200 hours (range 1100 to 1400 hours). On 5.10.70, echosoundings were performed at 1200, 1800 and 2400 hours, and again at 0600 hours on 6.10.70 along the six lines of transect.

Transects were also performed in the main basin and northern arm (5.8.70, Fig. 18), in the main basin and south-west basin (8.8.70) and western arm (14.8.70). Echosounding was always performed in the same direction along a given line of transect. Recording chart speed was maintained at 12.7 cm per hour, chart sensitivity at maximum and boat speed at about 8 knots. Echosounding was carried out in calm weather only, so that wave action would not alter the boat speed, produce excessive eddies under the boat, or interfere with the operating efficiency of the echosounder. As no echoes were recorded within 1.8 m of the transducer, large areas of shallow terrace around the shore of the south basin were unsuitable for echosounding using the equipment available.

Total beam reflection was recorded from the bottom and distinct elongate marks or dots were recorded from targets scattered between the bottom and the surface (Fig. 16). Discrete dots were each marked with a small circle on the echotrace and regarded in numerical analysis as individual fish. In order to represent graphically the relationship of the targets to the surface, middle and bottom thirds of the water

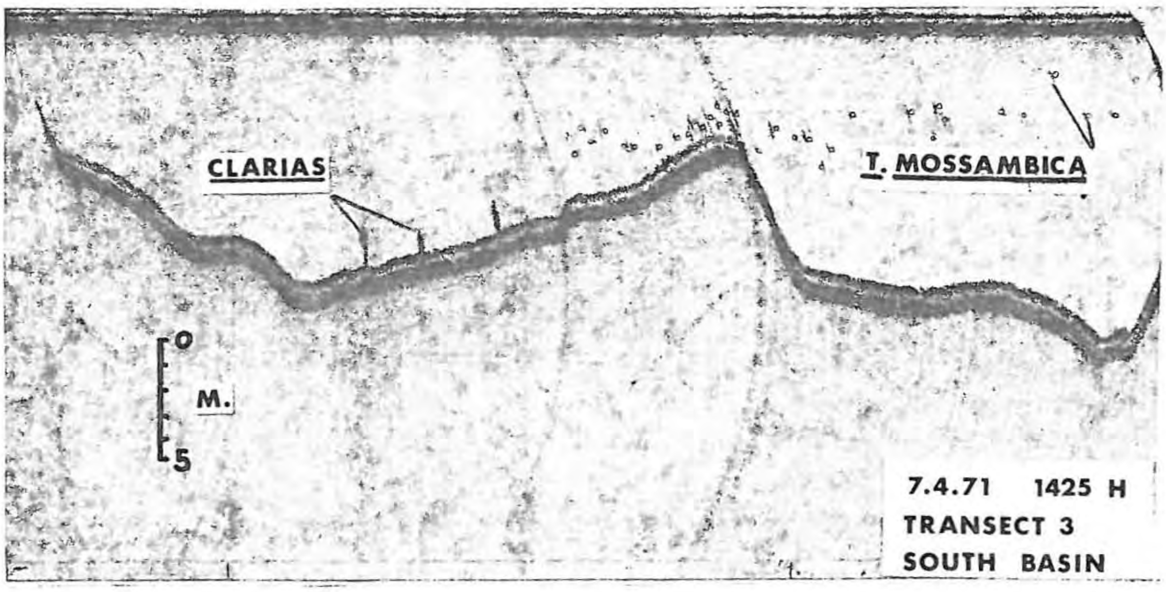


Figure 19: Reproduction of an echotrace indicating targets thought to be Clarias.

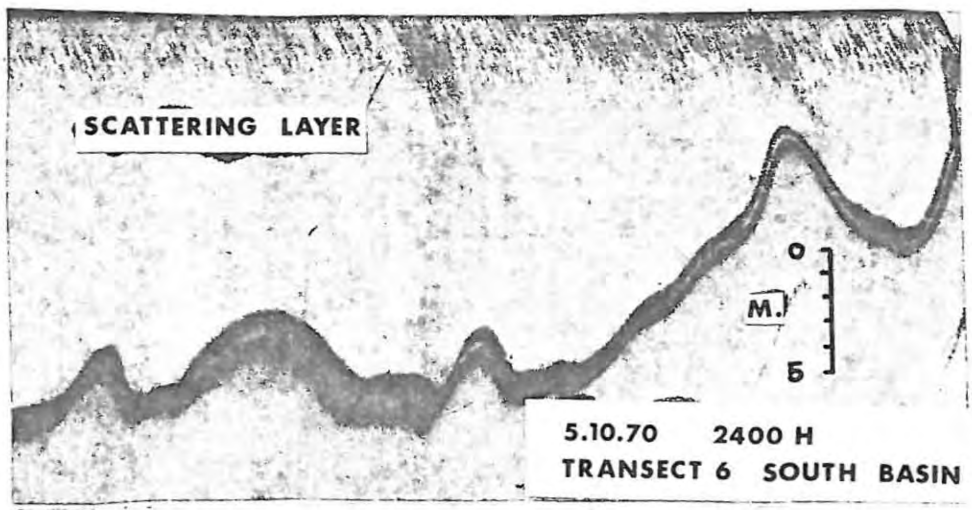


Figure 20: Reproduction of an echotrace showing the scattering layer produced by a large number of small targets at midnight.

column, the distance of each target from the bottom and to the surface was measured on the echotrace. These data were plotted on a scatter diagram and the number of dots in each third of the water column in each depth zone was summed. Distribution polygons were drawn from these data.

Validity of the method: There can be little doubt that the discrete targets recorded are fish, especially those with swim bladders since the reflective capacity of fish has been attributed largely to this source (Cushing and Richardson, 1955; Barham, 1966).

No other large pelagic animals are known from Sibaya except for crocodiles, hippopotami and diving birds, all of which can hardly be accounted for as target objects seen. There is little evidence of gas bubbles and particulate wastes in the limnetic zone sampled, and this source may be discounted.

Of the 16 species of fish known from Sibaya (Appendix 1), only *Clarias gariepinus*, *C. theodorae*, *T. rendalli*, *T. sparrmanii*, *T. mossambica*, and *Gnathonemus macrolepidotus* are sufficiently large to produce a discrete echo. Experiments have indicated that echoes are recorded from *Tilapia* 12 cm SL or larger. As *T. rendalli*, *G. macrolepidotus* and *C. theodorae* are comparitively rare, and according to the available data, confined largely to sheltered inlets in Sibaya, it is unlikely that they constitute a significant proportion of the targets recorded in the limnetic zone. Due to their large size the echo produced by *C. gariepinus* (a dot several times larger than that produced by *Tilapia* (Fig. 19) is clearly distinguishable. *T. sparrmanii*, a small species rarely reaching 12 cm SL, has only been recorded using fishtraps in water less than 3.6 m deep, or associated with the substrate. A scattering layer produced by dense aggregations of small targets was recorded near the surface during the transects carried out at night at 1800 and 2400 (Fig. 20). The echoshape of a scattering layer is clearly distinguishable from that of an individual large fish.

Gillnets were laid in the areas traversed by the echosounders. The catch of these nets, which sampled T. mossambica in the range 12-16 cm SL and Clarias longer than 30 sm TL, indicated that T. mossambica was the dominant species in midwater. The catches consisted of 61.4% T. mossambica, 37.1% C. gariepinus and 1.5% T. sparrmanii. Pike (1969) using gillnets ranging in size from 38 mm to 190 mm caught the following proportions of Tilapia species: T. mossambica 92%, T. sparrmanii 5%, and T. rendalli 3%. However, the proportion of small barbel producing 'Tilapia sized' dots on the echotrace is not known.

In summary, the data from the other fish collection equipment in Sibaya suggest that T. mossambica is the dominant limnetic fish over 12 cm SL but it must be stressed that confirmation of this supposition is required using high speed trawls in midwater before the targets, or rather the majority of targets, can be assigned to a particular species. Targets recorded in shallow water (less than 5 m deep) in sheltered bays are probably produced by a number of different species. Data collected through seining and fishtrapping operations has indicated that T. mossambica is the dominant species over 12 cm SL in these habitats.

FISH MEASURING AND RECORDING TECHNIQUES

The data collected during netting and trapping operations were tabulated on blank data forms. Details of the procedures for determining the various parameters of the fish sampled are described in this section:

Species identification: Adults of the three species of Tilapia present in the lake are easy to identify but juveniles of standard length less than 8 cm may cause confusion. The field characters used in this study for the identification of juveniles are given in Table 2. The vertical black bars mentioned in the table are only displayed by T. mossambica juveniles when the fish is alarmed, e.g. after netting. The normal colouration is plain silver, occasionally with a single horizontal black stripe. The other cichlid present in the lake (Hemihaplochromis philander) is readily distinguished by the rounded caudal fin (truncate in Tilapia), the lack of a tilapia spot and the yellowish-olive flank colouration.

TABLE 2

Field characters for distinguishing Tilapia juveniles

Character	T. mossambica	T. sparrmanii	T. rendalli
Vertical black bars (when present)	3 - 4	7 - 9	5 - 9
Colour of head	silver	blue-green	silver
Colour of flanks	silver	silver-green	silver
Colour of breast	silver	silver-green	pink
Vertical bar through eye	absent	present	present
Number of gillrakers	16	7 - 12	8 - 12
Length of gillrakers	long	short	short
Dark spot on operculum	absent	present	present

Length: Standard (SL) and total (TL) lengths were measured in the conventional way. The sampling error was highest in larger fishes (over 15 cm SL) as the exact point at which the caudal peduncle ended was difficult to determine. Standard lengths proved to be more reliable than total lengths as fishes were sometimes encountered with damaged caudal fins. The factor contributing most to inconsistencies in length measurement was probably the variation in the pressure applied in placing the closed jaw against the stop of the measuring board. The relationship between SL and TL for Sibaya T. mossambica is shown in Figure 21.

Weight: Weight was measured in grams as wet weight with the water drained from the fish's buccal cavity, except in the case of mouthbrooding females in which cases the buccal cavity was not drained. Weights were measured on an Ohaus Triple Beam balance accurate to 0.5 gram from

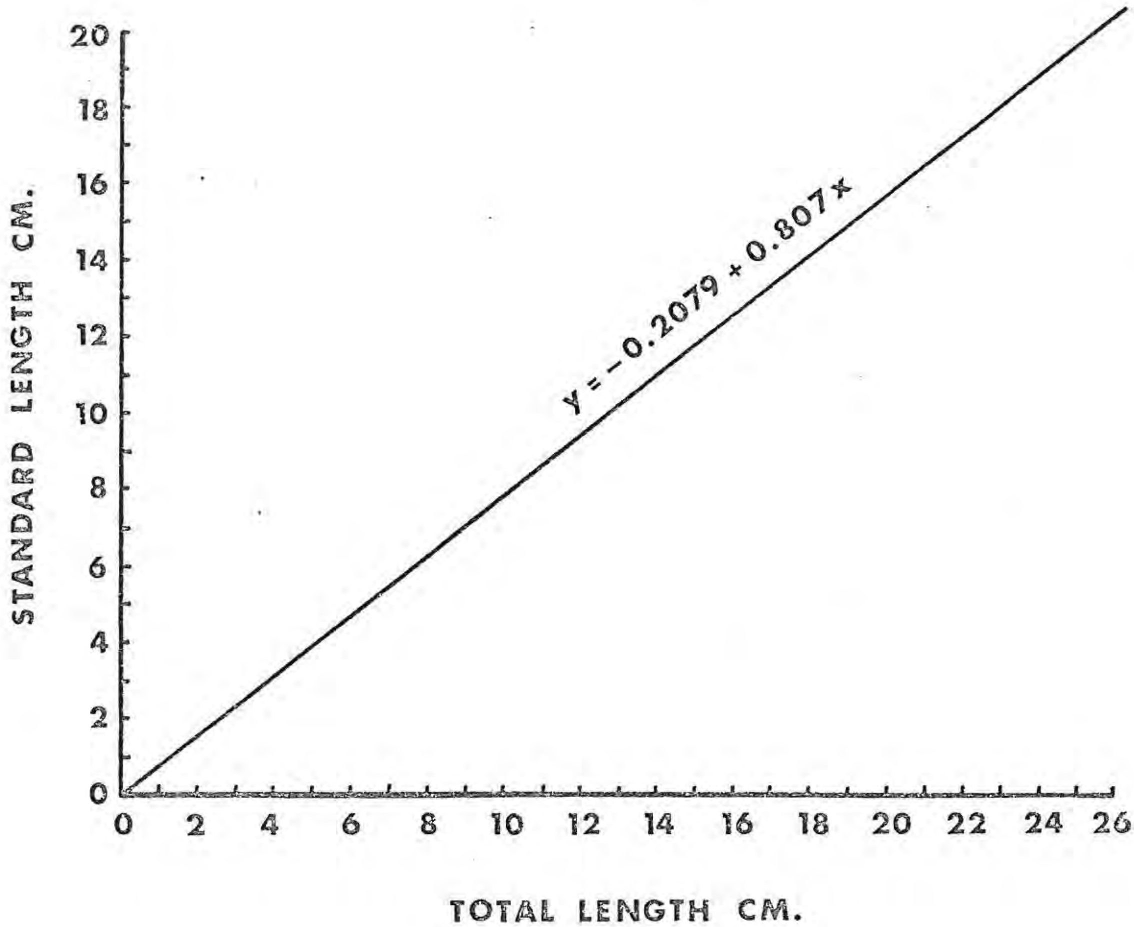


Figure 21: Regression line showing the relationship between standard length and total length for <u>T. mossambica</u> from Lake Sibaya. R = 0.98. N = 150.

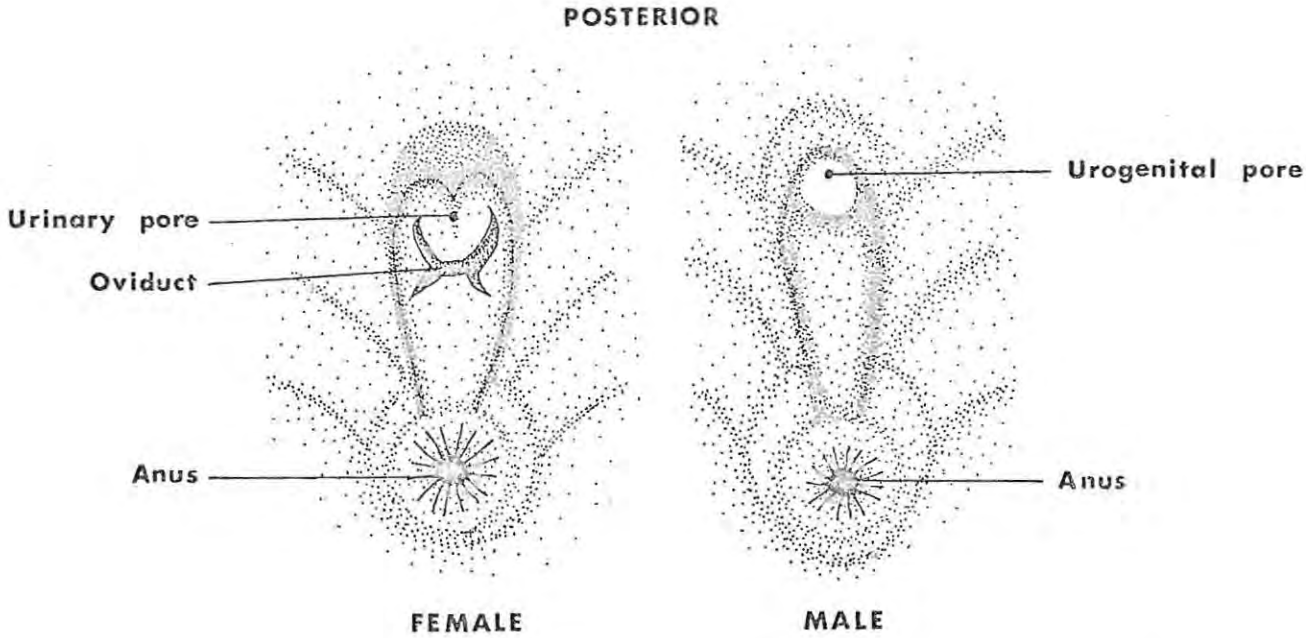


Figure 22: Genitalia of female and male T. mossambica. Diagram redrawn from figure of Vaas and Hofstede (1952).

21.1.1970 until 22.12.1970, on an Avery self-indicating scale type 1217, accurate to 2 grams from 22.12.1970 until 7.12.1971, and on an Ohaus Dial-o-gram scale accurate to 0.1 gram from 7.12.1971 until the conclusion of the study.

Sex: In fishes sacrificed and sampled for stomach contents, sex was determined by examination of the gonads. However, as the vast majority of fishes were used in growth and mark, release and recapture experiments, sex was usually determined by inspection of the external genitalia and the secondary sexual characters. The sex of fish of SL less than 8 cm can be diagnosed by determining the number of openings in the anal region. Thus, with the aid of a blunt crochet hook (size 23) the three openings on the female, the oviduct, the urinary pore and the anus can be distinguished (Fig. 22), while the male has two openings with a single urogenital pore on the genital papilla. This method has been used successfully by Vaas and Hofstede (1952) and Pike and Oosthuizen (Pers. comm., 1972) on *T. mossambica*. The sex of fish larger than 8 cm SL can be determined by visual examination. In the male the genital papilla is conspicuous, as is the opening of the oviduct in the female. Breeding males were recognised by their breeding colouration: black or grey upper head and flanks, bright white lower head and breast with scarlet colouring on the borders of the pectoral, dorsal and caudal fins. The non-reproductive colour in the male is grey. As the change from non-reproductive to reproductive colouration in the female was slight (plain grey to silver) the presence of young in the mouth was used as the criterion for distinguishing a breeding (or 'brooding') female.

Condition: Condition factors were calculated using the formula:

$$CF = \frac{W \times 100}{SL^{b}}$$

CF = condition factor

where W = weight in grams

SL = standard length

b = ratio of length to weight

as recommended by Tesch (1968).

Vaas and Hofstede (1952) found a value for 'b' of 3.08 in males and 3.02 in females in T. mossambica. A value of 3 has been used for calculation of 'condition factor' in T. mossambica from Lake Sibaya. As noted by Tesch (1968), 'b' is likely to change at various crises in the life of the fish, for instance at maturity. For this reason, condition factors of juvenile and adult fish have not been compared. Furthermore, no attempt has been made at this stage to distinguish between weight increases which are a normal consequence of growth, and weight increases brought about by the temporary accumulation of gonadal material. Condition factors have been used merely as an indication of the seasonal changes in the 'fatness' of T. mossambica.

General notes: Notes were made on injuries and parasites on the fishes sampled. Fishes were carefully examined for damage caused by the seine nets or gillnets, or, in the case of recaught tagged fish, for wounds caused by the tag. Notes were made on the presence of secondary sexual characters such as breeding colouration, expansion of the buccal cavity in females, or evagination of the mandibular teeth or of the genital papilla in males.

Mouth-brooding females were divided into five categories:

(i) carrying ova

(ii) carrying young fry (SL less than 6 mm)

(iii) carrying medium fry (SL 6-9 mm)

(iv) carrying advanced fry (SL more than 9 mm)

(v) carrying any combination of the above.

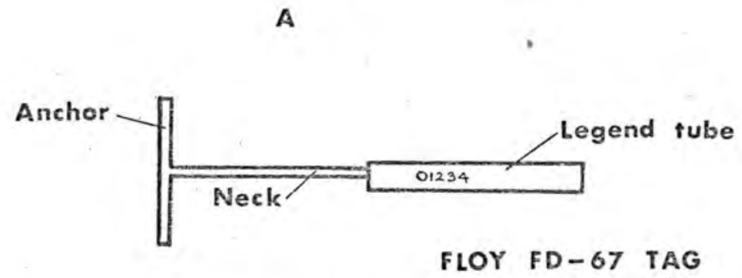


Figure 23: Floy FD-67 tags were used during the study (Fig. 23A). Preliminary experiments were carried out using Floy FTF-69 fingerling tags (Fig. 23B).

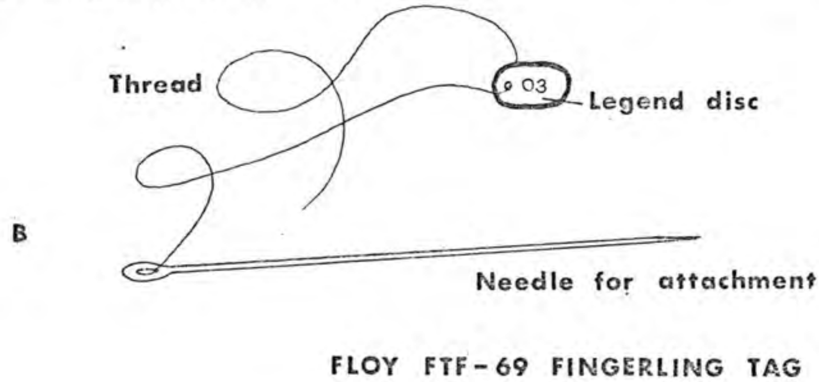


Figure 24: Position of application of the Floy FD-67 tag to T. mossambica using tag applicator.

FISH MARKING TECHNIQUES

Mark, release and recapture methods using rags for individual recognition, and finclips for batch recognition, were used to study growth and migration, and as an aid in estimating population size.

Tagging: FD-67 spaghetti-type plastic anchor tags, obtained from Floy Tag and Manufacturing Inc., Seattle, were used for individual marking of *T. mossambica* over 8 cm SL. The tag consists of a plastic anchor and neck fused to a numbered yellow legend tube (Fig. 23A). The tag applicator, identical to the instrument used to attach clothing tags, was purchased from Glendale Enterprises in Port Elizabeth.

The tag was inserted into the dorsal musculature between the anterior interneurals of the dorsal fin, as shown in Figure 24. The tag anchor was either inserted right through the body to lie on the right flank, or inserted so as to straddle interneurals within the musculature. "Synalar" antiseptic was applied to the tag wound.

Some fishes showed a shock reaction after tagging resulting in reduced swimming ability. Fishes were thus kept in containers for five minutes after tagging, and then released at the point of capture. Fishes which had been caught in shoals were released in batches. The success of the tagging operation was noted for each fish on an arbitrary scale: A : successful; B : slight difficulty due to continued flapping of fish or jamming of applicator; C : extreme difficulty due to a broken tag or other cause. Over 98% of the tagged fish fell into category A.

The effectiveness of FD-67 tags for marking *T. mossambica* is discussed in Appendix 2.

Finclipping: Fishes of SL less than 8 cm were finclipped by amputating one or both pelvic fins using a pair of fine scissors. The pelvic fin peduncle was not harmed. The disadvantage of finclipping is that the mark is not permanent, as the fin regenerates. However, fish in which regeneration of the clipped fin had taken place are

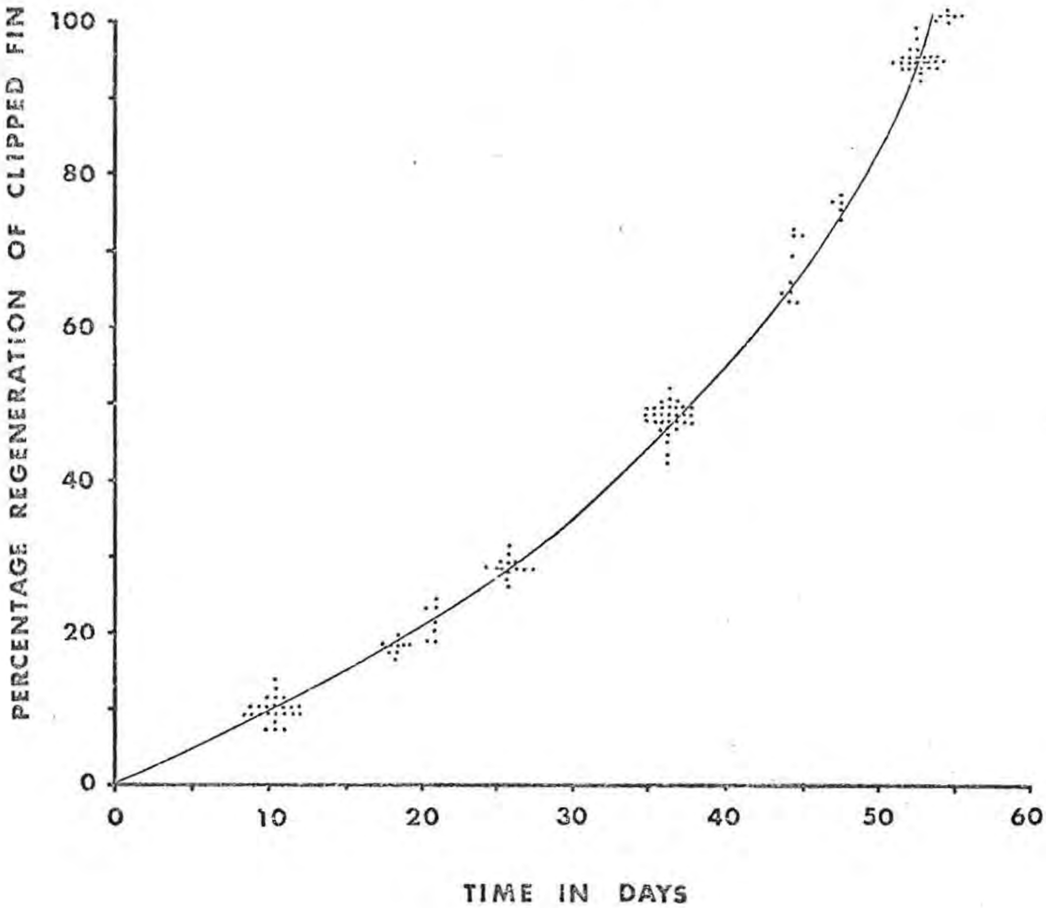


Figure 25: The rate of regeneration of pelvic fins of juvenile T. mossambica. The percentage regeneration of the clipped fin was obtained by comparison with the length of the unclipped fin. The fishes used in the fin regeneration experiment were held in an aquarium at water temperatures ranging from 20°- 23°C.

recognisable because of the altered pattern of branching of the fin rays. To assist in the identification of previously cut fins a suggestion of Arnold (1965) was followed whereby the vital dye, Sudan Black B, was applied to the cut fins. This produced a black line on the fin sometimes visible after regeneration. Although it is not possible to recognise individual finclipped fishes on recapture, fishes from different localities can be identified through the use of a code. Three codes of pelvic fin clipping were used in the south basin. The right pelvic fin was clipped on fish caught on the north-east shore (sites 2, 7, 11, 13 (Fig. 3)), the left pelvic on fish from the south-east shore (sites 8, 9, 14) and half of each fin for fish caught on the western shore (site 3).

The rate of regeneration of clipped pelvic fins was determined so that the time of liberty of recaptured fish could be calculated by noting the percentage regeneration of the clipped fin. Forty finclipped _T. mossambica_ (SL 5.5-6.9 cm) were introduced into an aquarium and the regrowth of the clipped fins was measured at intervals to the nearest millimetre. The percentage regeneration was calculated by comparison of the length of the clipped and unclipped fins. Both left and right pelvics were clipped. The data were combined as it was found that regeneration was not markedly different. The fishes were provided with excess amounts of natural food. Aquarium water temperatures varied between 20° and 23°C which approximates the average water temperature in the lake (about 23°C). Five fishes died during the experiment, which was discontinued after 58 days. As shown in Figure 25, 50% regeneration took place after 37 days after which the rate of regeneration increased. 100% regeneration took place after 50 to 54 days.

REMOVAL AND PREPARATION OF HARD PARTS FOR AGE ANALYSIS

Scale sampling: Scales removed from sampled fish were used as an aid in assessing growth rates. Five scales were removed from each fish.

Scales from the pectoral region below the lateral line were found to be most suitable as these scales were large and symmetrical with relatively clear rings and a constant ring count. The scales from each fish were placed in separate marked envelopes and cross referenced to the basic data on the field data sheet. The scales were then cleaned, dried, mounted in Cemedine (a transparent glue) on microscope slides, and examined on a Fresnel screen mounted on a Zeiss compound microscope. In order to avoid possible bias when counting scale rings, fish standard lengths were written onto the slide labels only after the scales had been read. Scales from 2223 T. mossambica were examined. 82% of the scales showed clear rings.

Removal of otoliths and opercula: Otoliths and opercula removed from subsamples of fish were also used as an aid in assessing growth rates.

The sagittal otolith was removed by severing the head from the vertebral column and removing the ventral lobes of the paired sacculi. The otoliths were soaked in warm water, dried, then ground on moist waterpaper on the distal surface to the plane of the nucleus. The ground otolith was washed, dried, and burnt by placing the ground surface on a heated piece of tin for 15 seconds. The burnt otolith was then mounted in Cemedine in the well of a hollowed microscope slide. When examined under a low power microscope clear subconcentric rings were visible on 96% of the otoliths sampled.

Opercula were removed by cutting away the pre-, sub- and inter-opercula. The opercula were then soaked in warm water, brushed, rinsed and dried. When examined under a low power microscope clear rings were visible in 40% of the opercula. 25 pairs of otoliths and opercula were examined. Otolith and opercula rings were counted without knowledge of the scale ring count or standard length of the fish, to avoid possible bias.

ESTABLISHMENT OF EXPERIMENTAL POOLS

Two pools were constructed for experiments on fish growth and the effect of the tags. The pools, measuring 10 by 12 metres, were dug on the lake shore and lined with black plastic sheeting. Pool 1 had an average depth of 1 m and Pool 2 of 1.4 m. Sand and detritus from the main lake were introduced into each pool. In addition aquatic macrophytes, molluscs, benthic and planktonic crustacea, and small numbers of cyprinodont fishes from the lake were introduced into each pool to simulate natural conditions in the lake. No artificial food was added to the pools. Water was pumped from the lake into the pools and a record of pool water temperatures was kept.

Marked and unmarked *Tilapia* were introduced into the pools and sampled at regular intervals using seine nets or fishtraps. Underwater observations on the feeding, breeding and territorial behaviour of *Tilapia* were made in the pools.

GENERAL BIOLOGY

Although *T. mossambica*'s ability to inhabit a wide variety of habitats is well known, few workers have had the opportunity of studying in detail the species' biology in a natural habitat. The results reported have described the way in which *T. mossambica* has adapted to living in a blocked marine estuary which has been transformed into a closed freshwater lake (Hill, 1969).

THE DISTRIBUTION OF *T. MOSSAMBICA* IN LAKE SIBAYA

The data are derived from a number of different methods, since what is appropriate to one region cannot be used in another. Consequently data from different regions of the lake cannot be compared in a strictly quantitative way since some of the methods did not allow of direct estimation of the population of fish in those regions. However, the catches were sufficiently different to show that the majority of the population appears in different regions at particular

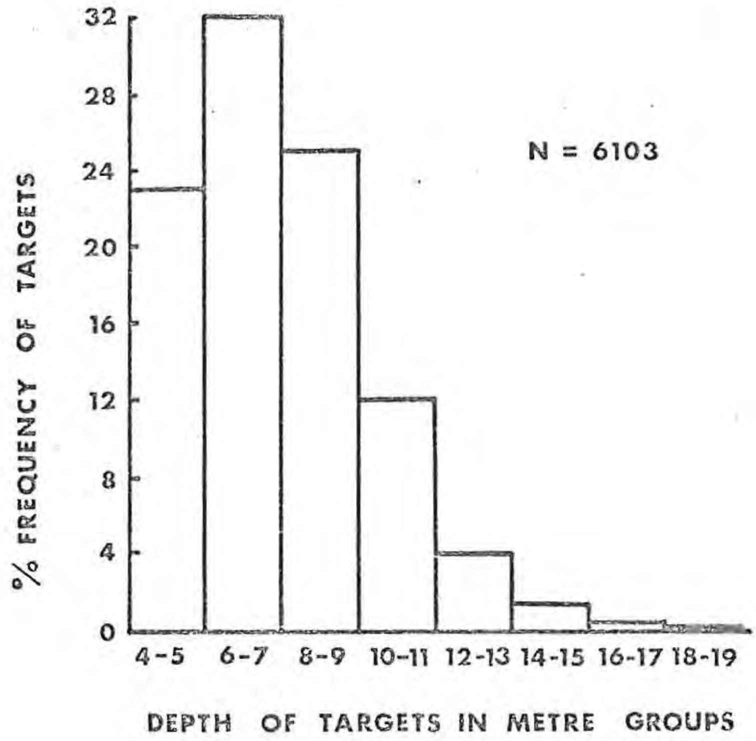


Figure 26: The percentage frequency in different depth groups of echosounding targets thought to be *T. mossambica*.

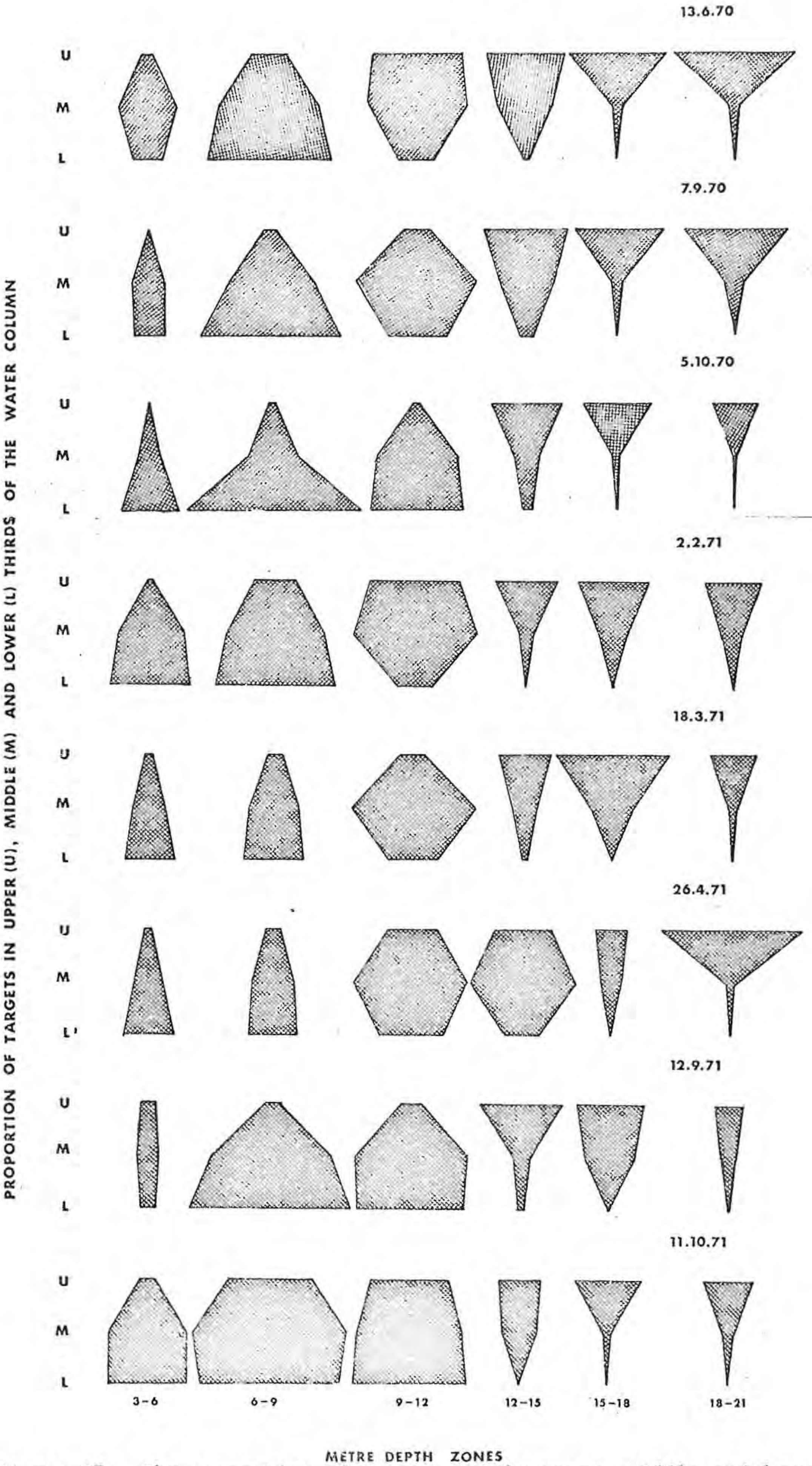


Figure 27: The proportion of targets in the upper, middle and lower thirds of the water column in different depth zones showing the changing relationship of targets with respect to the bottom. The data are derived from discrete dots on the echotraces which were plotted in a scatter diagram of water depth vs. target depth.

times of the year.

a) The vertical limitation of adult and juvenile fish:

Tilapia mossambica adults appear to be limited to water less than 18 m deep although juveniles may reach greater depths. Gill nets laid to a depth of 13 m only caught fish up to 9 m. Fish traps laid to a depth of 24 m in the south basin and 39 m in the main basin gave a catch per unit effort of 2.4 to a depth of 7 m. The catch per unit effort decreased to values less than 1 from 7-12 m and no T. mossambica were caught deeper than 12 m.

A total of 25 hours underwater was spent using SCUBA to confirm this distribution of fish. Observations were made at 28 different stations and to a maximum depth of 30.4 m in the main and south basins of Lake Sibaya. T. mossambica were positively identified to a depth of 8.5 m, and often encountered to a depth of 5 m. Although Hemihaplochromis philander and Tilapia sparrmanii were observed at 30.4 m, T. mossambica were not seen at this depth. Large faecal ropes of Tilapia have been reported at depths of 20 m on the substrate in Lake Sibaya (Boltt, Hill and Forbes, 1969). This, however, does not necessarily indicate that large Tilapia occurred near the substrate at these depths, as faecal ropes probably retain their form after having dropped onto the substrate from midwater.

Information on the distribution of fishes in water deeper than 3 m was also assessed using the echosounder. As suggested in the section on methods, the majority of the echosounding targets appear to be T. mossambica. Most of these targets occurred shallower than 13 m (93%, Fig. 26). The deepest targets were recorded at 18 m, although larger targets, thought to be Clarias gariepinus, occurred in deeper water (cf Fig. 19). The data indicate further that, throughout the year, more fishes occurred at depths of 4-5 m (23%) or over 9 m (20%) (Fig. 26), although the transects traversed large areas deeper than 8 m. In Figure 27, the proportion of targets in

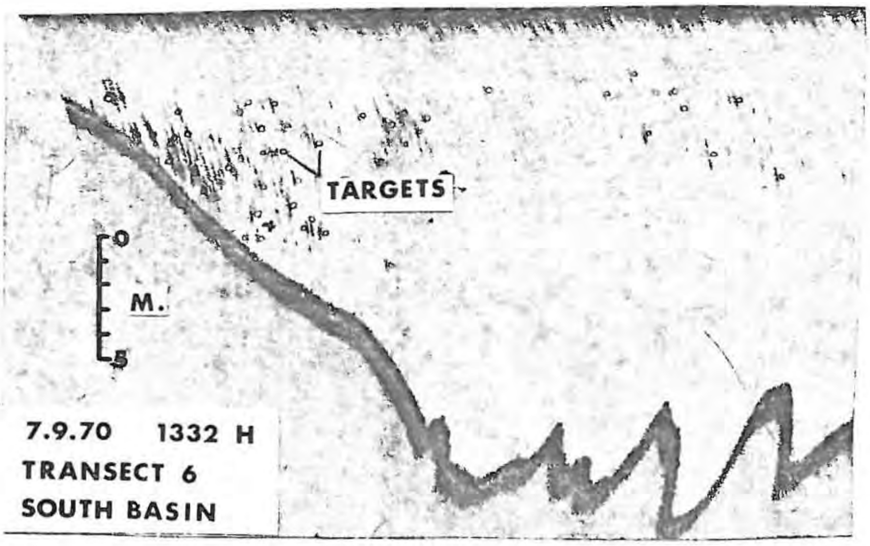


Figure 28: Reproduction of an echotrace showing a typical pattern of target distribution with increasing depth.

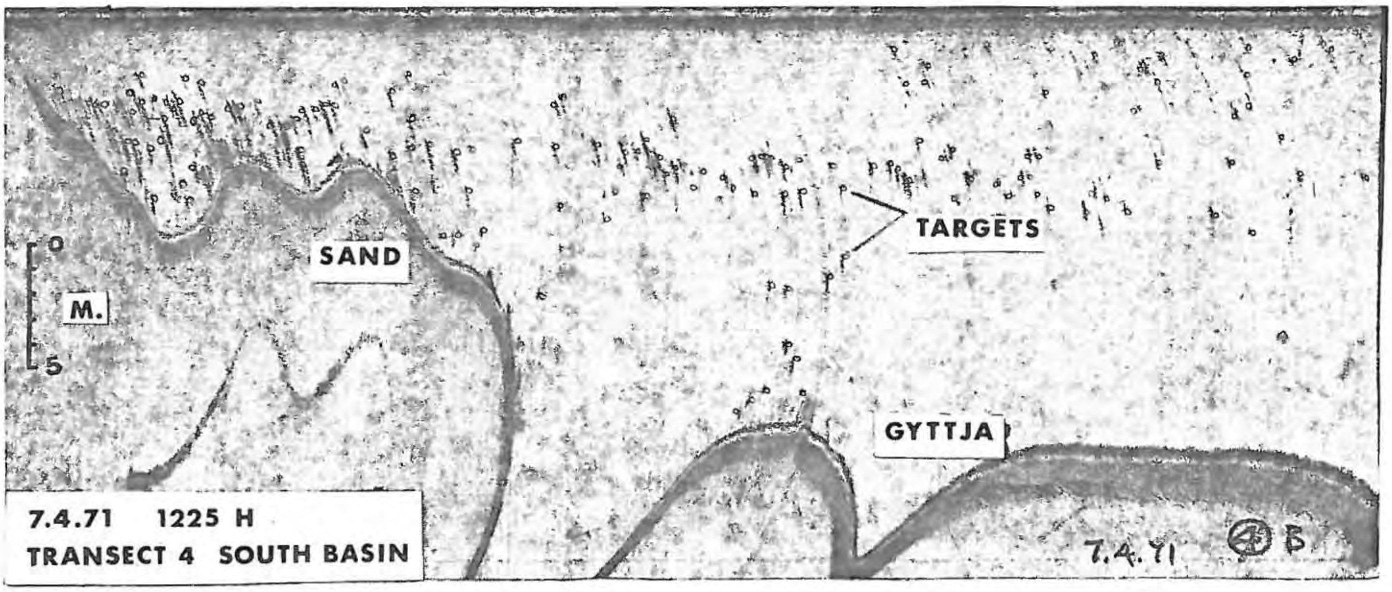


Figure 29: Reproduction of an echotrace showing the pattern of target distribution in relation to water depth. The figure also shows the wide diffuse trace produced by gyttja, and the narrow trace formed by sand.

the upper, middle and lower thirds of the water column is given for 8 sets of transects performed in the south basin. The data indicate that targets were associated with the substrate at depths from 3-12 m (i.e. occurred in the lower third of the water column), but occurred near the surface in water deeper than 12 m. A typical target distribution is illustrated in Figures 28 and 29. In water deeper than the preferred depth (about 12 m) T. mossambica occur in the surface third of the water column.

The lower depth limit of T. mossambica in Lake Sibaya was thought to be so important in the species biology that a series of laboratory experiments were initiated at Rhodes University by Caulton (1972) to investigate the reason behind the limitation. No physical factors limiting the distribution to depth of T. mossambica in Lake Sibaya except hydrostatic pressures are known. The recorded water temperature range in different seasons in the limnetic zone (30^{o}-17^{o}C) is within the range of the species. Thermal discontinuities of one to two degrees at the most do exist for short periods of time (Minshull, 1968; Allanson and van Wyk, 1969), but these are unlikely to restrict the vertical movement of T. mossambica. Similarly, the minimum recorded percentage oxygen saturation (60% at 38 m in summer; Allanson and van Wyk, 1969) is known not to be limiting to T. mossambica. The effect of pressure on T. mossambica was thus investigated. Using a continuous-flow, water-filled, temperature-controlled pressure chamber, Caulton exposed fishes to simulated depths by increasing and decreasing the water pressure. As the chamber was completely filled, there was no change in the oxygen partial pressure with a change in hydrostatic pressure, and conditions therefore resembled those in the lake. The experiments were conducted at a constant water temperature of 22^{o}C. The depth tolerances of male and female adult T. mossambica (TL average 17.7 cm, range 13.7-20.5 cm), and juvenile T. mossambica (TL 40-80 cm) were determined. After 24 hours at the 'surface', the

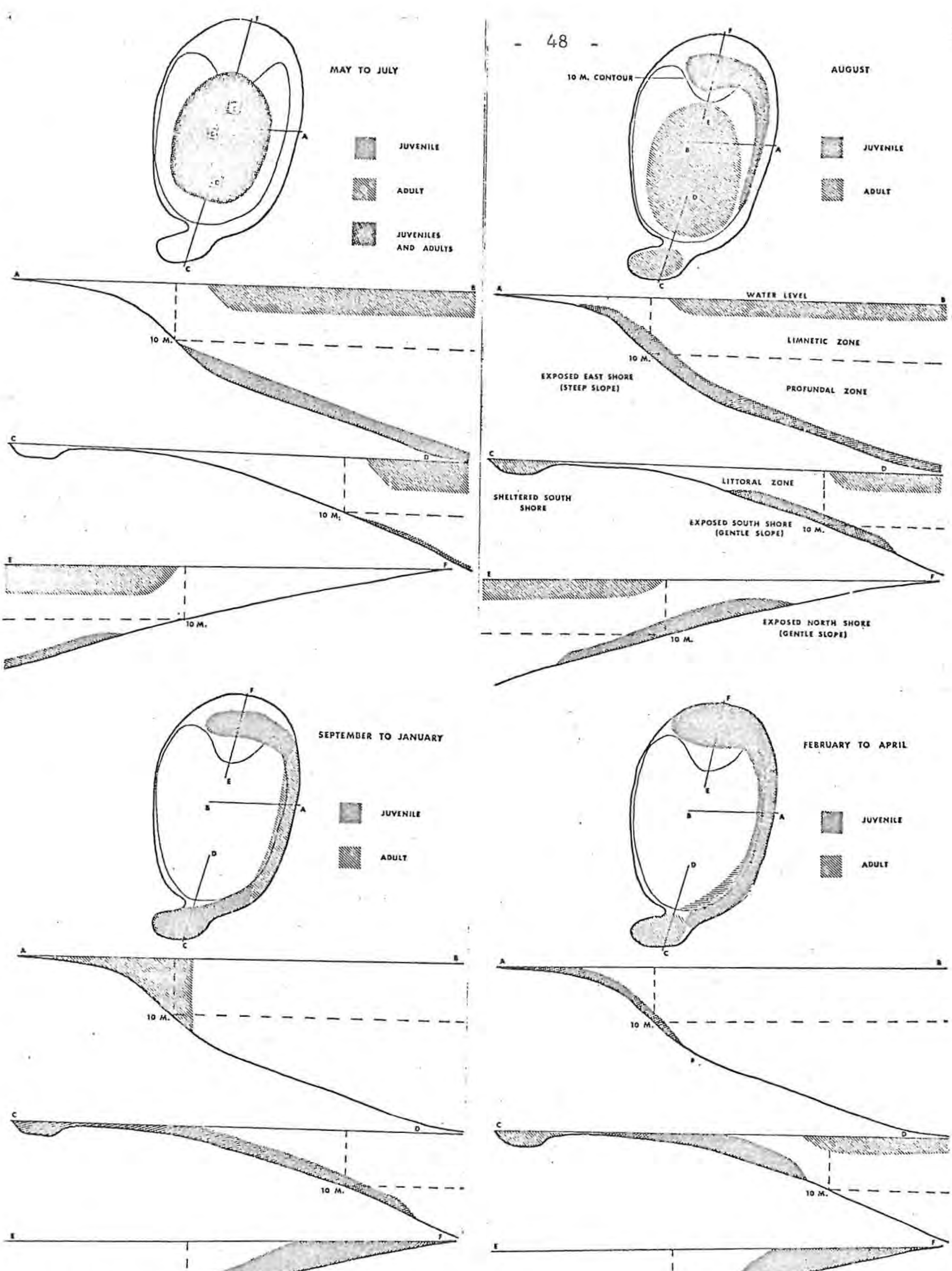


Figure 30: Diagrammatic representation of the horizontal and vertical distribution of the main juvenile and adult population *T. mossambica* in an annual cycle. In each of the four figures, the upper diagram, a simplified map of the south basin, illustrates horizontal distribution, and the lower three diagrams, which are profiles of the shore, illustrate vertical distribution. The position of each profile is given by the letters A to F. Profile A to B represents a scoured eastern shore, Profile C to D a sheltered bay and southern deposition shore, and Profile E to F a northern deposition shore.

fish were exposed to a simulated depth of 5 m for 12 hours, and thereafter, to further increases in depth of 2 m every 12 hours. The behaviour of adult and juvenile fishes, even under high pressure was found to be normal. Male and female T. mossambica were shown to have a marked difference in their ability to achieve neutral buoyancy at different depths. Males were able to compensate to a maximum depth of 20 m, but females to only 12.8 m. These maximum compensation depths were maintained despite acclimation time totalling 120 hours at intermediate depths, and exposure to 25 m for 36 hours. Adult fish tolerated a 16% swimbladder volume change brought about by rapid vertical movements. Thus a fish equilibriated to 20 m was capable of moving rapidly in a zone from 15-25 m. Juvenile T. mossambica of TL 40-80 mm tolerated a pressure change equivalent to 33 m in 10 minutes, by firstly adjusting their fin beat rate, and then becoming neutrally buoyant.

This experimental finding supports the observation reported by Boltt, Hill and Forbes (1969) that T. mossambica juveniles occur to a depth of 20 m in the main basin of Lake Sibaya. Caulton's results confirm my findings, that the lower depth limit of adult T. mossambica in Lake Sibaya is about 18 m. The echosounding data have further indicated that the majority of adult fishes are restricted to depths of less than 12 m.

b) Seasonal changes in the horizontal distribution of T. mossambica in Lake Sibaya:

The general trend is a movement from the shallows into deeper water in the cooler season, and a return to shallow water in the warm season when breeding takes place. The seasonal distribution of T. mossambica in Lake Sibaya is diagrammatically depicted in Figure 30 A, B, C, D.

In the cool season (May to July) T. mossambica are in general in very low numbers in shallow water near the edge of the lake. The

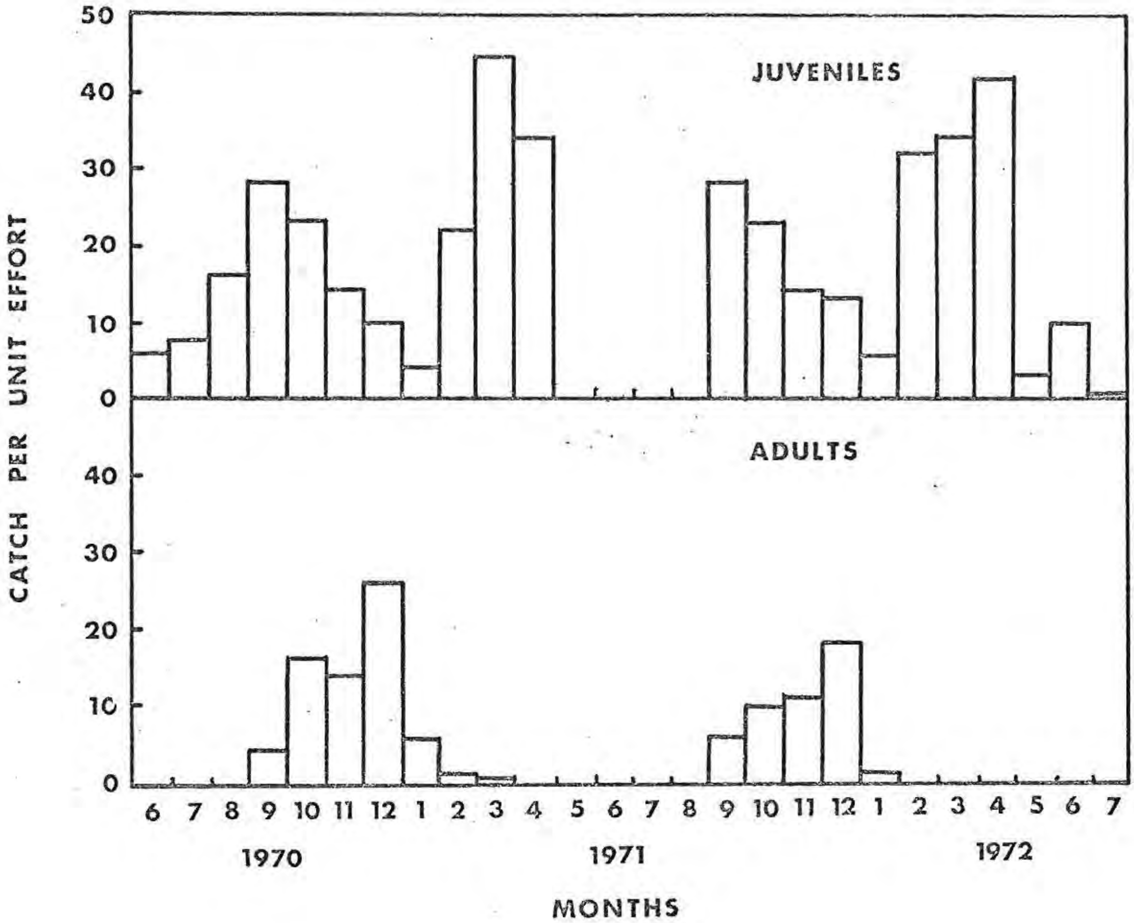


Figure 31: The catch per unit effort of juvenile and adult T. mossambica on the terrace and slope in the south basin by means of the slope seine net. No netting was performed in the period May to August 1971.

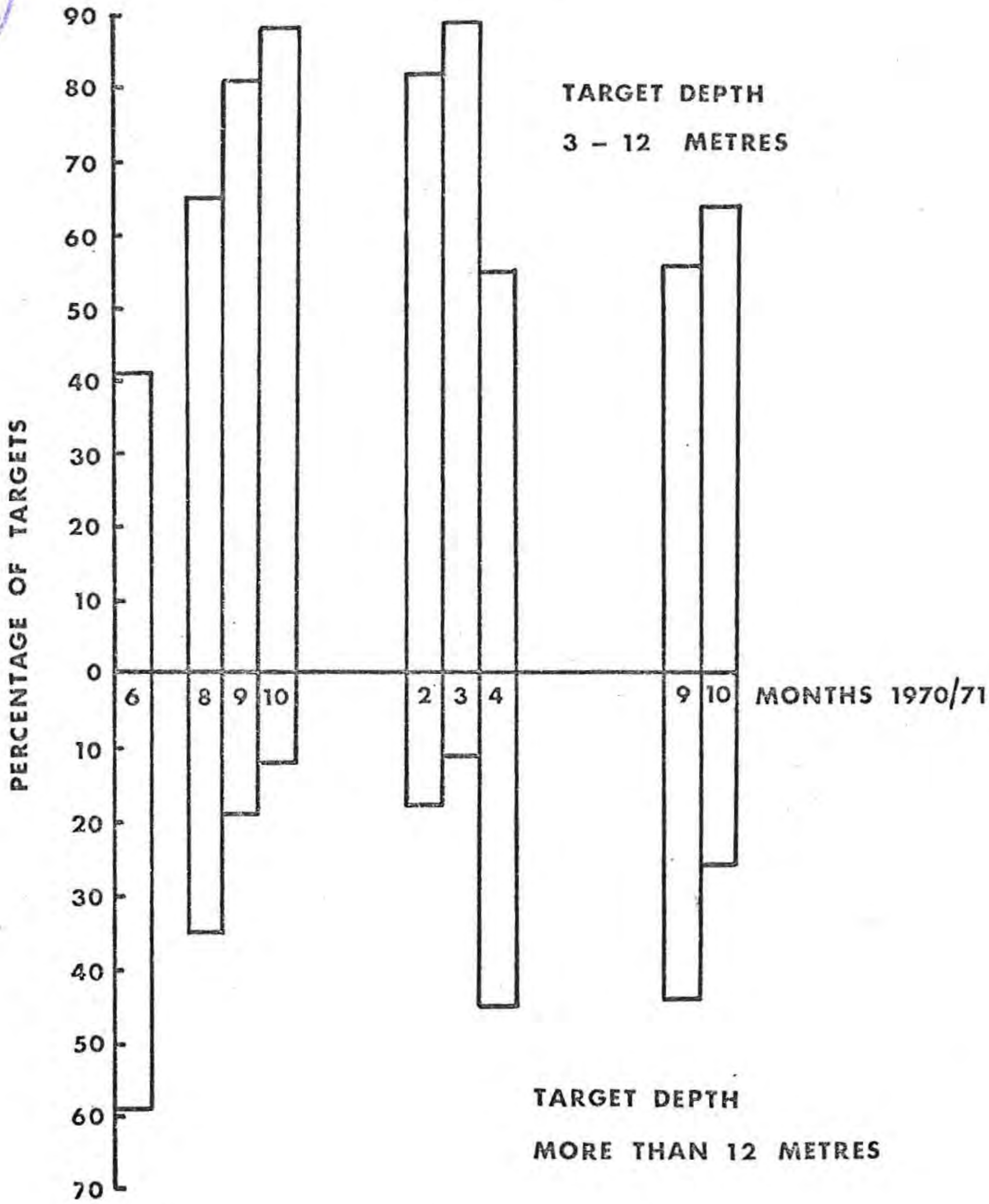


Figure 32: The percentage of echosounding targets in water 3-12 metres deep, in nine sets of transects performed in the south basin. Targets were most abundant in shallow water in summer, and least abundant in shallow water in the transition periods and in the cool season.

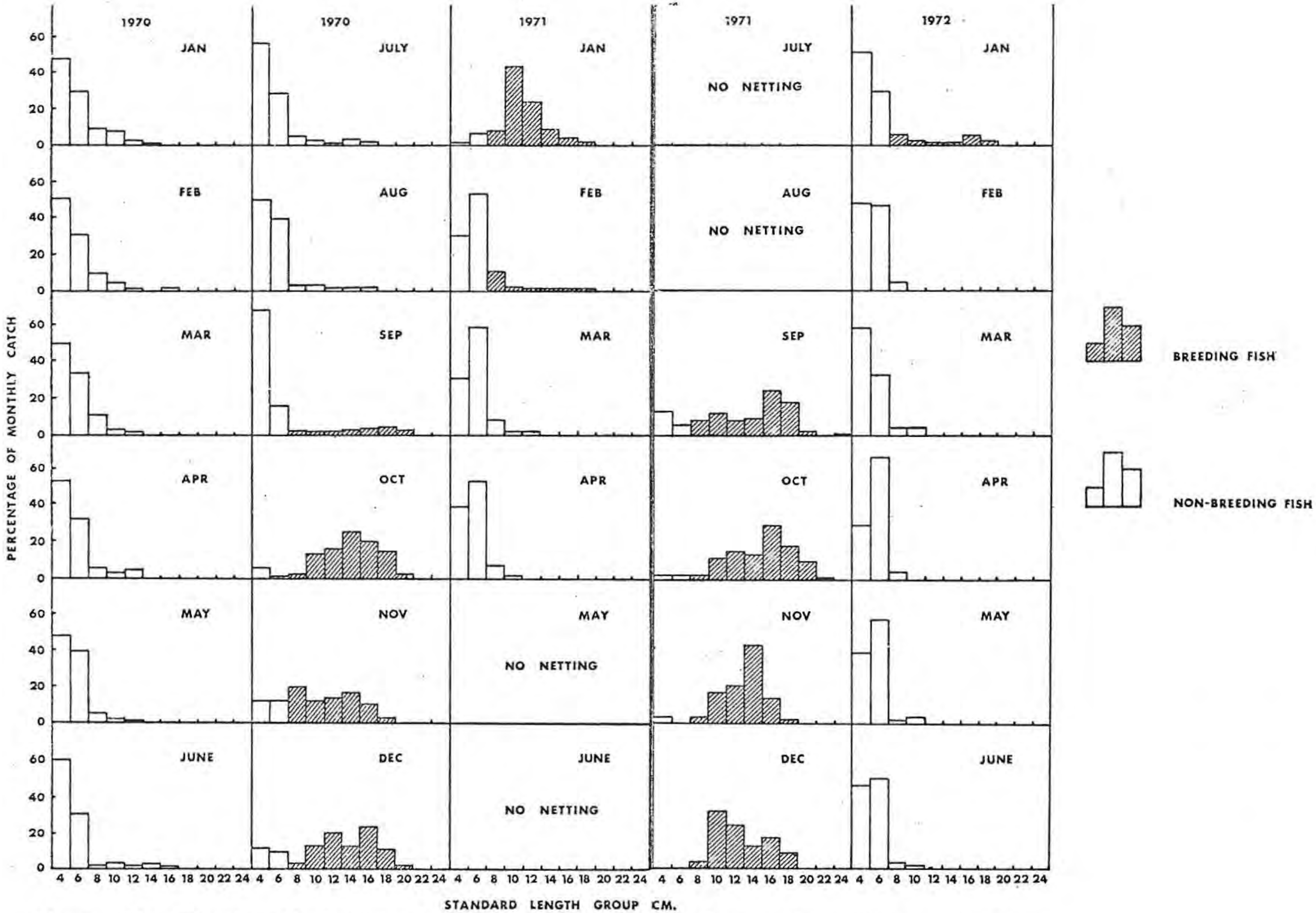


Figure 33: The length frequency of T. mossambica caught on the terrace and slope in the south basin by means of the seine nets.

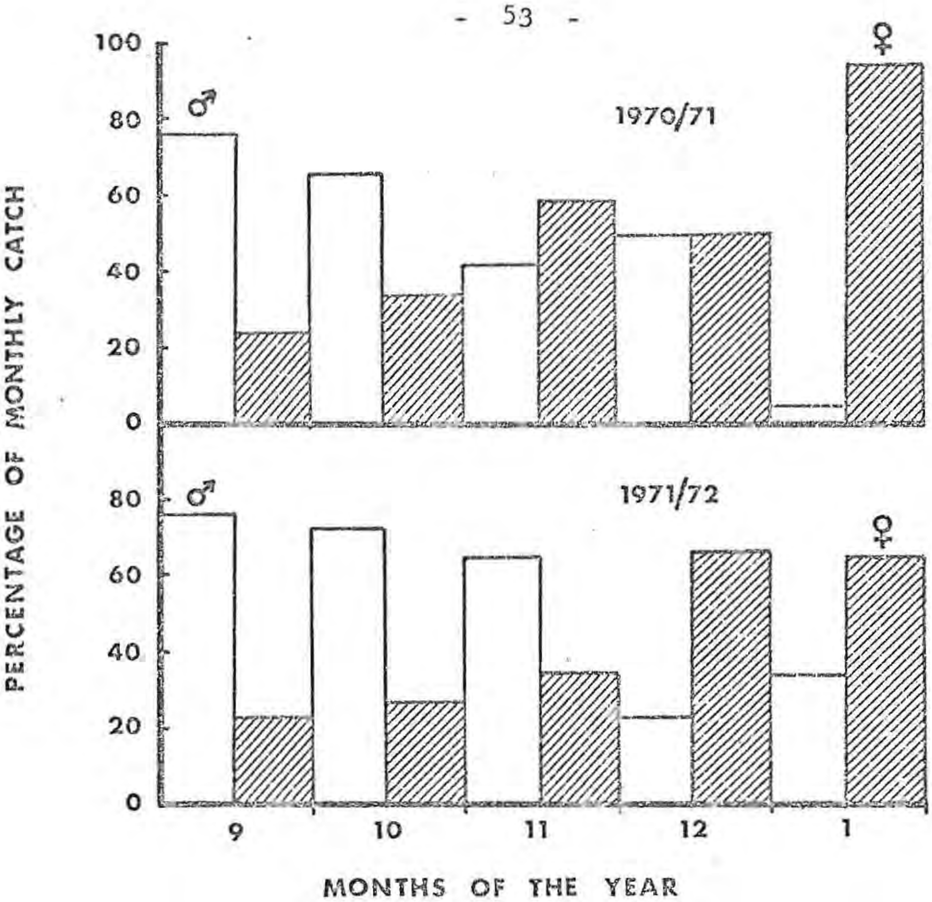


Figure 34: The percentage of adult male and female T. mossambica in monthly seine net catches in the south basin in the summers of 1970/71 and 1971/72. The data were obtained from fishes caught in exposed, partially exposed and sheltered littoral areas.

catch per unit effort (CPUE) from seining in water shallower than 7 m falls to nil for adults during this period, while in juveniles the CPUE in all cases averaged less than 12 (Fig. 31). As suggested in Figure 32 the major part of the population is over or in deeper water away from the shore. The predominance of echosounding targets over deep water in the cool season is shown in Figure 30A.

As indicated in the previous section, these targets, thought to be adult fishes, appear mainly in the surface third of the water column when over deep water. On the other hand, juvenile fishes in deep water occupy the lower third of the water column.

Following the cool season there is a general movement of fishes towards the shallows near the edge of the lake (Fig. 30B).

In the cool to warm transition period (August and the first half of September) the movement of fishes from deep to shallow water takes place as depicted in Figure 30B. Juvenile fishes move into littoral waters in August, followed in September by the adults as shown in Figure 31. Thus in 1970 the CPUE with the seine net for juveniles increased from 7 in July to 16 in August, and 29 in September, whereas the CPUE of adults increased from 0 in July and August to 4 in September.

The adult fishes moving into shallow water in September were largely breeding sized individuals (Fig. 33), most of which were found to be males, as shown in Fig. 34.

In the warm season (late September to January) the number of adult fishes in shallow water increased. This trend is shown by rise in the seine catches in the warm season (Fig. 31) and the increased percentage of echotargets in shallow water (Fig. 32). The apparent decrease in the number of juveniles caught (Fig. 31) is possibly due to the recruitment of juveniles into the adult population.

An analysis of length distribution of adult fish (SL 8 cm+) caught on the terrace with respect to sex is of interest since, while the females show regularly declining numbers with increased length, the

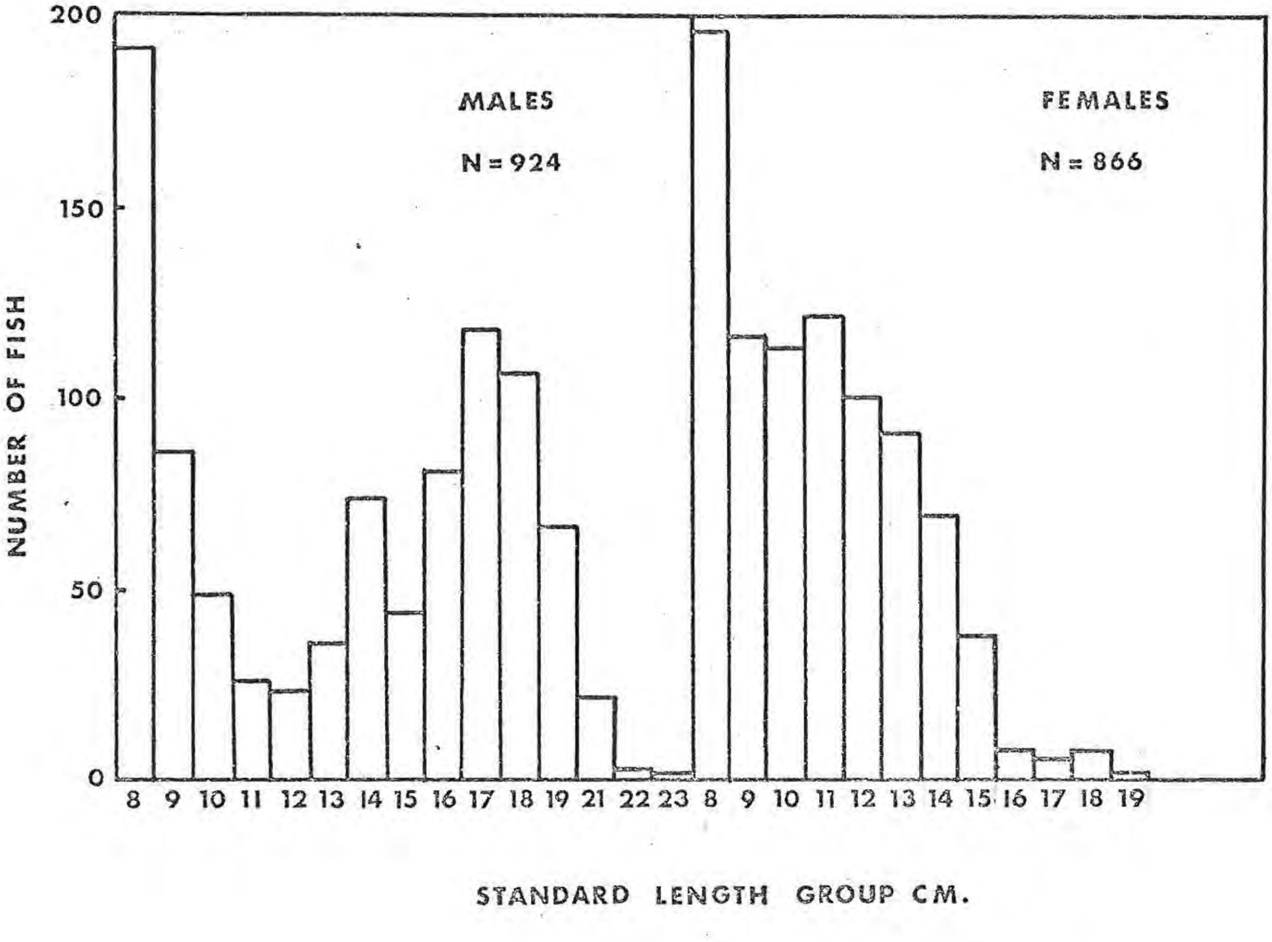


Figure 35: The length frequency of male and female T. mossambica above 8 cm SL caught on the terrace and the slope in the south basin in the summer of 1970/71 using seine nets.

TABLE 3

Time at liberty and distance moved of tagged T. mossambica released and recaught in the south basin in 1970 and 1971. The numbers in the column labelled "sites" refer to the netting sites marked on Fig. 2.

	TAG NUMBER	MONTH CAUGHT	MONTH RECAUGHT	DAYS FREE	MINIMUM DISTANCE MOVED M.	SITES
FREE FOR OVER 300 DAYS	358	11.70	6.72	570	-	12
	864	3.71	1.72	304	-	7AS
	750	3.71	1.72	310	10	7AM → 7AS
FREE FOR LESS THAN 1 DAY	518	2.71	2.71	6 hours	30	7AN → 7BS
	855	3.71	3.71	2 hours	10	7AN → 13S
	861	3.71	3.71	3 hours	30	7BS → 7AN
	1004	9.71	9.71	4 hours	60	2N → 7AN
	136	10.71	10.71	2 hours	10	2S → 2N
	397	12.70	12.70	3 hours	-	7AN
	103	10.71	10.71	2 hours	-	7AS
CAUGHT AND RECAUGHT IN THE SAME BREEDING SEASON	375	12.70	12.70	17	-	13
	402	12.70	12.70	2	-	7AN
	407	12.70	12.70	2	-	7AN
	414	12.70	12.70	2	-	7AN
	469	12.70	12.70	14	-	7AS
	361	12.70	12.70	3	-	13
NON-BREEDING. RECAUGHT AT SAME SITE	801	3.71	3.71	4	-	7AN
	803	3.71	3.71	4	-	7AN
	807	3.71	3.71	7	-	7AN
	960	4.71	4.71	9	-	11
	1010	9.71	9.71	6	-	2N
NON-BREEDING. RECAUGHT AT DIFFERENT SITE	489	12.70	2.71	54	30	13 → 7BS
	516	2.71	2.71	4	30	7AN → 7AS
	1018	9.71	10.71	34	500	7AS → 11
	737	3.71	4.71	16	800	9 → 7AM
	745	3.71	4.71	16	800	9 → 7AM
	787	3.71	3.71	14	1100	7AN → 14B
	854	3.71	3.71	10	1100	7AN → 14B

males are distributed bimodally with few fish of about 11 cm to 13 cm (Fig. 35). It would be expected that during this period growing male juveniles would move into this size class length as appears to be the case in the female population. It has been noted that while there is a decline in fish echosoundings during this time, a residual population does remain in the limnetic zone (Fig. 32). Probably the small adult males missing from the shallow waters have moved into the limnetic zone and are represented on the echo-traces as targets at this time.

In the warm to cool transition period (February to April) adult fishes moved off the terraces (Figs 31 and 33) leaving juveniles, which reached peak densities on the terraces in this period (Fig. 31). The percentage of echotargets in water shallower than 12 m (82%, 89% and 55% in February, March and April (Fig. 32)) indicates that the majority of adult fishes had not moved beyond the sublittoral zone, i.e. into water deeper than 12 m. Fishtrapping in sheltered littoral areas showed that large numbers of adults had moved into the sheltered littoral in February, March and April, from the terraces. Thus the CPUE of adult T. mossambica in the fishtraps increased from 0.1 and 2.3 in the warm season months to 10.4 in February, March and April. These data suggest that, at the conclusion of the breeding season, there is a movement of adult fishes from exposed to sheltered littoral areas. Data from tag returns supported the hypothesis that there is an increased movement of fishes around the shores after (and before) the breeding season. Twenty-eight tagged adults released into the south basin were recaptured (Table 3). Three fishes which were free for over 300 days, and seven fish free for less than one day do not concern us here, but of the 18 remaining fish, 6 were released and recaught in the same breeding season and at the same site, and 12 were recaught in the period just preceding or subsequent to breeding. Of the 12 non-breeding fishes, 5 remained at the same site, and 7 were recaught at different sites. The latter 7 fish moved distances from 30 m to 1100 m. These results indicate that, whereas breeding fishes are largely resident, non-breeding fishes may perform movements around the shores.

Both juvenile and adult fishes move back into deep water in the cool season (May, June) as shown by the low catches in shallow water in this period (Fig. 31).

Two major points emerge from this study of horizontal and vertical distribution. Firstly, adult fishes appear to be unable to occupy the profundal zone due to a depth limitation. Secondly, there is an exodus from shallow water in the cool season. Other workers have found a depth limitation in Tilapia, though few have commented on the importance of this feature in the species biology. Poll (1956) reported that T. tanganicae, which is common and wide-spread in Lake Tanganyika, is seldom found in water more than 10 m deep. Coke (1967) found that in Lake Kariba T. mortimeri above 20 cm TL only penetrate to 15 m, although the lake has a maximum depth of 110 m. Gee (1968) analysed the catches of 235 shallow and deep water trawls in Lake Victoria and reported that T. variabilis occurred to a depth of 13 m and T. esculenta to 30 m, though the latter species was most common at depths of less than 13 m.

Large areas of the deeper lakes would appear to be beyond the normal range of the genus Tilapia. In Lake Sibaya, a depth limitation of 10 m would preclude habitation of 55% of the area of the lake floor, at least to the adults. As T. mossambica in Lake Sibaya is a benthic feeder (Minshull, 1969) this means that large areas of potential food resources are not available for direct utilization.

The migrations into shallow water take the form of a convergence on certain selected sites for the purpose of breeding or feeding. The return to deep water is probably in response to unfavourably low water temperatures in shallow water. Similar movements between deep and shallow water have been found in Tilapia in other systems, e.g. T. lidole in Lake Malawi (Lowe, 1953), T. variabilis in Lake Victoria (Fryer, 1961) and T. macrochir in Lake Mweru (Carey, 1965).

HABITAT SELECTION

a) Adults: Little is known of the habitats selected by adults in the cool season beyond the fact that the fish occur over deep water at a depth of about 3-12 m, i.e. in limnetic and sublittoral areas (Fig. 6). In Sibaya the water temperature in the limnetic zone remains between 21° and 17°C in the cool season (Fig. 8), water temperature at any given moment being homothermal to about 0.5°C. These conditions, though cool for Tilapia mossambica, are more stable and less extreme than those on the terrace, where water temperatures fluctuate between 28°C and 12°C in the cool season. Selection of the limnetic habitat in the cool season is probably dictated by thermal requirements. The distribution of echotargets indicates that adult T. mossambica can also occur in deeper sublittoral waters in the cool season, at depths from 7-12 m on the northern and eastern shores.

In the cool-to-warm and warm-to-cool transition periods (August, and February to April), part of the population of adult T. mossambica, but by no means all, moves into sheltered littoral areas such as sites 12, 6, and 10 in the south basin (Fig. 3). These areas, protected either by a shallow tombola, as for sites 12 and 6, or by a peninsula of land, as for site 12, have very narrow terraces, steep well-vegetated slopes, and are rich in plant and animal life. Site 6 has been examined in detail using SCUBA. The terrace ends in a steep sandy slope which is sparsely vegetated with Potamogeton pectinatus on the upper edge. At a depth of 5-7 m the slope levels off. The sandy substrate on the floor of the bay is covered with a layer of gyttja up to 80 cm deep over sand. In January, strands of Myriophyllum spicatum and Ceratophyllum demersum protrude through the gyttja, forming dense beds on the edge of the layer.

In the period September-March, adult *T. mossambica* invade exposed littoral areas for the purpose of breeding. As shown in Figure 34 male fishes are more common on the terraces in the early part of the breeding season, but less commonly in the latter half.

b) The habitat preferences of breeding male *T. mossambica*: The habitat preferences of breeding male *T. mossambica* as indicated by the seine net are given in Table 4. Breeding males were absent from well-vegetated protected areas, although SCUBA observations revealed a low population as judged by the presence of a few nests at site 6.

TABLE 4

Habitat preferences of breeding male *T. mossambica* on the south basin from September to December, 1970, as revealed by the seine net.

CPUE = Catch per unit effort.

The degree of macrophyte cover is scored as follows:
+ = sparse: less than 5 plants per metre
++ = moderate: 5-10 plants per square metre
+++ = dense: more than 10 plants per square metre.

	SITE					
	6	12	15	2	7A and B	13
CPUE Breeding Males	0	0	1.2	3.5	12.4	13.5
Habitat type	protected littoral	protected littoral	exposed littoral	partially exposed littoral and terrace	partially exposed littoral slope and terrace	partially exposed littoral slope and terrace
Degree of macrophyte cover	++++	++++	+	++	++	++

On the other hand, breeding males were common in partially exposed, sparsely vegetated areas. The preferred areas coincided with the known nesting grounds.

c) Nesting Distribution: A series of surveys on nest distribution were

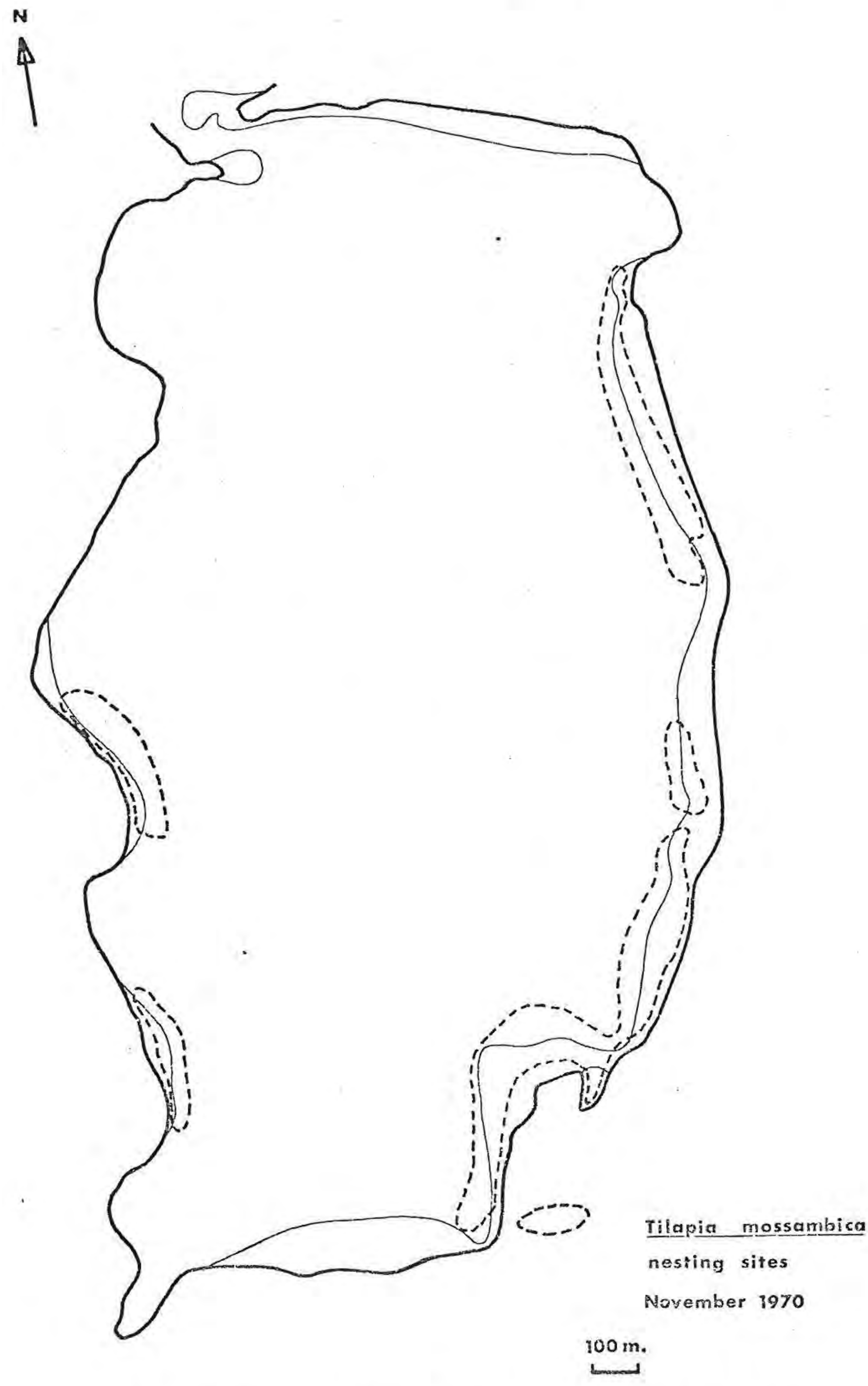


Figure 36: The distribution of the main T. mossambica nesting sites found in the south basin in November 1970. The data were obtained from free-diving observations in 1970, and confirmed using SCUBA in January 1971.

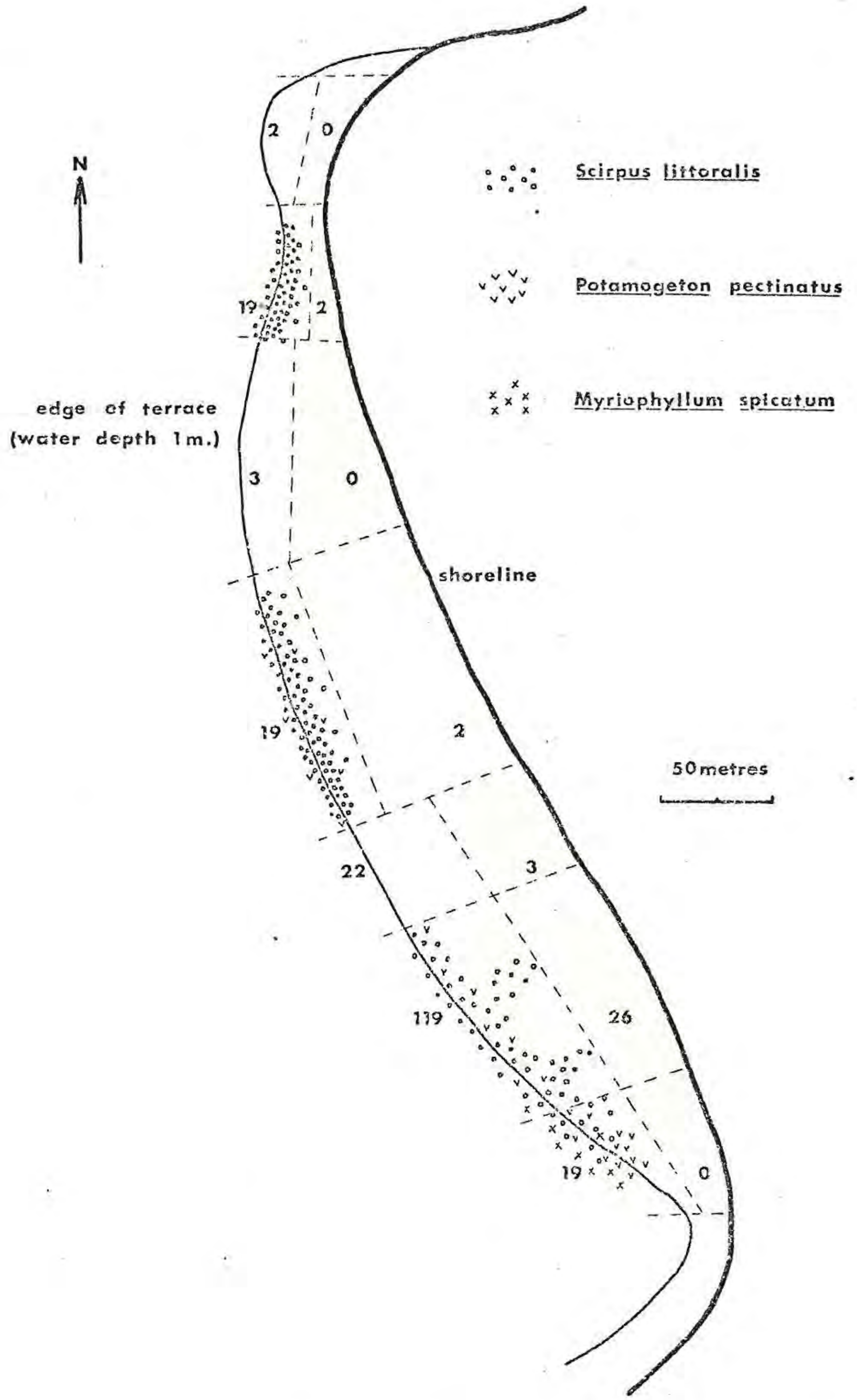


Figure 37: Detail of the north-eastern shore of the south basin showing the number of T. mossambica nests in various zones on the terrace. The distribution of three aquatic macrophyte species on the terrace is also indicated.

carried out using free diving equipment and SCUBA. Nests were found on the terrace, on the slope, and on deeper substrates below the slope. Figure 36 depicts the distribution of the nesting grounds in the south basin in November, 1970. Nests were absent from the exposed windward northern and south-western shores, but abundant on partially exposed eastern and south-eastern shores, and in restricted areas of the western shore.

An analysis of nest distribution in relation to various types of areas where they occurred showed that the greatest proportion of nests were associated with Scirpus and Potamogeton, and on the lakeside of the terrace (Table 5, category 1 and Fig. 37).

TABLE 5

Number and density of T. mossambica nests on the north-eastern shore of the south basin in four types of areas on the terrace and slopes of the south basin.

The nests were divided into four distribution categories:

(1) Associated with Scirpus littoralis and Potamogeton pectinatus on the deep edge of the terrace (green area on Fig. 37);

(2) in shallow protected water shoreward of a S. littoralis fringe (brown area on Fig. 37);

(3) on the deep edge of a barren terrace but closely associated with the Scirpus fringes to the north and south (white area on Fig. 37);

(4) on barren terraces shoreward of Category 3, and not associated with aquatic macrophytes (yellow area on Fig. 37).

Category	1	2	3	4
Number of nests	176	30	27	3
Nests per 1000 sq. m	13	5	7	1

The least favoured area was an open weedless terrace in shallow water (Table 5, category 4). Nests were reasonably common, but not abundant in shallow water on the terrace, where it was fringed with weed at the lakeward edge (Table 5, category 3), and at the lip of the terrace and onto the slope with weed associated on either side (Table 5, category 4).

164 nests from categories 1-4 were examined further with respect to the plant associations in which they were found. The results are given in Table 6.

TABLE 6

Plant associations of 164 T. mossambica nests on the north-east shore of the south basin.

The density of the plant cover in the immediate vicinity of the nest has been scored as follows:

+ = 1-3 stems of P. pectinatus, S. littoralis or Scirpus roots
++ = 4-6 " " " " " " "
+++ = 7+ " " " " " " "

Nests associated with two species of plants are included twice in the table.

T = total number of nests associated with a particular plant species.

	Potamogeton pectinatus				Scirpus littoralis				Scirpus roots			No plant association
Plant density	+	++	+++	T	+	++	+++	T	+	++	T	Nil
Number of nests	35	36	16	87	38	37	18	93	14	5	19	2

Ninety-nine percent of the nests examined were associated with P. pectinatus and S. littoralis, with no preference for either plant. The nests were most often associated with sparse or moderately dense, rather than dense, stands of aquatic plants. Nineteen nests were associated with Scirpus stands in which only the roots remained.

The distribution of nests on substrates deeper than the terrace was also determined. On the north-eastern shore of the south basin, off sites 7, 13 and 12, a dense band of nests was found at a depth of 2-6 m below a S. littoralis fringe, i.e. offshore of category 1 nests. All the nests were associated with stands of P. pectinatus and were constructed on a steep sandy slope.

Nests were also found in deep water off the southern and western shores of the south basin among Myriophyllum spicatum at depths of 1-5 m. These nests were most abundant on the fringes of the

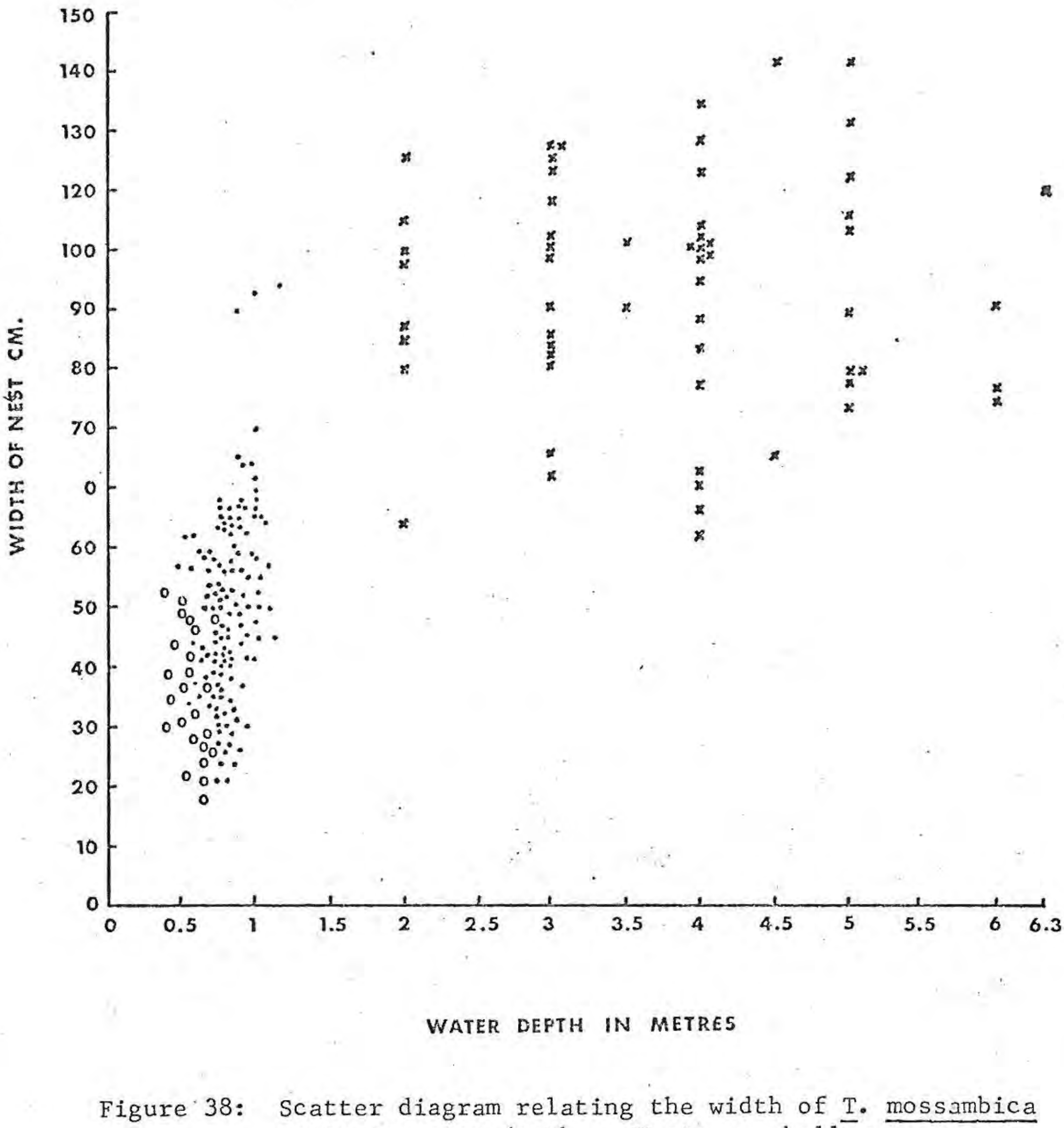


Figure 38: Scatter diagram relating the width of T. mossambica nests to water depth. Nests on shallow terraces shoreward of a Scirpus fringe (open dots), in the macrophyte fringe (closed dots) and on the slope (crosses) are included in the figure.

Myriophyllum beds, but occasional nests were also found among the dense *Myriophyllum* stands. These nests were overhung on all sides by *Myriophyllum* strands, and were noted to be more deeply excavated (up to 30 cm deep for a 35 cm diameter nest) than nests of the same size found in less vegetated areas. Incumbent males were often seen to conceal themselves among *Myriophyllum* strands next to the nest. Nests in water deeper than 4 m were not always associated with plants. A group of 11 large nests (diameter 1.5-2 m) was found on a barren substrate on a small plateau at a depth of 4.5 m off site 11, offshore of a *Scirpus* fringe.

In the main basin, nests were found on the eastern shores at depths of less than 1 m, on the terrace, and on the slopes from 1-8.5 m. Nests were also found on the southern shores, being associated with *P. pectinatus* from 3-5 m, and *M. spicatum* from 5-7 m.

The diameter and water depth of 221 nests were measured by means of a fibreglass measuring tape and (for depths greater than 2 m) a 'La Spirotechnique' depth gauge. In Figure 38 the diameter of the nests is plotted against water depth. The wider nests were recorded from deeper water. Nests on the shallow terrace inside of the *Scirpus* fringe (open dots on Fig. 38) were smaller than nests within the macrophyte fringe (closed dots) which in turn were smaller than nests on the slope (crosses). The minimum water depth of a nest was 41 cm and the maximum 6.3 m, though nests were found to 8.5 m in the main basin. The minimum nest diameter was 20 cm (at depth 0.6 m) and the maximum 142 cm (at depth 5 m). The width of nests on the terrace and on the slope averaged 51 cm and 97 cm respectively, giving a mean diameter for all nests measured of 74 cm.

Boltt, Hill and Forbes (1969) reported that the mean diameter of 30 *T. mossambica* nests on the south-eastern shore of the main basin was 1 m. This closely approximates the value obtained in the present study for offshore nests (97 cm).

Nests in the macrophyte fringe were found to be closer together (average distance apart about 1.1 m) than nests on barren substrates (average distance 2.1 m). Three nests in a *Scirpus* fringe were found to have their rims in contact with that of an adjacent nest, and a further 11 were separated from the nearest nest by less than 25 cm. In these cases, the area covered by the nest must have constituted the larger part of the territories of the incumbent males.

Fryer and Iles (1972) have suggested that some *Tilapia* species may deliberately construct nests in close proximity, the resulting group of nests forming an arena. Four distinct groups of *T. mossambica* nests were found during the present study (Table 7).

TABLE 7

Characteristics of the groups of *T. mossambica* nests found in the south and main basins of Lake Sibaya.

Date of observation	Number of nests	Average water depth metres	Location	Plant cover
6.11.70	8	0.3	East shore, main basin	nil
24.1.71	11	4.5	Site 7, south basin	nil
12.1.71	25	5	south-east shore, main basin	sparse *P. pectinatus*
14.1.71	18	5.2	south-east shore, main basin	sparse *P. pectinatus*

The nests in any one group were separated from one another by less than one metre, and the groups separated from adjacent groups or individual nests by extensive areas of terrace. In the beginning of the breeding season extensive aggressive encounters among nesting males were observed, but towards the end of the breeding season aggression was less overt, probably because communication to neighbours was achieved by more subtle means as suggested by Lorenz (1966). Arena nesting behaviour may have a homeostatic function in the sense of Wynne-Edwards (1962) such that areas suitable for nesting are only acquired by males which are best able to establish and defend territories. Communication within one arena would be achieved by symbolic aggression, and between arenas possibly by sound production, as Rodman (1966) has shown that male T. mossambica may emit sounds during threat behaviour in defence of territories. Supernumery males would be repulsed and thus would not contribute to breeding, and may return to deep water. This may explain the apparent scarcity of small males in the breeding population as indicated in Figure 35.

The majority of the nests in the south basin were constructed in areas partially protected from direct wave action. In the south basin, the prevailing winds blow from the north and the south. Most protection is afforded to these sites on the western and eastern shores with a macrophyte fringe, and least to those on the northern and southern shores with no macrophyte fringe. Nests were found to be most abundant on the relatively sheltered eastern shores, in areas where the topography of the shore and the presence of macrophytes dampened wave action, or at a depth of 4-5 m off exposed shores, where the effect of wave action is reduced by the depth of the water.

The Tilapia nests may be associated with plants for reasons other than protection from wave action. Plants may act as landmarks and assist the fish in finding the nest, or may provide refuges for males avoiding predators. T. mossambica males have been seen to hide among Myriophylum stems on the approach of a SCUBA diver, an observation also reported by Boltt, Hill and Forbes (1969) in Sibaya. Conversely, plants adjacent to a Tilapia would provide lairs for ambushing predators.

d) The habitat preferences of breeding female T. mossambica: During the warm season, female T. mossambica are engaged, at least for part of the time, in mouth-brooding. As shown in Table 8, mouth-brooding females were found to be most common in littoral areas with dense

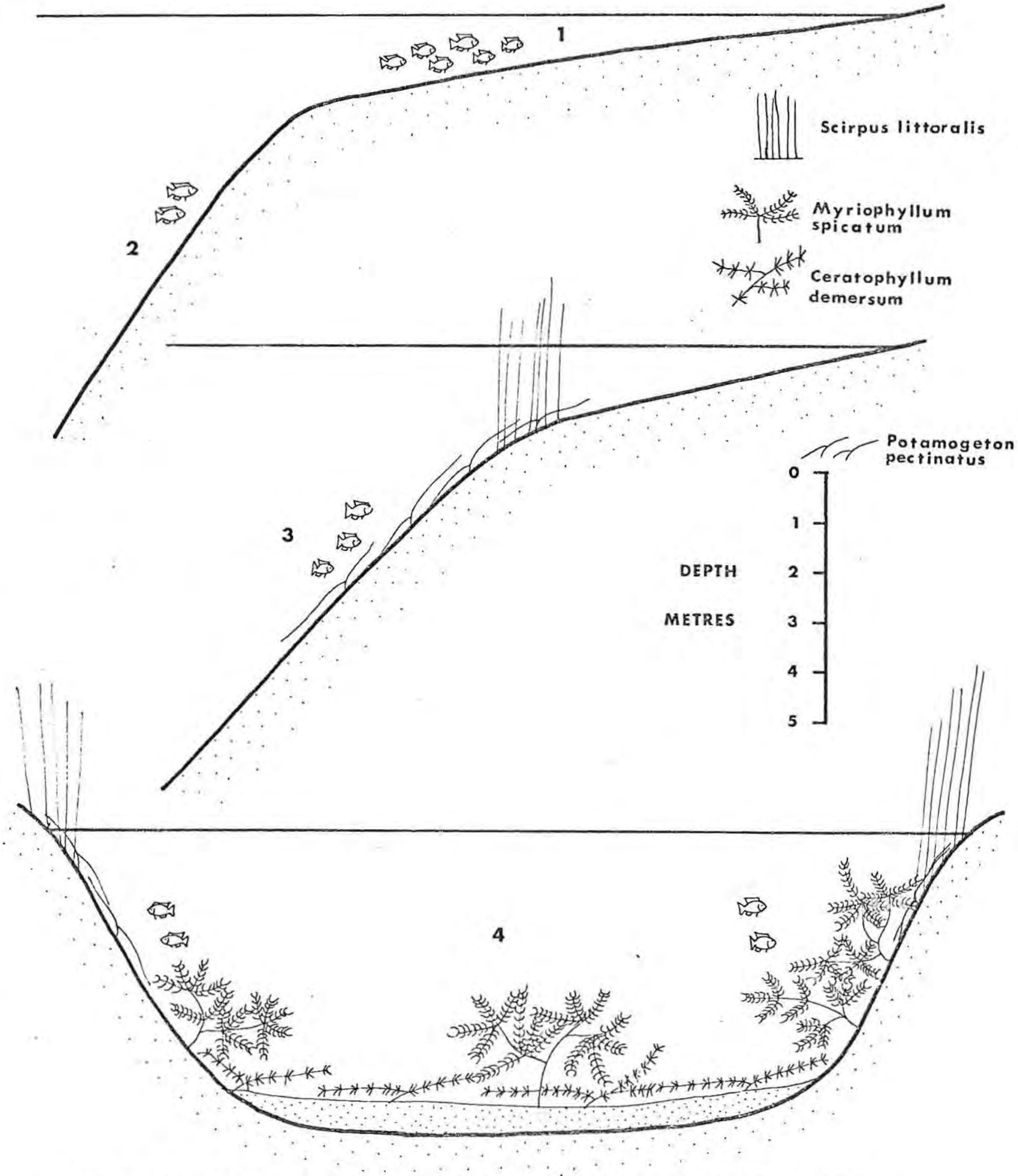


Figure 39: The four habitat types of the littoral zone of the south basin.
1 : Terrace. 2 : Barren slope. 3 : Sparsely-vegetated slope.
4 : Well-vegetated bay.

M. spicatum cover, less common in areas with sparse M. spicatum and P. pectinatus cover, and uncommon in areas with moderate P. pectinatus cover. The protection afforded by M. spicatum, which has bushy fronds and is suitable for concealment, would appear to be the criterion for the choice of habitat by mouth-brooding female T. mossambica. Exceptions to the rule are always found, and mouth-brooding female T. mossambica have been caught on exposed barren terraces. In the section on 'breeding behaviour', the shoaling habit of mouth-brooding females on the terrace under certain special conditions will be described.

TABLE 8

The habitat preferences in the littoral zone of mouth-brooding female T. mossambica in the south basin. The data are derived from fishes brooding eggs and fry.

CPUE = Catch per unit effort with the slope seine.

Plant cover	Dense M. spicatum and P. pectinatus	Sparse M. spicatum and P. pectinatus	Moderate P. pectinatus
Habitat type	Sheltered littoral	Partially exposed littoral slope	Exposed littoral slope
CPUE October to January 1970/71	12.2	8.1	0.5

e) The habitat preferences of juvenile and fry T. mossambica: Juvenile T. mossambica in Lake Sibaya have been recorded from shallow and deep sublittoral and littoral areas in the lake. Most of the data presented here concern their habitation of the littoral, as little is known of their occupancy of deep water.

The littoral zone may be divided into four parts - the terrace; barren slope; sparsely vegetated slope and well-vegetated bays. In Table 9 the preference of T. mossambica juveniles for these four habitat categories, as revealed by catch per unit effort data from the seine net, is given. The four habitats are illustrated in Figure 39.

TABLE 9

Habitat preferences of juvenile T. mossambica in the south basin in the period September, 1970 to May, 1971, as shown by seine net catches. The habitats are shown in Figure 39.

CPUE: catch per unit effort.

	HABITAT			
	Terrace	Barren slope	Sparsely vegetated slope	Densely vegetated bay
Depth	0-2 m	2-7 m	2-7 m	1-7 m
CPUE	66.5	21.2	15.1	4.1
No. of pulls of seine net	56	40	115	42
No. of juvenile T. mossambica caught	3727	843	1738	172

Juvenile T. mossambica were most abundant on the terrace, common on the slope, and uncommon in densely-vegetated littoral areas. Fry were found to be most common in shallow littoral and eulittoral areas. It is necessary at this point to examine the conditions found on the terrace in the hope that the marked preference of young T. mossambica for this habitat will be, in part, explained. Two features of the terrace environment - water temperature and depth - are considered here.

On 10 and 11.3.1971 a 26 hour temperature survey was carried out in the south basin to determine the nature of the temperature gradient on different types of shores, and the extent of the diurnal water temperature fluctuations. Seven sites were selected along the eastern and southern shores of the south basin to include all types of shores, i.e. exposed, sheltered, weeded, barren, with and without marginal pools, steep and shallow with narrow and wide terraces. At each site 3 points were selected for temperature measurement, the first in water less than 10 cm deep close to the shore, the second in the middle of

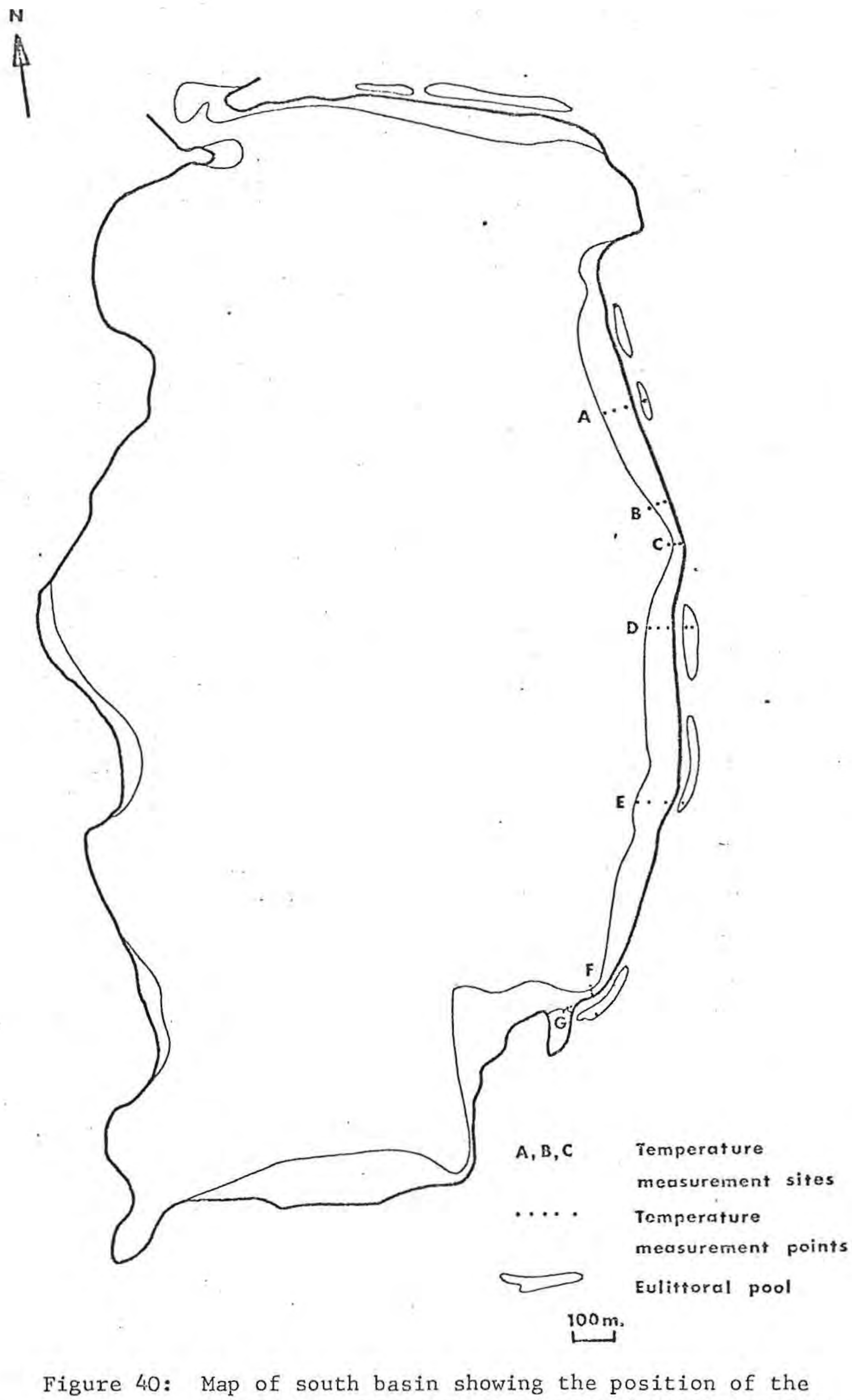


Figure 40: Map of south basin showing the position of the temperature measurement sites and points used in the temperature survey. The thin black line indicates the deep edge of the terrace.

Figure 41.

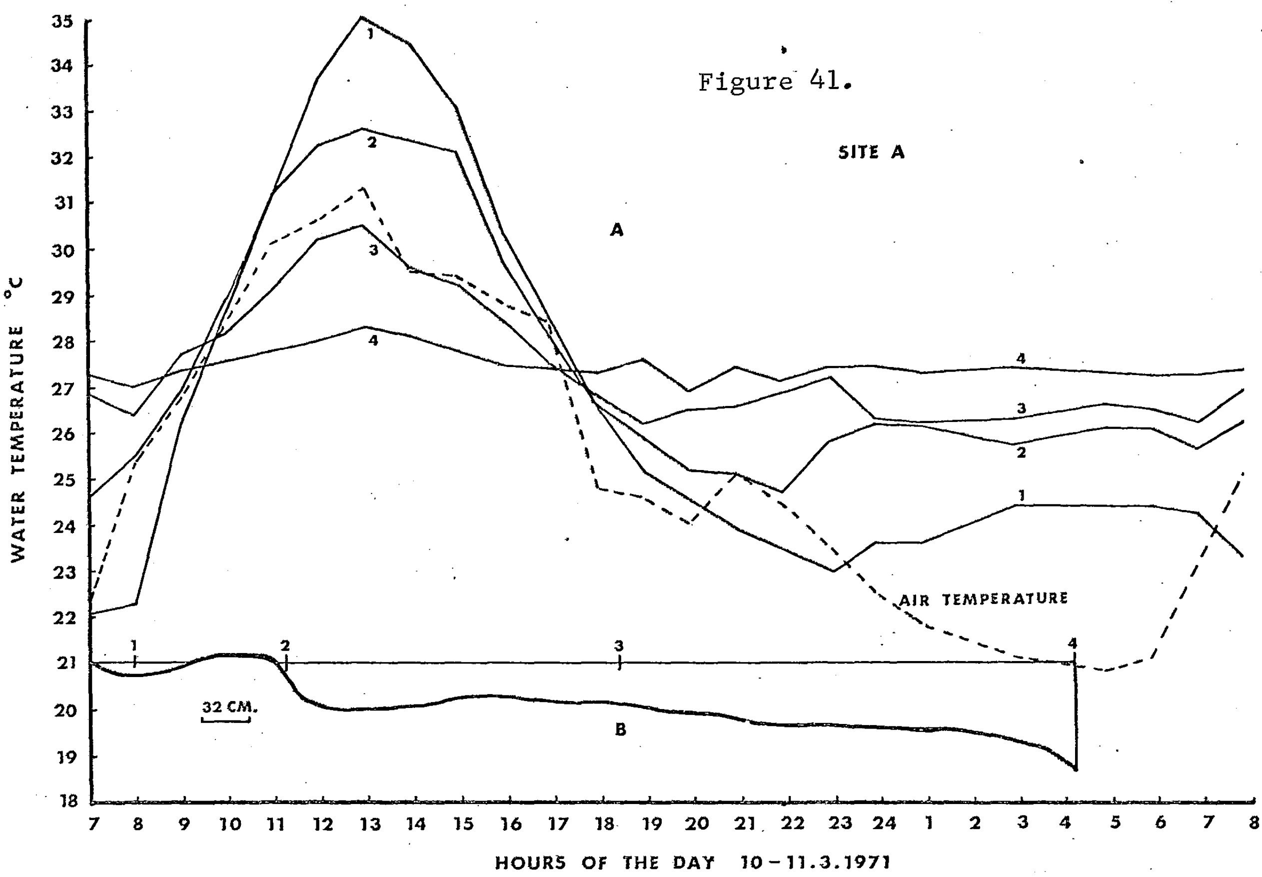
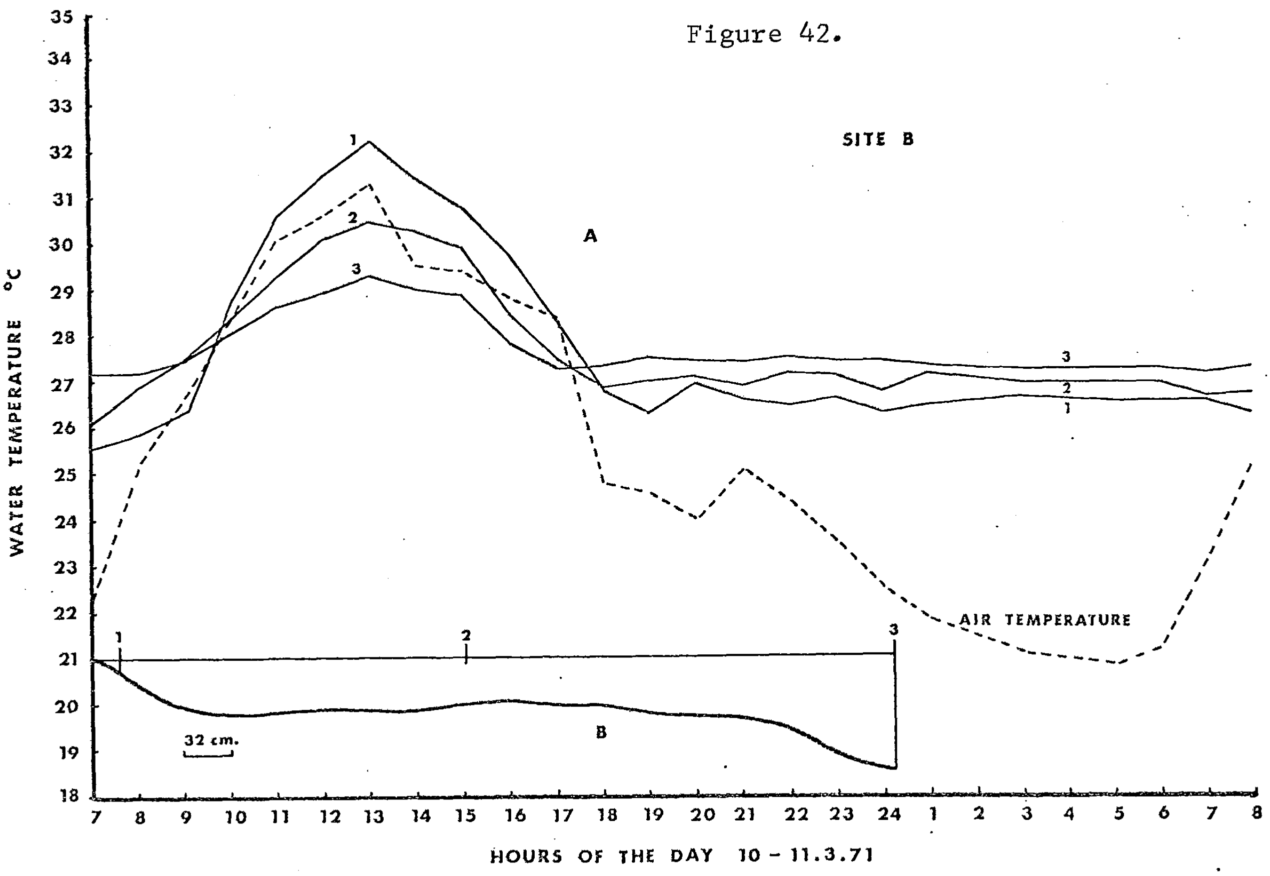


Figure 42.



Figures 41A to 47A: Water temperature profiles for sites A to G as shown in Figure 40 during the temperature survey on 10 and 11.3.1971. Temperature profiles for the different measurement points at each site are numbered 1 to 4. These numbers correspond to the positions across the terrace at which the temperatures were measured. The profile of the terrace is given in each figure.

Figure 43.

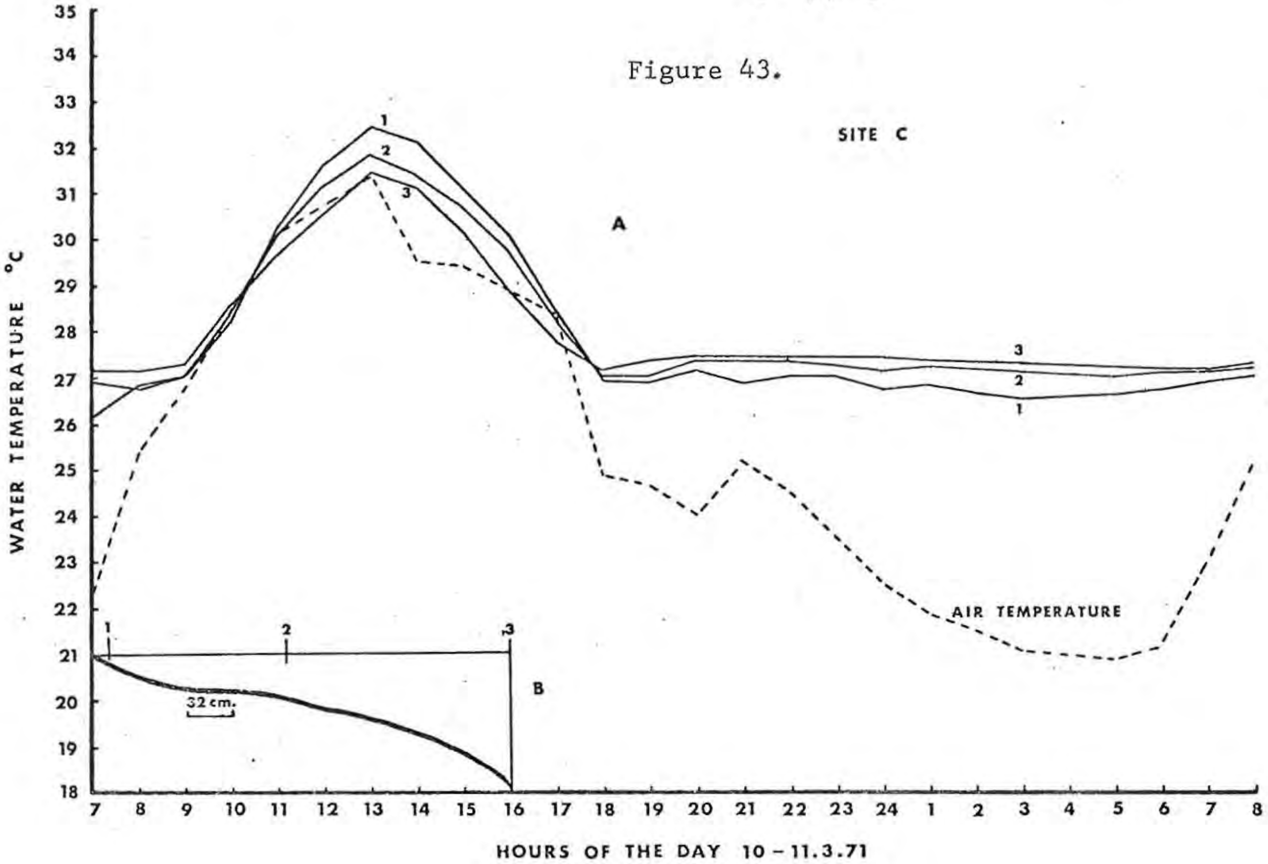
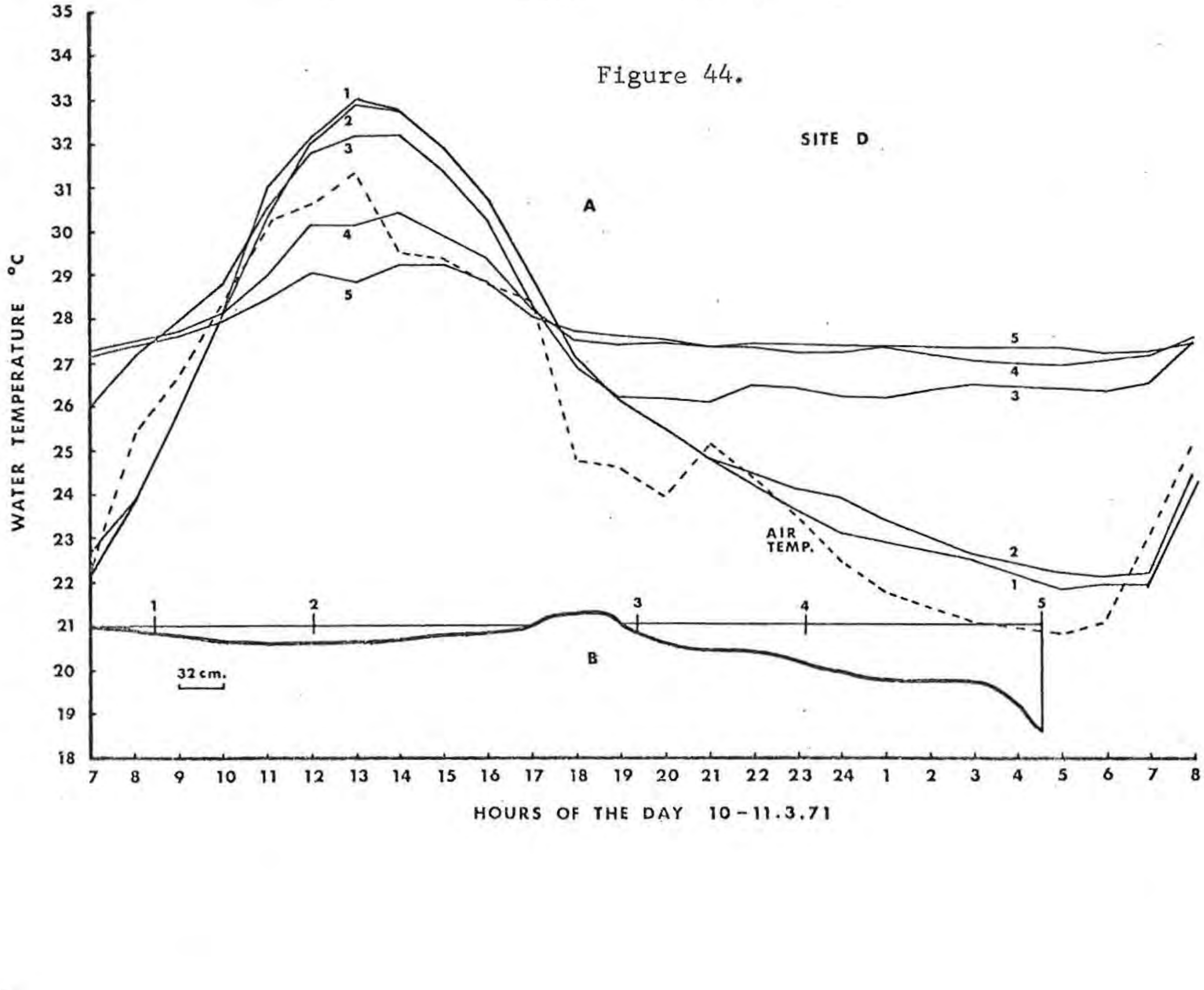


Figure 44.



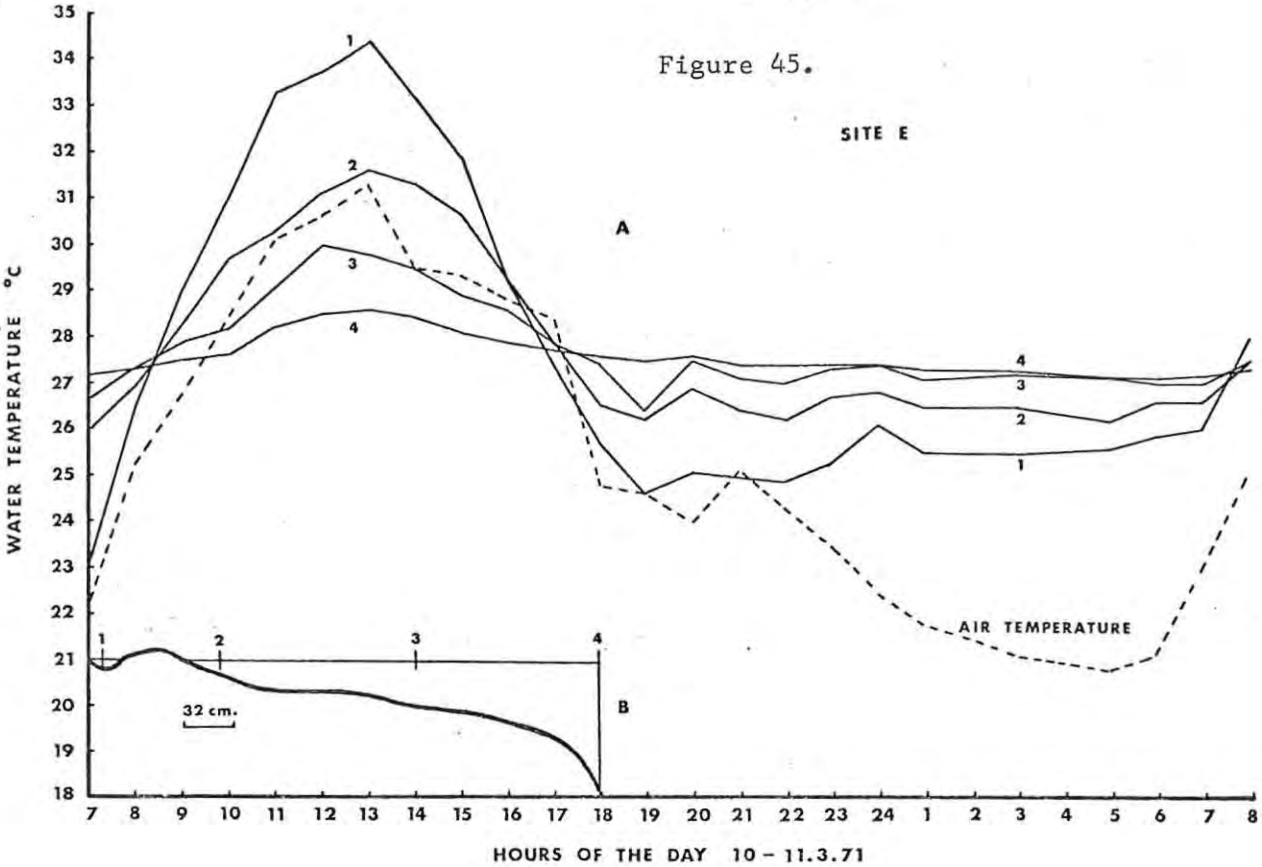


Figure 45.

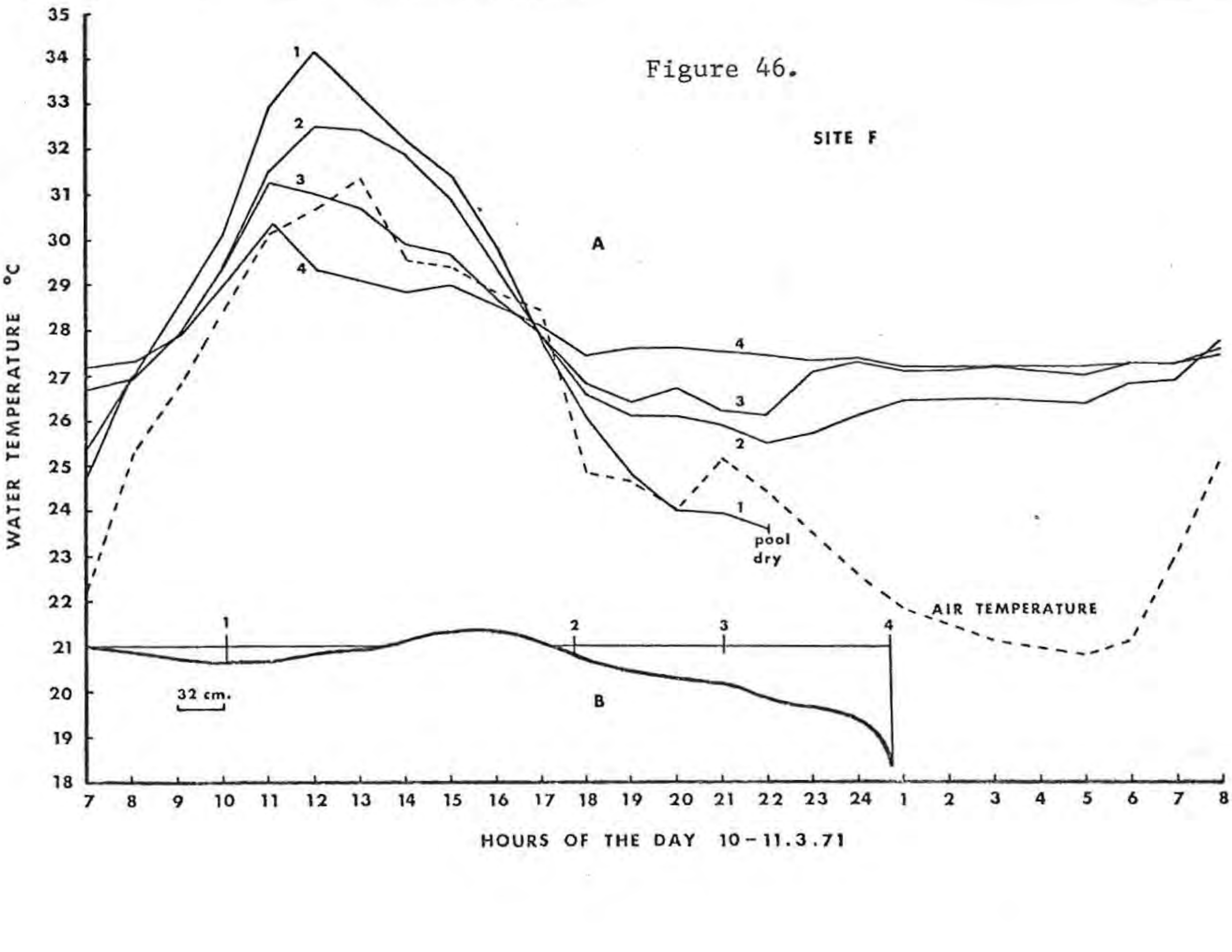
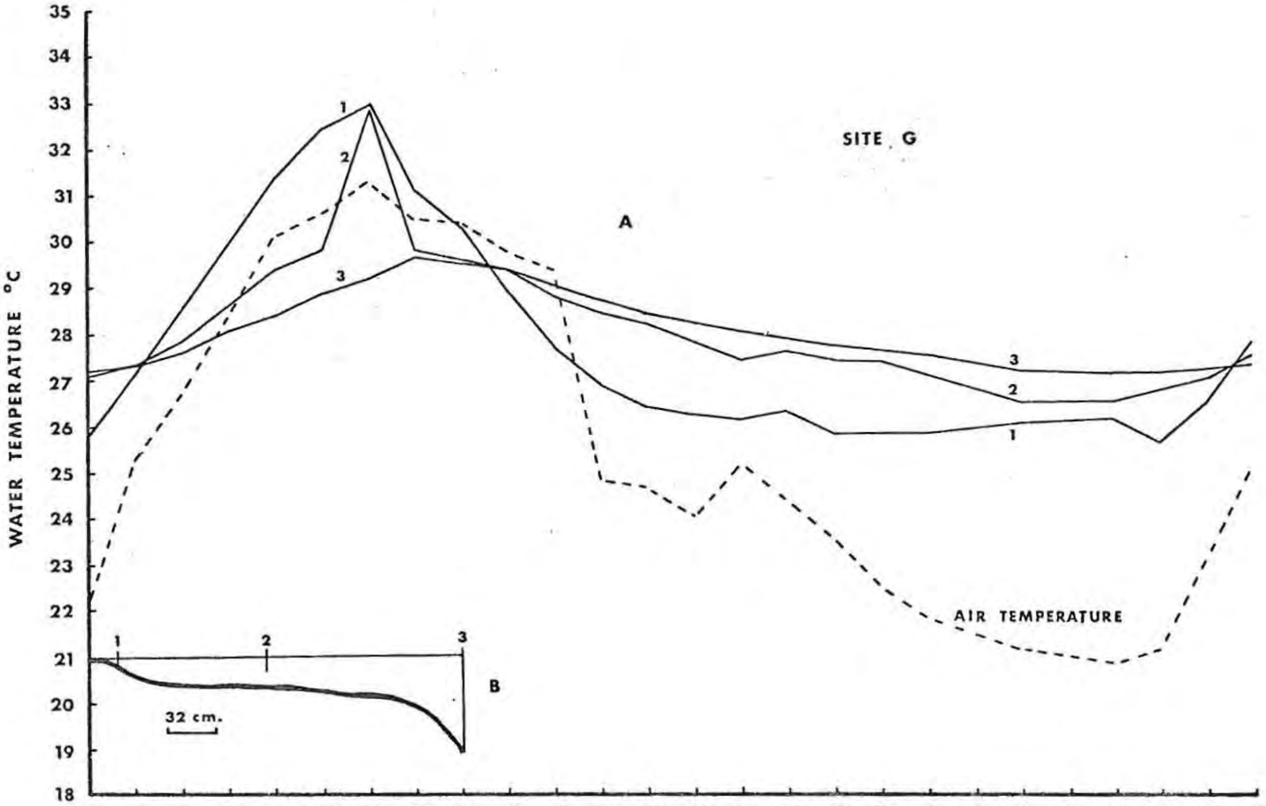


Figure 46.

Figure 47.


SITE G
A
B
AIR TEMPERATURE
32 cm.
WATER TEMPERATURE °C
HOURS OF THE DAY 10-11.3.1971
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 1 2 3 4 5 6 7 8
1
2
3

the terrace and the third at the edge of the slope. Where a eulittoral pool was present one or two measurement points were selected in the pool. The seven sites (A - G) and 26 temperature measurement points are shown in Figure 40. Temperatures were measured using a standard thermometer graduated to 0.1^{o}C. The survey was carried out from 0700 on 10.3.1971 until 0800 on 11.3.1971. Temperature measurements were taken at site A on the hour and concluded approximately 25 minutes later at site G. Readings were taken with the thermometer shaded from the sun, and the bulb 5-8 cm below the water surface. A diagrammatic representation of the slope of each site is given in Figures 41B to 47B.

In general there was a warming of the water over the terrace from just after sunrise up to about 1300 hours, when the highest temperatures were recorded. Thereafter the temperature declined, reaching steady levels in the water over the terrace at about 1800 hours, although further cooling was observed in the eulittoral pools. This pattern is very similar to the results obtained in more extensive series of measurements over a period of 15 days on terrace waters in the main basin, reported by Allarson and van Wyk (1969) for 1968. Also in agreement with the findings of Allanson and van Wyk, it was shown that the inshore water was much warmer than the lakeside water during the whole period of warming from 0800 hours to about 1800 hours, resulting during the day in a gradient of higher temperature towards the shore on the terrace. Between 1800 and 0800 hours, the gradient was reversed, and resulted in a gradient of higher temperature towards the deep edge of the terrace at night.

Table 10, in which site A is used as an example, shows that temperature variation was least on the deeper edge of the terrace and greatest in the eulittoral pool.

TABLE 10

Temperature variation at site A (see Figure 41) over 26 hours.

Temperature measurement point	Depth cm	Maximum T°C	Minimum T°C	Range T°C
Marginal pool 1	8	35.0	22.0	13.0
Shallow terrace 2	13	32.6	24.7	7.9
Middle terrace 3	27	30.5	26.2	4.3
Deep terrace 4	72	28.3	26.9	1.4

Water temperature gradients were most marked at the hottest time of the day (between 1100 and 1300 hours) and least between 1700 and 1800 hours. Gradients were more marked during the day than at night. However, as all the temperature measurements were taken at a depth of 5-8 cm, the degree of mixing of water on the deep edge of the terrace was not determined. The data of Allanson and van Wyk (1969) were obtained from three thermistor probes, one of which was on the substrate at a metre depth on the deep edge of the terrace. The other two probes were placed near the surface, the one over the deep edge of the terrace, and the other over shallower water. Their data indicate that during the day a wedge of cooler water, homothermal with the main lake body, extends over the lip of the shelf a short distance onto the terrace. This would have the effect of further increasing the temperature gradient on the terrace at substrate level during the day. Complete mixing of terrace waters was recorded at night. As a result, the gradient of water temperatures was less marked, and equal at substrate and water surface levels.

Another important result obtained by Allanson and van Wyk is that the magnitude of the temperature gradient varies widely from day to day according to weather conditions. Higher temperature gradients were recorded on the terrace on calm, clear days than on windy overcast days.

Along with my observations, the main trends of fish distribution on the terrace and in eulittoral pools were noted. Fry occupied very shallow water during the day but moved into water deeper than 15 cm at night. Juveniles entered terrace waters at about sunrise (0720 hours) when the terrace water temperature slightly exceeded that of the deeper water. Over the hottest period of the day (1200-1500 hours) juveniles occasionally entered very shallow water (less than 15 cm) but usually remained in water deeper than 15 cm. Juveniles left the terrace waters when shallow water temperatures dropped below those of the main water body at sunset. During the period of the survey, fry occupied water ranging from 22-35°C, and juveniles from 27-33°C.

These temperature preferenda for small T. mossambica correspond with those recorded experimentally by other workers. Badenhuizen (1967) found a preferred temperature range for small T. mossambica of 27.0-33.5°C, depending on previous thermal history. Donnelly (1969b) found upper temperature preferenda of 36.2 and 36.5°C for small T. mossambica (TL 20 - 40 mm) acclimated at 24.5 and 29.5°C respectively, and 34.3 and 36.5°C for larger T. mossambica (TL 100-120 mm) acclimated at 24.5 and 29.5°C respectively.

During the course of the survey, small T. mossambica remained within their preferred temperature range (PTR, taken as 27-33°C) by occupying deeper water at night, and shallower water by day. Movement into very shallow areas at the hottest time of the day allowed the fishes to operate for a short period at temperatures near the upper limit of the PTR. These thermoregulatory movements appeared to be initiated more as a response to temperatures of the lower limit of the PTR than to higher temperatures. Temperatures in very shallow water were not recorded to approach the upper lethal limit which has been found to be 38.2°C in T. mossambica 8-12 cm TL (Allanson and Noble, 1964) and 41.7°C in T. mossambica 2.5-3.5 cm SL

(Kemp, 1966). However, should T. mossambica become isolated in an eulittoral pool and exposed to very high temperatures, their rapid rate of temperature acclimation ($1^{o}C$ per 150 minutes for fishes 8-12 cm TL, Allanson and Noble, 1964) and high upper lethal temperature would ensure their survival unless water temperatures exceeded $41^{o}C$.

Welcomme (1964) and Donnelly (1969a) found a movement similar to that reported above of young Tilapia from the shallows when temperature reversal occurred. Donnelly, following Fryer (1961) and Welcomme (1966) applied the term 'primary' and 'secondary' nurseries to the habitats occupied by fry and juvenile fishes respectively. In Sibaya the shallow eulittoral pools and shallow verges of the terraces (1-15 cm deep) could conveniently be termed 'primary' nurseries, although, as indicated above, the fry may leave these areas at night. Juvenile T. mossambica (SL 3-8 m) inhabit the deeper terrace waters during the day, occasionally entering water shallower than 15 cm and the eulittoral pools, between 1300 and 1500 hours. Their habitat, which is probably defined by both temperature and depth preferenda, is sufficiently distinct from that of the fry to merit the name of 'secondary' nurseries.

Welcomme (1964) applied the term 'gradient shores' to shores in which a thermal gradient perpendicular to the shoreline is maintained for at least part of the day, and found them to be the typical habitat of the young Tilapia in Lake Victoria. The terraces of Lake Sibaya may also be classed as gradient shores, and, as in Lake Victoria, are the typical habitat of the young Tilapia.

The diurnal movement of young T. mossambica into shallow water recorded during the survey described above was confirmed by the catch per unit effort data from seine netting. As shown in Table 11, the number of T. mossambica (SL 4-8 cm) caught on the terrace increased during the morning to a peak between 1300 and 1500 hours, and then decreased in the late afternoon. The high catches between 0900 and 1000 hours reported in Table 11 may reflect a higher catchability at a time when fishes are congregated on the deep edge of the terrace prior to distributing themselves horizontally when the terrace water increases.

TABLE 11

Catch per unit effort (CPUE) of 4670 T. mossambica (SL smaller than 8 cm caught on the terrace from September 1970 to April 1971.

	TIME OF DAY - HOURS						
	9-10	10-11	11-12	12-13	13-14	14-15	15-16
CPUE SEPTEMBER-JANUARY	35.2	11.0	20.6	12.8	33.8	36.1	14.0
CPUE FEBRUARY-APRIL	30.1	18.1	33.4	32.1	43.0	55.5	23.7
AVERAGE	32.6	14.5	27.0	22.4	38.4	45.8	18.8

Fish distribution in relation to water temperature on the terrace was noted throughout the year. The maximum and minimum water temperatures recorded on the terrace in the warm season were 38.1°C and 19.8°C. In the cool season, the mean lake temperature falls below this minimum value to about 18°C, and terrace water temperatures may fall as low as 12.8°C at night, and rise to 28°C during the day. The temperature gradient on the terraces is present in the cool season, and reverses diurnally as in summer. In the cool season, juveniles were usually seen on the terrace at the hottest time of the day between 1100 and 1400 hours when water temperatures exceeded about 19°C. Minshull (1968) reported shoals on the terrace at a temperature of 16.5°C in June. In July, August and September, the number of degree/hours over 20°C in terrace waters increased, and juvenile T. mossambica were present for increasingly longer periods in the day.

The slope habitat must now be considered. As shown in Table 9, juvenile T. mossambica inhabit barren and sparsely-vegetated slopes, although this habitat is not preferred to the terrace during the day. The slope is inhabited by juvenile T. mossambica during the night in the warm and transition seasons, and for the greater part of the diurnal cycle in the cool season. One of the striking features of the slope habitat is that, especially on the steep eastern and western shores, very little detritus collects on the substrate. This is in contrast with the terrace and profundal regions where a rich detritus layer often accumulates. This paucity of detritic deposits is probably due to the steepness of the slope, which results in material being carried into deeper water by water currents, and deposited on a more level substrate.

Another feature of the slope habitat is that the majority of the submerged aquatic macrophytes are confined to this area, both on the steep-sided slopes of the western and eastern shores, and on the more extensive gently sloping northern and southern shores. This favours species feeding on periphyton or directly on the macrophytes. However, as mentioned above, dead plant material is washed away, and there is little superposition of the photosynthetic and decomposition zones in the slope environment. Other features of the slope habitat include water temperatures nearly homothermal with those of the main water body, and a lower visibility than in shallower littoral areas.

In well-vegetated littoral areas, where T. mossambica juveniles appear to be relatively uncommon (Table 9), there is a permanent superposition (Ruttner, 1966) of the photosynthetic and decomposition zones, resulting in the formation of a gyttja layer in some areas, e.g. sites 6, 8, 10 and 12. The gyttja, which consists of fine oxidised, decomposed organic detritus, and the abundant aquatic macrophytes, mainly Myriophyllum spicatum and Ceratophyllum demersum, support a wide variety of fish species which are a feature of these sheltered littoral areas. As there is likely to be considerable interaction between T. mossambica and these other fish species, it is important at this stage to discuss briefly the relative abundance of the various fish species in sheltered littoral areas. Thirteen

TABLE 12

Habitat preferences of 4 cichlid species (4-8 cm SL) in the south basin in the period September to May 1970 as revealed by the slope seine net.

Habitat No.	Habitat	Depth metres	Pulls of slope seine	CATCH				
					T. mossambica	*T. sparrmanii*	*T. rendalli*	*H. philander*
1	Terrace	0-2 m	56	No. *% CPUE	3727 98.1 66.5	25 0.6 0.4	3 0.1 0.1	47 1.2 0.8
2	Barren slope	2-7 m	40	No. % CPUE	843 61.5 21.2	179 13.1 4.5	7 0.1 0.1	341 24.8 8.5
3	Sparsely vegetated slope	2-7 m	115	No. % CPUE	1738 64.5 15.1	508 18.9 4.4	7 0.3 0.1	439 16.3 3.8
4	Densely vegetated slope	1-7 m	42	No. % CPUE	172 19.4 4.1	175 19.8 4.2	0 0 0	539 60.8 12.8
	Total		253	No. % CPUE	6480 74.0 25.6	887 10.1 3.5	17 1.9 0.1	1366 14.0 5.4

* Percentage of total catch for all fishes in one habitat type.

species have been recorded from these areas, consisting of 4 cichlids (T. mossambica, T. rendalli, T. sparrmanii, H. philander); one barbel Clarias gariepinus; one goby Glossogobius giurus and 7 other species, which are either uncommon (Gnathonemus macrolepidotus); or very small species (Barbus paludinosus, B. viviparus, Aplocheilichthys katangae, A. myaposae, Atherina breviceps and Gilchristella aestuarius). Both C. gariepinus and G. giurus are common. The relative abundance of the 4 cichlid species in sheltered littoral areas, as revealed by the seine net catches, is given in Table 12. The figures for T. rendalli are unreliable as this species readily escapes the seine net. H. philander were found to be numerically dominant, constituting over 60% of the catch. T. mossambica were less than a third as common, and occurred in the same proportion as T. sparrmanii.

In order to distinguish between fish inhabiting the weedbeds and the slope in well-vegetated areas, pairs of fishtraps were laid, one trap on the slope and the other in the bed of macrophytes. As only 144 cichlids were caught, further data are required before definite conclusions can be drawn. T. mossambica were more common on the slope (CPUE 3.4) than over the gyttja layer (CPUE 0.7) whereas T. sparrmanii and H. philander were more common over the gyttja.

These results are confirmed by underwater observations using SCUBA. T. mossambica were fairly common on the fringes of the weedbeds in sheltered areas, and uncommon among the plants compared to H. philander, T. rendalli and T. sparrmanii. Barbel were often encountered.

Competition for food and space among the cichlids, and interference from predators such as Clarias, appear to be a feature of sheltered littoral areas. This is in contrast to the terrace and slope habitats, which are dominated by T. mossambica (Table 12). On the terraces, T. mossambica constituted 98% of the catch, and on barren and sparsely-vegetated slopes, 61% and 64% of the catch respectively

(Table 12).

Finally, mention must be made of the profundal zone (Fig. 6). T. mossambica juveniles are thought to enter this zone, but little confirmatory evidence has been collected as yet. The substrate in the profundal zone consists mainly of sand which is overlain in some areas by a layer of gyttja up to 1 m deep, and in others by a thin layer of mulm. Boltt (1969) found that the infauna of the bottom sediments, which consists mainly of small crustaceans, is mainly confined to sandy substrates; whereas the epifauna, comprised mainly of several molluscs and the crab Hymenosoma orbiculare was more generally distributed. The most common fish species in deeper water, as assessed by fish trapping, are G. giurus (CPUE of 12 fishtraps each laid for 36 hours : 66 fishes) and H. philander (CPUE : 3 fishes). These species, as well as T. sparrmanii, have been seen by the author to a depth of 30.4 m in the main basin. C. gariepinus, Croilia mossambica and Silhouettea sibayi have also been recorded from the profundal zone.

In the case of the adults, habitat preferences are dictated by the conflicting requirements of breeding and feeding. The terraces, a habitat too shallow and cold for all-year habitation, are used specifically for nest building by the males in the warm season. Adult females only enter terrace waters for the brief courtship. After the breeding season, all the adults abandon the terrace and move into deeper water. Here their requirements are dictated by the need to occupy nutrient-rich areas when water temperatures are still high enough for feeding, and to occupy deeper littoral, or limnetic, regions when water temperatures fall below about 20°C. Thus the adults occupy habitats in the warm season which they share, at least in the case of the male, almost esclusively with juveniles of their own species.

In the cooler seasons, habitats are shared with the other fish species in the lake.

Their greater tolerance of extremes of temperature in shallow water allows the juveniles to inhabit terrace areas throughout the year.

BREEDING, SHOALING AND FEEDING OF T. MOSSAMBICA IN LAKE SIBAYA

As indicated in the previous two sections, T. mossambica occupies a wide variety of habitats in the course of the year, and at different stages of the life cycle. In each of these habitats, distinct activities take place. Baerends and Baerends-van Roon (1950), Vaas and Hofstede (1952), Neil (1966) and others, have described the behaviour of T. mossambica. Only those features of interest in the Sibaya context, or examples of behaviour which are not fully documented, will be described here.

a) Movements and behaviour of adult T. mossambica

In August, when lake water temperatures average 17-19°C, adult T. mossambica were noted in small groups near the water surface several hundred metres from shore. However, only in early September, 1970, 1971 and 1972 were the first adult fishes noted in the littoral zone. These fishes were seen to move in loose aggregations just beyond the slope. Seine hauls and rod-and-line catches, showed that all these fishes were males. In the second half of September, when water temperature offshore exceeded 19°C and rose to 26°C on the terrace, large numbers of male, and a few female, T. mossambica moved into shallow water. Males were numerically dominant in September and October, approximately equal proportions of males and females were caught in November and December, but females became more abundant in December and January (Fig. 36). These data were obtained from catches in all littoral areas - sheltered, partially exposed and exposed. Breeding sized fishes caught in February, March and April were all females.

During the early part of the occupancy of the shallows by the males, intraspecific aggressive encounters commenced, and continued throughout September and the first half of October with progressively more fishes establishing territories and excavating nests in the shallows.

By late October, the majority of males in the shallows had established territories, and were engaged in nest-digging, cleaning and protection. Territorial aggressive encounters consist of broadside displays, chasing, and jaw locking. Opened mouths and aggressive black-and-white colorations are typical of attack and threat behaviour. A characteristic of threat behaviour is that, as in many other animals such as agamid lizards (Bruton, 1969), the aggressive conflicts between territorial males usually takes the form of threat displays rather than actual fighting. Thus, as suggested by Tinbergen (1953) and Lorenz (1966), natural selection has favoured the development of a symbolic display which achieves the functions of fighting without reducing the ability to fight, but does not result in harm to conspecifics. However, male T. mossambica do occasionally fight and inflict injuries on one another. 10% of 323 breeding males which had been carefully examined were found to have injuries. This figure is markedly higher than that for females (2%) and suggests that the injuries were sustained in aggressive encounters between males. Injuries to male fish were recorded in the dorsal fin (11 fish), flanks (5)m caudal fin (4), pectoral fin (4), mouth (2), eye (3), operculum (2), anal fin (1) and premaxilla (1). Except for the eye injury, which may have been caused by a free-swimming leech Limnatus which have been seen to attach themselves to the eyes of Tilapia in Lake Sibaya, the majority of the injuries may have been caused by mouth-biting. The aggressive encounters would serve to divide the nesting grounds among the breeding males, thus possessing an epidiectic function in the sense of Wynne-Edwards (1962). Weak, surplus or small animals would fail to establish territories, and therefore fail to reproduce. The aggressive encounters would then serve as a density-dependent factor controlling population numbers if areas for breeding were limiting.

The first females entered the nesting grounds from deep water in September and early October, but their numbers reached a peak in late October, November and December. The increasing importance of females in the breeding population in the littoral in October, November and December is shown in Figure 34.

After the brief courtship the female takes the ova into her mouth and retreats into deeper, more sheltered water off the terrace to brood the eggs for about 20 days. At the conclusion of the incubation period, the female moves back onto the terrace and releases the fry into very shallow water, thereafter retiring to deeper water again. Mouth-brooding and fry-releasing behaviour will be discussed in more detail below. The behaviour of an egg-carrying female T. mossambica (SL 15.1 cm, weight 127 gms) in an aquarium was observed. The length of the eggs averaged 3.2 mm (range 3.0-3.5 mm) and the diameter 2.8 mm (range 2.5-3.0 mm) when the female was introduced into the aquarium. Aquarium water temperatures averaged 22°C (range 21.2-22.8°C). Very little somatic development of the eggs had taken place. As judged from Vaas and Hofstede's (1952) report that one-day-old embryos of T. mossambica had discernable pigmented somatic tissue lying on top of the yolk mass, the eggs brooded by the female studied had probably been fertilised not more than one to two days before introduction into the aquarium. The female ventilated the eggs by regular chewing movements in which the mouth was opened wide then closed completely, and the branchiostegal membrane moved up and down. These ventilatory movements alternated with the normal respiratory movements. The female first ejected the fry after 12 days, but readily retrieved them at the slightest sign of danger. After 19 days, the fry voluntarily left the mouth of the female, and after 21 days, the female abandoned the shoal of fry. Thus the entire brooding cycle took about 22 days in the female examined. No feeding by the female was observed during this period. On dissection, the female was found to have the ovary fully distended with ova approximately 1 mm in diameter. Incubation periods for T. mossambica in other systems range from 13 to 21 days (Vaas and Hofstede, 1952). Baerends and Baerends-van Roon (1950) report an incubation period of 10-12 days, and Hickling (1950, in Vaas and Hofstede, 1952) of 10 days in T. mossambica. The relatively long incubation period of the Sibaya fish may have been brought about by the artificial environment of the aquarium.

Mouth-brooding females were caught from September to March in 1970/71 and 1971/72, and probably produced several broods. Minshull (1967) was of the opinion that Sibaya females produced at least two batches of eggs during a breeding season.

He found that a mouth-brooding female may have newly formed eggs in the ovary, an observation confirmed by Vaas and Hofstede (1952) and myself. With an incubation period of about 22 days, and allowing a week between each incubation period, the entire cycle of mouth-brooding in T. mossambica from Lake Sibaya would take a minimum of about 30 days, but probably more. As mouth-brooding fishes were recorded over 169 and 159 days in the summers of 1971/72, four and possibly five broods may be produced each breeding season. This suggestion is supported by field data from Crass (1964) who reports a brood every 6 or 7 weeks in summer for T. mossambica from Natal, and Jubb (1967) that a single female may spawn as many as four times during summer.

Counts were made of the number of young in the mouths of females which were carefully caught and thought to have lost no young during sampling (Table 13). The highest number of eggs (579) was carried by a 15.6 cm SL female, and the highest number of fry (226) by a 13.2 cm SL female.

TABLE 13

Number of eggs or young carried by mouth-brooding female T. mossambica caught in the south basin in 1970/71.

MOUTH-BROODING FEMALES		NUMBER OF YOUNG CARRIED	
SL cm	Weight grams	Eggs	Fry
12.5	59	110	-
13.7	90	164	-
15.6	119	579	12 young*
15.8	158	370	-
10.6	40	-	78 medium*
12.2	50	-	146 advanced*
12.8	78	-	127 young*
13.2	92	-	226 young*
13.4	80	-	74 medium*
13.7	93	-	222 young*
16.6	154	-	204 young*

* young fry: SL 6 mm; medium fry: SL 6-9 mm; advanced fry: SL 9 mm +.

Egg brooding is characteristic of the female population although two male T. mossambica brooding eggs or fry were caught. The first (SL 18.2 cm, TL 22.8 cm, weight 215 gms) was caught on the nesting grounds in October, and was found to be brooding young fry. As no other mouth-brooding fish were caught in that particular netting, the fry were not picked up by the male in the net or in the bucket. The second male (SL 17.7 cm, TL 22.3 cm, weight 213 gms), was caught on the nesting grounds in December, and was found to be brooding eggs. Although no other T. mossambica brooding eggs were caught at the time, one female brooding advanced fry was caught in the same net. Lowe-McConnell (1957) found that at times Tilapia fry may take shelter in the mouths of fishes other than the parent fish. However, Welcomme (1967) and Hyder (1970) found no evidence that adult T. leucosticta will 'easily' part with eggs or fry. Vaas and Hofstede (1952) found in Java that 'male mossambica in a few exceptional cases, also incubated the eggs, but as a rule, the female was active in this respect'. Liebman (1933) suggested that in the various Tilapia species both sexes may brood the young but not in equal proportions. Fryer and Iles (1972) report that T. multifasciata and T. galilaea are bi-parental brooders - both sexes play an equal part in brooding, and that T. macrocephala is a paternal mouth-brooder. With the exception of the two male fish reported above, mouth-brooding in T. mossambica from Lake Sibaya is performed in the vast majority of cases by the female.

The mouth-brooding females leave the brooding grounds when the fry have reached 9-10 mm SL and enter shallow terrace waters where the fry are released. A remarkable pattern of fry-releasing behaviour was observed in female T. mossambica in Lake Sibaya. This behaviour will be documented in some detail here, as no previous record of this phenomenon is known in Tilapia. Mouth-brooding females were found to form large shoals which occasionally entered very shallow water. Shoaling of mouth-brooding females was observed on three occasions, all of which were preceded by heavy rain. The first shoals were observed in November, 1971. The fishes were seen to move rapidly along the terrace parallel to the shore, in a compact group in water 0.3 to 1.5 m deep in hot calm weather at 1130 hours. The fishes occasionally entered very shallow water and released fry. The shoal remained on the terrace until 1330 hours, after which the fishes entered deeper water. A part of the shoal was caught by means of a seine net, but more than 7/8 of the fishes escaped. As the seine catch totalled 101 fishes, the whole shoal probably numbered over 800 fishes. The shoal consisted entirely of mouth-brooding females (83 fishes), or females in which the branchiostegal membrane was distended (18 fishes), which indicates that the young had been released very recently, probably during the netting operation. It was noted that 81 of the 83 females which retained their young were brooding fry, whereas only 2 fishes were brooding eggs.

The preponderance of fry as opposed to egg-carrying, females was also noted in another shoal of mouth-brooding females in which fry-carriers were found to be nine times as common as egg-carriers. This shoal totalled 169 fish and was found to consist of 150 mouth-brooding females, 13 non-brooding females, 2 adult male *T. mossambica* and 4 juvenile fish. The non-brooding females may have been caught over the slope as the net was laid over the edge of the slope in order to encircle the shoal on the terrace.

The fry-releasing behaviour of a third large shoal of mouth-brooding females was followed in December, 1971. The shoal assembled in shallow terrace waters on the southern shore of the main basin on the 4th December. Light rains (3.4 mm) had fallen on the 2nd, followed by heavy rain on the 3rd (38.0 mm) and the 4th (116.6 mm; total 158 mm), with the result that very extensive pools had formed in the eulittoral zone. Large shoals of fishes, estimated to number several hundred individuals, were seen swimming along the terrace in water 0.5 to 1 m deep. Occasionally small shoals were seen to leave the large shoal and enter water less than 4 cm deep on the edge of the terrace where the fry were released. Many females swam up the very shallow (1-3 cm) inlets and into the eulittoral pools. As the water was too shallow for normal swimming, these fishes swam on their sides. 44 fishes which entered eulittoral pools were all found to be mouth-brooding females (SL mode 13 cm, range 11-15 cm) with a low condition factor (28.8). These fish were seen to release fry on the edges of the pools, where water temperatures at the time of the observation reached 32.0°C. After releasing the fry, the females swam back across the inlet of the eulittoral pool and into terrace waters, where they rejoined the shoal and later moved into deeper water beyond the slope. The release of fry reported above was thought to be the final release as females are unlikely to move off the terrace and into deeper water and then return later to retrieve the fry for further brooding.

The shoaling of mouth-brooding female T. mossambica in Lake Sibaya requires some comment. Similar behaviour of female Tilapia is reported briefly by Fryer and Iles (1972) who mention that brooding female T. variabilis in Lake Victoria 'often congregate in considerable numbers in 3 or 4 metres of water' on beaches with gently sloping rock bottoms. Lowe (1952) reported a shoal of several hundred adult female T. lidole swimming just below the surface above a spawning ground in Lake Malawi.

Fryer and Iles (1972) have suggested that shoaling may have a protective significance. Observations on mouth-brooding fishes have indicated that they may be very vulnerable to predators over barren substrates, especially when the fry have to be gathered into the mouth by the female. Protection by shoaling, they suggest, is afforded by the 'confusion effect' whereby a predator confronted by a shoal receives a number of conflicting stimuli which block the feeding response.

The movement of adult females into deep water after the release of the fry marked the end of the breeding season. As shown in Table 14, breeding fishes were caught over 172 days from 14.9.70 to 4.3.71 in the summer of 1970/71, and over 175 days from 12.9.71 to 4.3.72 in 1971/72. In both summers, breeding females entered the littoral after the males, and departed to deep water after the males.

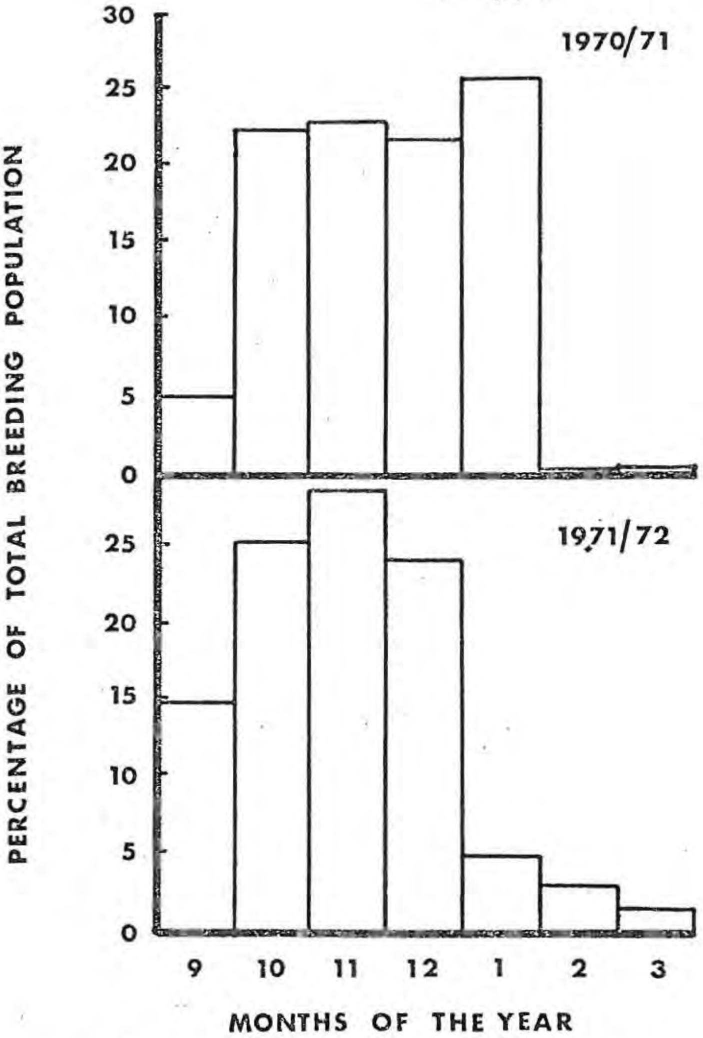


Figure 48: The percentage of the total sample of breeding *T. mossambica* caught per month for the summers of 1970/71 and 1971/72, showing the months of major breeding activity. The data are derived from fishes caught in the south basin by means of seine nets with the netting activity reduced to a similar value for each month.

TABLE 14

Duration of the breeding season of T. mossambica in Lake Sibaya.

		1970/71	1971/72
♂ Adults	First capture	14.9.70	12.9.71
	Last capture	16.1.71	7.12.71
	Duration	125 days	87 days
♀ Adults	First capture	17.9.70	28.9.71
	Last capture	4.3.71	4.3.72
	Duration	169 days	159 days
♂&♀ Adults	First capture	14.9.70	12.9.71
	Last capture	4.3.71	4.3.72
	Duration	172 days	175 days

Discussion of breeding behaviour: The major point to emerge from this study of the breeding behaviour is that T. mossambica in Lake Sibaya has a cyclical breeding pattern. After a quiescent stage from April to August, breeding activity takes place from September through to March.

Although breeding took place during seven months, intense breeding was only recorded over three or four months. Thus in the summer of 1970/71, with the fishing effort per month reduced to the same figure, 93% of the breeding fishes were caught from October to December (Fig. 48).

Cyclical breeding behaviour is well known in Tilapia, and has been recorded in species from sub-tropical lakes, in which environmental conditions vary seasonally, as well as in tropical lakes, in which only slight seasonal changes occur (Fryer and Iles, 1972). One might expect the species which have definite breeding seasons to be those which inhabit lakes in which seasonal changes are marked. However, this is not always the case. Thus Lowe (1952) reports that in Lake Malawi, in which seasonal changes are slight, T. saka breeds during the hot season preceding the rains, whereas

T. squamipinnis breeds during the rainy season. As pointed out by Fryer and Iles (1972), different stimuli must be responsible for the onset of breeding in these species.

In Lake Sibaya, T. mossambica breed during the warm season. Unfortunately, meteorological data for the area have only been collected for a short period, thus correlations between changes in external factors and the duration of the breeding cycle are of little value. Rainfall has been measured since May, 1968 and has shown an erratic pattern with a tendency for most rain in the warm to cool transition period (February and March) and least rain in the cool season (June, July, August, Fig. 7). Lake water temperatures in 1968 and 1969 showed a seasonal variation of 13°C from 17-30°C, reaching a peak in January (Minshull, unpublished field notes, Fig. 8). Mean day length data are only available from Durban, which is 330 km south, and 1°40' longitude west of Sibaya. As Sibaya is closer to the equator than Durban, seasonal changes in day length would be less extensive. In 1972, day length in Durban varied from about 10 hours in July to 14 hours in December (Hydrographic Office, S.A., 1972).

It is tempting to assign factors such as increasing day length and water temperatures as precipitative factors for breeding, and heavy rainfall as a terminating factor. Correlations of this sort have been made for T. leucosticta in Lake Naivasha by Hyder, 1970. However, insufficient meteorological data are available for Sibaya at present for the definition of regular cyclical changes, if any, in external factors and therefore no correlations can be drawn. Furthermore it is the author's opinion that experimental data on the effect of changes of the various external factors, such as day length, are required before factors precipitating and terminating breeding in T. mossambica in Lake Sibaya can be pinpointed.

The movement of T. mossambica into the shallows for breeding purposes is well known for many other species in the genus Tilapia, for example, T. lidole in Lake Malawi (Lowe, 1953); T. variabilis in Lake Victoria (Fryer, 1961) and T. macrochir in Lake Mweru (Carey, 1965). However, little data are available indicating whether adult fishes return to the same breeding grounds in successive seasons or not. Three recaptures of Sibaya T. mossambica which were breeding when tagged, have been made in the following breeding season. Two of the fishes, both males, were recaught at, or within 10 m, of the site of original capture, i.e. they had returned to the same breeding ground in the following breeding season. The other fish caught and released over a nesting ground at site 2 in the south basin, was recaptured 351 days later on a nesting site on the south-east shore of the main basin. This fish, a large male, had migrated over 3100 m to a site some distance from that used for breeding in the previous summer. The fish was noted to be in breeding colouration on release and recapture.

b) Shoaling and other activities of fry and juveniles:

After release by the female, the fry form large shoals in water 1-15 cm deep (the primary nurseries), either on the shallow margins of the terrace or in the eulittoral pools. This observation is confirmed by Minshull (1970) who, using fishtraps, found that the modal length of fishes in water 15 cm deep was 1.5 to 1.9 cm TL, which corresponds with the length of fry which have recently been released by the female. The fry were observed to occupy shallow water during the day, but to move into deeper terrace waters or onto the slope at night.

The fry occupy deeper water during the day as they grow larger, and at a length of 3-8 cm are frequently caught in terrace waters 15 to 100 cm deep (secondary nurseries). Minshull (1970) also recorded T. mossambica's occupancy of deeper and deeper water by juveniles of increasing size. Thus at a depth of 45 cm on the terrace, the modal fish length was 55 cm, and at 100 cm, 7.5 cm.

As indicated in the data relating to the temperature survey, juveniles occupy the terrace waters by day, and deeper water over the slope at night. An idea of their behaviour at night was obtained during two night SCUBA dives carried out on the eastern shore of the main basin. Observations indicated that large numbers of small T. mossambica (about 6 cm SL) were present on the slope after dark where, during the day, small T. mossambica were infrequently encountered. The fishes were found lying motionless on the substrate at approximately three metres depth, or swimming slowly in midwater. When alarmed they dispersed as individuals, and not as a shoal. Minshull (1970) reported that at night T. mossambica may congregate under a stationary boat over the deep terrace, an observation confirmed by the author at Sibaya. The latter observation suggests that temperature preferenda is not the only factor determining night distribution of T. mossambica, and that light intensity may also be involved. Other workers have noted that the shoaling habit of Tilapia breaks down at night. Thus Capart (1955) in Fryer and Iles, 1972, using an echosounder in Lake Kivu, found that T. nilotica shirana live in shoals during the day, disperse at dusk, and reform shoals at dawn.

During the day, juvenile T. mossambica formed large shoals on the terrace which reached a peak size in March and April and a minimum size in the cool season. The shoals were usually made up of a limited range of sizes with the modal two centimetre length groups comprising 40-60% of the shoal. Small fractions of the large shoals found in March and April, estimated to contain over 2000 fish at times, were encircled by a seine net. One shoal, driven into a eulittoral pool, covered an area later calculated to be 682 square metres. The largest single catch made with the seine net (330 T. mossambica juveniles) was made at 14.45 hours at site 11 on 1.4.71. Other catches, constituting parts of large shoals, were 206 T. mossambica

(14.10 hours, 19.3.71 at site 7AN); 242 (12.00 hours, 10.4.71 at site 11). These large catches were all made between 10.00 and 1500 hours in March and April on the terraces of the eastern shore of the south basin.

It was noted that the juveniles formed small shoals (less than about 200 individuals) when feeding, but large shoals (more than 200 individuals) when alarmed or moving rapidly across the terrace parallel to the shore.

In late April, and during the cool season, juvenile T. mossambica formed small shoals (20-100 individuals). In September and October, those juveniles which had not reached adult size formed isolated small shoals which frequented terraces not used by the adults for breeding.

c) Feeding behaviour of T. mossambica in Lake Sibaya:

Feeding by fry is predominantly from the mulm in eulittoral pools although particulate matter floating on the water surface may also be taken. The movement of fry into eulittoral pools in February, March and April corresponds with the time of deposition of large quantities of allochthonous detritus, which are washed into the terrace waters from the shore by the heavy rains, and autochthonous detritus, which result from the post-summer dieback of aquatic macrophytes in the lake. The mulm which results from the decay of this detritus was found to be rich in diatoms (Minshull, 1968). These diatoms were found to constitute the main food source of the fry of T. mossambica in Lake Sibaya (Minshull, 1969), though stomachs may also contain small amphipods and some insects including Thysanoptera. Allanson (pers. comm., 1972) examined the stomach contents of a large number of fry from a eulittoral pool and found that the fishes had consumed numerous Harpacticoid copepods. This is interesting, as Le Roux (1956) found that under pond conditions, young T. mossambica under 5 cm TL prefer zooplankton as food. The evidence suggests that the fry are opportunistic feeders, consuming zooplankton when available, but relying on diatoms as the main source of food. This conclusion is supported by the results of Vaas and Hofstede (1952) who found that fingerling T. mossambica feed on diatoms, unicellular green algae and small crustacea.

Juvenile T. mossambica in Lake Sibaya were observed to breed predominantly on the mulm which accumulates on the sand in terrace waters, and occasionally on mulm deposits in the eulittoral between 10.00 and 14.00 hours. These observations are confirmed by Minshull (1970). Feeding by juveniles on periphyton on Myriophyllum spicatum and Potamogeton pectinatus was also noted.

The mode of feeding on periphyton and mulm differed. When removing periphyton from Myriophyllum or Potamogeton stalks, the fish turns on its side, encloses the stalk with its mouth, and executes a series of sucking and scraping movements which remove the attached flora without damage to the plant. Occasionally leaves of Myriophyllum are severed, sucked and then discarded. Balance is maintained by means of the pectorals. Feeding was accomplished in bursts lasting up to 15 seconds, with intervals of 30 seconds to 5 minutes or longer. When feeding on the mulm, the fish adopts a posture of 45^{o} from the substrate, digs the open mouth into the mulm, retreats a few centimetres, mouths the particles, ejects sand grains through the opercular opening, and resumes feeding. Minshull (1970) found that the gut contents of juvenile T. mossambica consisted mainly of algae, in which diatoms common in the mulm, predominated. After an examination of stomach and rectal contents, he concluded that diatoms were the only algae to be digested. Other authors have confirmed that diatoms are the major food source of juvenile T. mossambica. Thus Vaas and Hofstede (1952) report that young T. mossambica feed almost entirely on diatoms, unicellular green algae, and small crustacea, occasionally taking periphyton; and le Roux (1956), Crass (1964) and Munro (1967) that young T. mossambica feed almost exclusively on diatoms. Utilisation of benthic and epiphytic food resources would restrict juvenile T. mossambica to areas adjacent to the substrate, and explain their absence from the limnetic zone where they have not been collected using fishtraps.

Besides the mulm, adult T. mossambica were found to feed on periphyton, aquatic macrophytes, insects floating on the water surface and, in the case of the largest specimens, other fishes. The stomach contents of 164 adult T. mossambica, caught at different times of the year in various habitats, were examined. The results indicate that the adult fishes may feed on different food sources in different parts of the lake, utilizing periphyton in protected well-vegetated areas, mulm in exposed areas, and floating insects and possibly plankton in the limnetic zone. 80 fishes caught in sheltered well-vegetated littoral areas were found to contain large quantities of naviculoid and nitzschioid diatoms, some plant fibres, and small quantities of sand. These fishes had apparently been feeding on periphyton. The stomach contents of adult fishes caught on the terrace varied according to the time of sampling. Thus all of 26 breeding fishes caught during October and November were found to have empty stomachs, whereas the stomachs of 30 adults caught after the breeding season were found to contain small quantities of diatom-rich mulm and sand. Feeding by T. mossambica in the limnetic zone, according to the stomach contents of 28 fishes, appeared to be on terrestrial flying insects of the Coleoptera and Formicidae which had fallen on the water. Fishes feeding at the surface in the limnetic zone have been seen as far as 900 m from shore over water 31 m deep. Six of the 28 stomachs examined were found to contain a green digested fluid which may have been derived from plankton. The possibility of plankton feeding in adult T. mossambica requires some comment, though no data are available at present. Several deposit-feeding Tilapia species are known to be facultative feeders utilizing both suspended phytoplankton and sedimented material of planktonic origin. In taking to plankton feeding these species probably used pre-existing rather than specialised structures, but the exact collection mechanisms are not known (Fryer and Iles, 1972). A study of Closterium sp., Anabaenopsis sp., Anabaena sp. and Melosira g. granulata and other planktonic algae in Sibaya has revealed that 'the algal standing crop as reflected by chlorophyll concentration and cell counts is relatively stable at a comparatively low level with different species involved as major and minor contributors at different times of the year' (Hart, 1971). Hart also reported that most of the phytoplankton species were more abundant in deeper water (30 m) than in the 0-5 m column. The diurnal distribution of the calanoid copepod Pseudodiaptomus hessei was also investigated. This zooplankter was found to inhabit deep water during the day, and rise to the surface at night. Marteifel (1961) found that the feeding intensity of predatory pelagic fish was lower in lower light intensities. Feeding by T. mossambica on plankters at night, if it occurs at all, is probably at a low intensity. Furthermore, the maximum depth restriction of adult T. mossambica of about 12 m would preclude utilization of plankton in deeper water. The volume of plankton available may be insufficient to support large obligatory planktophagous fishes, but sufficient for facultative feeders relying on other sources of food.

In summary, adult T. mossambica in Lake Sibaya, according to available data, feed on the diatom-rich mulm, periphyton, floating insects and possibly plankton. Minshull (1969) reports similarly for T. mossambica from Lake Sibaya. The gut contents of 40 T. mossambica were found to consist of the following constituents by settled volume: 41% algae, chiefly diatoms; 25% sand; 9% insects, all of which were terrestrial flying forms including Coleoptera, Lepidoptera and Formicidae; 8% Crustacea, including amphipods and ostracods; 7% fish in the form of small cichlids; 6% plant fibres and 4% gastropods and Hemiptera. Minshull noted that fish remains were only recorded for larger T. mossambica over 200 gms in weight. Adult T. mossambica from some other systems have been found to rely on food sources other than diatoms. Thus Le Mare (1951) reports that T. mossambica shows a preference for planktonic crustacea in well-fertilized ponds in Singapore, and Vaas and Hofstede (1952) that adult T. mossambica feed mainly on higher plants in Indonesia though 'bottom diatoms play an important part'. Other workers have found a preference for diatoms and higher plants. Thus Munro (1967) reports that filamentous algae and diatoms predominated in the food (52%), and that higher plants were also common (31%). The evidence suggests, and most authors agree, that T. mossambica is an omnivorous feeder relying on whatever food sources are available.

PREDATORS AND PARASITES

a) Predators:

The predation rate, by man, birds and fishes appears to be low in Sibaya compared with many other systems inhabited by Tilapia, many of which are fished commercially, or have large populations of piscivorous birds and fish. The local Africans take juvenile and adult T. mossambica by spearing and trapping, but the fishery is by no means well developed. Piscivorous birds, while common, are not abundant. The barbel Clarias gariepinus probably has the most impact as a predator. In the following section, the author's observations on predation of T. mossambica in Lake Sibaya are presented. The data available are very incomplete, and quantitative surveys are clearly required.

As with many other fish species, the youngest stages of T. mossambica, especially the fry, appear to be the most vulnerable. In well-vegetated areas, where the adult females brood their young, the omnivorous cichlid Hemihaplochromis philander was common (Table 13). These fishes were observed to prey on T. mossambica fry in the experimental pool, and may take some fry in the lake. Minshull (1969), however, reports no fish remains in the stomach contents of 12 H. philander, but this sample is very small, and is unlikely to be a true reflection of their food preferences. Predation on fry by the barbel Clarias gariepinus has been observed in protected littoral areas, and fry have been recorded in the stomach contents of this omnivore on two occasions. However, once the fry have been released by the female into shallow littoral or eulittoral areas, they appear to be safe from predation by Clarias. Clarias do occasionally enter the eulittoral pools for the purpose of spawning; but the stomachs of 37 barbel which had entered an eulittoral pool for spawning were empty.

Fry appear to be vulnerable to bird predators when carried by the females into shallow eulittoral pools just prior to their release. Heavy mortalities among brooding females were witnessed on three occasions in November and December 1971. Piscivorous birds including fish eagle, Haliaëtus vocifer, purple heron, Ardea purpurea and yellow-billed kite, Milvus aegypticus were seen to take adult fish and consume the body, leaving the head, with the consequent death of the fry. On other occasions, certain birds including the purple heron and grey-headed gull, Larus cirrocephalus pecked the opercula away and fed on the fry, leaving the body of the fish undamaged. Mortalities among fry-releasing T. mossambica are also incurred by man. After heavy rains on two or three occasions each year, the Africans gather in eulittoral areas and spear or club fry-releasing Tilapia. Mortalities among the fry also result from the drying up of eulittoral pools. However, it was noted that fry congregated in larger numbers in eulittoral pools which maintained an entrance to the lake, which pools occurred mainly on eastern and western scoured shores, and not on northern and southern deposition shores.

Juvenile T. mossambica also fall prey to C. gariepinus, piscivorous birds and man. Clarias is common in sublittoral and sheltered littoral areas during the day, and enters terrace waters at night. The stomach contents of 88 C. gariepinus were examined immediately after capture. 22 stomachs (25%) contained fish, of which 5 (5.6%) contained identifiable T. mossambica remains; 46 contained invertebrate remains, and 12 were empty. The identifiable T. mossambica consisted of 8 juveniles (SL less than 8 cm) and 3 adults. Allanson and Campbell (unpublished field notes, 1967) and Minshull (1969) also found Tilapia in the stomach contents of C. gariepinus from Lake Sibaya. Allanson and Campbell examined 35 Clarias, and recorded fish remains from 13 stomachs (37%) including cichlid remains from one stomach (2%) and identifiable Tilapia remains from three stomachs (8%). Minshull examined 53 Clarias, and reported that fish remains, consisting mainly of small cichlids and Glossogobius giurus constituted 32% of the settled volume of the combined stomach contents, and Crustacea 44%. The above data indicate that, although Clarias feeds mainly on Crustacea, fish including T. mossambica constitute a large part of their diet. Studies in other systems have indicated that C. gariepinus may rely almost entirely on invertebrate food. Thus Munro (1967) concluded after examining the stomach contents of 979 barbel of all sizes, that the young feed on insect larvae and the adults on zooplankton. In Lake Sibaya, which has a low plankton biomass (Hart, 1971) Clarias feeds on the Crustacean macrobenthos, and also to a considerable extent on fishes including T. mossambica.

A series of 6 bird surveys carried out in March 1970 around the shores of Lake Sibaya indicated that the most abundant avian piscivores were reed cormorant, Phalacrocorax africanus (289 birds counted, 47% of the total count), white-breasted cormorant, P. carbo (93 birds), little egret, Egretta garzetta (74) and pied kingfisher, Ceryle rudis (50).

Field observations have indicated that cormorants feed exclusively over offshore waters, and not on the terrace, an observation confirmed by Junor (1969) in Lake Kyle. Thus during the day, at least after 0800 hours and before 1800 hours, the majority of T. mossambica, being on the terrace, would not be subject to cormorant predation, whereas Hemihaplochromis philander, T. sparrmanii, and other small fish species, would. However, it was noted that the cormorants feed most intensively in the early morning between 0500 and 0700 hours. During this period, juvenile T. mossambica still occupy slope waters and may be subject to considerable predation by cormorants. Data from other systems in which both Haplochromis-type and Tilapia species occur in abundance indicate that the former were preferred over the latter by a factor of over 38 in number of prey caught (Fryer and Iles, 1972, citing the data of Cott). The protection afforded to T. mossambica juveniles by occupancy of the terrace may result in cormorants relying on offshore species for food in Sibaya.

Juvenile T. mossambica are also caught by the local Africans in baited and unbaited 'umono' traps, sometimes laid in association with reed barricades. As many as 53 juvenile T. mossambica may be caught overnight, though this is exceptional. A survey revealed that 2-5 traps were laid daily in the south basin in the summer of 1970/71, catching an average of 5 juvenile T. mossambica per trap per day.

Breeding adult fishes are preyed on by Clarias, birds, crocodiles and man. T. mossambica up to 15 cm SL have been recorded from the stomach contents of C. gariepinus. Avian predators include the fish eagle, which is able to take large T. mossambica, e.g. on 28.9.71 a fish eagle took an adult male T. mossambica (SL 19.8 m, TL 24.7 cm, weight 268 gms) immediately after the fish's release after tagging. Fishing intensity is high at times - a single fish eagle caught and consumed 4 large T. mossambica (identified by the remains left on the beach) in 3½ hours in November, 1971. Non-

TABLE 15

The incidence of parasites on 5210 juvenile and adult T. mossambica caught in the south basin.

Number of fish examined		Parasites					
		Eustrongylides?	Argulus	Ichthyothirius	Ascaris	Limnatus	Total and percentage of N
Juvenile	4670	7	5	3	3	0	18 0.38%
Adult ♂	323	22	9	0	0	1	32 9.9%
Adult ♀	217	21	2	0	0	0	23 10.6%
Total adults	540	43	11	0	0	1	55 10.1%

breeding T. mossambica near the surface in the limnetic zone of the lake are also taken by fish eagles. Predation on females is particularly intense during fry-releasing activities. The local Africans are aware of the migration of large T. mossambica into the shallows in the warm season and take advantage of the higher catchability of the breeding fishes by concentrating their fishing effort in the lake in October, November, and December. Nest-guarding males are speared, and fry-releasing females clubbed and speared after being blockaded in eulittoral pools.

The population of nile crocodile, Crocodilus niloticus, in the south basin was estimated at 17 animals over 1 m length in 1970 and 1971. The total crocodile population of the lake has been tentatively estimated at between 100 and 120 individuals from night and day counts and a single aerial survey. In the south basin crocodiles were most often recorded from well-vegetated bays (sites 10 and 12) or on densely vegetated terraces (site 3) but often entered sparsely vegetated terrace waters at night. Feeding crocodiles were observed on 48 occasions. In the majority of cases (35), they were found feeding on the remains of T. mossambica or C. gariepinus left on the beach by fish eagles. However, nothing is known of the feeding of crocodiles on live T. mossambica.

b) Parasites:

The incidence of parasites on juvenile and adult T. mossambica caught in the south basin is low (Table 15). The percentage of juvenile T. mossambica recorded with parasites (0.38%) was markedly lower than that of adult fish (10.1%).

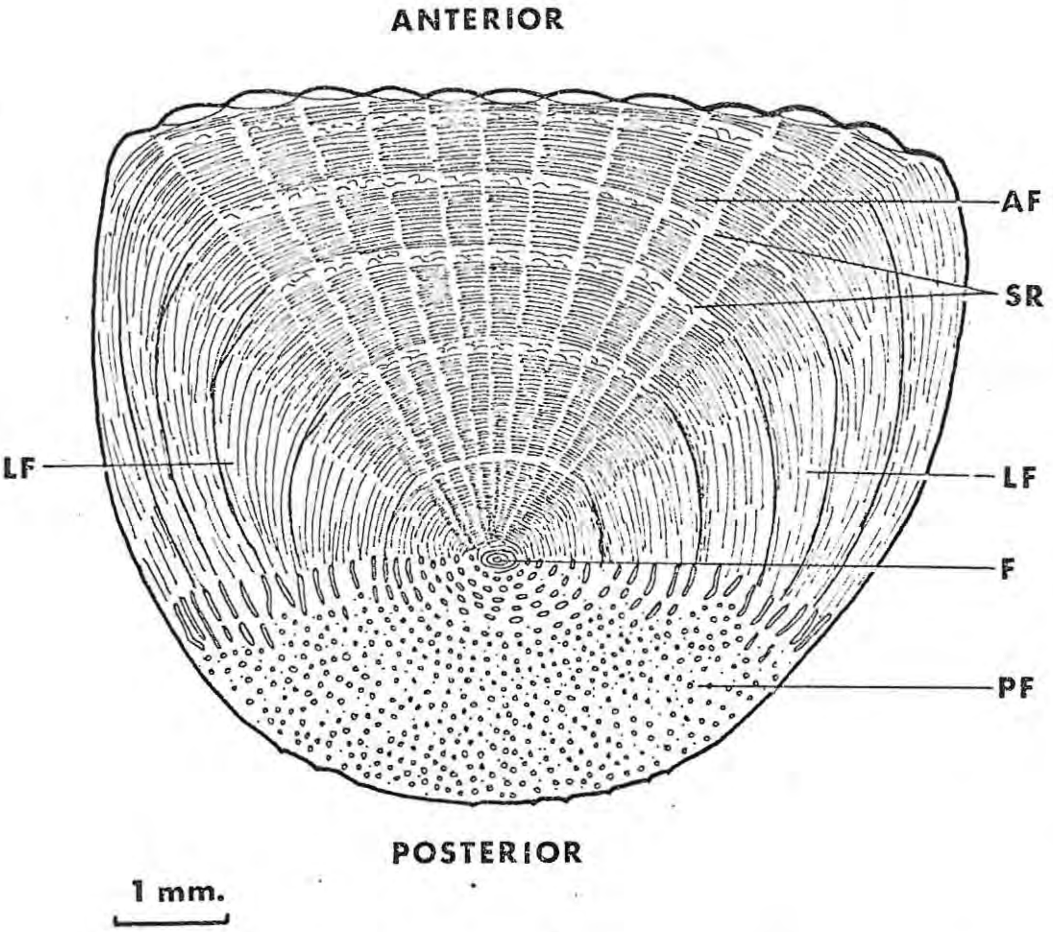


Figure 49: Diagram of a ctenoid scale of T. mossambica from the region immediately dorsal to the pectoral fin, showing the anterior field (AF), lateral field (LF), posterior field (PF), scale rings (SR), and focus (F).

AGE AND GROWTH

The most frequently used method of age determination in fishes is the counting of growth zones formed as rings on the bony parts during alternate periods of faster or slower growth, reflecting environmental and internal physiological changes. Lake Sibaya, which is situated in a subtropical coastal climatic zone, experiences some seasonal climatic variation with a well-defined warm season. The average difference in water temperature, for example, between warm and cool seasons is $10^{o}C$ (28^{o}-$18^{o}C$). Well-defined rings formed on the scales of *T. mossambica* from Lake Sibaya are perhaps tied in with the seasonal events of the lake. If so, these rings could be used for age determinations. In this chapter, after an introductory description of the scales and scale rings, a method is described whereby the time of scale ring formation was determined. The time of ring formation was then related to concurrent ecological changes in an attempt to explain the factors bringing about ring formation. With the time of ring formation established, growth rates can be calculated. These calculated growth rates were compared with growth rates obtained from marked fishes in the lake, and with *T. mossambica* from other systems. The results of preliminary determinations of the number of otolith and opercular rings are also given.

DESCRIPTION OF SCALE AND SCALE RINGS

The structure of the scenoid scales of *T. mossambica* has recently been described by Alletson (1972).

The scales of *T. mossambica* have an anterior field consisting of regular concentric circuli which are subdivided into sectors by radii originating from the focus (Fig. 49). The concentric arrangement of the circuli continues through the lateral field and into the posterior field where the circuli are replaced by rows of ctenii. A ring is formed when the regular arrangement of the circuli in the anterior and lateral fields is interrupted by irregularly arranged

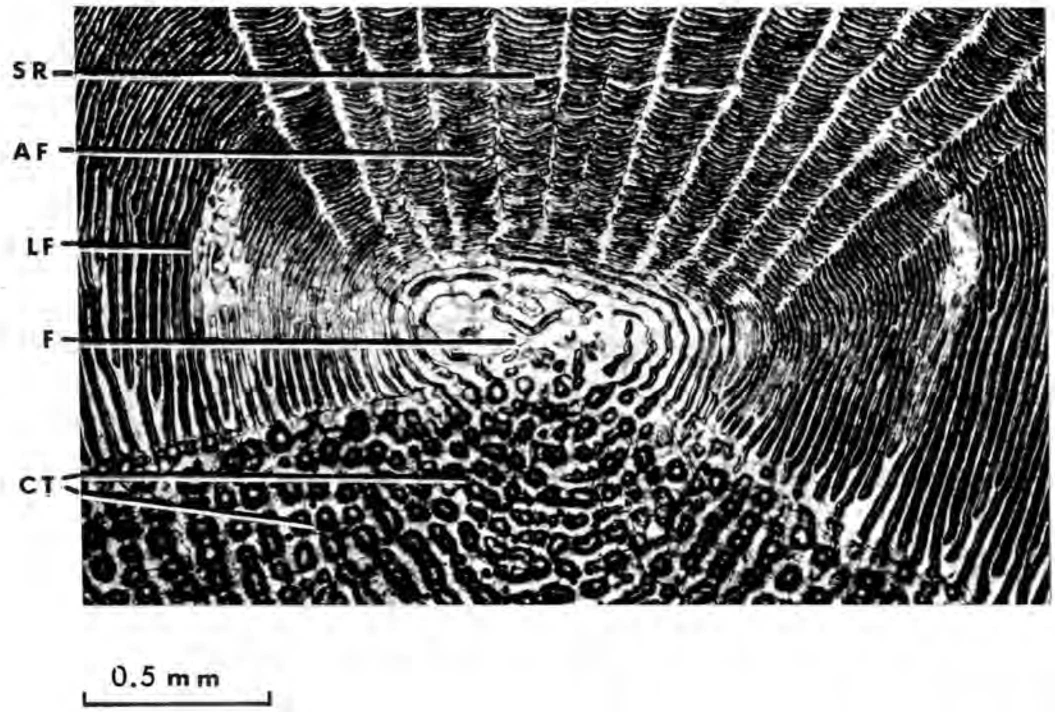


Figure 50: Scale of T. mossambica showing focus (F), Anterior field (A), Lateral field (L), Scale Ring (SR) and Cteni (CT).

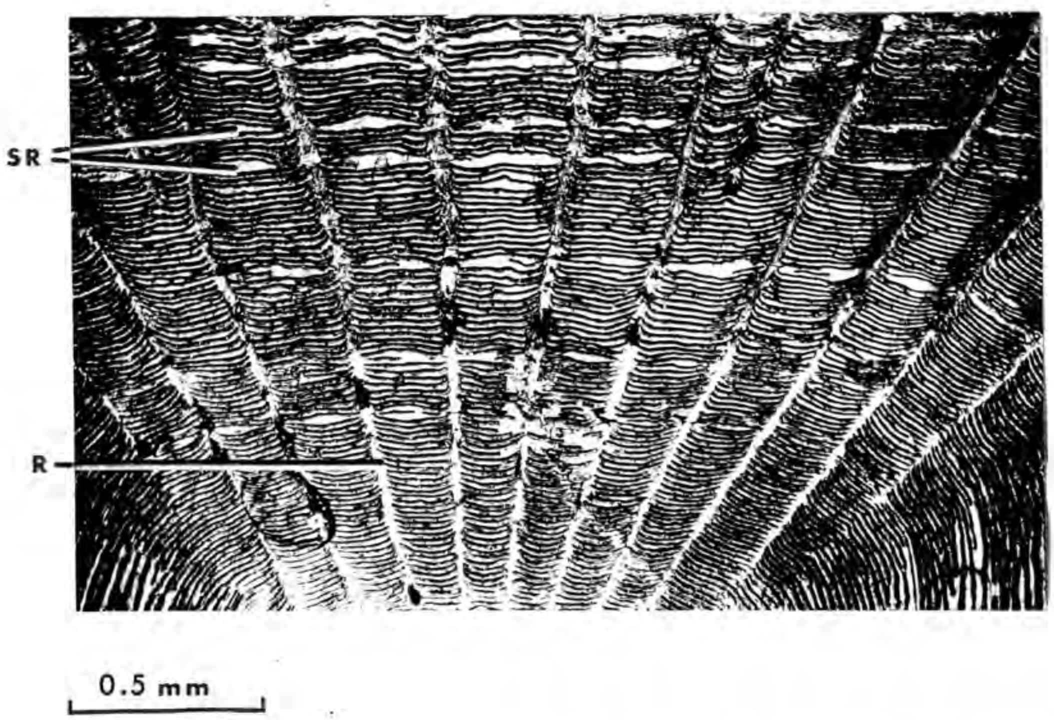


Figure 51: Scale of T. mossambica showing Radii (R) and Scale Rings (SR).

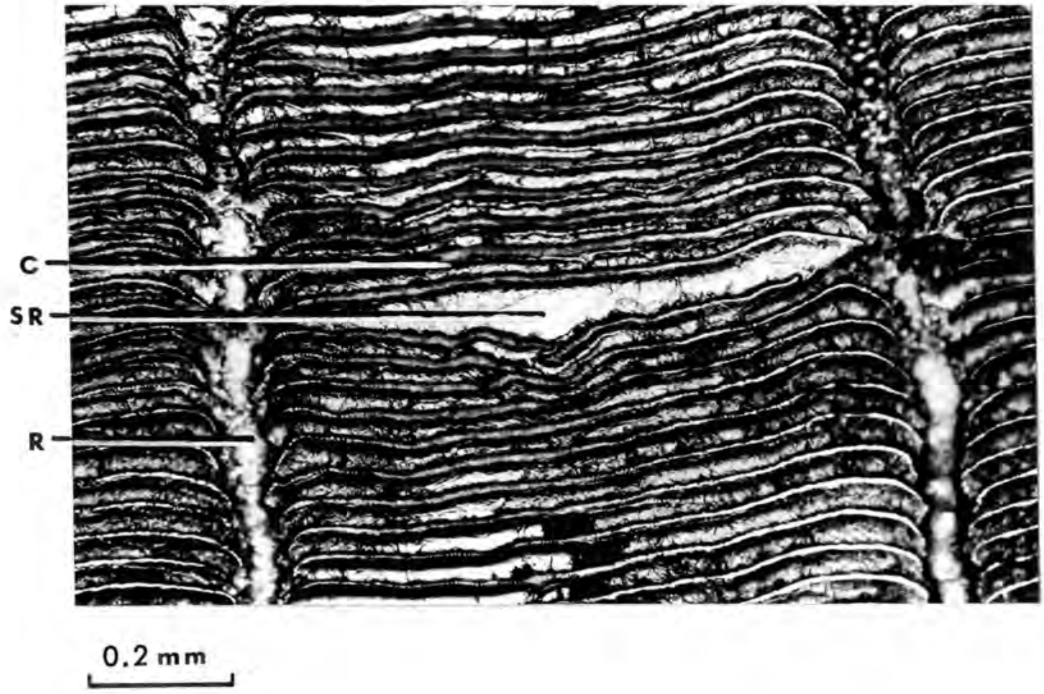


Figure 52: Scale of T. mossambica showing wide gap between circuli (C), forming a ring (SR). A radius (R) is also shown.

Figure 53: Scale of T. mossambica showing fragmentation and wide spacing of circuli (C).

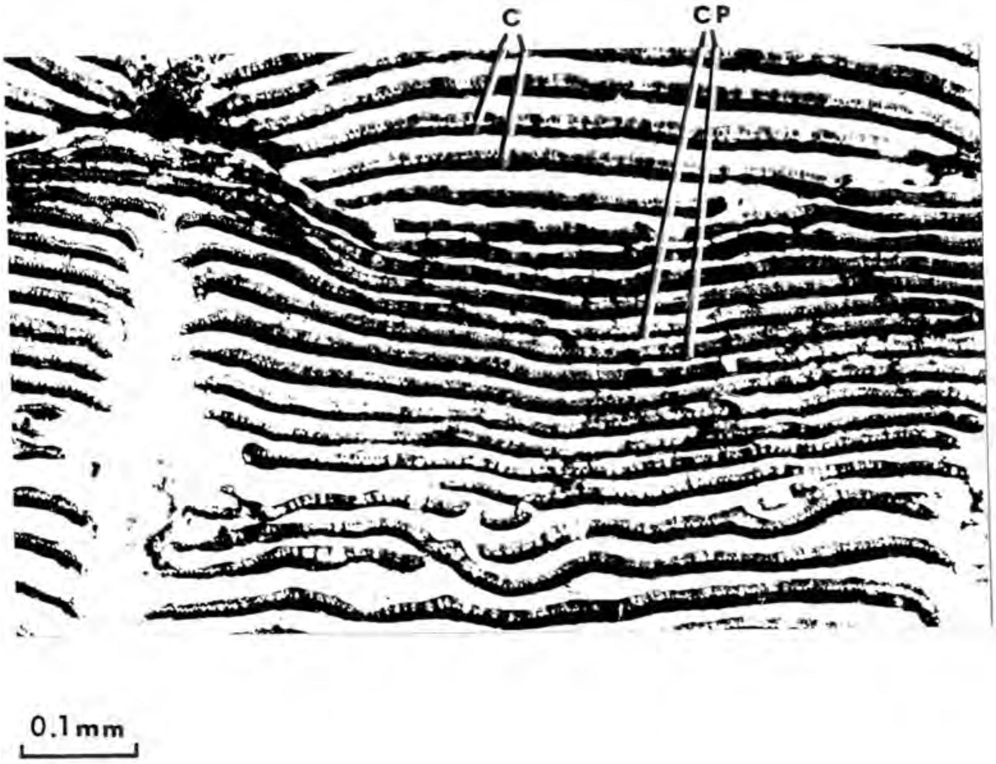


Figure 54: Scale of T. mossambica from Lake Sibaya showing close-packed circuli (CP) forming 'slow growth' ring, and normally spaced circuli (C).

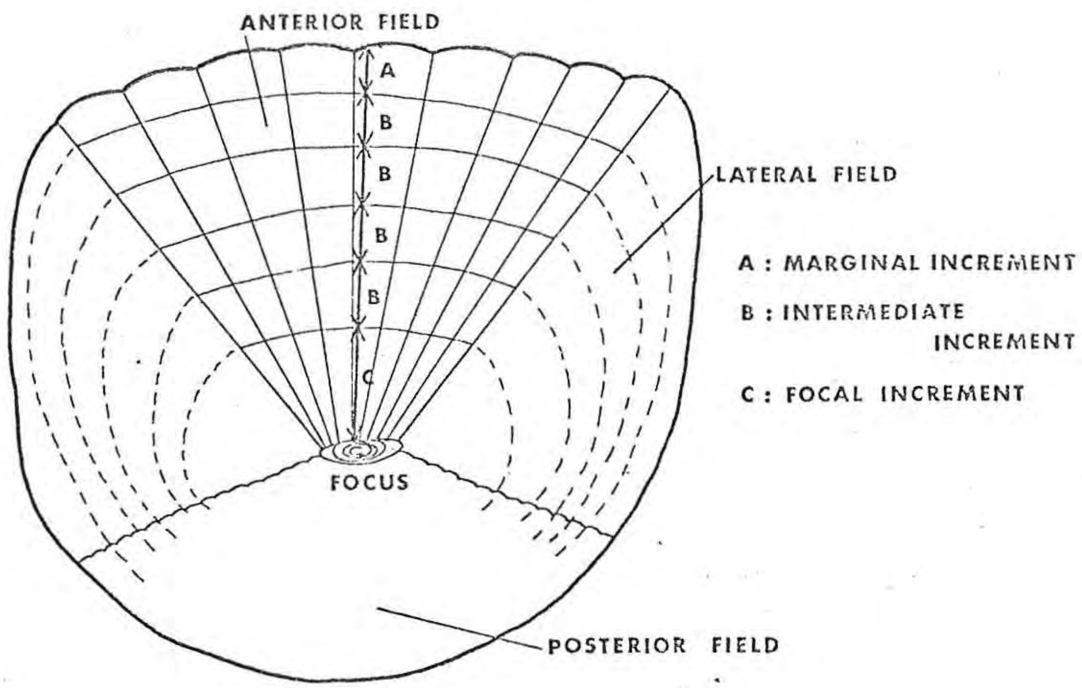


Figure 55: Diagram of a scale of T. mossambica from the region immediately above the pectoral fin. The position of various parts of the scale referred to in text are indicated.

circuli. Rings which did not extend from one lateral field across the anterior field and into the opposite lateral field were regarded as false rings, and were not used in age determinations. Circuli forming rings were 'irregularly arranged' in two different ways. In the majority of scales examined (over 96%), rings were formed by widely-spaced circuli (Figs 50, 51, 52 and 53), but a small number of scales with rings formed by closely-packed circuli were also found (Fig. 54). Only rings formed by widely-spaced circuli were used for age determinations. These rings were of two kinds. Those closest to the focus were formed by the looping of one or two intact circuli, thus forming a gap which is widest at a point midway between radii (Fig. 52). The other type of ring, always close to the anterior edge of the scale, and only present on scales with more than four rings, was formed by wide-spacing of circuli, which were usually fragmented to a greater or lesser degree (Fig. 53). The gap so formed is as wide on the line of the radii as between the radii. Wide-spaced rings formed by intact and fragmented circuli on the same scale are illustrated in Figure 51.

In this account, the focal increment of a scale is defined as the distance from the focus to the first scale ring (Fig. 55), and the marginal increment as the distance from the anterior edge of the scale to the most anterior scale ring. If no rings have been formed, there is no marginal increment. The distances between the rings are termed the intermediate increments.

The number of circuli in the focal increment averaged 30 (range 24 to 36). The number of circuli in the intermediate increments varied widely, there being on average, no more circuli in the anterior than in the posterior intermediate increments, except when more than 8 rings were present. In scales with less than 8 rings, the average was 8 circuli in intermediate increments.

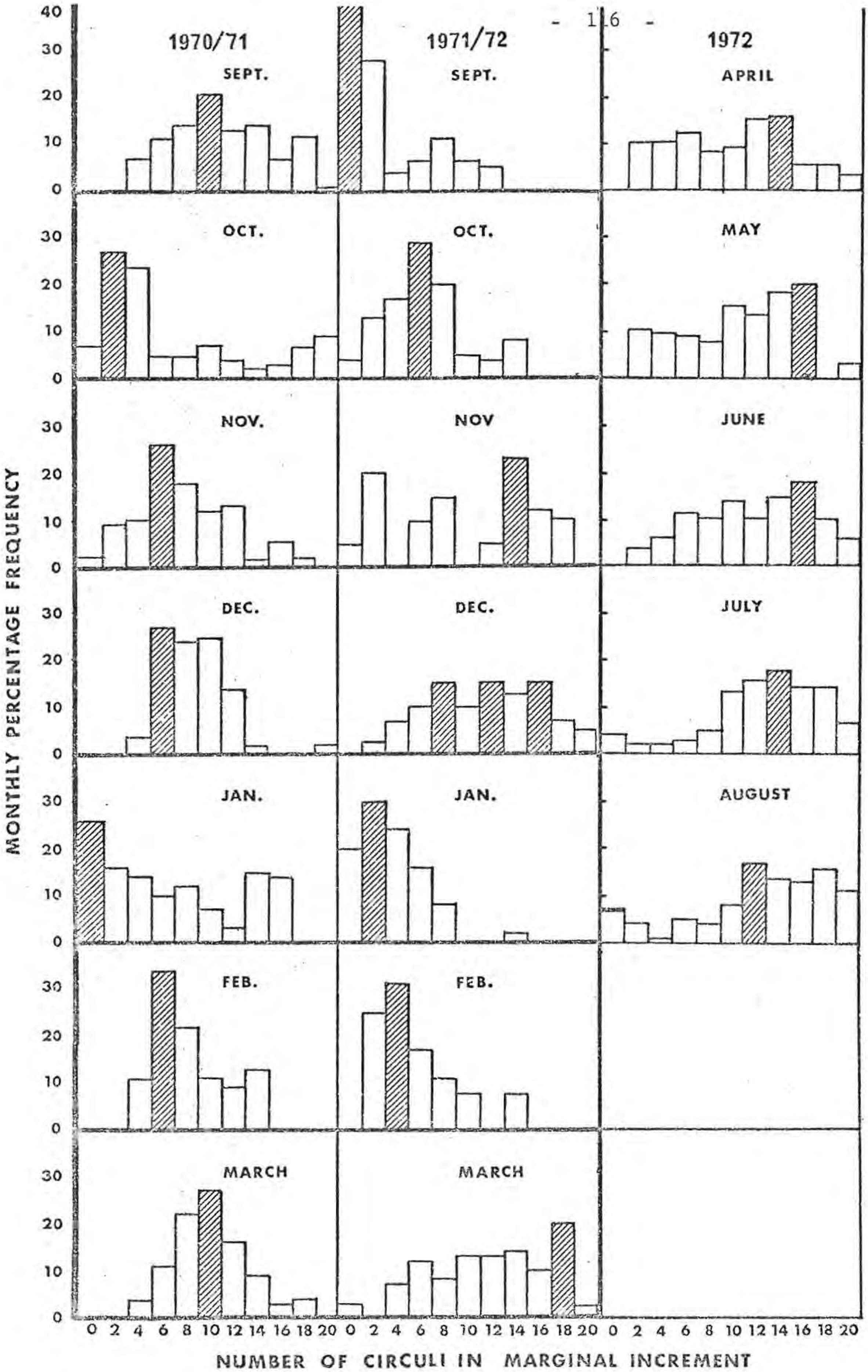


Figure 56: The percentage frequency of circuli in the marginal increment of 2223 T. mossambica scales. The circuli have been combined into groups of two. The data are derived from scales with one or more rings.

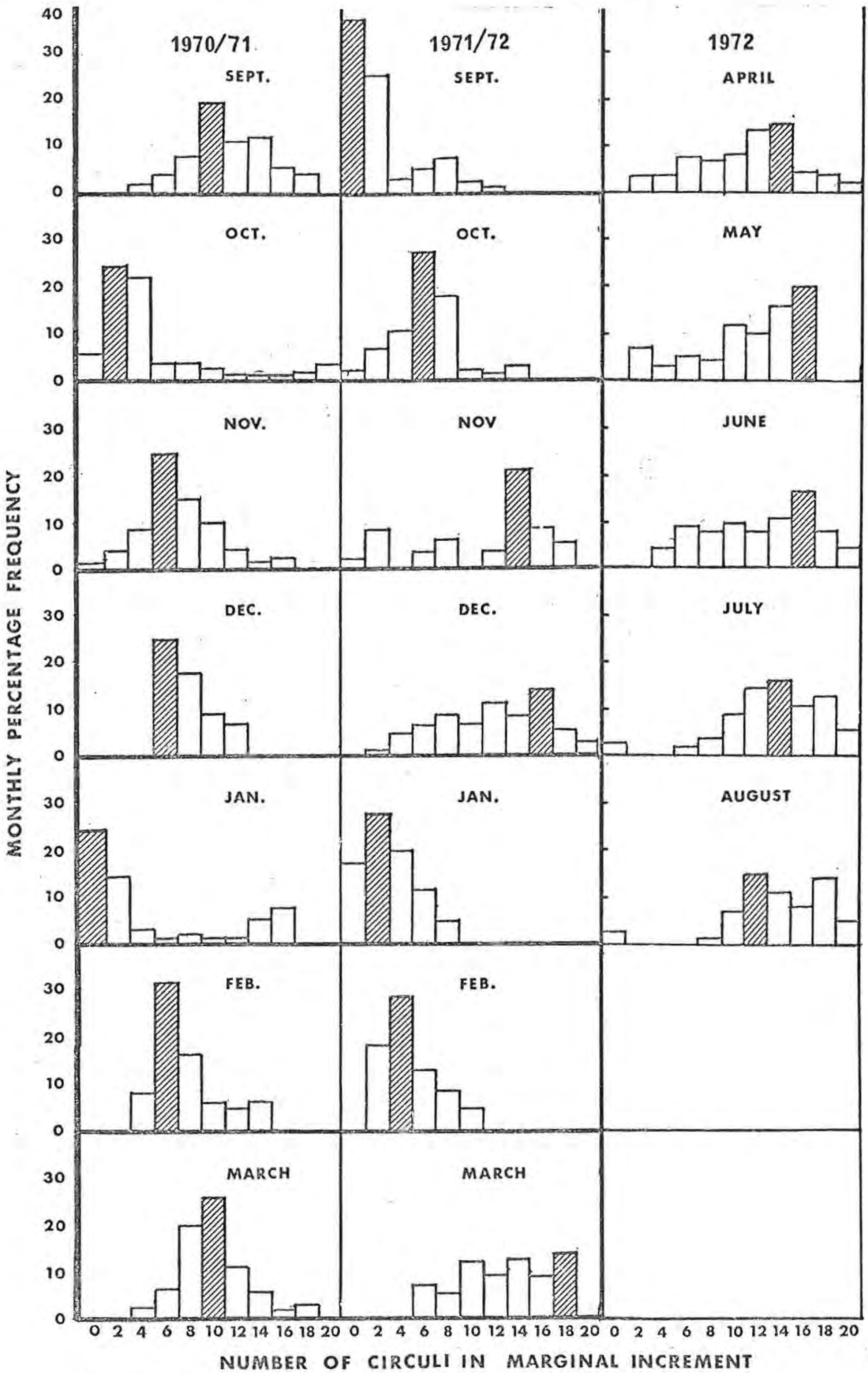


Figure 57: The percentage frequency of circuli in the marginal increment of T. mossambica scales. The data are derived from scales with less than 8 rings.

DETERMINATION OF TIME OF SCALE RING FORMATION

The number of circuli in the marginal increment depends on the time of sampling. Thus, in fishes sampled immediately, or shortly, after a ring has been formed, the ring is on the anterior margin of the scale, and there are no, or few circuli in the marginal increment. Therefore, if a large sample of scales is taken at particular times throughout the year and the number of circuli in the marginal increment of each scale is determined, the time of scale ring formation can be obtained.

The number of circuli in the marginal increment of scales from 1032 and 919 T. mossambica caught during the period September 1970 to March 1971, and September 1971 to August 1972 respectively, was determined. These results are represented as histograms in Figure 56 showing the percentage frequency per month of circuli in the marginal increment.

In Figure 56, a shift to the left of the mode of the frequency distribution occurs in October 1970, January and September 1971, and January 1972, indicating that new rings were formed by the majority of fish sampled in these months.

Since there are less circuli in the marginal increment after 8 rings, an analysis of circuli in the marginal increment with scales of less than 8 rings is presented in Figure 57. The shift of the mode is exactly similar showing that in the warm season of 1970/71, the ring was formed in October. In November and December, the number of circuli in the marginal increment increased gradually. In January a further ring was formed, followed again by a gradual increase in the number of circuli in the marginal increment. In the summer of 1971/72, a ring was formed in September, and again in January. On the other hand, there is no marked movement of the mode to the left in the period April to August 1972, indicating that, in the majority of the fish sampled, no new rings were formed during

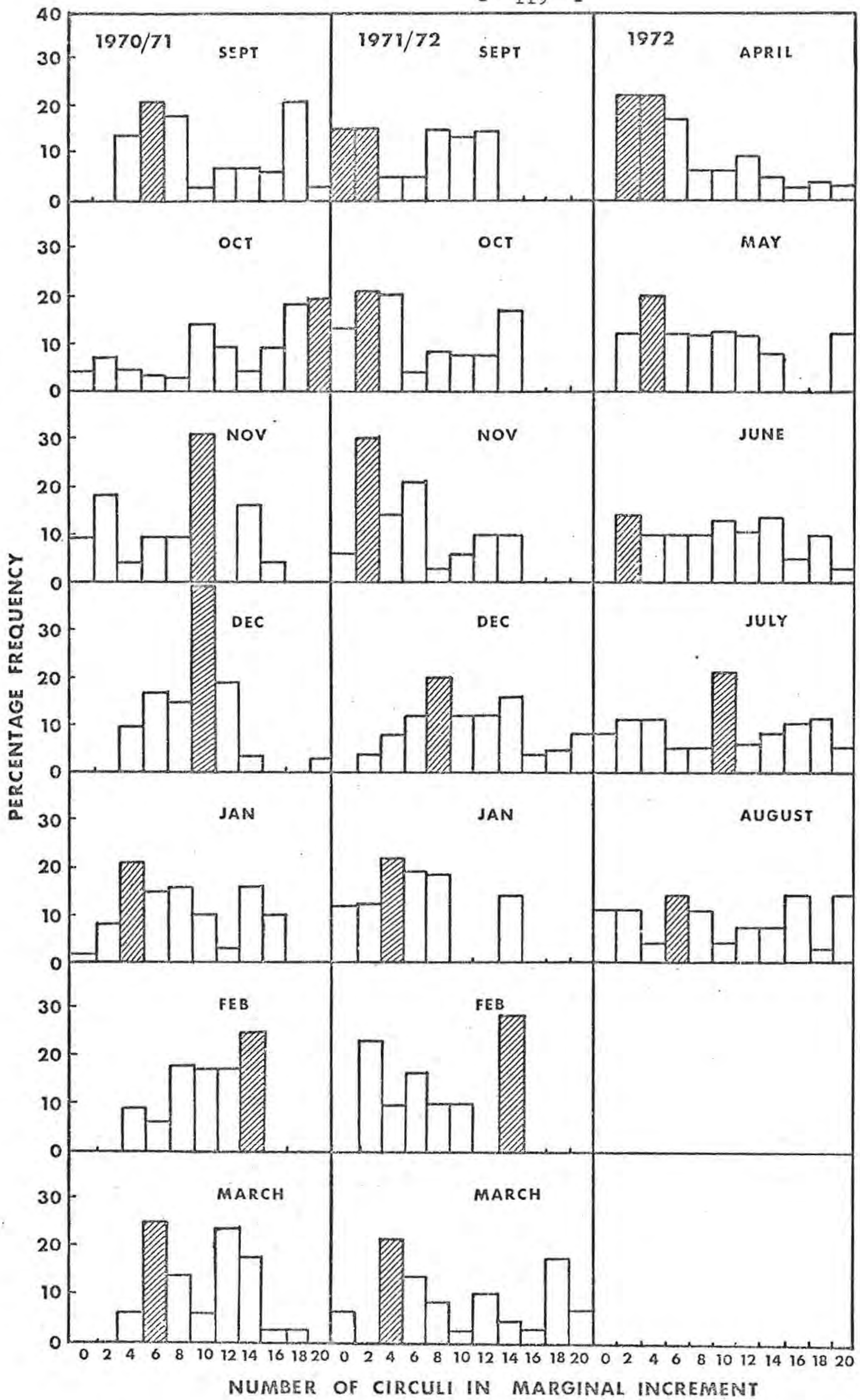


Figure 58: The percentage frequency of circuli in the marginal increment of T. mossambica scales with more than 8 scale rings.

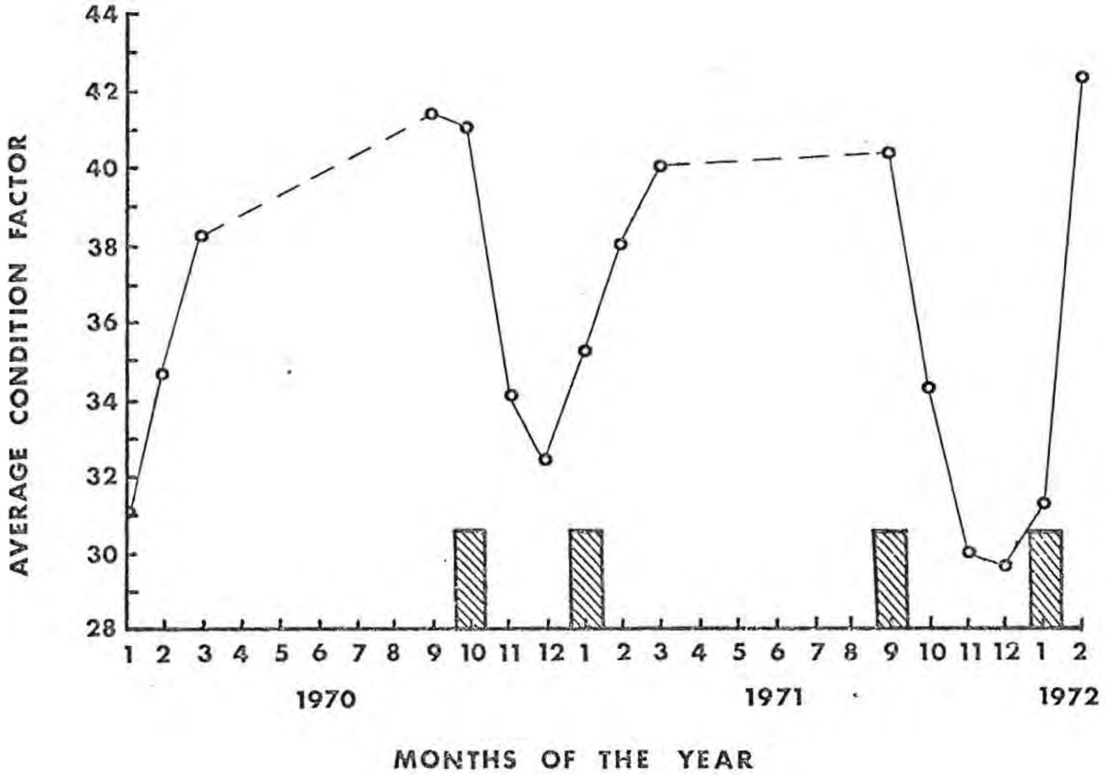


Figure 59: The changes in average condition factor of adult T. mossambica in the south basin over a period of 26 months. No data are available for the period April to August as few adult T. mossambica were caught in the period. The cross-hatched histograms indicate the suggested time of scale ring formation.

the cool season. Thus by eliminating those fishes with more than 8 scale rings, the pattern of scale ring formation becomes clearer.

The number of circuli in the marginal increment of scales with more than 8 rings was also plotted per month (Fig. 58). In general the modes of the circuli distribution are not as clear, nor is there a well-defined pattern of a gradual movement of the mode from the left to the right, though ring formation is suggested in September 1971 and April 1972. Rings would appear to be formed at less regular time intervals in fishes with more than 8 scale rings than in fishes with less than 8 scale rings.

The data presented above indicate that two rings were formed each summer in the majority of fish examined during 1970/71 and 1971/72. As there was no evidence of ring formation in the cool season, growth determination will be made on the assumption that two rings were formed per year.

FACTORS ASSOCIATED WITH RING FORMATION

Data from fishes caught in the seine nets and fish traps gave evidence of several events coinciding with early and late summer ring formation. The events coincident with early summer ring formation were:

(1) movement of a large number of T. mossambica into littoral areas (Fig. 33)

(2) initiation of breeding activity

(3) high condition factors relative to midsummer (Fig. 59).

Events concurrent with late summer ring formation were:

(1) movement of adult fishes from exposed to sheltered littoral areas (Table 16)

(2) termination of intensive breeding

(3) marked increase of average condition factors to a post-summer peak (Fig. 59).

Figures 60 and 61:

Regenerated scales of T. mossambica showing wide spacing of circuli (C) near focus (F).

Figure 60

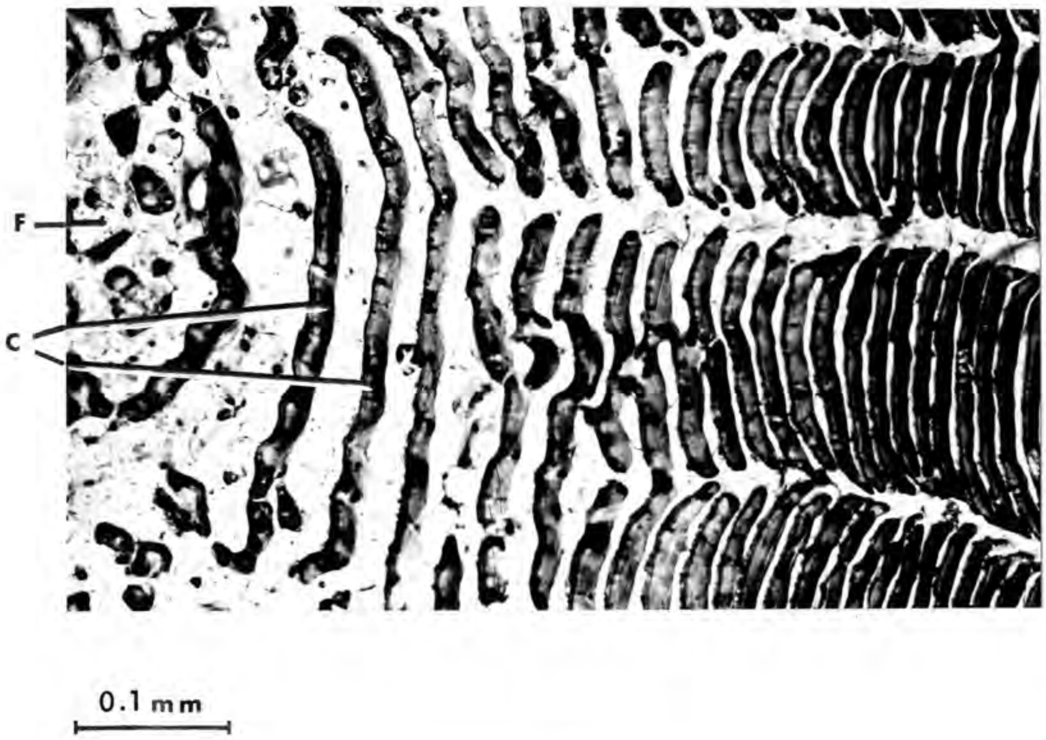


Figure 61

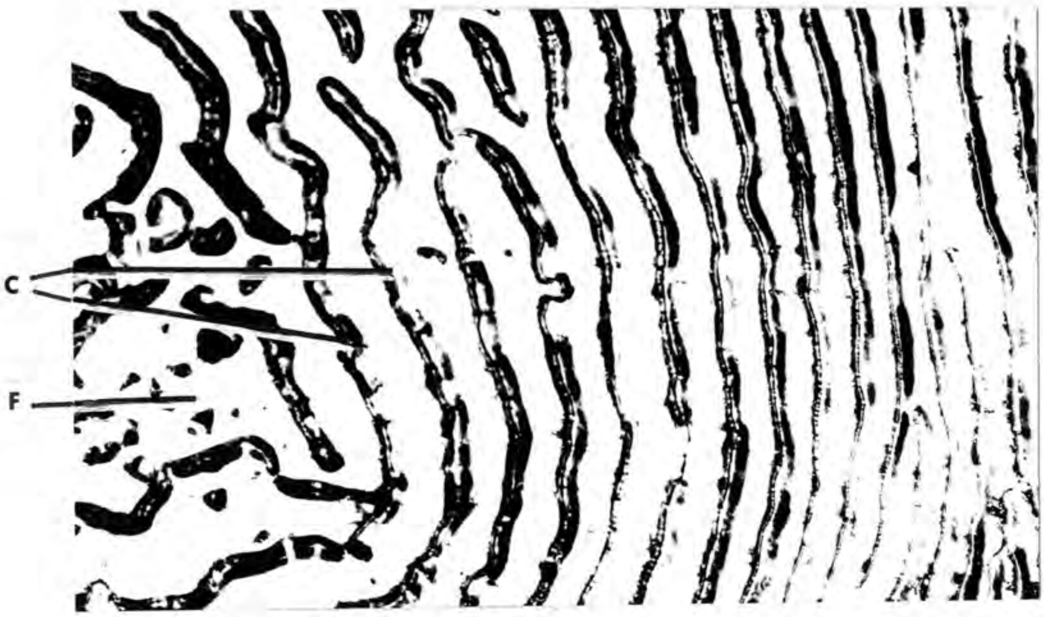


TABLE 16

The catch per unit effort of adult T. mossambica using type 2 fishtraps in sheltered and exposed littoral areas suggesting the movement of the population into the sheltered littoral zones in February, March and April.

CPUE	OCT NOV DEC	JAN	FEB MAR APR	MAY JUNE JULY	AUG SEPT
Adults on exposed littoral	8.3	0	0	0	0.2
Adults on sheltered littoral	0	2.3	10.4	0.1	3

Ring formation took place shortly before, and shortly after intensive breeding activity, at a time when condition factors were relatively high, or increasing to peak values (Fig. 59), and when feeding in well-vegetated bays took place.

A close look at a scale ring shows that the discontinuity is formed by a wider spacing of circuli than is normally the case (Figs 50, 51, 52 and 53). The circuli of a regenerated scale (Figs 60 and 61) are also widely spaced. Recovery of previously tagged fish from which key scales had been removed, indicated that regenerated scales replace the lost scales within 3 to 4 weeks. Obviously regenerated scales are fast-growing relative to normal scales, so that the arrangement of their circuli might reflect the arrangement of the circuli on a scale which is growing more rapidly than normal, i.e. wide spacing of circuli would appear to indicate rapid scale growth, which was found to be the case.

The available data suggest that the time of scale ring formation coincides with times of feeding, and attainment of peak condition factor and, as will be shown later, accelerated growth rates. If growth of body and scale are isometric, (their linear relationship indicates that they are), rings are formed at a time of rapid scale growth by wide spacing of the circuli. Wide spacing of the circuli would result if the basal plate of the scale showed a growth acceleration which tended to separate circuli in the inter-radial region. On the other hand, poor feeding and slow growth would result in a close packing of circuli, as shown in Figure 54. Fragmentation of widely spaced circuli, which was encountered in old fish only, is possibly brought about by re-absorbtion of calcium at a time when feeding is minimal, as suggested by Garrod and Newell (1958).

The conclusion reached, namely that the amount of food consumed is the factor controlling scale ring formation, is supported by experimental studies performed by Gray and Setna (1931) and Bhatia (1932, both in Pickford and Atz, 1957). Working on the rainbow trout Salmo gairdneri, these authors found that circuli are formed close together when the food supply is limited, but that in well-fed fish they are more widely spaced. By alternating the food supply of the rainbow trout, Bhatia was able to induce the formation of alternating bands of broad and narrow rings. It was shown that temperature had no effect, although, as pointed out by Pickford and Atz in nature it may be indirectly involved in correlation with the seasonal availability of food. Pickford (1953, in Pickford and Atz, 1957) found that administration of growth hormone to Fundulus heteroclitus elicits a resumption of scale growth in hypophysectionised fish, accompanied by the formation of a ring.

Other workers have suggested that scale rings comprised of widely-spaced circuli are formed not as a result of sudden growth acceleration; but by growth deceleration, loss of condition and/or maturation of the gonads (Holden, 1955; Garrod, 1959; De Bont, 1967); or as a result of low water temperatures (Jensen, 1957; Le Roux, 1961). Garrod and Newell (1958) found that the rings on the scales of T. esculenta from Lake Victoria, consisted of regions where the otherwise evenly-spaced concentric circuli were irregular. They suggest that the irregularity is related to the withdrawal of calcium during the period in which the gonads were maturing, and the young were being brooded. This withdrawal took place in order to maintain a reasonable level of calcium ion in the blood-serum of non-feeding breeding individuals. Garrod (1959) found that the T. esculenta of the northern waters of Lake Victoria had two distinct breeding periods each year, and that the 'maturation rings' were formed twice a year.

It is possible that scale rings formed by widely-spaced circuli are precipitated by different factors, or different responses to the same factors, in different ecosystems. The evidence from Lake Sibaya, however, indicates that rings are formed at a time of high food intake, when a sudden but temporary growth acceleration takes place prior to, and just subsequent to breeding. Without knowledge of the pre- and post-summer feeding migration of Sibaya T. mossambica, the cause of scale ring formation could erroneously have been assigned to the initiation and termination of breeding.

AGE DETERMINATION FROM OTOLITHS AND OPERCULAE

Otoliths and opercula were removed from 25 T. mossambica and prepared for examination as described in the section on methods.

Well-defined rings were present on 96% of the otoliths examined (Table 17). Otolith rings took the form of dark concentric rings alternating with light concentric rings of equal width. Otolith ring counts were found to correspond closely with scale ring counts (Table 17). Thus, as scale rings are laid down twice a year, (in the majority of fish for years in which data are available), otolith rings may also be bi-annual. However, the use of otoliths for age determinations is not compatible with the use of mark, release and recapture techniques, as fishes must be sacrificed for the removal of the otoliths. Preparation of the otoliths for examination is tedious and time-consuming if large numbers of fishes are to be examined. The method holds promise though as a means of cross-checking results obtained from examining scales once the frequency of otolith ring formation has been determined.

TABLE 17

Scale, otolith and opercula ring counts of 25 *T. mossambica* from Lake Sibaya.

UC = Unclear definition of rings.

number	scale ring count	otolith ring count		operculum ring count	
		left	right	left	right
1	10	UC	UC	4	UC
2	10	10	11	UC	UC
3	10	9	10	UC	UC
4	10	9	UC	UC	UC
5	10	9	10	UC	UC
6	9	9	9	UC	UC
7	9	9	9	5	5
8	9	9	8	UC	UC
9	8	10	9	4	4
10	8	8	9	4	4
11	8	8	9	4	4
12	8	8	8	UC	UC
13	8	7	8	4	UC
14	8	7	8	UC	UC
15	8	8	7	UC	UC
16	8	8	UC	UC	UC
17	7	7	7	4	4
18	7	7	UC	UC	UC
19	7	6	UC	3	UC
20	7	8	UC	UC	UC
21	7	8	7	UC	UC
22	7	6	UC	UC	UC
23	6	5	6	UC	UC
24	6	6	6	3	3
25	6	6	UC	3	UC

Age assessment (Table 17) using opercula bones was found to be unsatisfactory, as the majority (60%) of the opercula showed

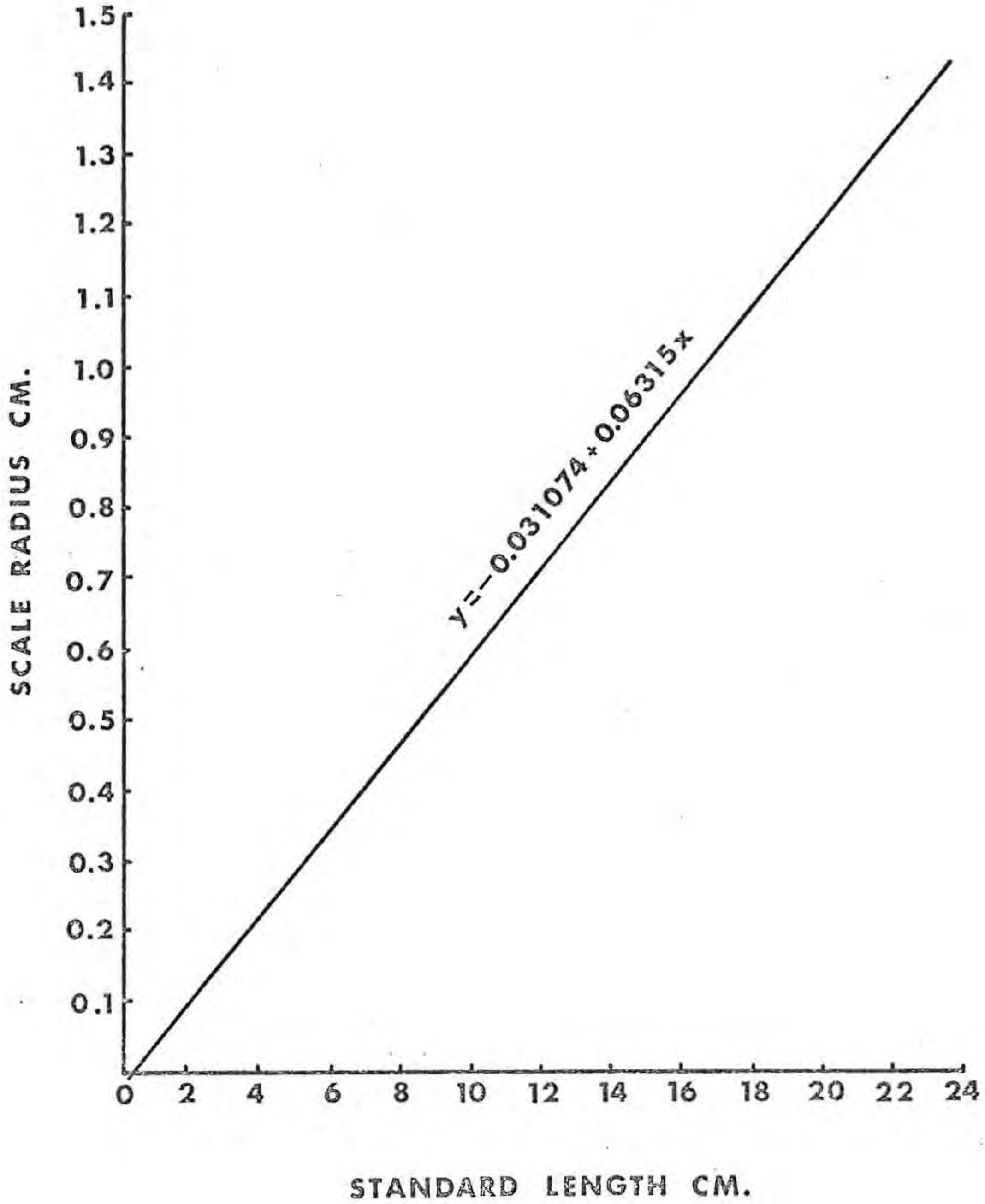


Figure 62: Regression line showing the relationship between standard length and scale radius of 128 T. mossambica. R = 0.766.

indistinct rings. Opercula bones were found to have light and dark zones. The dark zones, which were a quarter or less as broad as the light zones, were counted. Opercula ring counts are half the scale ring counts (Table 17), indicating that opercula rings may be formed once a year. Jubb (1967) reports that in T. mossambica, opercula bones will 'usually be found to have clearly defined growth zones, which by their spacing, can be used to compare the rate of growth of specimens. Widely spaced zones would indicate good growth under good conditions.' Lowe (1952) however, found in Tilapia from Lake Malawi that dark zones on the opercula bones coincided with annual periods of greatest phytoplankton abundance. The zones were interpreted as indicating spurts of growth. The author supports the suggestion of Jubb that light zones are formed by growth acceleration. Thus in the T. mossambica from Lake Sibaya the light zones may reflect good or normal growth in the warm part of the year, and the dark band a cool season growth check.

GROWTH DETERMINATIONS FROM SCALES

Back-calculations of growth history were made on the assumption that two scale rings are formed per year. Choice of a formula for back-calculations from scale data is determined by the relationship between fish growth and scale growth. The standard lengths of 128 T. mossambica of all size groups caught throughout the year in Lake Sibaya were plotted against their corresponding scale radii (scale radius = distance from the focus to the midpoint of the anterior scale edge). In the standard length range, 4 to 24 cm SL, the scale radius:fish length relationship was found to be linear. The regression line drawn from these data cut the abscissa at 5 mm (Fig. 62). According to Tesch (1968) a scale radius:fish length relationship which is linear, and intercepts the abscissa near the origin, is described by the following formula (a modification by Fraser and Lee of the direct proportionality formula of Lea (1910)):

$$l_n - c = \frac{S_n}{S}(l - 5)$$

where l_n = SL when ring 'n' was formed

c = intercept on abscissa = 5 mm

S_n = radius of ring 'n' (at length l_n)

S = total scale radius

l = SL when sampled

Annual length increments were calculated using this modification of Lea's formula for 450 T. mossambica collected from Sibaya at all times of the year.

As the direct proportionality formula used for back-calculations of growth rates relies on isometric scale growth and a constant relationship between body and scale growth, allometric scale growth would give inaccurate results. Some workers have found in Tilapia that under conditions of stress such as starvation or loss of condition, growth of body and scales are not necessarily concurrent or isometric (e.g. de Bont and Ceillie, 1966, in T. rendalli; de Bont, 1967, in Tilapia). From their results it is clear that growth rates cannot be accurately determined unless the ontogeny of the scale is well-documented and corrections have been made for allometric growth.

No corrections have been made for allometric growth in the present study. A test of the reliability of the growth curves obtained by back-calculations, however, indicates that the curves are fairly accurate: A growth curve was compiled using data from 72 fishes which were found to have the outer scale ring on the anterior edge of the scale, i.e. the ring had been formed very recently. These fishes, consisting of 35 female and 37 males, were all caught in the post-summer feeding period when the late summer ring, i.e. the ring completing the couple formed per year, was found to be laid down in the majority of fishes sampled. The standard

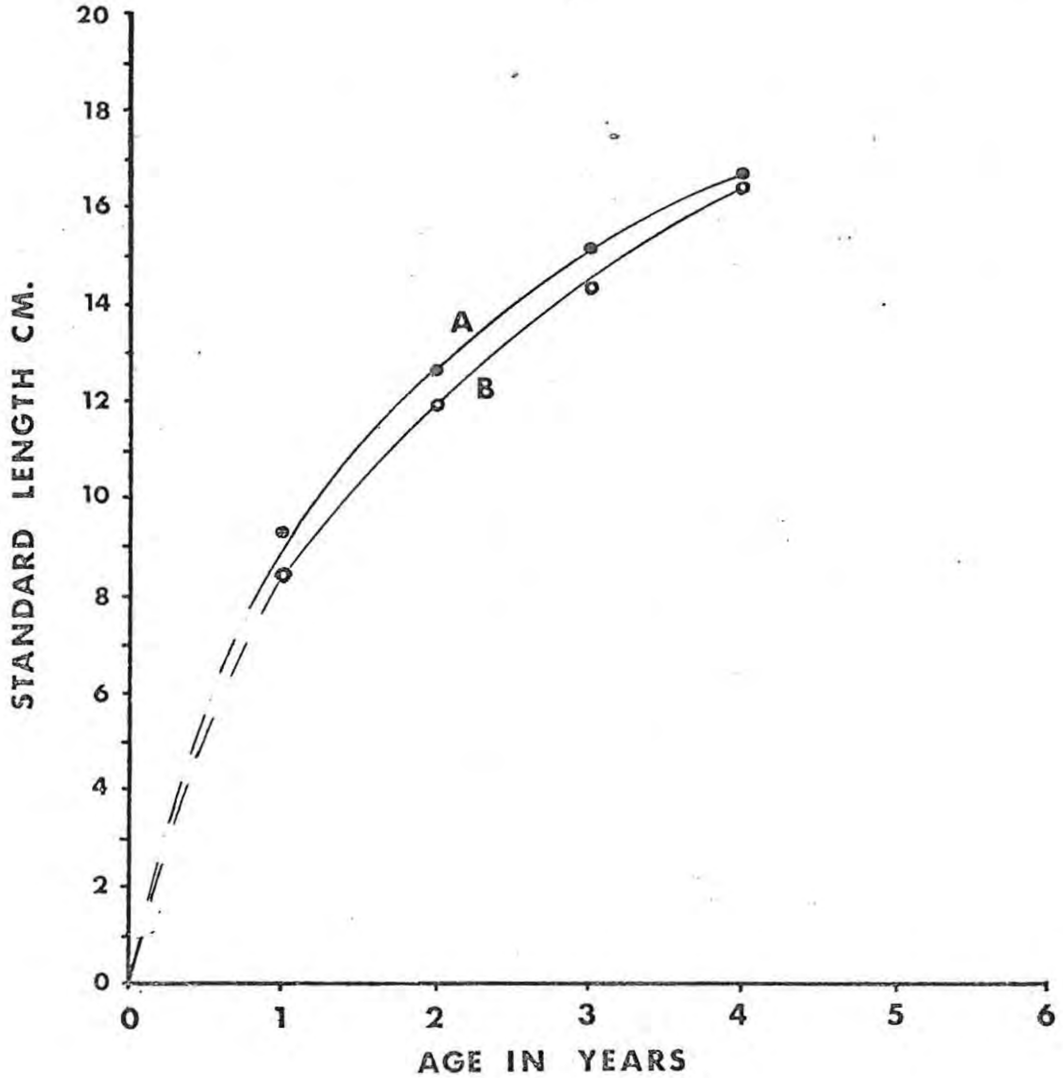


Figure 63: Linear growth rates of T. mossambica from Lake Sibaya calculated (A) using scales in which a ring had very recently been formed; (B) using back-calculations from a modification of Lea's (1910) formula.

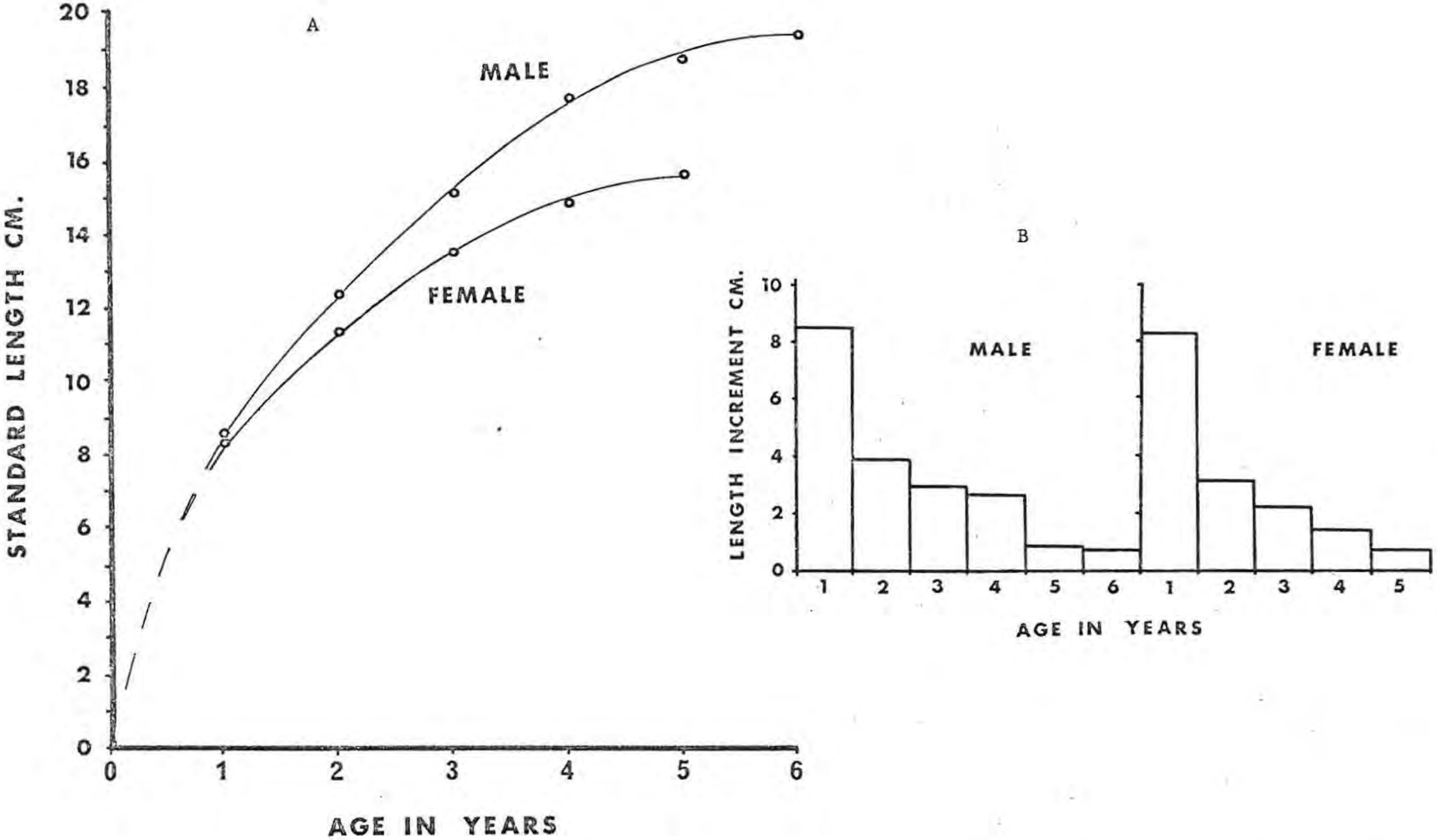
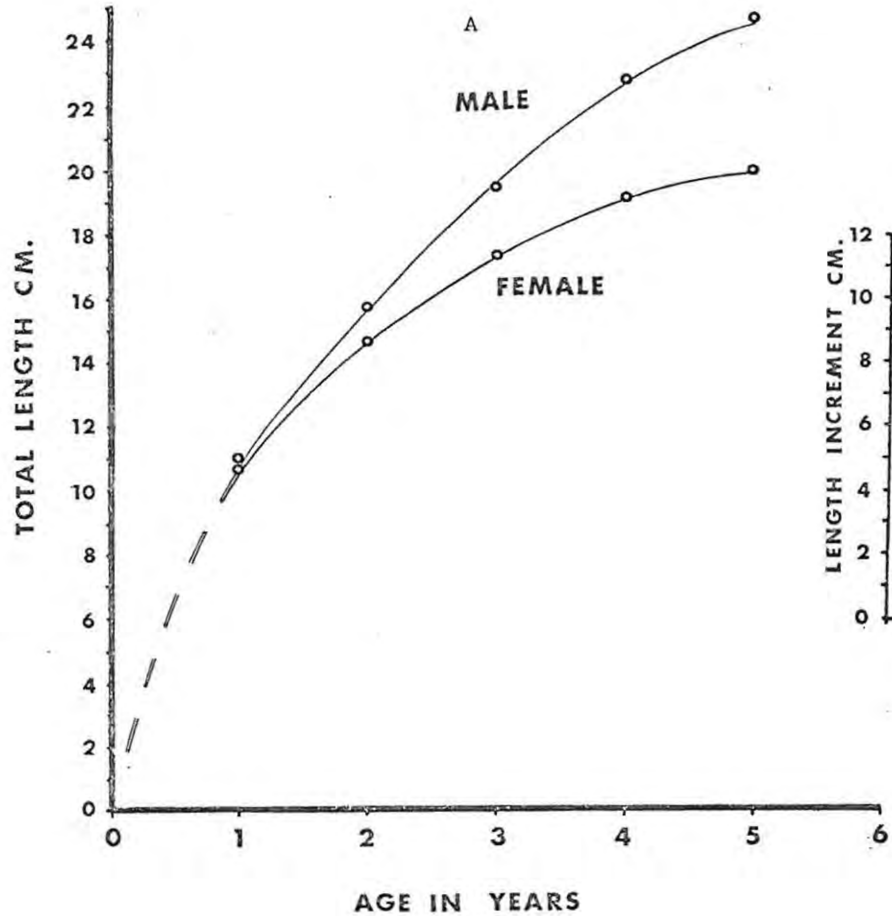


Figure 64: Linear growth rates in standard length (A) and length increments (B) of male and female T. mossambica from Lake Sibaya.



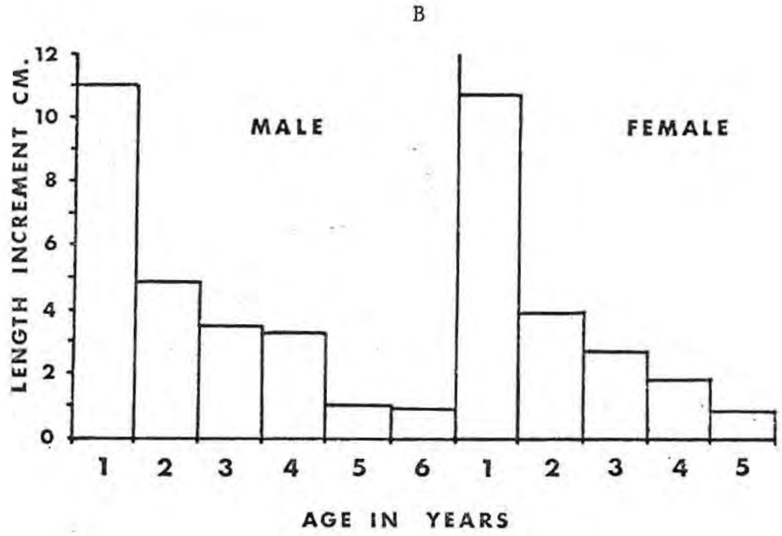


Figure 65: Linear growth rates in total length (A) and length increments (B) of male and female <u>T. mossambica</u> from Lake Sibaya.

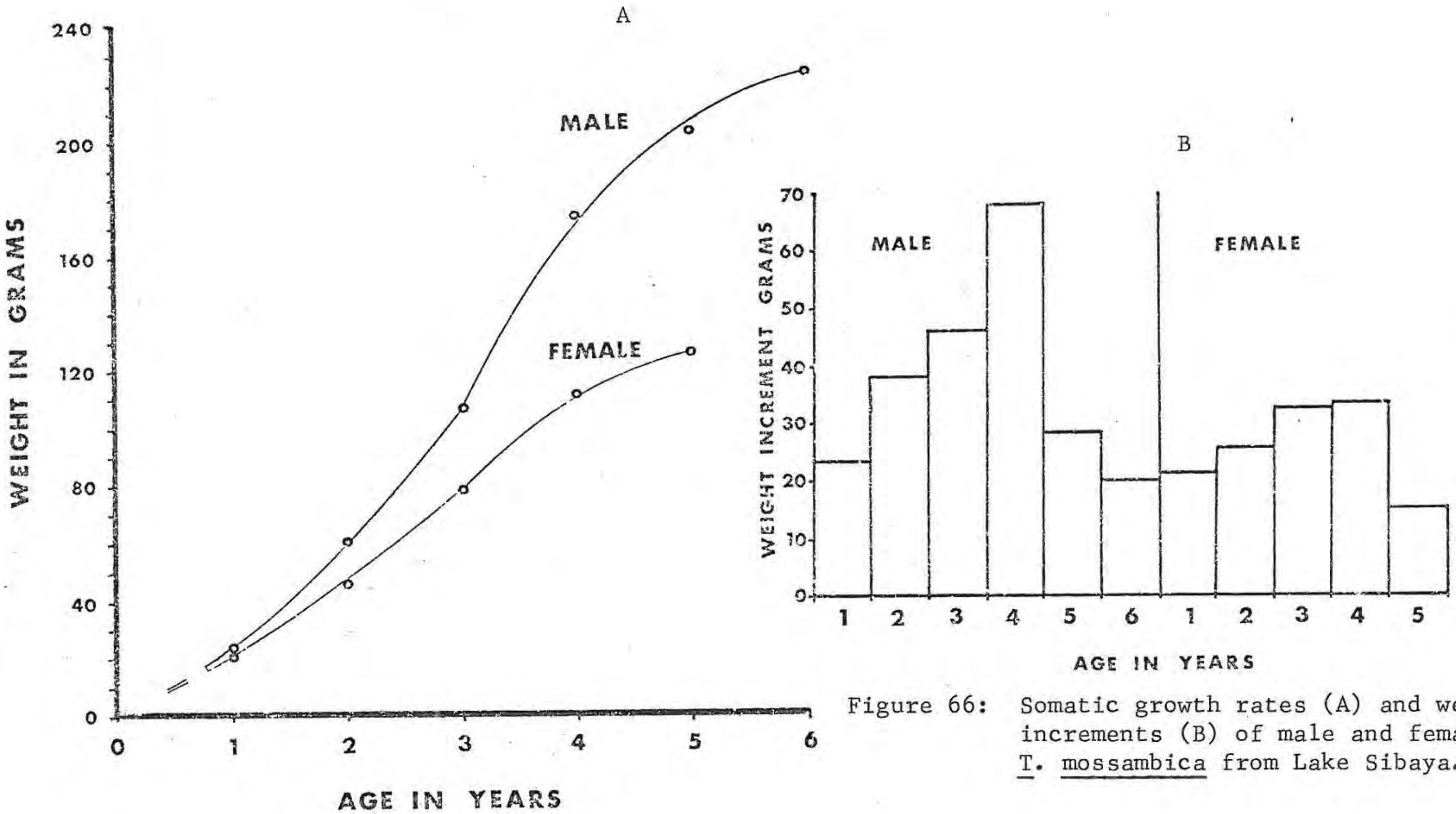


Figure 66: Somatic growth rates (A) and weight increments (B) of male and female T. mossambica from Lake Sibaya.

lengths of the 72 fishes sampled were regarded as the standard lengths at year 1, 2, 3, 4 and 5, depending on whether the fish had 2, 4, 6, 8 or 10 rings on the scale, (thus assuming that 2 rings are laid down per year). The growth curve obtained in this way (curve A in Fig. 63) was compared with the growth curves obtained using back-calculations from Lea's formula from 450 fish caught in the lake (curve B). The curves show a close fit, indicating that growth of body and scale is reasonably isometric, and that the growth curves obtained by back-calculating are sufficiently accurate at least for a general statement on growth.

GROWTH CURVES OF *T. MOSSAMBICA* FROM LAKE SIBAYA

Growth curves and annual increments calculated for standard length and total length (using Lea's formula) and weight of male and female *T. mossambica* from Lake Sibaya are given in Figures 64, 65 and 66.

As shown in Figures 64 and 65, male *T. mossambica* grew faster than females after the first year. In both sexes, the linear growth rate was highest in the first year, but decreased progressively thereafter. In males, the linear growth increment in the first year is double that in the second year, and approximately equal to the combined increments of the 2nd, 3rd and 4th years. In females, the 1st year increment is also double that in the 2nd year, and equals the combined increments of the 2nd to 5th years.

Somatic growth curves (i.e. increases in weight, Fig. 66A) indicates that in the male and female fishes, there is a gradual increase in weight in the first three years, reaching a peak rate in the fourth year. The somatic growth rate decreased markedly in the 5th year. Annual weight increments (Fig. 66B) were highest in the 4th year for male and female *T. mossambica*. Minshull (1970) suggested that juvenile *T. mossambica* from Lake Sibaya have a very slow growth rate. He found a bimodal length distribution in fishes caught in shallow water in fishtraps and concluded that the length increment between the two modes (2 cm) represented a year's growth. It is thought that the traps were laid in slightly different water depths and that Minshull mistook two size classes of juveniles of approximately the same age, for fishes of two different year classes.

Four other characteristics related to growth in T. mossambica from Lake Sibaya are conveniently mentioned here: the size and age at first maturity, the length composition of the breeding population, the mean longevity, and the final size of the fishes.

To determine the size at first maturity, 754 T. mossambica from 2.5 to 8.3 cm SL were examined for the degree of maturation of the gonads in the period January to March 1970. The fishes were arranged into centimetre length groups, and divided into three categories: immature; mature males; and mature females (Table 18). A fully developed white testis was regarded as the criterion of maturity in males, and an ovary containing eggs the criterion in females. Females in the sample were found to have matured at a smaller size than the males. The smallest mature females measured 6.8 cm and 7.8 cm SL, and the smallest mature males 10.4, 10.5 and 10.9 cm SL (all measured in January). The smallest actively breeding fishes caught in the lake measured 12.0 cm SL (male) and 8.4 cm SL (female).

TABLE 18

Percentage of immature and mature male and female T. mossambica in different length categories sampled from January to March 1970.

Centimetre length group	% of sampled population immature	% of males mature	% of females mature	Number of fish examined
4-5	100	0	0	112
6-7	99	0	1	319
8-9	97	0	6	220
10-11	64	38	60	49
12-13	23	60	83	39
14-15	0	100	100	37

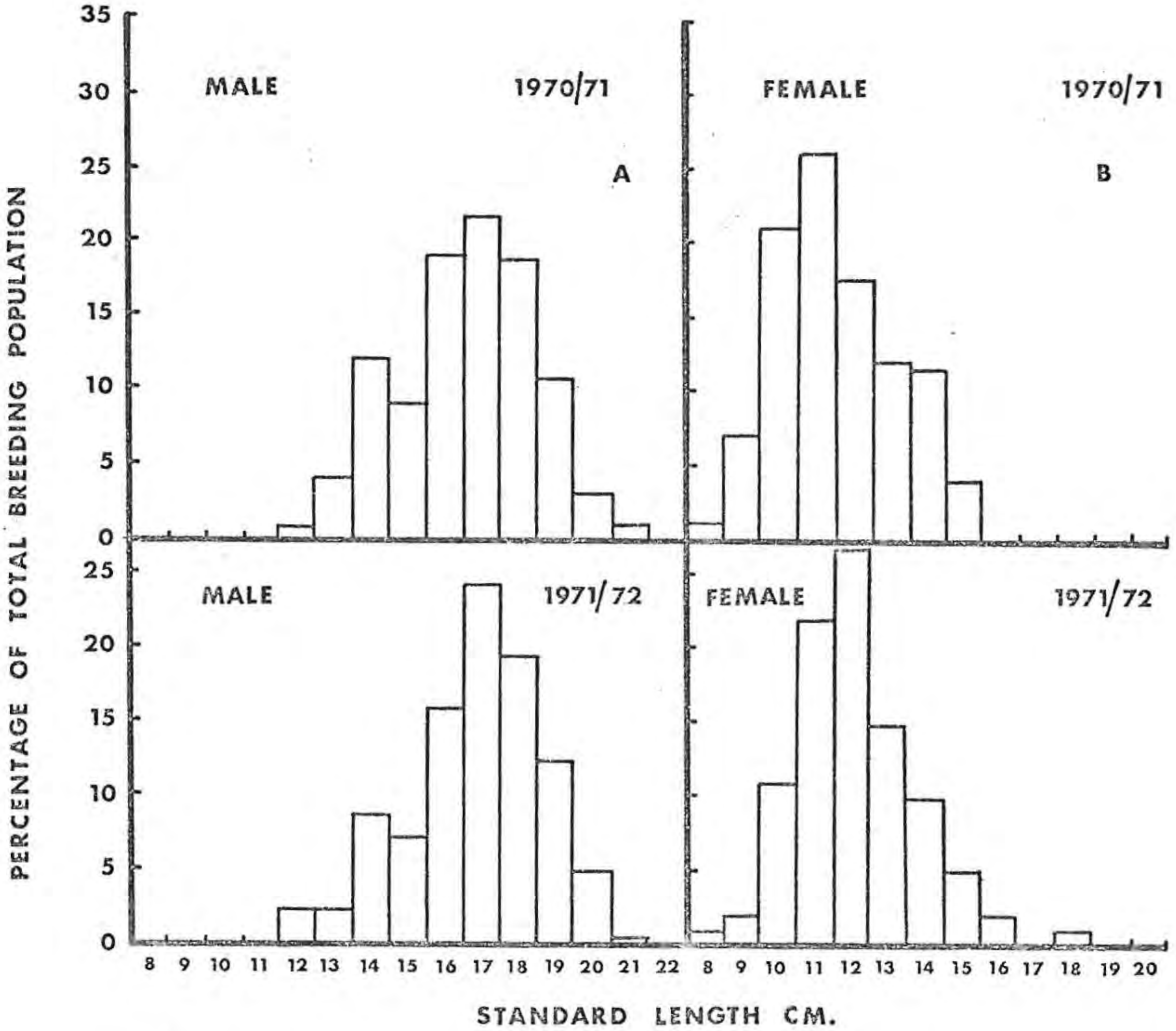


Figure 67: The length composition of seine catches of breeding male and female T. mossambica caught in the south basin in the summers of 1970/71 and 1971/72.

According to these data the size at first maturity is 10 cm in males and 8 cm in females. Extrapolation of these lengths onto Figure 64 indicates that females first breed after one year (i.e. in their second summer), whereas males first breed after two years. The average weight of maturity (27 gms in females, 57 gms in males) is approximately 12% and 17% of the maximum weight for females and males respectively. The length frequency of the breeding population catches in the warm seasons of 1970/71 and 1971/72 are given in Figures 67A and B. In males, the mode fell at 17 cm SL, and in females at 11-12 cm SL.

As regards longevity, little can be said with certainty as scale rings in excess of 8 were often ill-defined as a result of excessive fragmentation, or re-absorption along the anterior scale edge. Reabsorption was only noted in large fishes (average SL 17.0 cms). Data from the few fishes in which rings in excess of 8 were well-defined, indicated that up to 16 rings may be formed in male fish, and 14 rings in females. If the rate of scale ring formation in these fishes was constant throughout life at 2 per year this would give a longevity of 8 and 7 years respectively. In the majority of fish examined, the number of rings did not exceed 12, giving a longevity of 6 years.

The maximum final size recorded for T. mossambica from Lake Sibaya was reached by a male which measured 23.6 cm SL (29.2 cm TL, weight 320.6 gms). Minshull (unpublished field notes, 1969) recorded male T. mossambica from Lake Sibaya up to 29.4 cm TL (354.4 gms), and 30.2 cm TL (343.0 gms). The largest female I caught measured 18.5 cm SL (22.8 cm TL, weight 215 gms).

AGE AND GROWTH DETERMINATIONS USING MARKED FISH

Tagged fishes recovered from the lake and experimental pools were used as an aid in establishing the time of scale ring formation, and for determining growth rates. Determinations of age and growth

TABLE 19

Scale ring counts of tagged T. mossambica recaptured in Lake Sibaya

Fish number	Scale ring count		Number of rings laid down	Days at liberty	Months at liberty	Change in weight AS % of weight on release
	On release	On recapture				
1	8	8	0	570	Nov-June	-2
2	6	7	1	351	Oct-Sept	+4.7
3	2	4	2	310	Mar-Jan	-12.5
4	2	4	2	304	Mar-Jan	+6.7
5	4	5	1	34	Sept-Oct	0
6	3	4	1	16	March	0
7	4	4	0	14	March	0
8	4	4	0	10	March	0

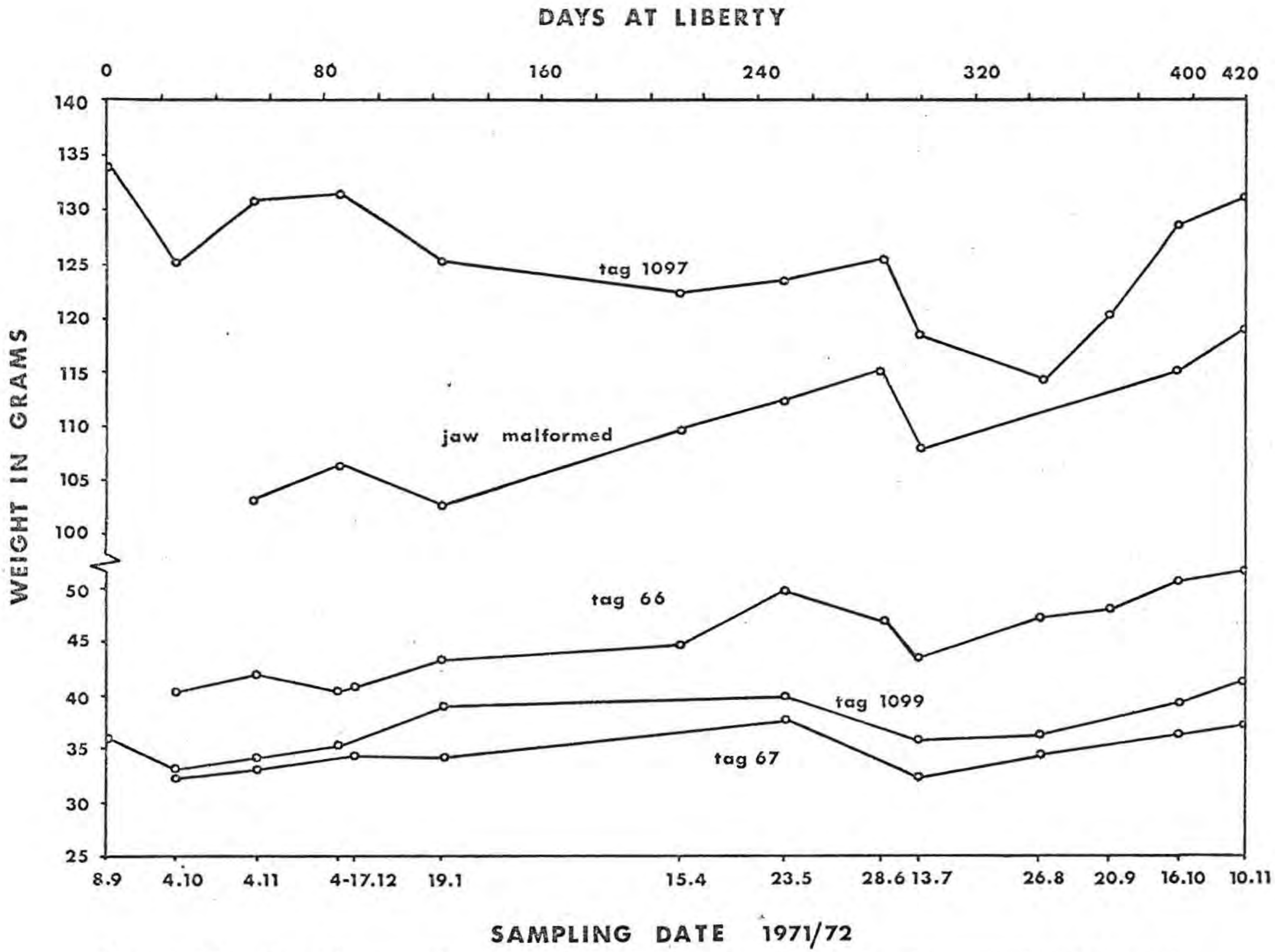


Figure 68: Somatic growth rates of adult T. mossambica in the experimental pool.

using tagged fishes were, on the whole, unreliable because of the variably detrimental effect of the tag on growth rates.

Seven recaught tagged fishes had clearly defined scale rings (Table 19). The data support the hypothesis that 2 rings are formed per year, at least in fishes with less than 6 scale rings. Thus, fishes 3 and 4, free for 310 and 304 days respectively, each laid down 2 scale rings. Fishes 1 and 2, with 8 and 6 scale rings respectively on release, formed 0 and 1 ring after 570 and 351 days. As indicated in the table, fishes 1 and 3 showed weight losses. Thus rings may be laid down even if the fish shows a nett weight loss between sampling periods. The other 4 fishes (numbers 5-8 in Table 19) were free for short periods from September to October, and in March. Two of these fishes formed rings, whereas ring counts for the other two fishes remained the same, although there was a slight increase in the number of circuli.

Tagged fishes recaptured from the lake showed erratic growth rates, possibly induced by the tag. Of 20 fishes recaught after more than 2 days, only 2 showed weight gains beyond the sampling error of 1 gram. Fish 103, free for 351 days, gained 10 gms, representing a 4.6% increase in body weight (weight on release 214 gms). Fish 489, free for 54 days, gained 2 gms, a 5% increase on the original weight of 39 gms. The other 18 fishes showed weight losses (7 fishes), or remained the same weight (11 fishes). Three fishes showed length losses of 3 mm.

Fortythree tagged fishes were introduced into the experimental pools. Initial overpopulation in the pool may probably be correlated with the severe weight losses recorded in all pool fishes. For this reason, all the fishes, with the exception of 4 tagged and one untagged fish, were subsequently removed. These 5 fishes showed positive growth (Fig. 68). Fish 1097, after an initial weight loss of 10 gms, gained weight in summer when the fish density in the pool had been reduced. This fish remained the same weight from January to June, lost weight in July and August, and gained weight in September and October. Three smaller tagged fishes (66, 67, 1099) grew slowly from October to May, gaining approximately 1 gram per month, lost weight in July, and gained weight at a rate of 2-4 gms per month in the period August to November. The four tagged fishes showed the same growth pattern - weight gains in the warm season, weight losses in July, and an increase in growth rate in the period September to November. These seasonal variations in growth rates are thought to have been caused by temperature fluctuations, as food was always available in the pool. The pool water temperature averaged 26°C in the warm season, but as in the main lake, decreased to 17°C in July, sufficiently low to inhibit feeding in *T. mossambica* according to Josman (1971).

A single untagged fish was introduced into the pool. This fish, despite a malformed premaxilla, gained an average of 2 gms per month from November to June, lost 12 gms in July, then increased in weight at a rate of 4.5 gms per month from August to November. This untagged fish showed the same growth pattern as the tagged pool fish, but gained weight more rapidly throughout the sampling period.

The increase in weight over a year of the tagged pool fishes (maximum 8 gms, fish 66) was considerably lower than growth rate postulated in Figure 66 (38 gms for a fish the same age as fish 66). The untagged pool fish also showed poor growth in relation to the data given in Figure 66.

GROWTH DETERMINATIONS BY THE PETERSON METHOD

The length composition of fishes in a population will often exhibit modes among the smaller fish which correspond to year-groups. These modes will be most pronounced in fish with a short spawning season. As the individuals in a population grow, the growth rate can be determined by noting the horizontal movement of the length

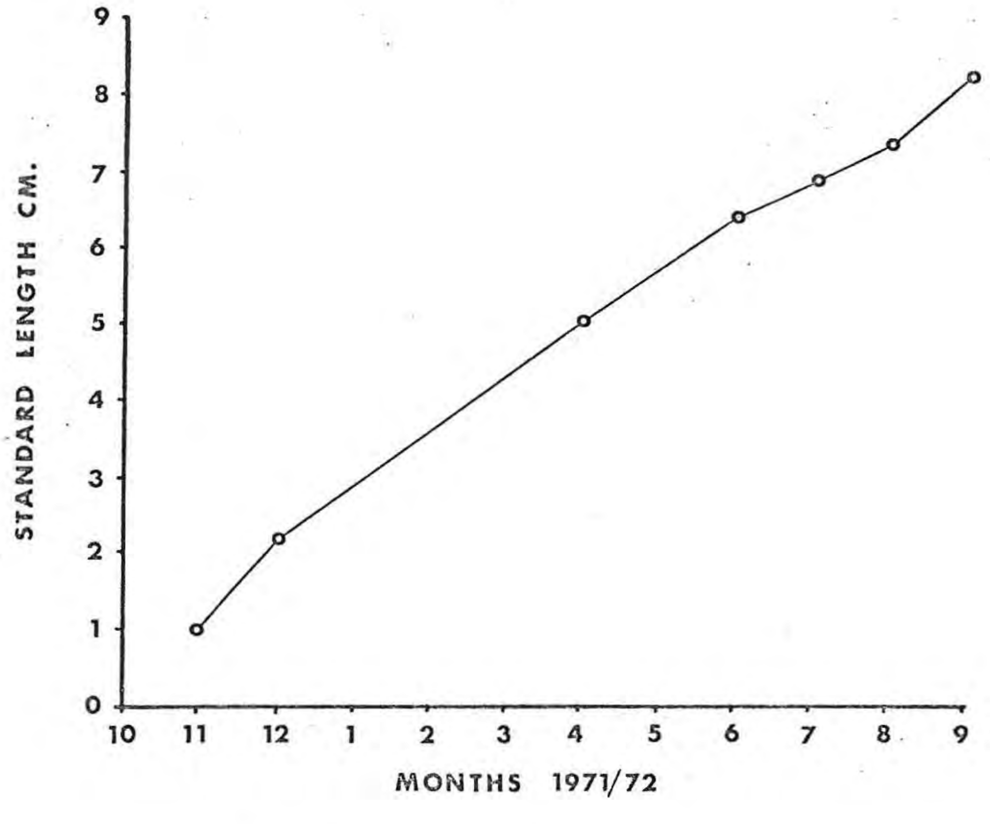


Figure 69: Linear growth rates of T. mossambica fry in the experimental pool.

frequency mode. T. mossambica from Lake Sibaya have been noted to have a spawning season lasting 6 months, with the result that length frequency modes are not well-defined, and this method is not applicable in the wild population. Some indication of the growth rate of T. mossambica fry in experimental pool 2 was obtained, however. Six mouth-brooding female T. mossambica were introduced into the pool from the lake. The fry, released within 10 days, were caught at irregular intervals over 11 months, and sampled for standard length. As shown in Figure 69, the growth rate was high, monthly increments averaging 8 mm. A modal size of 8.5 cm was reached after 11 months. This result also shows that Minshull's (1970) suggestion that juveniles grow slowly is in error.

COMPARISON OF GROWTH RATES WITH OTHER T. MOSSAMBICA POPULATIONS

There is no published study on the growth rates of T. mossambica in a natural system. A single study on growth rates in impoundments was traced. Le Roux (1961) reported on growth rates of T. mossambica from various impoundments in the Transvaal. The growth rate was found to vary widely in different waters. The fastest growing population reached 10.1 cm TL in the first year, which is exceeded by T. mossambica from Lake Sibaya, which reach 10.9 cm TL. However, as the error on the growth rate estimation is about 1 cm (Fig. 63) this difference is not significant and the populations would appear to grow at the same rate. In subsequent years, the Transvaal fish grew faster than the Sibaya fish.

The growth rates of T. mossambica in culture ponds vary widely. The data are of little relevance here, except to illustrate the spectacular growth plasticity of the species. Thus Le Mare (1950, in Hickling, 1970) reports that T. mossambica in brackish water culture may reach 36 cm TL in eight months. Koura and el Bolock (1958) found that growth of T. mossambica in culture ponds in Egypt was good, fishes reaching 14.9 cm in the first year, and a final size of 38 cm and 1015 gms. Donnelly (pers. comm., 1970) reports that in the closely related species T. mortimeri in Lake Kariba, the fish reach 12 cm TL in the first year, and 25 cm in the second year. The modal length of adult fish, which varies from year to year, was about 44 cm in males and 38 cm in females. T. mossambica from Lake Sibaya showed a similar first year growth, but the growth rate in subsequent years was well below that of the Kariba population. The modal lengths of adult T. mossambica from Lake Sibaya (21 cm TL in males, 15 cm TL in females) is less than half the modal values for the Kariba population of T. mortimeri.

According to Donnelly (pers. comm., 1970), T. mortimeri reach maturity after 3 years at a total length of about 30 cm. T. mossambica from Lake Sibaya reach maturity after one to two years, at total lengths of 14 cm. The rapid maturation of the gonads of T. mossambica from Lake Sibaya means that fishes are breeding at a relatively small size. Many workers, e.g. Vaas and Hofstede (1952) have shown that the growth rate of Tilapia decelerates after maturity. The growth rate after maturity of T. mossambica from Lake Sibaya thus follows the pattern, but not the dimension, of the growth rate of other Tilapia which have reached maturity. Vaas and Hofstede followed the growth rate of T. mossambica in mixed and monosex cultures. In the mixed cultures, growth rates decelerated when breeding was commenced. In monosex cultures, the fishes maintained good growth rates throughout the experiment. These authors also noted that male T. mossambica grew to a larger size than females in mixed cultures. However, in monosex cultures, the growth rates of male and female fish were found to be equal. The different growth rates of male and female T. mossambica may be due to a different effect of spawning and mouth-brooding on the growth of the fish. Male fish may occasionally take in food while nest-guarding. Baerends and Baerends-van Roon (1950) suggest that in mouth-breeding female T. mossambica the whole feeding instinct is suppressed as a mechanism to protect the young from being eaten. Mouth-brooding would appear to have a more detrimental effect on growth rates than spawning and nest-guarding. This effect would be marked in Sibaya, where females breed a year earlier than males.

If the pool data are to be relied upon, the growth pattern of T. mossambica from Lake Sibaya is characterised by a temporary check in the cool season. Growth deceleration on reaching maturity is clearly shown by age/growth analyses from fish from the lake.

The cool season growth check is almost certainly as a result of lowered water temperatures. Allanson and van Wyk (1969) report that in the cool season water temperatures decrease to 18.5-19°C in Lake Sibaya. Minshull (1968) reports that from the 29th June to 13th July 1968, the main water body of the lake was homothermal at 17.2°C and water temperatures did not exceed 19°C until August. Data from several laboratory experiments indicate that T. mossambica is a thermophilic species with an optimal temperature range of 20-36°C. Thus Long et al (1961) give a normal range of 20-36°C and a lower sublethal range of 20-16°C. Josman (1971) after extensive laboratory investigation, concluded that the oxygen absorbing system is maximally efficient between approximately 25.0 and 38.0°C. Badenhuizen (1967) and Donnelly (1969B) found that the preferred temperatures for juvenile T. mossambica are 27-33.5°C and 34.3-36.5°C respectively, and Fukosho (1968 in Josman, 1971) showed that similar sized T. mossambica have a maximum cruising performance at 32°C. Donnelly (1969A) and I have shown that under natural conditions, young T. mortimeri and T. mossambica respectively have a diurnal rhythm of migration, moving into warm shallow waters, at the hottest time of the day, and returning to deeper warmer waters at night. From field observations, Jubb (1967) gives an optimal range for T. mossambica of about 21.1 to 26.7°C ('70-80°F').

Lowered temperatures have a proven detrimental effect on T. mossambica. Thus Job (1969A and B) and Josman (1971) found respectively that oxygen consumption and ventilatory rates in T. mossambica decreased with a decrease in water temperature. Josman (1971) suggests that the lowered metabolism of T. mossambica under low temperature conditions (less than 20°C) reduces the amount of energy available for the various physiological processes such as ventilation, osmoregulation, motility, digestion, etc. Josman also found in fresh water at temperatures below 16°C that T. mossambica became very lethargic, would not feed, did not grow, and showed little sign of gut peristalisis or ventilatory movements. Coe (1966) reports that T. mossambica held in freshwater at 14°C were found to show degenerative changes in kidney microstructure, seen also in fish after 4 days at 11°C (Allanson, 1966; Allanson and Cross, 1970) and possibly associated with the decreasing urine production that has been reported under these conditions (Minshull, 1967). Bok (1968) and Allanson et al (1971) report significant decreases in plasma osmolarity and in plasma sodium and chloride concentrations in fish held in fresh water at 11°C.

These data clearly illustrate that T. mossambica is a thermophilic species, and that at cool season water temperatures in Lake Sibaya (17-19°C) metabolism may be retarded. Retardation of metabolism could effect growth in two ways: firstly the lowered metabolic rate would have the general effect of reducing feeding and digestion rates. Secondly, lowered water temperatures may directly effect the growth-stimulating hormones secreted by the pituitary gland. No data on the latter point were collected during the present study, but the results of an investigation by Swift and Pickford (1965) on the growth of the perch (Perca fluviatilis) are of interest here. They found that seasonal variations in the growth hormone content of the pituitary gland. The amount of growth hormone was found to be low in the cool season, and high in the warm season, with consequent slow growth in winter and fast growth in summer. Seasonal variations in water temperature may have the same effect on the growth hormone content of the pituitary, and on the growth rate of the T. mossambica from Lake Sibaya. Swift and Pickford (1965) found in the perch that a rapid use of the growth hormone content of the pituitary at the beginning of the warm season reduced the available stock, with the result that little growth took place during the rest of the warm season after the initial growth period. They conclude that the perch pituitary appears to be adapted to a short growing season. It would be interesting to know whether the pituitary of T. mossambica from Lake Sibaya is adapted to two short growing seasons (pre- and post-breeding), or one long growing season (September to March) which is bisected by the breeding season.

Although the seasonal availability of growth hormone may have some effect on growth rates in an annual cycle, the direct effect of suboptimal water temperature on metabolism is likely to be important as well, at least in the coldest months.

Growth deceleration after maturity is thought to be brought about by two factors, the one more important than the other. The most important factor is a direct consequence of the little-feeding-while-breeding behaviour of T. mossambica, i.e. reduced feeding time. The second factor is related to size. The effect of a reduced feeding time will be discussed first.

Low water temperatures in June and July suggest that little feeding takes place during these months. Of the remaining ten months of the year, five are used for breeding, and five for feeding. The feeding months are August, and February, March, April and May, these being the months when water temperatures are sufficiently high for feeding, but conditions are unsuitable for breeding. Thus, compared with non-breeding fishes, which may feed for ten months, breeding individuals could only feed for five months. Furthermore, assimilated material in mature individuals would be used boty for somatic growth and gonadal development. If food is scarce, or water temperatures suboptimal, resulting in a reduced feeding rate and/or a low level of growth hormone in the pituitary, assimilated material would be directed into the development of the gonads, to the detriment of linear growth. In addition, food reserves utilized in the non-feeding breeding period would have to be replenished before positive linear growth could be resumed.

The long breeding period, cool midwinter, and the need to replenish used reserves and gonadal material, result in a poor growth rate of mature fishes, despite a total of five months feeding per year.

The size of fishes which have reached maturity may also have some connection with the growth deceleration of adult fishes. As indicated in the section on feeding T. mossambica above about 10 cm SL, i.e. adults, rarely enter terrace waters to feed, nor do they enter the profundal zone, because of minimum and maximum depth restrictions. The adult fishes feed in sublittoral or sheltered littoral areas, where they must compete with the other fish species in the lake for available food. Lower availability of food to adult fish would result in slower growth rates in comparison with juvenile fish.

POPULATION ESTIMATIONS

The technique of indirect estimation of population numbers used is based on the appearance of previously marked fish in the catch. This method involves:

(1) the capture and liberation of a number of marked fish (m) into a population

(2) the subsequent capture of marked (r) and unmarked (u) fish from the population, and

(3) the computation of population size ($\hat{N}$) from the proportion of m, r and u by

$$\hat{N} = \frac{m(u+r)}{r}$$

The Petersen method uses this formula in its simplest form, and is applicable when a large number of marked fish are first liberated, after which a substantial sample is recovered for the estimation of the proportion of u to r. The methods of Schnabel (1938), Schumacher and Eschmeyer (1943), and Chapman (1952) make use of the accumulating values of u and r during the processing of a large population. The latter methods make it possible to estimate populations in instances where netting effort is relatively low. If individual catches are very small in relation to $\hat{N}$, and when removals are also negligible, the method of Chapman (1952) is most suitable. The proportion of fish not caught is used as an estimate of N. Chapman's method was used in the present study. The standard error was calculated using the formula of Robson and Regier (1968). The calculations were made by means of a computer, using a programme compiled by Blaber and Greener (pers. comm., 1971) at Rhodes University.

Samples for the population estimation study were collected in the following way: Over a period of one to two days, seine nets were pulled at 17 sites around the shores of the south basin (Fig. 3). T. mossambica over and under 8 cm SL were tagged and finclipped respectively, and released at the site of capture. Recaptured fish were noted as recaptures and released. A period of at least 4 days, and usually 14 days, was allowed before the next sampling period, during which the cycle of sampling was repeated. Marked fish recaptured in a given sampling period were not entered as recaptures in the catch statistics, whereas marked fish recaptured in the following, or any subsequent sampling period, were regarded as recaptures. As the seine nets only sampled littoral and sublittoral areas, the estimates of N only apply to these areas.

Certain basic assumptions must be fulfilled before mark-and-recapture methods can be used to estimate the population. If any of the assumptions are not met in the field, data must be collected for the development of corrective factors if resultant values of $\hat{N}$ are to be satisfactory:

(1) the marked fish must become randomly distributed throughout the population,

(2) the marked fish must be no more or less vulnerable to the sampling apparatus than are the unmarked,

(3) loss by mortality must be proportionally the same for marked and unmarked fish,

(4) the marked fish must not lose their marks,

(5) all marks must be recognised and reported on recapture,

(6) recruitment by growth or immigration to the population must be negligible during the time recoveries are being made.

Each of these assumptions will be examined with reference to tagged and finclipped T. mossambica.

(1) Random distribution: At least four days, and usually 14 days were allowed for redistribution of tagged fish in the population. Analysis of data from recaptured tagged fish indicated that little movement occurred during the breeding season, whereas some movement took place in the non-breeding season (average 54 m per day). Because of the lack of movement of breeding fishes, and the low number of recaptures in the breeding season, estimates of N for the breeding season are unreliable (Table 22, p.156). However, the extent of movement in the non-breeding period, as indicated by the tag recovery data, is thought to have been sufficient to redistribute tagged fishes in the wild population. This redistribution of fishes would not have taken place around the entire littoral and sublittoral shores of the south basin, but only in localised areas, such as the

north-eastern shore, the south-eastern shore, and the southern shore. Information on the redistribution of finclipped fishes is less precise than that gained from tagged fishes, as movements between three large areas could only be defined. Of the 209 finclip recoveries made, 20 moved from one shore to another, a minimum distance of 410 m. Field observations during the sampling period indicated that the shoals of juveniles moved rapidly over the terraces with considerable mixing of shoals. Finclipped fish were released in batches which quickly rejoined wild shoals soon after release. Mixing and redistribution of clipped fishes, at least on localised shores, was thought to be thorough. This introduces a query: Is random distribution in localised populations sufficient if N is estimated for the whole littoral, or should the fishes be randomly distributed along the whole shore? If both approaches to randomness meet the requirements of the population estimation formula, then estimations of N for the 'localised populations', which are then summed, and for the whole population, would be approximately equal. In order to test whether both approaches to randomness meet the requirements of the basic population estimation formula (Petersen Formula), a simulated mark, release and recapture experiment was carried out. Five 'populations' of known size (200, 400, 600, 800, and 1000 individuals) were made using uniform slips of paper. Small numbers of 'individuals' (about 5% of N) were marked in each population. Each population was then sampled eight times (total number of samples = 40), and N was calculated, using Petersen's formula. To simulate the condition of 'localised populations', N was estimated separately for the 40 different small populations, and the estimates of N were then summed. To simulate the condition of randomness along the entire shore, the values of m, u, r, and c in the Petersen formula for the 40 samples were summed separately, and N was calculated from the summed values. The results of the two estimates are given in Table 20.

TABLE 20

The results of two simulated population estimation experiments using Petersen's (1910) Formula. N is actual population number; $\hat{N}$ estimated population number.

	Number of samples	N	$\hat{N}$	$\hat{N}$ as % of N
Method 1 summation of $\hat{N}$	40	24,000	26,814	111
Method 2 summation of Petersen formula components	40	24,000	25,927	108

As indicated in Table 20, $\hat{N}$ calculated by summing N for local populations, and by summing statistics for the whole population, was approximately the same (26814:25927). Both estimates were reasonably accurate. This simple test indicates that randomness of marked individuals in localised populations is sufficiently real to allow estimation of N in the total population comprised of the localised populations. As near-random distribution in localised populations appears to take place, at least in the non-breeding season, this requirement of the mark and recapture method used is met.

(2) Vulnerability: As tagged fish observed in aquaria and in pool 1 showed no signs of reduced swimming efficiency, or changes in behaviour, they were thought to be no more or less vulnerable to the sampling apparatus than tagged fish. In some instances the caudal fin of smaller fishes caught in the seine net was damaged. 2044 unclipped juveniles and 94 finclip recoveries caught in the seine net were examined for the condition of the caudal fin. As shown in Table 21, 3% of the juveniles captured for the first time were found to have damaged caudals, but in all cases damage was slight. Damage to the caudal was more frequent among fishes caught a second

time (recognisable because 'key' scales had been removed from both the right and the left flanks). In some cases the damage was sufficiently severe to impair swimming. Approximately 15% of the fishes (CD + CVD) fell into this category. An attempt was made to improve netting efficiency after this survey. The net was landed in deeper water and the fishes were removed more carefully from the net. The proportion of fishes with damaged caudal fins was reduced to less than 5%. Severely damaged fish were regarded as mortalities and entered as 'I' in estimations of SE($\hat{N}$).

TABLE 21

Condition of caudal fin in *T. mossambica* juveniles caught in the seine nets

First capture			Second capture						
Total caught	CSD		Total caught	CSD		CD		CVD	
	No.	%		No.	%	No.	%	No.	%
2044	62	3.03	94	27	28.7	9	9.6	5	5.3

CSD = caudal slightly damaged, i.e. rays parted. CD = caudal damaged i.e. few rays broken. CVD = caudal severely damaged, i.e. many rays broken.

According to Baerends and Baerends-van Roon (1950) the pelvics do not contribute to actual locomotion since they can only act when the fish is already moving, and then as horizontal rudders. It is thought that amputation of the pelvic fin did not affect catchability.

(3) Mortality: Tagged fish were shown to have abnormal growth rates, but the mortality in Pool 1 among tagged fish was no greater than among untagged fish. The wound made during tag insertion usually healed within 1-2 months. Tagged fish appeared to be unaffected by handling except for an initial shock reaction from which they recovered in seconds. A tagged fish caught after 570 days was found to be in good condition, though no growth had occurred.

No evidence suggesting that amputation of the pelvic brings about increased mortality was found. Fredin (1950) found that of seventeen species fish finclipped, only one appeared to be harmed by the amputation. Van Someren and Whitehead (1959) found that finclipping had little or no effect on Tilapia juveniles.

(4) Loss of mark: Tag retention when the tag was inserted into the dorsal musculature was found to be poor in fishes released into the experimental pools. Of 43 fishes sampled a total of 55 times, seven had lost the entire tag and two the legend tube only. The number of days between tag application and loss averaged 108 (range 75-182). The two legend tubes were lost after 75 and 83 days. The high rate of tag loss was thought to have been brought about by repeated netting in the dense vegetation. As no tagged T. mossambica released into the lake was caught more than once, tag loss brought about by netting was probably low.

No tag losses from fishes in which the tag was inserted right through the dorsal musculature have been recorded. This modification of the tagging technique was introduced on 15.3.1971 (tag 726).

Fish which had lost the tag could easily be recognised (after at least 200 days) by the presence of the tag wound in the dorsal muscles. No fishes caught in seining operations in the lake had tag wounds from previous tagging.

The positive bias of $\hat{N}$ introduced by loss of the tag in wild-released fishes was thought to be negligible.

(5) Mark recognition: There is no loss of the mark in finclipped fishes. All tagged fish which were recaptured were recognised as tagged fish, and reported as such. The number of identifiable finclip recoveries would be reduced if fin regeneration is rapid and the regenerated fin not easy to recognise. However, in Lake Sibaya T. mossambica samples, finclip recoveries were easily recognisable because the finrays regrowth produced a kink near the line of the original amputation.

The presence of a black line of Sudan Black B made recognition of the regenerated fin in some fishes even easier, and very few clipped fins are thought to have escaped recognition.

Van Someren and Whitehead (1959) found that Tilapia regenerated clipped fins in 30 days, and that it was possible to recognise the marked fish because of the altered pattern of branching of the finrays. Bailey (1969) reported recognisable finclip recoveries in the longnose sucker Catostomus catostomus after four years.

(6) Recruitment: A well-defined pattern of migration of adult (='taggable') T. mossambica into shallow water in summer and into offshore waters after summer was found. Large fish invade the shallow terraces first. During January and February most of the larger fishes leave the terrace to be replaced by smaller adults in the period February to April. The populations of larger and smaller adults appear to remain distinct except in January when intermixing occurs. Because of the almost complete change in the population of adult fish inhabiting the terrace between October and April an estimate of the population number (N) using data from this whole period would be inaccurate as the reduction of r in January would result in a positive bias in $\hat{N}$. In order to reduce the effects of emigration, N has been estimated separately for the October-December summer population, and the February-April post-summer population, and no estimate has been made for January. Migrations of individuals during either 3 month period are likely to have occurred as often in tagged as in untagged fishes, and would not introduce a bias into $\hat{N}$.

Recruitment into the "taggable" population also took place by growth of smaller fishes into the + 8 cm SL group. However, as the sampling periods were only three months long, the positive bias resulting from this cause was thought to be slight. To minimize

TABLE 22

Estimation of standing crop of *T. mossambica* over 8 cm SL in littoral and sublittoral on the southern and eastern shores of the south basin in summer 1970/1971.

I = number of injured fish discarded from sample
$\hat{N}$ = estimate of population number
SE(N) = standard error on $\hat{N}$

Sample No.	Date	Catch	Recaptures	Unmarked catch	Cumulative unmarked catch	I	$\hat{N}$	SE($\hat{N}$)
1	1.10.70	44	0	44	44	-	-	-
2	30.10.70	90	0	90	134	-	-	-
3	7.11.70	25	0	25	159	-	-	-
4	20.11.70	36	0	36	195	-	-	-
5	27.11.70	86	0	86	281	-	-	-
6	10.12.70	111	1	110	391	-	24,577	1,672
7	24.12.70	35	1	34	425	-	112,539	8,273

TABLE 23

Estimation of standing crop of *T. mossambica* over 8 cm SL in littoral and sublittoral areas on the southern and eastern shores of the south basin in the post-summer period 1971.

I = number of injured fish discarded from sample
$\hat{N}$ = estimation of population number
$SE(\hat{N})$ = standard error on $\hat{N}$

		CATCH STATISTICS		SUMMARY STATISTICS				
Sample No.	Date	Catch	Recaptures	Unmarked catch	Cumulative unmarked catch	I	$\hat{N}$	$SE(\hat{N})$
1	15.2.71	66	0	66	66	-		
2	19.2.71	55	2	53	119	-	1815	1189
3	26.2.71	65	1	64	183	-	3811	673
4	5.3.71	21	0	21	204	-	3270	1238
5	17.3.71	106	0	106	310	-	5875	503
6	22.3.71	33	7	26	336	-	1593	197
7	1.4.71	114	4	110	446	-	1764	165
8	10.4.71	15	1	14	460	-	1327	94
9	20.4.71	2	0	2	462	-	1277	87

TABLE 24

Estimate of standing crop of *T. mossambica* SL less than 8 cm in littoral and sublittoral areas on the southern and eastern shores of the south basin before and during the summer of 1970/71

I = number of injured fish discarded from sample
$\hat{N}$ = estimate of population number
SE($\hat{N}$) = standard error on $\hat{N}$

		CATCH STATISTICS		SUMMARY STATISTICS				
Sample No.	Date	Catch	Recaptures	Unmarked catch	Cumulative unmarked catch	I	$\hat{N}$	SE($\hat{N}$)
1	30.6.70	104	0	104	104	-	-	-
2	30.7.70	3	1	2	106	-	312	229
3	21.9.70	427	0	427	533	-	45,998	15,893
4	30.10.70	16	0	16	549	-	10,002	4,348
5	27.11.70	48	1	47	596	-	7,052	1,303
6	24.12.70	45	0	45	641	-	7,969	1,747

TABLE 25

Estimate of standing crop of *T. mossambica* less than 8 cm SL in littoral and sublittoral areas on the southern and eastern shores of the south basin in the post-summer period 1971.

I = number of injured fish discarded from sample
$\hat{N}$ = estimate of population number
SE($\hat{N}$) = standard error on $\hat{N}$

		CATCH STATISTICS		SUMMARY STATISTICS				
Sample No.	Date	Catch	Recaptures	Unmarked catch	Cumulative unmarked catch	I	$\hat{N}$	SE($\hat{N}$)
1	31.1.71	24	0	24	24	-	-	-
2	6.2.71	196	1	195	219	1	4,704	3,530
3	15.2.71	152	2	150	369	2	12,695	4,138
4	19.2.71	295	14	281	650	3	6,420	1,157
5	26.2.71	334	16	318	968	3	6,353	660
6	5.3.71	347	12	335	1,303	2	7,182	509
7	19.3.71	854	37	817	2,120	1	8,331	379
8	29.3.71	643	14	627	2,747	0	12,134	493
9	10.4.71	709	38	671	3,418	3	11,942	363
10	20.4.71	105	12	93	3,511	0	10,819	296

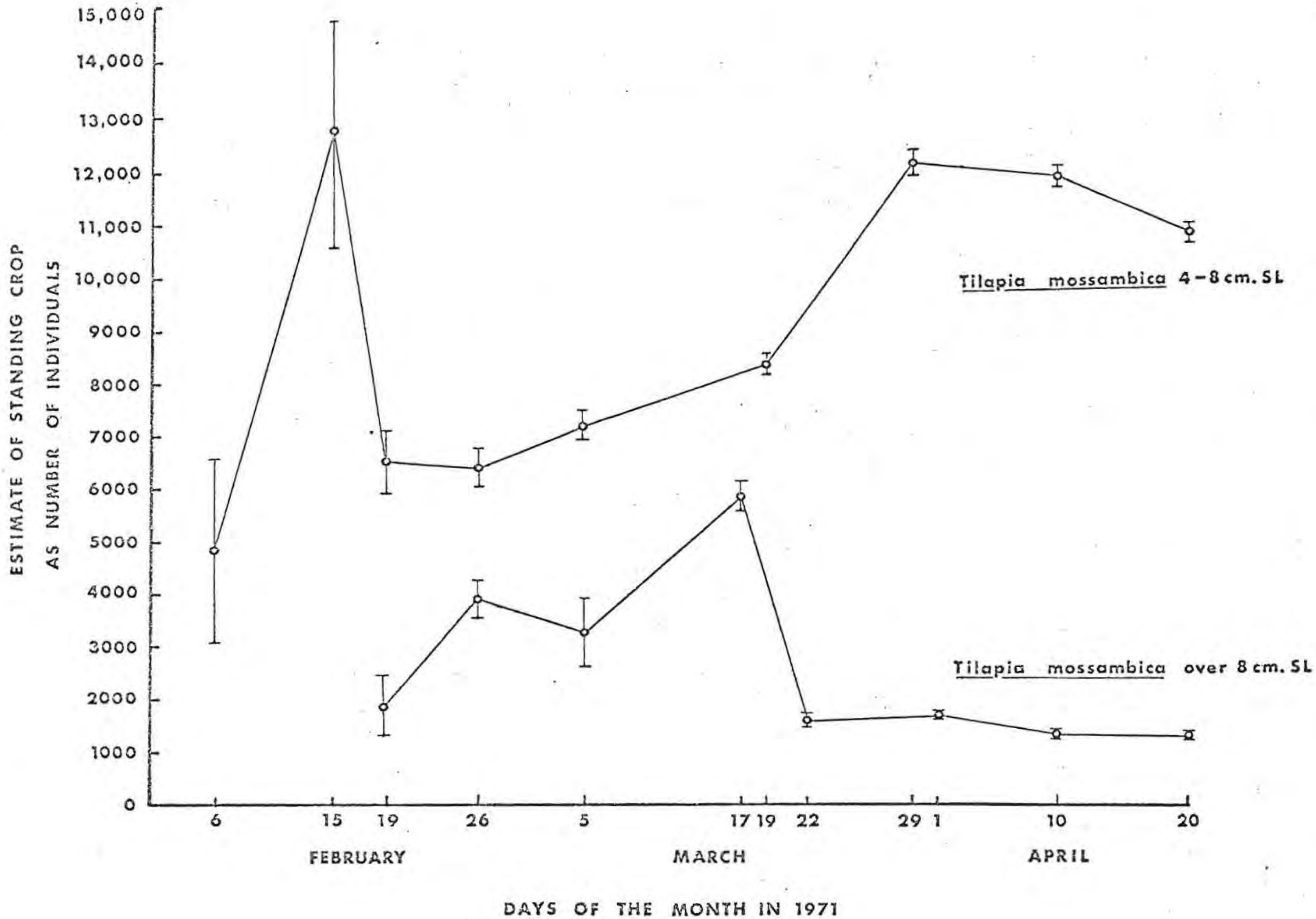


Figure 70: Estimates of the standing crop of T. mossambica on the eastern shores of the south basin at various sampling dates. The estimates were calculated using the formula of Chapman (1952).

the bias brought about by recruitment of juveniles, either through growth or immigration, N was also calculated separately for juveniles caught from June to December, 1970, and from January to April. Estimates of N for the pre-summer and summer populations of juveniles are unreliable, as evidence was obtained that substantial migrations of fishes into and out of the sampled areas took place during the sampling period. On the other hand, no evidence of large scale migrations of juvenile T. mossambica into and out of the littoral and sublittoral zones sampled was obtained during the post-summer sampling period, and bias on the estimation of $\hat{N}$ from this source is thought to be small. Recruitment by growth into the catchable juvenile population also took place, resulting in a gradual increase in the number of fishes. The short interval between sampling periods is thought to have offset the bias from this source as newly recruited fishes would regularly be caught, marked and released and would thus be quickly assimilated into the sampled population.

1173 tagged and 4788 finclipped T. mossambica were released into the lake. 17 tag and 209 finclip recoveries were made. The catch and summary statistics, and $\hat{N}$ and SE $(\hat{N})$ for the summer and post-summer stocks of T. mossambica over and under 8 cm SL are given in Tables 22 to 25.

The estimations of $\hat{N}$ for summer (Tables 22 and 24) are unreliable as too few recaptures were made. However, in the post-summer period, recaptures were frequent, resulting in low standard errors and reliable estimates of $\hat{N}$ (Tables 23 and 25, Fig. 70). $\hat{N}$ for large and small T. mossambica increased during February and March, to reach a combined peak of 14200 fishes on 19.3.71 for the sampling area. Thereafter the number of large T. mossambica decreased, while the number of small T. mossambica in the littoral and sublittoral increased, and $\hat{N}$ combined for the two size groups did not exceed 14000 again.

The south basin has an area of 2.1 sq km shallower than 10 m. On the 17th-19th March 1971, when the standing crop of T. mossambica reached a peak, the density of fishes over 8 cm SL was 1 fish per sq m, and that of fishes 4-8 cm SL, 6 fishes per sq m. Thus the density of smaller T. mossambica on the terrace exceeded that of the large fishes by a factor of over 200, indicating that, at least in March, the number of fishes smaller than 8 cm SL in the population is very large.

The gradual increase in the number of T. mossambica 4-8 cm SL in February and March reflects the continual recruitment of fry (SL less than 4 cm) into the juvenile population.

According to these data, the rate of recruitment was about 2400 fishes per month in February and March. No further recruitment took place in April, approximately 3 weeks after the end of the breeding season.

DISCUSSION

In the introduction I pointed out that a large body of experimental data on environmental tolerances such as temperature are available for T. mossambica. This study has allowed integration of some of these data with observations on the species' biology in a natural system.

As may be expected, tolerances in the field are narrower than in experimental situations. This point was noted by Odum (1971) who suggested that 'accessory factor interaction', and the metabolic cost of physiological regulation at extreme conditions, reduces the limits of tolerance in the field at both upper and lower levels. Accessory factors may include biological interactions, such as a predator-prey relationship, or abiotic interactions. For example, Caulton's experiments have shown that adult male T. mossambica may penetrate to 20 m in a simulated environment. My observations, however, suggest a maximum depth for adults of only 18 m, with the majority occupying water shallower than 12 m. Similarly, experiments have shown a temperature tolerance range of 14°-$41^{\circ}C$ for T. mossambica in the laboratory, whereas observations in the field indicate a preferred range of 17°-$36^{\circ}C$. These sort of data coupled with our knowledge of cichlid ethology allows an assessment of the way in which the species has exploited the resources of the lake.

The distribution of T. mossambica is quite neatly divided into two phases: a cool season limnetic phase changing to an onshore migration in September and October; a littoral breeding phase followed in January and February by a movement to feeding grounds also in the littoral. While T. mossambica is undoubtedly a herbivore, feeding almost exclusively upon benthic diatoms, the distribution of the diatom flora upon which it feeds is not known in Lake Sibaya. While at first sight it would appear obvious to expect rich diatom assemblages in the shallow littoral, our knowledge of the distribution

Figure 71:
A view southwards at site 16 in the south basin in November 1971 showing low lake level and a reduced terrace. Lake level 19.7 m above mean sea level.

Figure 72:
A view southwards at site 9 in the south basin in November 1972 showing a high lake level and flooded eulittoral. Lake level 20.3 m above mean sea level.

Figure 73:
A view northwards at site 16 in the south basin showing a high lake level and flooding of macrophytes in the eulittoral - November 1972. Lake level 20.3 m above mean sea level.

of hydrophytes such as *Myriophyllum* which form the substrate for a periphyton complex suggests that feeding could take place in weed beds offshore. In addition to this food source, the littoral and eulittoral of the lake receives large quantities of allochthonous detritus washed in from the dune forest on the eastern shore as well as detritus from fragmented *Juncus*, *Scirpus* and *Typha* which line the shores. This detritus becomes the substrate for a rich periphyton or "aufwuchs" (Ruttner, 1966) and together with the interstitial material in the sandy substrates would also provide food. It must be stressed that unequivocal evidence that these are indeed the food resources is not yet available. The availability of this possible resource is subject to fluctuations in lake level which varied, from extreme exposure with lowering lake level in November 1971 to inundation in November 1972 (Figs 71, 72, 73).

The importance of allochthonous materials in the productivity of shallow water has also been noted by Fryer (1959) who suggested that in Lake Malawi the 'high productivity of the littoral zone may be due in part to its favourable position to receive salts swilled into the lake from the surrounding land.' Pieczynska (1970) and Welcomme (1970) have also noted the high trophic levels in flooded littoral areas brought about by the decay of terrestrial plants, and increased fish production.

The characters ensuring successful utilisation of the cyclically-renewed littoral area of the lake would be the same as those required to succeed in the ancestral riverine habitat, i.e. an ability to feed on a wide variety of foodstuffs, wide temperature tolerances, and the ability to inhabit widely differing habitats. Retention of these characters by *T. mossambica* has meant that the colonisation of a shallow lake with a fluctuating littoral has presented few problems. Conversely, it may be that *T. mossambica* have selected for occupation those areas of the lake which most closely resemble the riverine habitat. One of the problems associated with habitation of the shallows is that of increased vulnerability to predators. This has been overcome to some degree by shoaling, e.g. by juveniles, and by fry-releasing females.

Generalised adaptable species are often regarded as primitive. In morphological terms, T. mossambica may be regarded as a generalised cichlid, since they very closely resemble the unspecialised Miocene fish fossils from which modern-day lacustrine Tilapia may have evolved (Fryer and Iles, 1972, citing Greenwood, 1951). Despite their resemblance to primitive, unspecialised fishes, their adaptability suggests, however, that they are in fact very advanced. An opinion expressed by Fryer and Iles (1969, 1972), which I support, is that this adaptability of Tilapia should be regarded as a form of adaptive radiation - a specialisation towards generalisation - rather than a primitive feature. Adaptive radiation has been defined as 'radiation from a primary stock to a number of different types adjusting to different modes of living', (Kenneth, 1963). Selection of adaptable features enabling a species to colonise unstable and young habitats, such as the littoral of Lake Sibaya, may be regarded as a form of adaptive radiation.

The other great branch of the cichlids, the Haplochromis-flocks, have taken an alternative evolutionary path - towards super-specialisation. This mode of evolution has resulted in speciation and represents the classical form of adaptive radiation.

Fryer and Iles (1969) have recently pointed out that Tilapia in Africa usually occupy habitats which are subject to cyclical and irregular changes, and thus preserve the characters of 'initial' ecosystems in the sense of Margalef, which is in contrast to the Haplochromis-flocks of the great lakes, which usually inhabit stable 'mature' ecosystems. Communities inhabiting 'initial' ecosystems ('initial communities'), they note, tend to be simple, and dominated by a *Tilapia* species. This condition may exist in Lake Sibaya in which an oligospecific assemblage of 3 *Tilapia* species dominated by *T. mossambica* is found. *Haplochromis*-flock is represented by only one species - *Hemihaplochromis philander*. Initial communities are also reported to have high reproductive rates and to occur in large breeding populations - once again fitting the case in Lake Sibaya.

T. mossambica in Lake Sibaya exhibit a further character of members of 'initial communities', namely, adaptive cyclomorphosis (which may be defined as a change in size in response to a change of environment) as they reach a final size of only 25 cm SL and 340 gms, which is smaller than that of individuals of the same species from other systems. Thus Coke (pers. comm. 1971) reports that *T. mossambica* grew to 36 cm SL in the Pongola river, 70 km west of Lake Sibaya; Crass (1964) that *T. mossambica* may reach 40 cm TL and 1700 gms in Natal; and Jubb (1967) that *T. mossambica* may reach 2953 gms in southern Africa. The Lake Sibaya *T. mossambica* can be regarded as a 'dwarf' population.

'Dwarf' populations of other *Tilapia* species in natural systems are known. Jubb (1960) found a population of *T. shirana* in Mapatamanga gorge, Malawi, in which the largest female caught measured 10.2 cm, compared with Lowe-McConnell's (1955) breeding size for this species of 20-25 cm. Copley (1952) records a population of dwarf *T. mossambica* from springs flowing into Lake Magadi in Kenya in which the fishes reach maturity at 6.3 cm and never grow larger than 10.2 cm.

Clearly, in certain circumstances, some advantages must accrue to dwarfed populations. Dwarfing of *T. mossambica* in Lake Sibaya does not merely involve a reduction in the final size of individuals, but also a greatly accelerated life cycle, achieved by reducing both the time taken to reach maturity, and the size at which maturity occurs. As shown in the chapter on growth, the growth rate of *T. mossambica* follows the pattern of that of *Tilapia* from other systems, but not the dimension. Thus the growth rate to maturity is high, but decelerates after maturity as in other populations. By breeding precociously at 8 cm in females and 10 cm in males, growth deceleration occurs earlier in the life cycle than in 'normal' populations, with the result that the final size of individuals is reduced.

At this stage it is necessary to comment on the use of the various terms stunting, miniaturisation, dwarfing, neoteny and pygmyism, which have been used rather loosely by Fryer and Iles (1972) and others. The confusion can be clarified by referring not to dwarfing (or the former two terms) but to 'precocious breeding', and applying this term to all populations in which the small size of individuals is phenotypic, i.e. in response to environmental factors. As these populations have the ability to assume normal populations again, they cannot be termed neotenous, for this term is usually applied to populations in which the individuals always breed at a juvenile stage of development.

Pygmyism on the other hand should refer to populations which do not retain the potential to grow to a large size if conditions improve, i.e. the small size is genotypic, as suggested by du Plessis (in Jubb, 1960).

Fryer and Iles (1969) have commented on the dwarfing of Tilapia as a result of precocious breeding, and consider it analagous with cyclomorphosis in certain 'simple' animals such as flatworms and Hydra which can adjust their biomass in accordance with available resources. Elsewhere Fryer and Iles (1972) have remarked that in the Haplochromis-flocks, which are generally small fishes, large size is a specialisation, whereas in Tilapia, in which large size is the norm, retention of the large size represents a generalisation. While I find this argument acceptable, I feel that it supports the hypothesis that precocious breeding in Tilapia, resulting in smaller fishes, should be regarded as a specialisation, and not a further generalisation. In fact, could it not be argued that Tilapia, by exploiting their phenotypic plasticity, have reached a level of specialisation akin to that in certain insects, e.g. the Lepidoptera, in which the juvenile stage is adapted to use the available food resources efficiently, whereas the adult is concerned mainly with maintenance and reproduction.

Fryer and Iles (1969) suggest that the advantage of 'dwarfing' is that the fishes can compensate for very high mortality rates in adverse environments, and that the rapid colonisation of new, or cyclically renewed habitats is possible shortly after these become available and when conditions are too severe for most other species. It was noted earlier that fry occasionally enter pools which dry up, resulting in a mass mortality of young fishes. High fry mortalities also occur when mouth-brooding females entering eulittoral pools for fry-release, are killed by avian predators. Precocious breeding, and a rapid population turnover, would tend to offset such losses.

However, in the Sibaya context, the small modal size of individuals in the population is probably more important as a means of increasing the efficiency of an opportunistic use of food resources which are cyclically available in eulittoral areas. Small T. mossambica are known to be more eurythermal than large T. mossambica. Thus small T. mossambica in Lake Sibaya enter water from 17-36°C whereas adults were only recorded in water from 19-32°C. Their ability to withstand greater temperature extremes than adults allows the juveniles to enter the shallower water for longer periods each day than adults, and this permits more frequent use of allochthonous and autochthonous detritus when these deposits become available. Small T. mossambica are also more eurytopic than larger individuals, and enter more shallower and deeper water than adults. This would facilitate greater utilisation of eulittoral and profundal detritus deposits. It is my contention that cyclomorphosis in the T. mossambica population in Lake Sibaya brought about by precocious breeding allows the most efficient utilisation of a particular feeding niche by increasing the proportion of fishes in the size classes which are best able to feed in shallow water. This adaptation would be necessary if food resources suitable for *T. mossambica* were largely confined to the shallow waters of the lake, and if competition for the food available in the deeper regions further reduced the amount of food available per individual compared with shallow areas. The 'dwarfing' of the fishes, if this hypothesis is correct, would thus not be related to an overtaxing of the food supply resulting in slow growth and a small final size, but to abundant food, fast growth and early maturity.

An interesting parallel has recently been reported by Welcomme (1970) who studied the ecology of fish in certain recently flooded shore regions of Lake Victoria. He noted that there was little or no mixing of lake and lagoon fishes. Populations of *T. leucosticta* in the lagoons showed a tendency to stunt, with stunting more marked in the more isolated lagoons. A mat of floating vegetation, by reason of the de-oxygenated conditions that existed under it, acted as a barrier so that fishes from the lake could only penetrate to the nearer lagoons, the populations in the more isolated lagoons remaining more or less segregated. Presumably higher algal productivity existed in the lagoons, emphasizing once again the possibility that precocious breeding results in a large number of small individuals and an increased population turnover, which may increase the efficiency with which the shallow water is utilised.

As regards the triggers of precocious breeding, the work of Cridland (1962) has shown that the increased temperature accelerates growth and the onset of maturity of *T. zillii* in aquaria. This factor may be important in high temperature tolerant juvenile *T. mossambica* in Lake Sibaya. Chen (1965, in Welcomme, 1970) found that living space, represented by surface area, may influence the growth rate: fish tend to grow faster in association with greater surface area. This factor may also be important in Lake Sibaya in which juvenile T. mossambica occupy extensive littoral areas. A further factor cited by Welcomme, namely the buildup of external metabolites which inhibit growth in restricted areas, is unlikely to be significant in the Sibaya context). The proximate external factors, whatever they are, would presumably have some effect on the pituitary gonadotropic hormones, which in turn would trigger the maturation of the gonads. One of the most interesting unanswered questions is: what stimulus results in the conversion of one type of population structure into another? Lake Sibaya would appear to be a perfect system in which to answer this question, and in so doing offer an attractive opportunity for ecologists and physiologists to work together.

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APPENDIX 1

FISH SPECIES RECORDED FROM LAKE SIBAYA

FRESHWATER

family MORMYRIDAE: *Gnathonemus macrolepidotus* (Peters), 1852.

family CYPRINIDAE: *Barbus paludinosus* Peters, 1852.
Barbus viviparus M. Weber, 1897.

family CLARIDAE: *Clarias gariepinus* (Burchell), 1822.
Clarias theodorae Weber, 1897.

family CYPRINODONTIDAE: *Aplocheilichthys katangae* (Boulenger), 1912.
Aplocheilichthys myaposae (Boulenger), 1908.

family CICHLIDAE: *Tilapia mossambica* Peters, 1852.
Tilapia sparrmanii A. Smith, 1840.
Tilapia rendalli (Boulenger) 1896.
Hemihaplochromis philander (M. Weber), 1897.

COASTAL LAKE, ESTUARINE OR MARINE

family GOBIIDAE: *Glossogobius giurus* (Hamilton and Buchanan), 1822.
Croilia mossambica J.L.B. Smith, 1955.

family ATHERIDAE: *Atherina breviceps* Valenciennes, in Cuvier and Valenciennes, 1835.

family STOLEPHORIDAE: *Gilchristella aestuarius* (Gilchrist and Thompson) 1917.
Silhouettea sibayi Farquharson, 1970.

APPENDIX 2

THE EFFECTIVENESS OF FD-67 TAGS FOR MARKING *T. MOSSAMBICA*

The FD-67 tags used to mark *T. mossambica* in Lake Sibaya were found to have a variable, usually detrimental, effect on fish growth. Tag retention was good in the wild, but poor in the pool where repeated sampling was carried out using a seine net. The tag legend was found to be clearly legible up to 570 days after the fishes release, though some tags were found to be covered with green algae which was easily removed. The tag wound healed rapidly in the majority of fishes. Other workers have found that spaghetti tags show poor retention when compared with other types of tags. Holden (in Jensen, 1969) reports that the return rate of Petersen discs was four times that of spaghetti tags. Jensen (1961, 1966) tagged 907 spiny dogfish and found that spaghetti tags gave the lowest percentage return when compared with Petersen discs and a combination tag with a Petersen disc attached to a spaghetti tube. Fink (1970) found that the retention of FD-67 tags in the herring *Sardinella* was poor. Duncan (1971) found a variable effect of the FD-67 tag on white bass. In one fish at liberty for 728 days the tag wound had healed, but in another at liberty for 696 days fungus had set in and an infection had spread across the back which affected tag retention. Other workers have found that tag retention was good. Duncan (1970) recovered an FD-67 tag from a white bass (33.1 cm TL) at liberty for 708 days. Duncan obtained a 10.5% recovery rate for 3,589 tagged white bass. Thompson (1970) found that 50% of FD-67 tagged fish recaught after 3 months had healed tag wounds, although healing can occur as soon as one month after tagging. Millenbach (1971) tagged 10,000 trout with FD-67 tags and obtained only a small number of recoveries. However, one tag recovery had travelled over 3000 miles across the northern Pacific and had grown from 28 grams to over

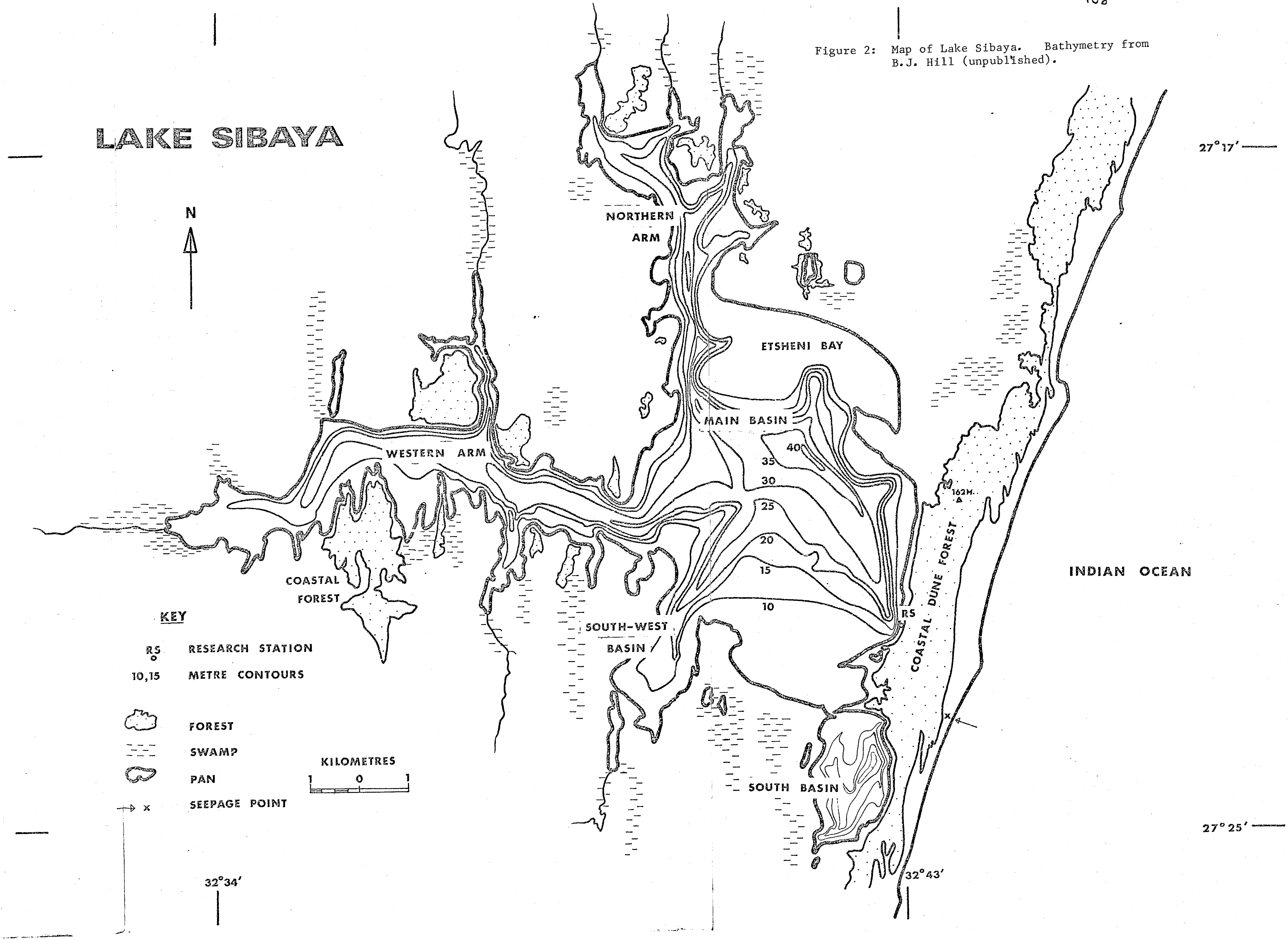
1800 grams. Mather (1968) recovered a Floy tag from a tuna after seven years and seven months.

These results indicate that tag retention was good in all tagged fishes larger than *T. mossambica* from Sibaya. The size of the tag and the diameter of the tag neck are probably too large in proportion to the size of fish tagged at Sibaya.

Van Someren and Whitehead (1959) recommend an individually numbered plastic strip attached through the dorsal musculature by means of a fine wire for tagging *Tilapia* above 6 cm TL. These tags were found to have no effect on the growth of *T. nigra*. Tag loss in pond fishes never exceeded 8% despite repeated monthly netting and handling. They suggest that in wild populations, or in populations handled less frequently, the tags are probably a life-long fixture.

Preliminary experiments using a Floy FTF-69 fingerling tag (see Figure 23B), which consists of a 5 x 3 mm white numbered plastic disc, a length of solid vinyl thread, and a needle for application, have been performed. Tagged fishes were found to show normal behaviour patterns. Tag retention was very good.

Figure 2: Map of Lake Sibaya. Bathymetry from B.J. Hill (unpublished).



SOUTH BASIN

Figure 3: Map of the south basin of Lake Sibaya. Bathymetry from B.J. Hill (unpublished).