STUDIES OF THE BIOLOGY OF THE SPECIES OF TILAPIA IN THE VOLTA LAKE

STUDIES OF THE BIOLOGY OF THE SPECIES OF TILAPIA IN THE VOLTA LAKE

A thesis submitted in April 1967

by

ADOLPHUS AMANOR WUDDAH, B.Sc. (LONDON)

in part fulfilment of the requirements of the University of Ghana, Legon, for the Master of Science Degree in ZOOLOGY.

From: The Department of Zoology,
University of Ghana,
LEGON.

CONTENTS

SECTION		PAGE
I.	INTRODUCTION	1
II.	LOCALITY	3
	- General description of the Lake. ..	3
	- Selection of localities.	4
III.	MATERIALS AND METHOD.	10
	- Sampling Equipment.	10
	- Ichthyological Data.	11
	- Preservation of Materials. ..	13
	- Hydrological and Meteorological Data.	16
IV.	SPECIES COMPOSITION	17
	- Changes in Relative Abundance of Fish.	25
V.	LENGTH-FREQUENCY DISTRIBUTION OF CATCHES	34
VI.	SEX RATIO IN *TILAPIA* SPECIES	53
VII.	MATURITY AND FECUNDITY	65
	- The Ovary.	66
	- The Onset of Sexual Maturity. ..	69
VIII.	SPAWNING.	81
	- The Coefficient of Maturity. ..	88
	- Sexual Maturity and Size of Fish. ..	96
IX.	DISCUSSION.	107
X.	SUMMARY.	111
XI.	ACKNOWLEDGEMENTS	114
XII.	REFERENCES.	116

-----0-----

I. INTRODUCTION

The damming of the Volta River in Ghana has stimulated an interest in the fisheries potential of the new Lake. Research projects have therefore been undertaken to study not only the biological changes but also the physical and the chemical changes which are taking place as the water body is transformed from a river into a lake. The earliest work on the condition of the water after the closure of the dam has already been reviewed (Ewer, 1965; Biswas, 1966).

After an initial brief boom of productivity there followed extreme deoxygenation with high turbidity, low light penetration and no thermocline. There was heavy fish mortality and the conditions were generally unsavoury, a situation common upon the immediate impoundment of water.

The altered environment to which the riverine fish are being subjected and their adaptation to the different ecological regime is a study of great interest and one which is of special importance because of its application to the large scale commercial fishery which it is hoped the Volta Lake may eventually support. Considering, however, the meagre data available on the fishes of the Volta as well as the scarcity of fisheries statistics of landed fishes, very little is yet really known.

From the data collected it was quite evident that *Tilapia* was likely to be particularly important and together with *Chrysichthys* and *Synodontis* species might form the largest component of the commercial gill-net fishery.

At the beginning of the present investigation the <u>Tilapia</u> population was sufficiently dense and the size of the fish sufficiently large to suggest that it would provide the basis for an experimental fishery designed to collect data concerning the biomass of the <u>Tilapia</u> species occurring in the Lake. The primary aim was to analyse these data in order to contribute to a knowledge of the life cycle of the <u>Tilapia</u> species in the conditions prevailing in the Volta Lake. This detailed work was undertaken in a scheduled time of field work from January to August 1966 to cover both wet and dry seasons. As will become clear, the early abundance of <u>Tilapia</u> was not maintained in the area under survey and as a result many of the data collected are based upon relatively small samples of fish. An attempt has been made, however, within the resulting limitations, to see what can be deduced concerning the biology of <u>Tilapia</u> and to indicate what further lines of research, both in subject and method, the present results suggest it would be profitable to pursue.

II. LOCALITY

GENERAL DESCRIPTION OF THE LAKE

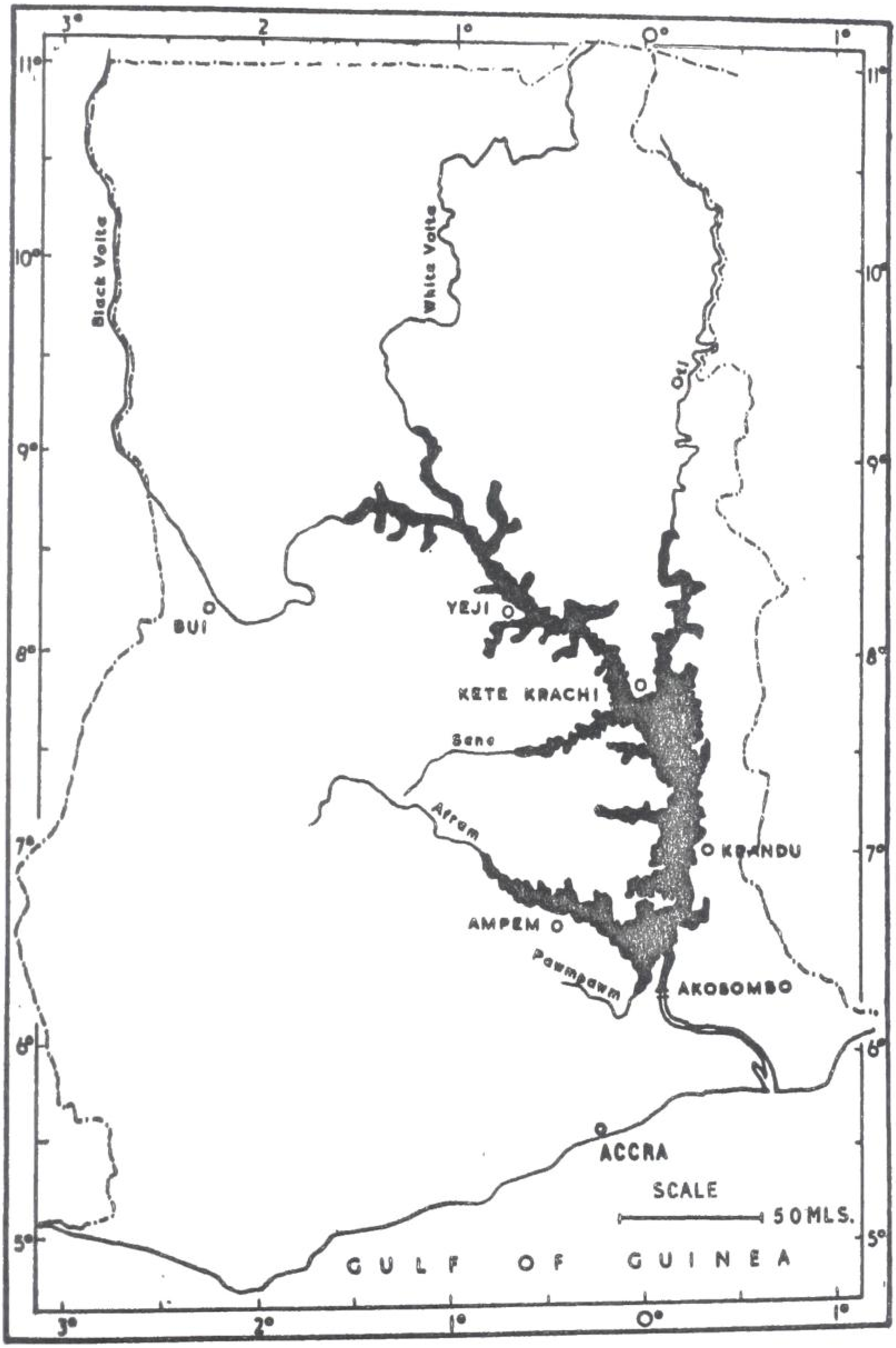
The Volta Lake, which was impounded from the old Volta River, is situated at a low altitude near the Equator between latitude 6 - 9° N and longitude 1° E and 1° W. It is set against low surrounding savanna country and also tropical rain forest. With the flow of its riverine tributaries and rain water, it started to fill in May 1964 when the dam was closed. At the present time, there is a large and continuous flow of water through the hydro-electric turbines at Akosombo.

The Volta Lake with its complex dendritic outline is estimated to cover an area of more than 3,000 sq. miles (about 8,000 km^2) and the perimeter of the shoreline will exceed 4,500 miles in length at maximum flooding. The lake is comparatively shallow, the average depth being 30m. These figures, naturally,may undergo considerable changes as a result of the periodic fluctuations of level from dry to wet seasons.

Very little has so far been published on the temperature and water chemistry of the Volta Lake. In a review of the position between May 1964 and May 1965, Ewer (1965) reported that at a station close to the Dam, apart from a transient daily heating of the most superficial water layer, there was no thermocline and the temperature decreased gradually with depth down to about 25., below which the temperature was almost uniform. The chemical composition of the water showed a reasonably clear-cut division into a surface layer extending down to about 10m., then a transitional layer to about 25m and finally a fairly uniform bottom layer. This layering was markedly displayed in both the iron and ammonia content of the water and also, but less distinctly, in the phosphate content. It was recognisably reflected as well in pH, alkalinity and in potassium. Furthermore, owing to the absence of a thermocline, a free mixing of the upper and lower water masses occurred, leading to marked turbidity and hence poor light penetration. More recent observations (Viner, 1967) show that these conditions are not typical for the Lake as a whole and that further north well marked thermal stratification may occur, while light penetration has improved over all the lake since the latter part of 1965.

SELECTION OF LOCALITIES

According to Petr (1967) an increase in the numbers of *Tilapia* was first observed by August 1965 in the Pawnpawn area, (Map I), a shallow bay formed by the flooding of a small tributary valley. Catches from another small and sheltered bay near Akosombo in October 1965 showed cichlids to constitute over 60% of the total catch. By the end of 1965, this trend was also strongly shown at Akosombo. Further north at both Kpandu and Ampem cichlids constituted at least three-quarters of the total catch by early 1966. These results are summarised in Table 1.



Map 1. Map of GHANA showing position of Volta Lake.

Table 1.

Abundance of Cichlids in catches from different areas of the Volta Lake. (Data from Petr (1967)).

Locality	Date	% Occurrence
Akosombo	Jan. - April 1965	0.18
Akosombo	Nov. - Dec. 1965	35.61
Kpandu	May - June 1965	7.56
Kpandu	February 1966	75.09
Ampem	February 1966	76.97
Kete Krachi	February 1966	18.10

This summary thus indicates that populations of Tilapia are widely distributed in the Lake.

For the present work, it was necessary to select one locality for intensive study. When the work was being planned, the following features were regarded as essential for any area selected as a site for study:

1. There must be an adequate stock of Tilapia.
2. It should be easy to set nets in as much of the selected locality as possible.
3. As much of the shore as possible should be reasonably close to a road.

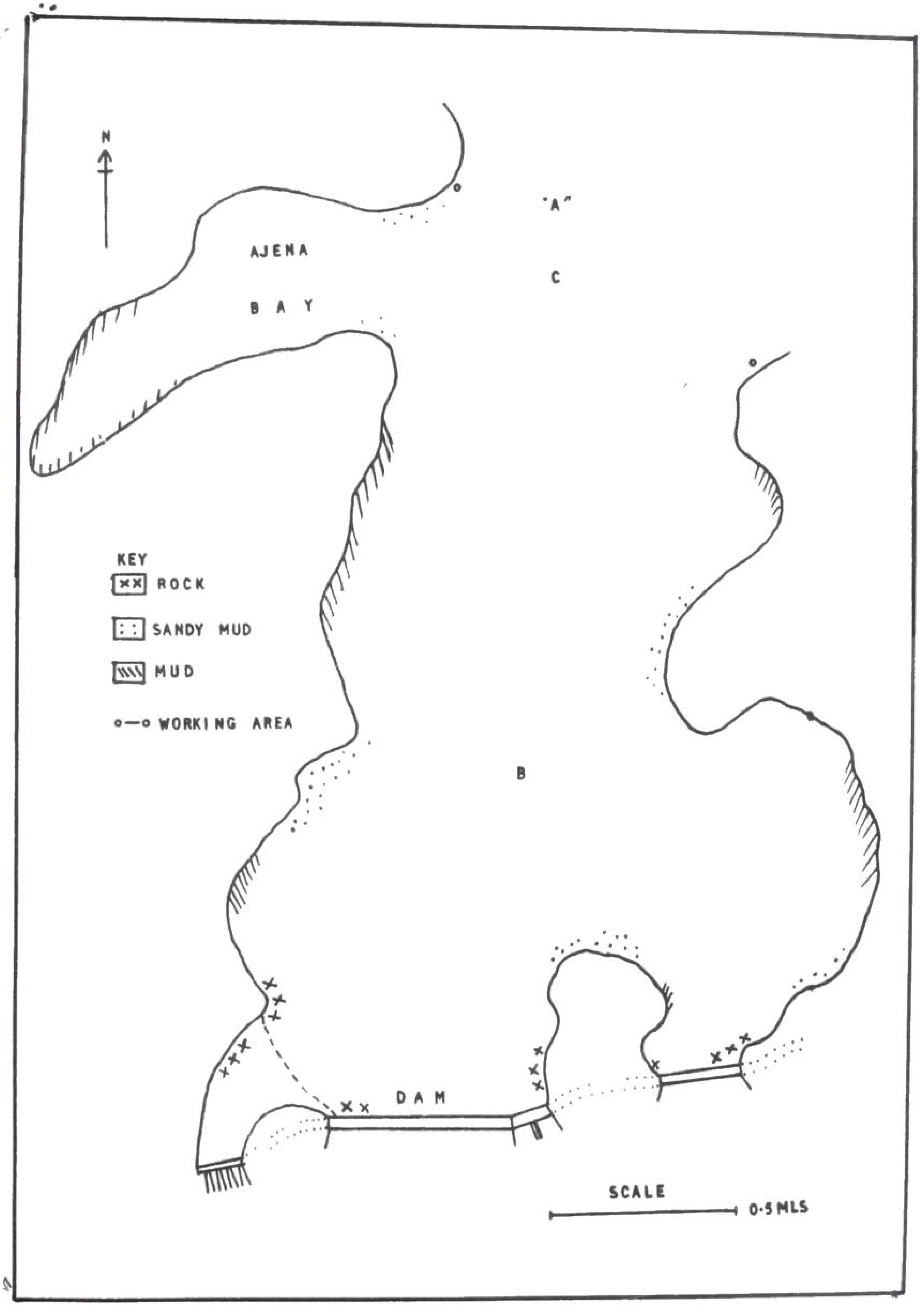
A few places were at first explored including Pawnpawnya fishing village and New Ajena, but none of these satisfied condition 3; moreover they lacked both easy communication facilities and accommodation. After a careful examination of all reasonably convenient areas, Akosombo in the extreme south of the lake was selected as the most suitable site. (See Map 1).

Work in this sampling area was restricted to a stretch of shoreline running up to three miles north of the Dam. The upstream limit of the area is the point marked "A" on map 2. This area is commonly referred to as the 'Gorge Region' and includes three bays, the largest of which is Ajena Bay. Compared with the surrounding flat country, this narrow area of the lake is lodged between steep-sided hills sloping abruptly towards the shoreline.

The vegetational cover is mainly composed of scattered terrestial plants such as Hygrophila laevis (Nees) Lindau, Cyperus lanceolatus Poir, Vossia cuspidata Griff., Denbollia voltensis Hutch, Indigofera paniculata Vahl ex Pers and Sphenochlea zelanica Gaertn which invade the marginal zones. In this part of the valley, the land was cleared of vegetation to a considerable extent but has recently been neglected. Decaying bushes and tree stumps are abundant along the eastern shoreline. When the annual rains start in March to April most of the steep shoreline becomes flooded.

The Lake bottom in this area, examined visually and by feel, varies to some extent. Apart from a rather limited rocky area adjacent to the Dam, (See map 2), the principal substrata in all other parts were either mud or muddy-sand. Of these, mud was by far the more abundant.

This part of the lake lacked any floating aquatic weeds during the latter months of 1965 but subsequently Pistia stratoites L. and



Map 2. Sketch map of the working area at Akosombo.

Ceratophyllum *demersum* L. became common, providing food as well as shelter for the cichlids.

III. MATERIALS AND METHOD (FIELD)

The first phase of this investigation was a gill-netting programme. Weekly visits were made to Akosombo and on each occasion a series of experimental gill-nets was set, usually for a period of three days i.e. 72 hours. As the nets had to be lifted once or twice daily for inspection and the removal of fish, it was not normally possible to investigate more than one locality at a time.

SAMPLING EQUIPMENT

A fleet of nets consisted of five white nylon gill-nets of diagonal mesh sizes of $1\frac{1}{2}$", 2", 3", 4" and 5", each net being only of one mesh size. Each net in the fleet measured 50 yards by 10 ft. deep when stretched and settings were made at the surface. In an attempt to ensure random sampling and to cover the area investigated with the same fishing effort, settings were made at different localities on each visit, either along the dam wall, in sheltered bays, off shore or close to the shores. When the location was inshore i.e. in the shallow areas and bays, the ends of the head rope of each net were stretched between inundated trees. It was not easy in some places to fish nearer the shoreline than 20 ft. since the nets became entangled in the submerged vegetation and much damage was done to them. In fact, two nets were damaged beyond repair in this way in an attempt to lift them out of the water for inspection. Off shore, floats were attached to the ends of the head rope and these were held in position by means of stone anchors. Here also some difficulties were encountered since, due to the great depth of the water (about 40 m), the anchors failed to reach the bottom and sampling was not satisfactory.

The scheme of setting the nets was either (a) in a long linear chain parallel to the shoreline as shown in fig.1, the positions of the nets being changed randomly at each setting, or in a serial manner with respect to the shoreline (fig.2), the positions of the nets also being changed at random.

By the use of the graded series of nets it was hoped to catch as many stages of Tilapia species as possible in order to estimate the structure of the entire Tilapia population and also to make possible the determination of the relative abundance of different age and length groups.

In this investigation there was a total of 87 fishing days and on days when no experimental fishing was undertaken samples of fish from the local fishermen operating from Akosombo as well as cast-net samples were examined.

ICHTHYOLOGICAL DATA

A record was made of the total weight and numbers of each species caught in each mesh size. Species other than Tilapia were identified by reference to Blache (1964), Daget (1954) and Irvine (1947). Tilapia species were identified with the aid of keys by McConnell (1955). In order to save time in the field, counting of fin rays etc. to distinguish T. melanopleura (Dum) from T. zilli (Gerv), were ignored, thus these two species are referred to subsequently as T. zilli/melanopleura.

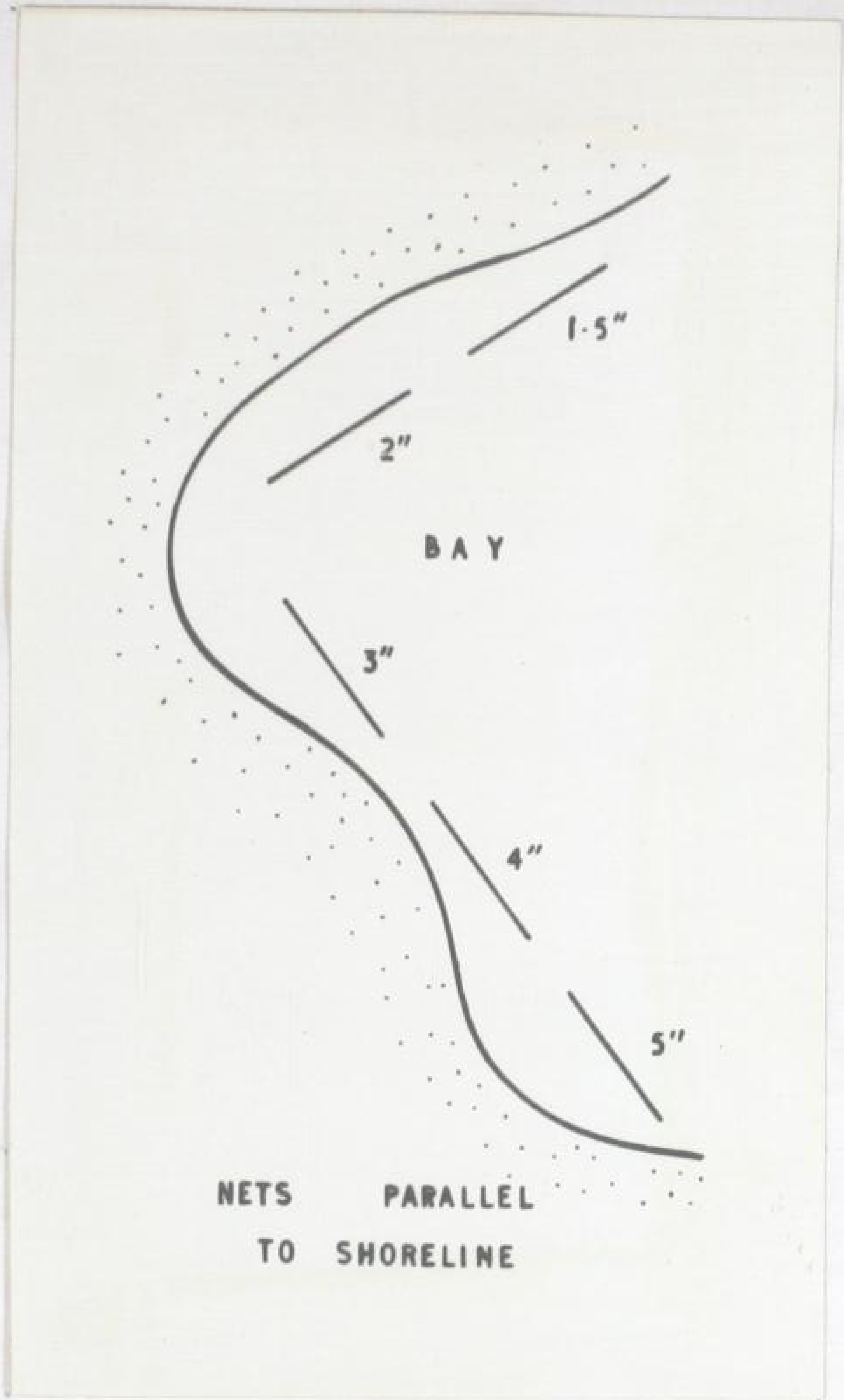


Fig. 1.

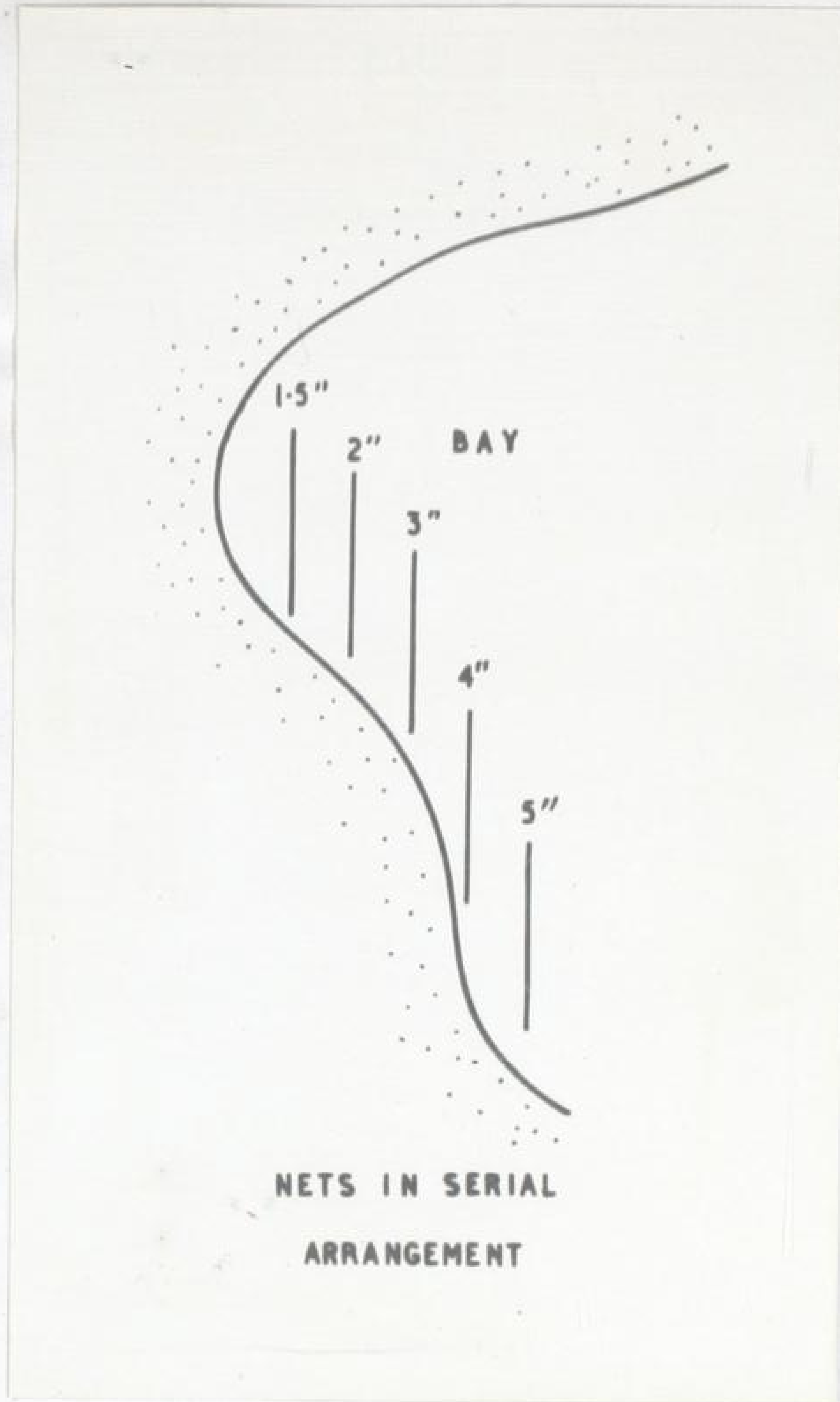


Fig. 2.

Sketch of position of nets with respect to shoreline.

A record was also made of the standard and total lengths (in cms.) of each specimen of Tilapia, its weight to the nearest g as well as its sex. In sexing, males were distinguished from females by the shape of the genital papilla, which is conical with one aperture in the male but broader and bluntly pointed with one aperture and a transverse slit in the female (McConnell, 1955). (See also fig.3).

Each fish was then dissected to remove the gonads, the stage of maturity being recorded using the scale proposed by Nikolsky (1963). Scales were taken from the region between the lateral line and the insertion of the anal fin. These scales which were put into marked envelopes were used for the examination of seasonal or spawning marks.

The identification of the fish and their measurement can be regarded as satisfactorily accurate but the records of the stage of maturity of the gonads can only give a rough guide since the distinction between the stages is not clear-cut and to this extent liable to error.

PRESERVATION OF MATERIAL:

The gonads were fixed and preserved in Bouin's Picro-formol (Picric acid sat. soln. 75 parts, 40% formalin 25 parts and glacial acetic acid, 5 parts). This fixative was chosen because the solution keeps indefinately and causes little shrinkage of tissue layers. It also stains the object yellow so that small specimens are easily seen during embedding and sectioning. Objects can also be left in it for a considerable time without injury and it gives excellent anatomical pictures (Guyer, 1953).

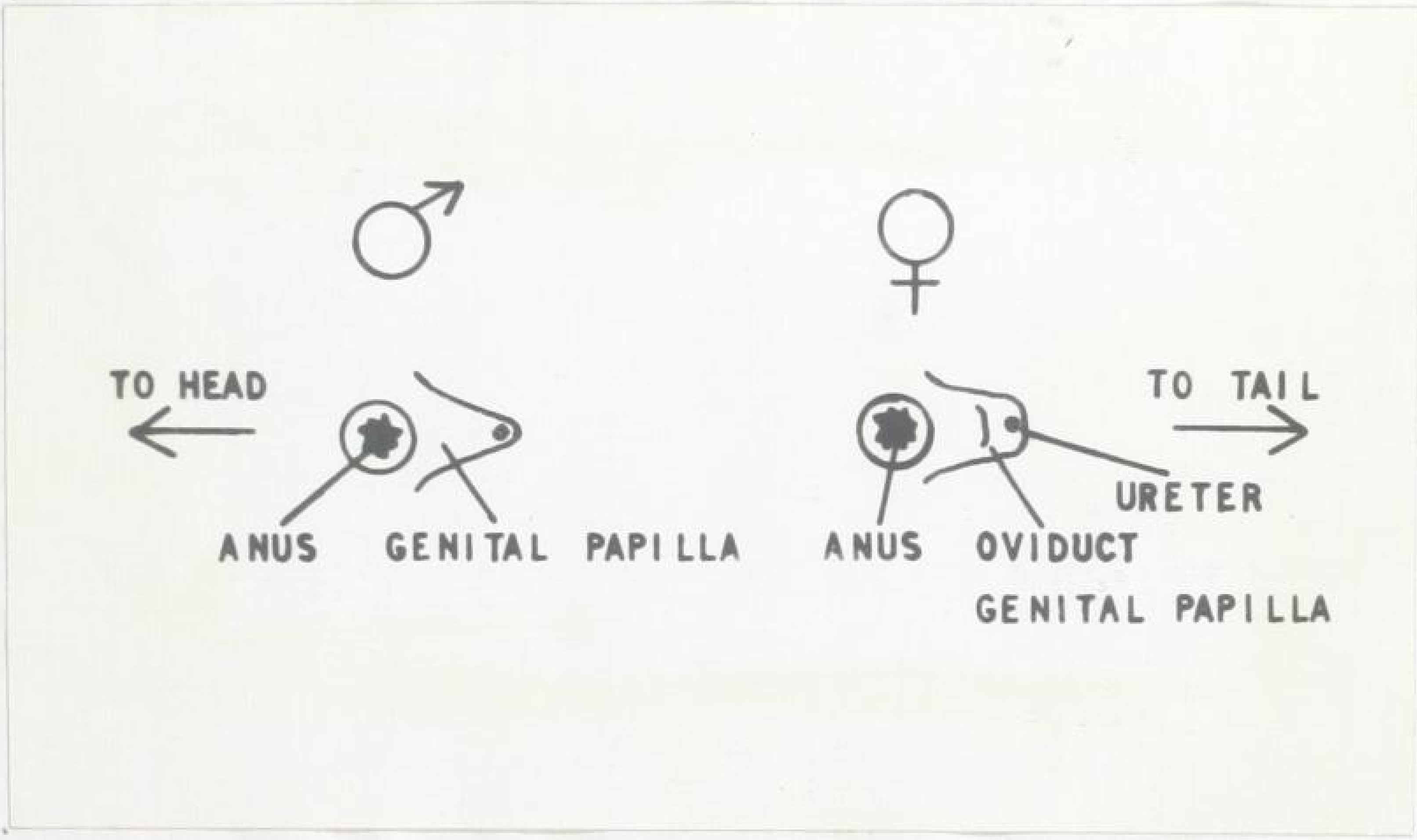


Fig. 3. Diagram of the genital papilla of <u>Tilapia</u> spp.

The fishes were preserved in 10% formalin but the scales required no preservation.

On returning to the laboratory the measurements were transferred from a field notebook onto record cards for easy reference.

The testes (apart from being weighed) were not subjected to any examination. Both ovaries with their outer ovarian capsules intact were weighed to the nearest mg and a weighed portion dissected under a binocular microscope. The number of eggs in the portion of ovary dissected was counted differentially with respect to size, appearance and stage of development. The various categories established for this purpose are described in section VIII. Eggs less than 0.19 mm. diameter were not counted. It was thus possible to calculate the number of eggs greater than 0.19 mm. diameter in the entire ovary.

The fixed material of ovaries was washed in 70% ethanol, dehydrated and sectioned at 15 μ. Sections were cut at three levels namely the anterior, middle and posterior regions. Satisfactory results were obtained if, before staining with haematoxylin, the sections were passed through a 1% solution of potassiun permanganate until brown and then treated with 1% oxalic acid until colourless, the acid being subsequently washed away in distilled water.

The sections were then stained in the usual way with haematoxylin and eosin. This preliminary treatment with potassium permanganate results in more vivid colouration of the sections (Guyer, 1953).

HYDROLOGICAL AND METEOROLOGICAL DATA:

Hydrological sampling was carried out to determine the influence of various factors on the fish populations. A station B (see map 2) was established at which routine hydrological investigations were carried out once a week at 0700 hrs. pH was determined with a Lovibond comparator and filter discs. Water samples were taken and oxygen concentrations determined later in the laboratory by means of the Winkler method (Mackereth, 1963). Temperatures of the air and of water at 0.3m below the surface were observed.

Data on water level as well as meteorological data were obtained from the Hydrological Unit of the State Construction Corporation.

These data were supplemented by observations made routinely by Dr. S. Biswas and Mr. R. Attionu at a sampling station shown as C on Map 2 and included pH, alkalinity as well as temperature and dissolved oxygen at a number of depths.

IV. SPECIES COMPOSITION AT AKOSOMBO.

The history of the formation of the *Tilapia* stock after the closure of the dam can be obtained from a study of the species composition of the catches. Data both upon the initial build up and subsequent changes in the size of the *Tilapia* population may be sought not only from routine nettings such as those undertaken in the present study, but also from records of fish caught commercially. These latter data are however of very limited value. Fishermen are inclined to use only large sizes of gill nets and hence commercial catches from gill nets give no indication of the numbers of young fish present in the Lake and due to be caught in the future. Furthermore, fishermen are apt to stop fishing when catches decline seasonally due to migration to other places and so their records do not provide adequate material for assessing fish abundance at any one place. Thus although these records have some value for general information they were not used for the present work which was a comparison of the changes in the occurrence of fish.

Comparative data of greater value can be obtained from routine observations made by the Fisheries Division at Akosombo from January 1965 (Fisheries Report, 1965). They show (Table 2 and fig.4,) the marked change in the relative abundance of *Tilapia* between the early months of 1965 and the final months of that year. Associated with this change was a striking decline in the abundance of *Alestes* species and an increase in that of *Chrysichthys* species, the latter displacing the former from its dominant position in the catch.

TABLE 2

% SPP OCCURRENCE IN DIFFERENT MONTHS
JANUARY-APRIL AND NOVEMBER-DECEMBER 1965

	Janua		Februar		March		A ril		November		December	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Alestes spp.	872	49.07	378	26.36	908	78.80	185	53.78	-	-	-	-
Lates	92	5.18	4	0.28	-	-	-	-	3	0.89	75	6.70
Labeo spp.	103	5.80	232	16.18	65	5.67	41	11.92	2	0.55	9	0.80
Hydrocynus	197	11.09	26	1.81	-	-	-	-	1	0.27	10	0.89
Barbus spp.	5	0.28	-	-	-	-	-	-	-	-	-	-
Bagrus spp.	2	0.11	-	-	-	-	-	-	-	-	-	-
Tilapia spp.	4	0.23	-	-	2	0.17	-	-	55	16.37	463	41.38
Citharinus cith	1	0.06	-	-	-	-	-	-	-	-	-	-
Clarias	3	0.17	2	0.14	51	4.45	-	-	-	-	4	0.36
Distichodus	1	0.06	169	11.79	23	2.01	10	2.90	22	6.55	4	0.36
Heterotis	-	-	-	-	1	0.09	-	-	-	-	-	-
+ Other spp.	497	27.95	623	43.44	101	8.81	108	31.40	-	-	-	-
Chrysichthys	-	-	-	-	-	-	-	-	253	75.37	550	49.15
Auchenoglanis	-	-	-	-	-	-	-	-	-	-	4	0.36
	1777		1434		1146		344		336		1119	

\+ Other spp. include : Synodontis, Ctenepoma, Hepsetus
Hemichromis etc. etc.

Data supplied by Fisheries Division, Akosombo.

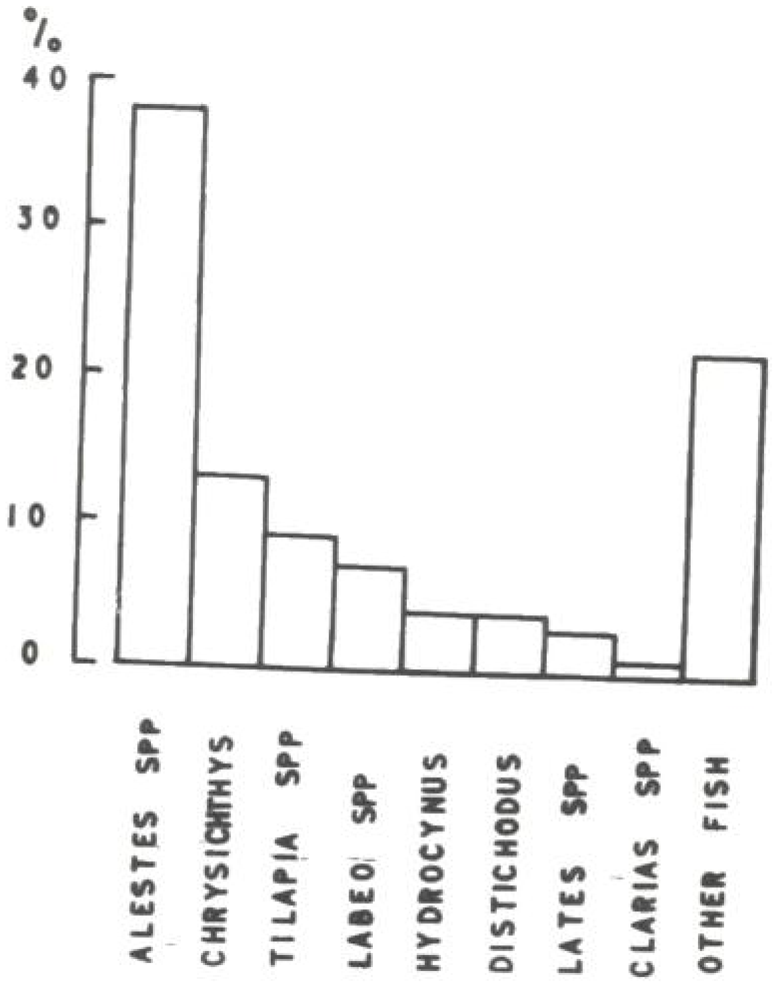


Fig. 4. Percentage species composition from Jan. to Apr. and Nov. to Dec. 1965. (Data from Fisheries Division, Akosombo).

The data collected by the Fisheries Division both during 1965 and 1966 are not beyond criticism. Their catches were mostly limited to 3" nets and a selection was made of the total catch, only specimens which could be considered as being in marketable condition being counted. It is clear that if data are to be collected which will be of value for comparison in subsequent years, a fleet of nets should be used and the total catch, regardless of condition, recorded so as to avoid any arbitrary selection based upon some subjective opinion which may itself vary with time.

The data shown in Table 3 and fig.5 summarise the total catches in the fleet of nets used in the present investigation between January and August 1966. No attempt is here made to differentiate between catches from the different nets and catches from different localities as described before. Out of a total of 4092 fish caught during the period, 1877 were Chrysichthys spp. representing 45.90% of the total catch. This genus was predominant in the total catch which included twelve other families of fish. Synodontis spp. was the next most abundant fish representing 19.20%, followed by Tilapia spp. (11.30%). Of those species regularly occurring in the catches, Auchenoglanis was least abundant, forming only 0.10% of the total catch. Certain other species of fish which occasionally appeared in the gill nets were nevertheless commonly caught by other types of gear. For example Clarias and Heterotis are often caught by hook and line.

The data shown in Table 4 and fig.6 summarise the catches made by the Fisheries Division over the same period. It will be seen that they reflect the same general picture with Chrysichthys as the dominant

% SPP. OCCURRENCE IN DIFFERENT MONTHS
JANUARY-AUGUST 1966

TABLE 3

pp.	January		February		March		April		May		June		Jul		Au ust	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
sichthys spp.	217	21.70	134	56.07	188	36.37	377	53.25	472	63.36	236	50.11	188	79.66	65	36.93
dontis spp.	530	53.00	6	2.51	121	23.40	57	8.05	17	2.28	9	1.91	6	2.54	38	21.59
ia spp.	108	10.80	84	35.15	104	20.12	80	11.30	36	4.83	24	5.10	9	3.81	18	10.23
be/Eutropius	53	5.30	-	-	29	5.61	78	11.02	63	8.46	9	1.91	25	10.59	12	6.82
opoma	7	0.70	-	-	7	1.35	36	5.08	33	4.43	126	26.75	-	-	10	5.68
chromis	3	0.30	2	0.84	8	1.55	27	3.81	66	8.86	21	4.46	1	0.43	10	5.68
es spp.	18	1.80	1	0.42	18	3.48	27	3.81	20	2.68	9	1.91	-	-	6	3.41
chodus spp.	15	1.50	-	-	9	1.74	6	0.85	14	1.88	17	3.61	4	1.69	-	-
spp.	2	0.20	-	-	9	1.74	1	0.14	9	1.21	7	1.49	-	-	6	3.41
spp.	22	2.20	9	3.78	1	0.19	1	0.14	-	-	-	-	-	-	-	-
terus	-	-	-	-	4	0.77	3	0.42	2	0.27	4	0.85	1	0.43	6	3.41
noglanis	-	-	-	-	2	0.39	-	-	2	0.27	1	0.20	-	-	1	0.57
spp.	25	2.50	3	1.25	17	3.29	15	2.13	11	1.47	8	1.70	2	0.85	4	2.27
	1000		239		517		708		745		471		236		176	

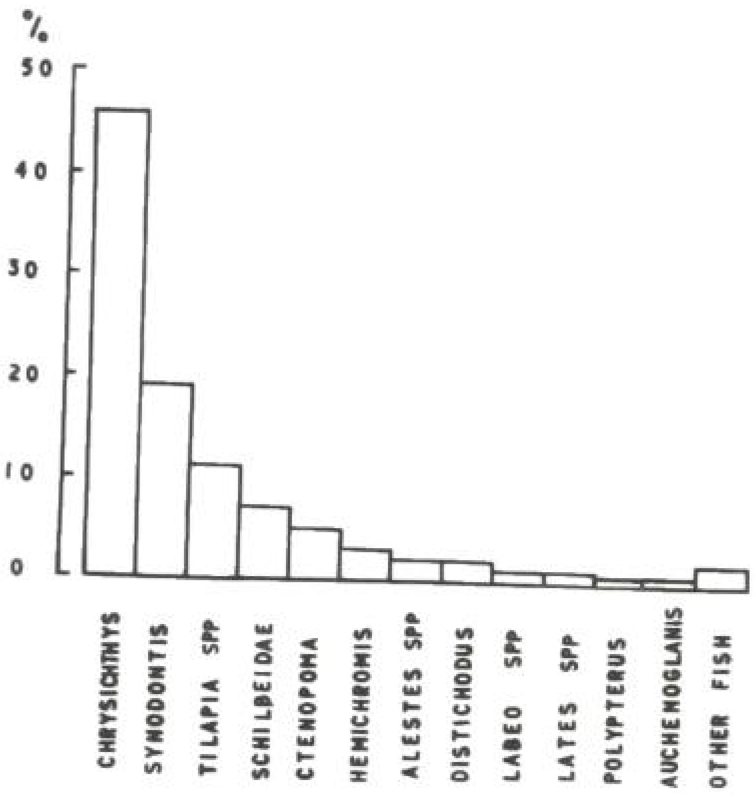


Fig. 5. Percentage species composition at Akosombo from January to August 196.

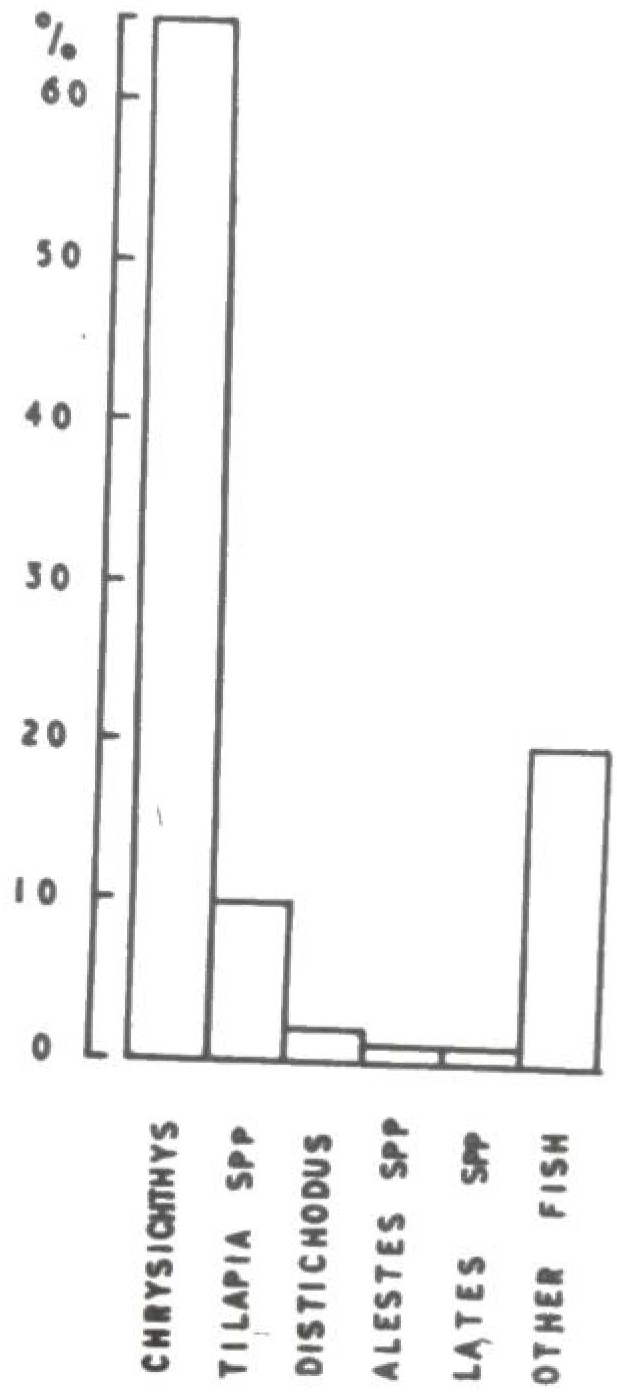


Fig. 6. Percentage species composition at Akosombo from January to August 196.
(Data from Fisheries Division, Akosombo).

TABLE 4

% SPP. OCCURRENCE IN DIFFERENT MONTHS
JANUARY-AUGUST 1966

Spp.	January		February		March		April		May		June		July	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Chrysichthys spp.	204	30.68	124	54.39	29	60.41	334	86.75	361	80.04	433	77.18	191	79.90
Alestes spp.	10	1.50	1	0.44	-	-	-	-	24	5.32	3	0.53	-	-
Distichodus spp.	10	1.50	-	-	1	2.08	6	1.56	10	2.22	26	4.64	4	1.68
Lates	22	3.31	13	5.70	-	-	-	-	-	-	1	0.18	-	-
Tilapia spp.	64	9.63	36	15.79	11	22.92	31	8.05	22	4.88	60	10.70	9	3.79
"Other spp."	355	53.38	54	23.68	7	14.59	14	3.64	34	7.54	38	6.77	35	14.64
	665		228		48		385		451		561		239	

Data supplied by Fisheries Division, Akosombo.

"Other spp." include Synodontis (majority); Schilbe/Eutropius, Hydrocynu
Ophiocephalus, Ctenopoma & Mormyridae.

species, followed in relative abundance by *Tilapia* and then by *Synodontis*. The number of *Synodontis* species is not noted but information indicates that the majority of fish lumped as "other fish" were in fact *Synodontis* species. Personal observations of the catches of the local fishermen showed a similar situation. It seems from figs.4 and 5 that species of fish can be classified into:

(a) Those with permanent or stable occurrence such as Bagridae and the cichlids and

(b) Those with seasonal occurrence such as *Distichodus* spp., *Lates* and *Labeo* spp.

CHANGES IN THE RELATIVE ABUNDANCE OF FISH DURING THE PERIOD OF INVESTIGATION

An examination of Table 3 shows that there are two distinct changes which occurred in the population of fish at Akosombo during the period of study. The first concerns the absolute numbers of fish caught. As can be seen, the total numbers of fish caught showed marked fluctuations from month to month. The total catch was exceptionally high in January partly owing to a remarkable abundance of Synodontis, fell sharply in February and then rose again during March, April and May to show a further steady decline during the remaining three months. At one time it seemed that the drastic decline in the number of fish caught might be due to the theft of fish from my nets, but remaining overnight in the vicinity of these nets in order to ensure that they were not interfered with led to no improvement in the catches. Unfortunately the data collected by the Fisheries Division cannot be used as a check on these observations as the fishing effort in any one month was variable and consequently total catch figures are of doubtful significance. There is, however, in these data the suggestion that the total fish population had started to decline in July and August. This was significant in T.galilaea in which the catch/fishing day was 10.69 in January and February and 2.02 from March to August, ($p < .01$). It is noteworthy that the commercial fishermen started to leave Akosombo for other fishing grounds towards the end of May and early June, a fact in keeping with the conclusion that the total catch had started to decline at this period of the year.

Comparisons of the relative abundance of different species within the catch of any one month are of uncertain validity and have to be approached with caution. Thus for example the percentage occurrence of Chrysichthys rose from 21.70% in January to 56.07% in February and fell again to 36.37% in March, (fig.7). It does not follow that these figures really reflect any absolute change in the abundance of this fish. If the February data are taken as a point of reference, it will be seen that the low value in January is primarily the result of the exceptional abundance of Synodontis and that had this not occurred the percentage abundance of Chrysichthys would have been 47%. Similarly in March the percentage abundance of Chrysichthys is again lowered by a greater abundance of Synodontis than in February. Had this change not taken place Chrysichthys would again have constituted 47% of the total catch. This is not to imply that the population density of Chrysichthys was constant, but simply to emphasise the limited value of the present type of data and the fact that the significance of abrupt changes in relative abundance from month to month must be assessed critically.

As far as Tilapia is concerned, the percentage abundance recorded in any month will be affected by invasions of other species in a similar manner to that of Chrysichthys and here again it is the sharp variations in abundance of Synodontis which is a major factor. It seems possible to arrive at a more accurate picture of the relative abundance of Tilapia in one of two ways. The first is to discard completely all counts of Synodontis; the second to express the abundance of Tilapia relative to

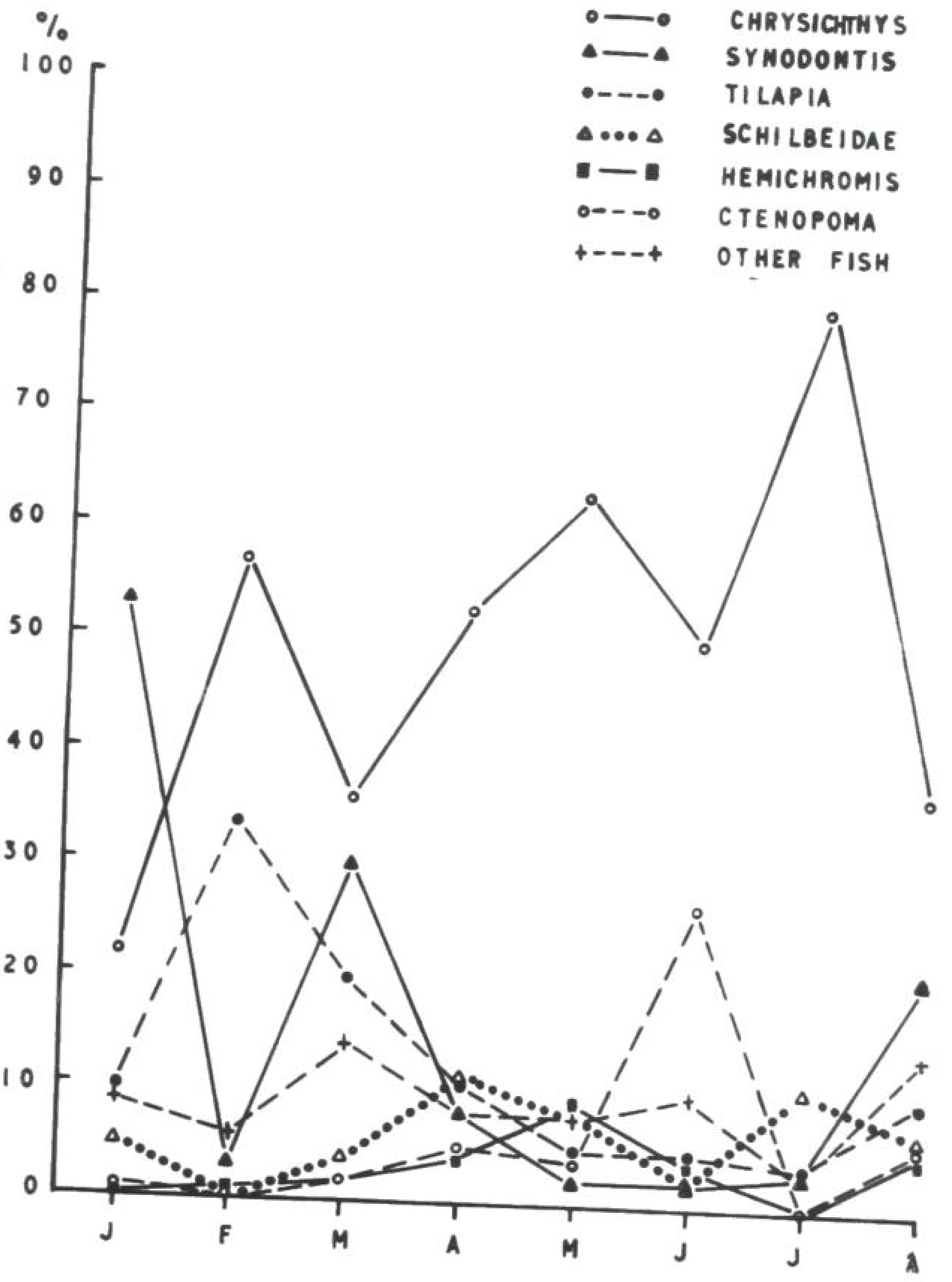


Fig. 7. Percentage proportion of different fish species in different months.

that of *Chrysichthys* as the only other fish occurring in sufficient numbers to make certain that small catches are not biasing the results. The outcome of such an analysis is shown in Table 5, in which it can be seen that the abrupt changes in relative abundance between January and March are markedly smoothed out by the two alternative methods of calculation. At the same time all the results point to a sharp fall in the relative abundance of *Tilapia* spp. after April.

Reviewing Table 3 as a whole it seems possible to recognise three patterns of change in relative abundance.

(a) A more or less constant relative abundance over the whole period of study. This would appear to be true of *Chrysichthys* and may also apply to some of the other species which appeared only rarely in the catch, but the numerical data are too few to permit any conclusion being drawn.

(b) A high relative abundance during the early months followed by a marked decline or complete disappearance, with some possible signs of recovery in August. This would appear to apply to *Tilapia*, *Synodontis* and *Lates*, although the last species showed no late recovery.

(c) A marked increase in relative abundance starting perhaps in March and becoming clear-cut in April, May and June. Such a pattern is shown by *Ctenopoma* and *Hemichromis* and by the two schilbeids.

These changes in relative abundance must be distinguished clearly from the general decrease in absolute abundance characteristic of June, July and August.

TABLE 5. % RELATIVE ABUNDANCE OF TILAPIA SPECIES IN DIFFERENT MONTHS. JANUARY - AUGUST 1966.

	% Occurrence of Tilapia of total catch	% Occurrence of Tilapia of total catch less Synodontis.	Tilapia as % of Tilapia plus Chrysicthys.
January	10.80	22.98	33.23
February	35.15	36.07	38.53
March	20.11	26.26	35.61
April	11.30	12.28	17.51
May	4.83	8.41	7.09
June	5.10	5.20	9.23
July	3.81	3.91	4.57
August	10.23	13.04	21.69

Fig.8 shows not only these data but also values for the mean monthly rainfall, lake level, temperature at 0.3 meters, dissolved oxygen from both the surface at the sampling site and from a depth of 5 m. at Ajena as well as Secchi disc readings from the station at Ajena. The last two values were obtained by Dr. S. Biswas and Mr. R. Attionu.

It will be seen that of these factors only rainfall and Secchi disc readings show any marked seasonal variation and it would appear probable that the decrease in relative abundance of Lates, Synodontis and Tilapia correlates with the advent of the small rains. The increase in relative abundance of Ctenopoma and Hemichromis shows a similar but opposite correlation. It is possible that the general decrease in the absolute numbers of fish after May may correlate either with the decreasing precipitation or, more possibly, with the rise in the level of the Lake which occurred towards the end of the period of observation. However, confirmation of this is required in the following year.

It is possible to recognise a variety of factors which could lead to these changes in the composition of the fish catch. Among these are:

(a) Seasonal migrations away from one region to another in search of preferred food. Such an event might perhaps be the origin of the disappearance of Lates which is a predator.

(b) Seasonal migrations away from a feeding ground to some preferred spawning area .

(c) Seasonal migrations into the area which is a preferred spawning ground but not favoured by the adults outside the breeding season.

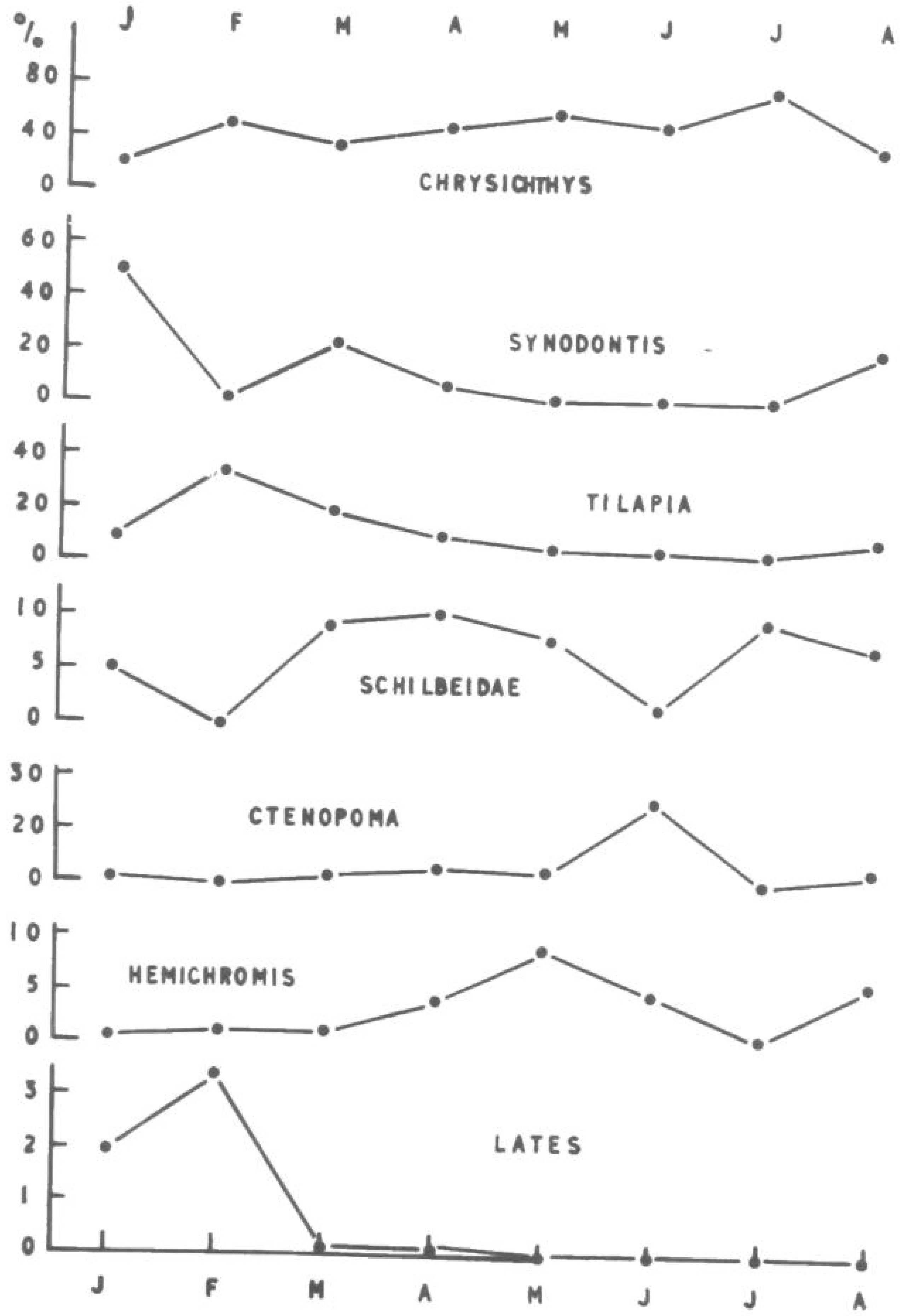


Fig. 8a. Percentage changes in Relative Abundance of fish. (Mean monthly values).

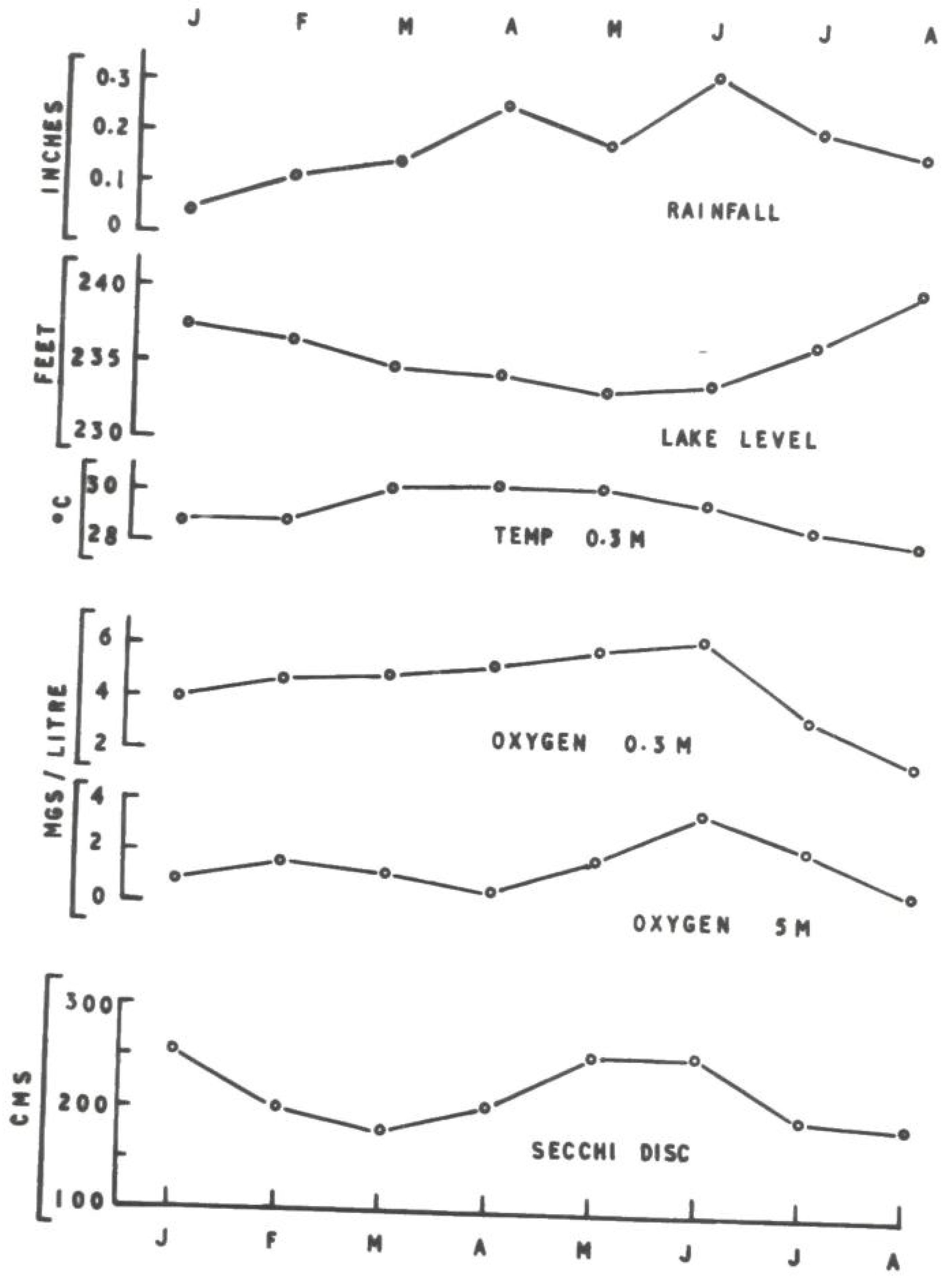


Fig. 8b. Mean monthly variations in Rainfall, Lake Level, Water Temperature, Oxygen concentration and Secchi Disc.

Clearly only the accumulation of further data and the intensive study of the habits and habitats of particular species will show whether these or other factors are the cause of the changes observed.

Finally, it seems possible that the rise in lake level may have resulted in a change in the general abundance and quality of food in the area with the result that it became generally less acceptable to the whole fish population.

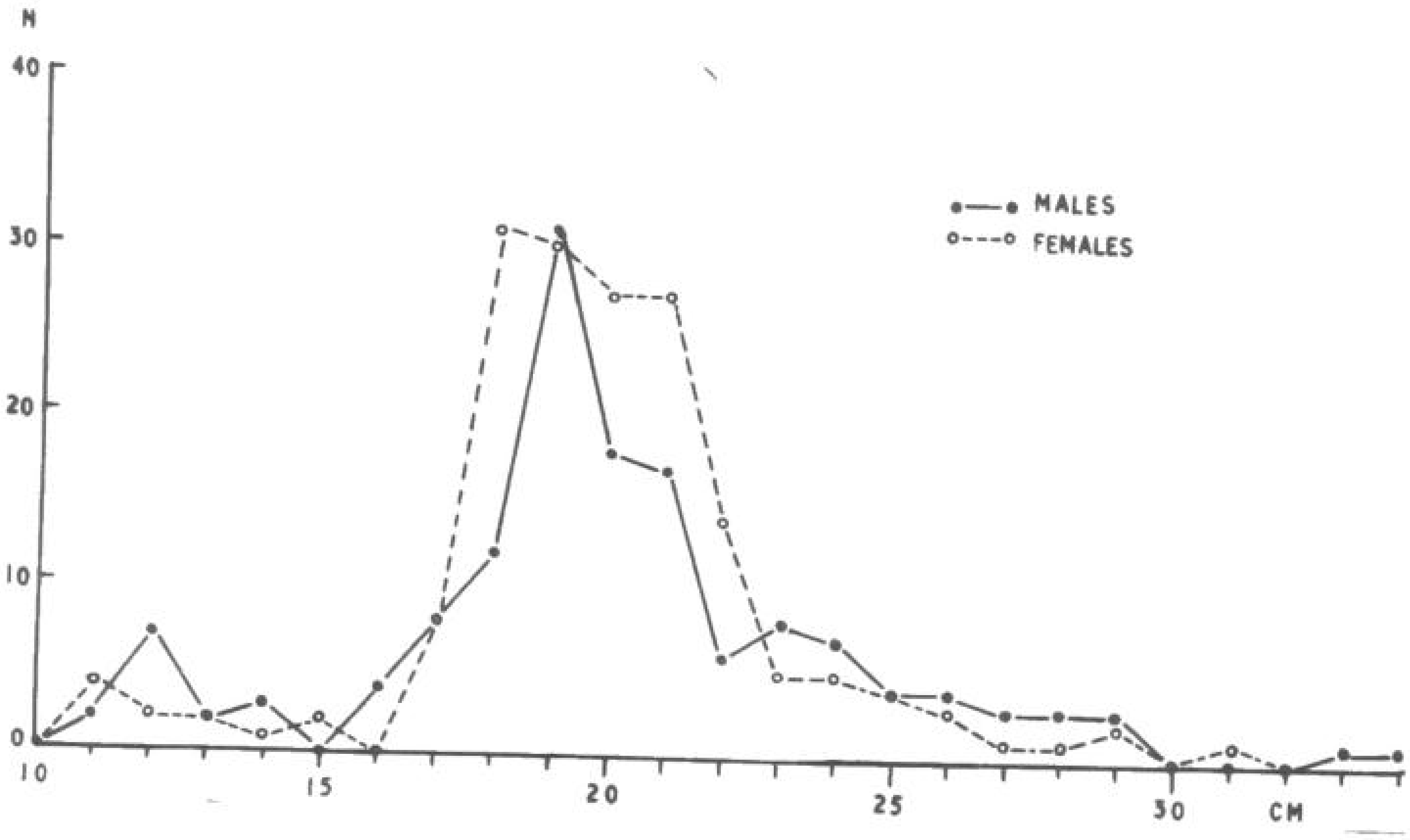


Fig.9.

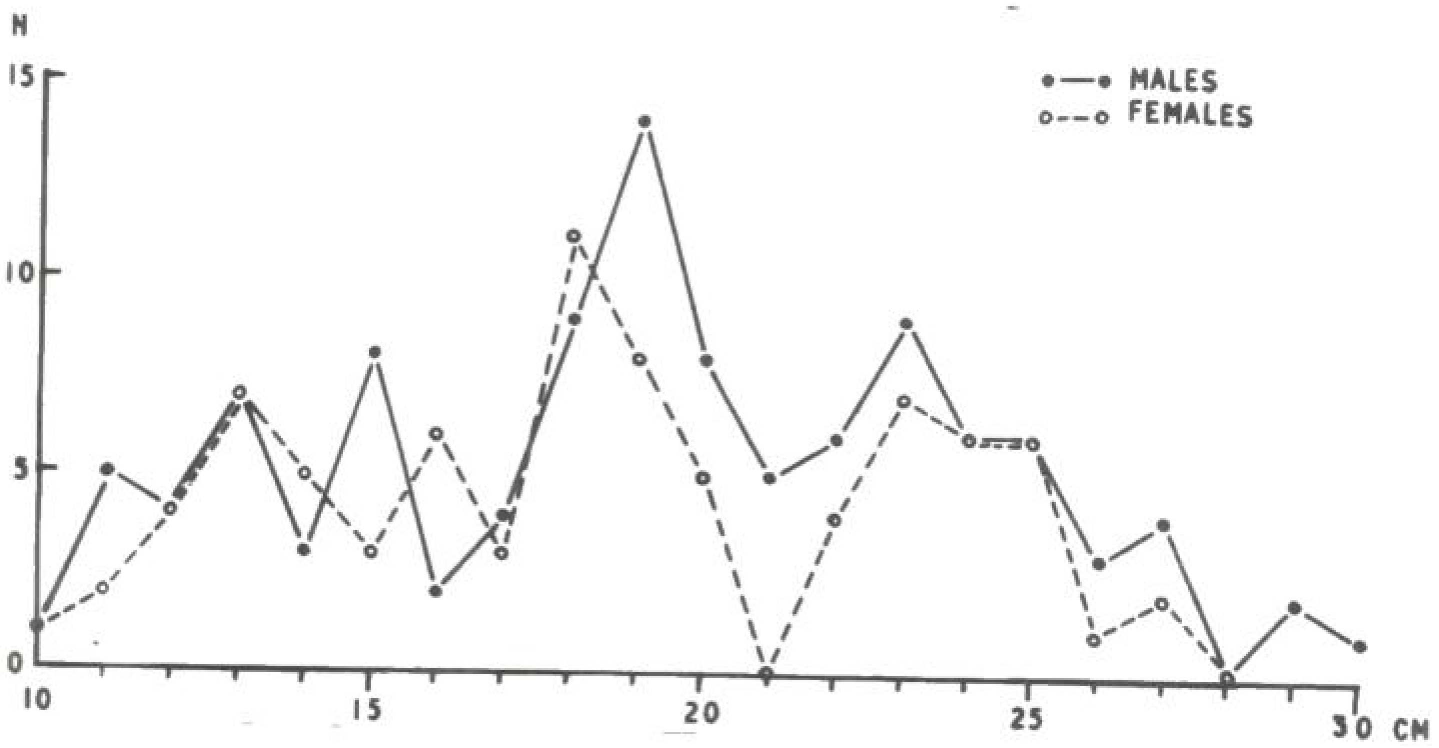


Fig.10.

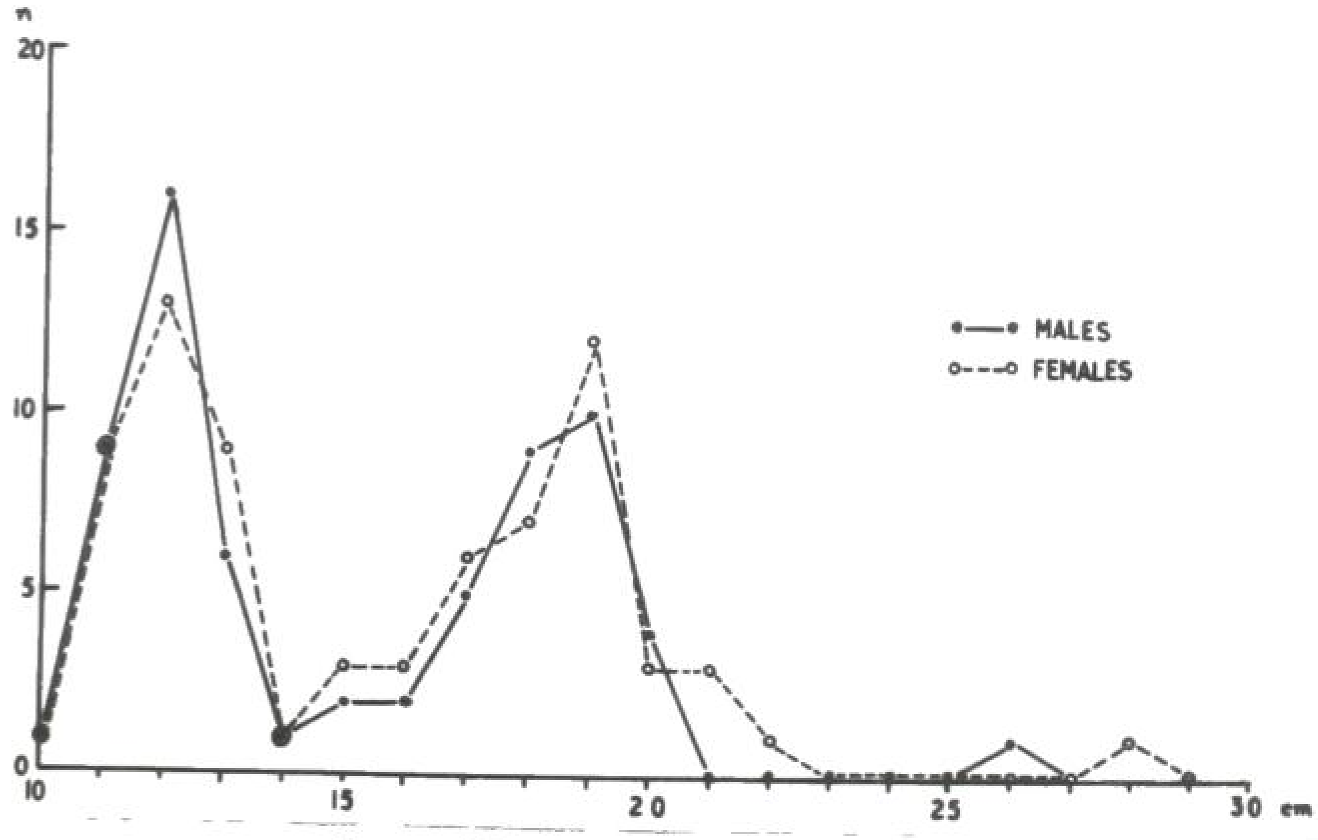


Fig.11.

Length-frequency distribution of

Fig. 9. T. galilaea (sexes separate).
Fig.10. T. nilotica " "
Fig.11. T. zilli/melanopleura ".

commonly subject to casualty. The present data do not allow any decision to be made between these possibilities.

Reports stating that Tilapia males are larger than females have been made from a number of localities; in other cases, however, no difference in maximal size between the two sexes has been found. These results have been summarised in Table 6 where it will be seen that in two localities, L. Muleyhe and L. Bunyoni of East Africa, females reached a greater maximal length than males. It is clear from these sometimes conflicting accounts that size differences between the sexes is slight and no explanation has been offered as yet to account for the differences between the results obtained by different workers with the same species from different localities.

Figs. 12, 13 and 14 show the same data replotted without regard to sex. An examination of the length-frequency distribution for Tilapia nilotica strongly suggests that four distinct size classes are represented in the population. The same tendency may perhaps be recognised in T.galilaea but in this case the catch is completely dominated by the size class arbitrary numbered II and the presence of representatives of the other three size classes is little other than a reasonable surmise. With T.zilli/melanopleura there are specimens whose modal lengths appear to agree well with the classes I and II recognised in T. nilotica, but beyond this it is not possible to recognise any distinct classes, although the results suggest that at least one further size class is represented by the largest individuals

TABLE 6

Size differences between the sexes of *Tilapia* species from different localities.

SPECIES	LARGER FISH	LOCALITY	AUTHOR
T. nilotica	♂ > ♀	L. Rudolf	Worthington & Ricardo (1936)
"	♂ > ♀	L. Baringo	Worthington (1929)
"	♂ = ♀	L. Rudolf	McConnell (1958)
"	"	L. Albert	
"	"	L. Edward	
"	"	L. George	
"	♀ > ♂	L. Muleyhe	McConnell (1958)
"	♀ > ♂	L. Bunyoni	
"	♂ > ♀	Buhuku lagoon (L. Albert)	Lowe (1958)
"	♂ > ♀	Kijani pond	
T. zilli	♂ > ♀	Teso Dams	E.A.F.R.O. (1953)
T. leucosticta	♂ > ♀		
T. melanopleura	♂ > ♀	Belgian Congo	De Bont & de Bont-Hers (1950)
T. mossambica	♂ > ♀	Indonesia	Vaas & Hofstede (1952)
T. nigra	♂ > ♀	E. Africa	Brown & van Someren (1953)
L. Jipe Tilapia	♂ > ♀	L. Jipe (Taveta pond)	E.A.F.R.O. (1953)
T. karomo	♂ > ♀	E. Africa	"
T. leucosticta	♂ > ♀	"	"
T. squamipinnis	♂ = ♀	L. Nyasa	Lowe (1956 b)
T. lidole			
T. esculenta	♂ = ♀	L. Victoria	"
T. variabilis			
T. variabilis	♂ > ♀	"	E.A.F.R.O. (1953)
*T. variabilis	♂ = ♀	E. Africa	"
*T. nilotica	♂ = ♀		
*T. zilli	♂ = ♀		

*Same rate of growth until mature and then differential growth determined by environmental

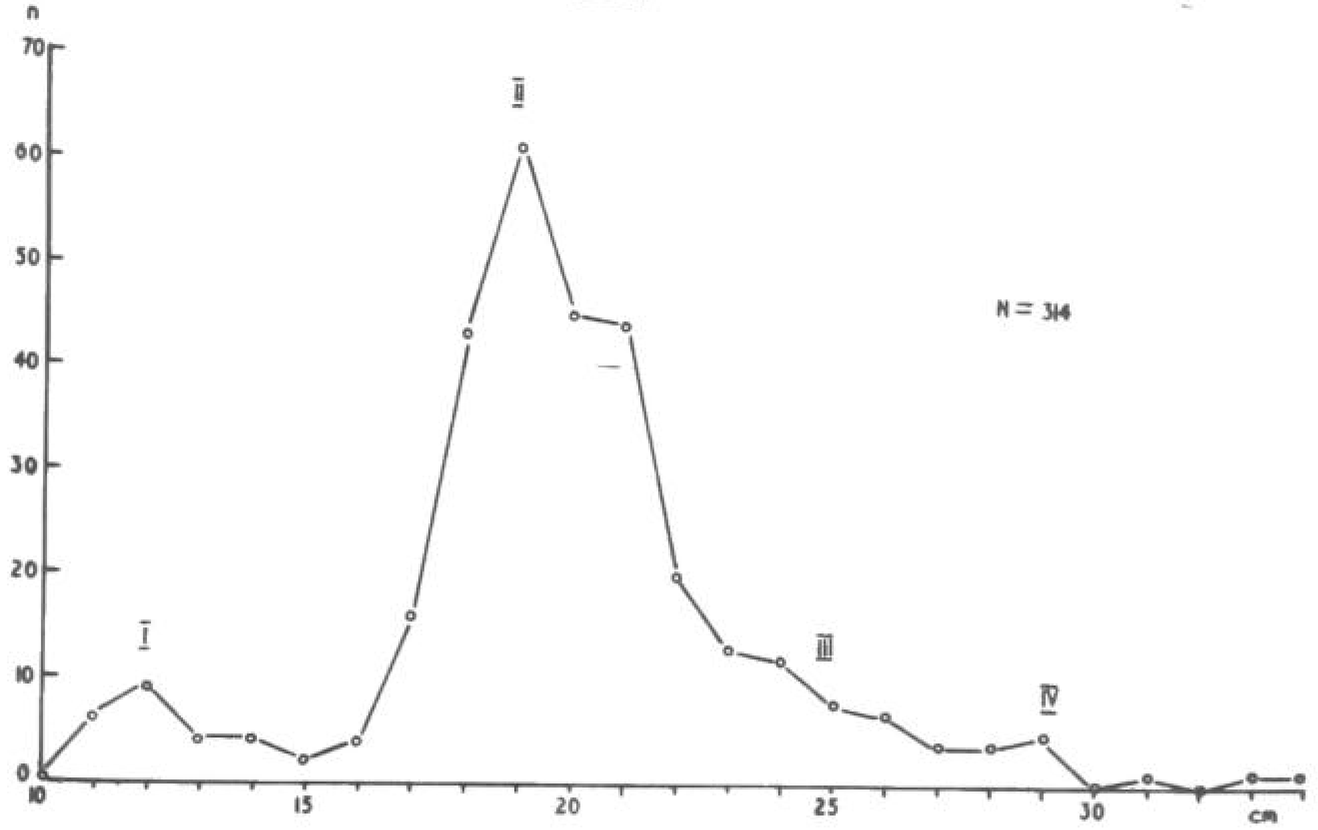


Fig.12

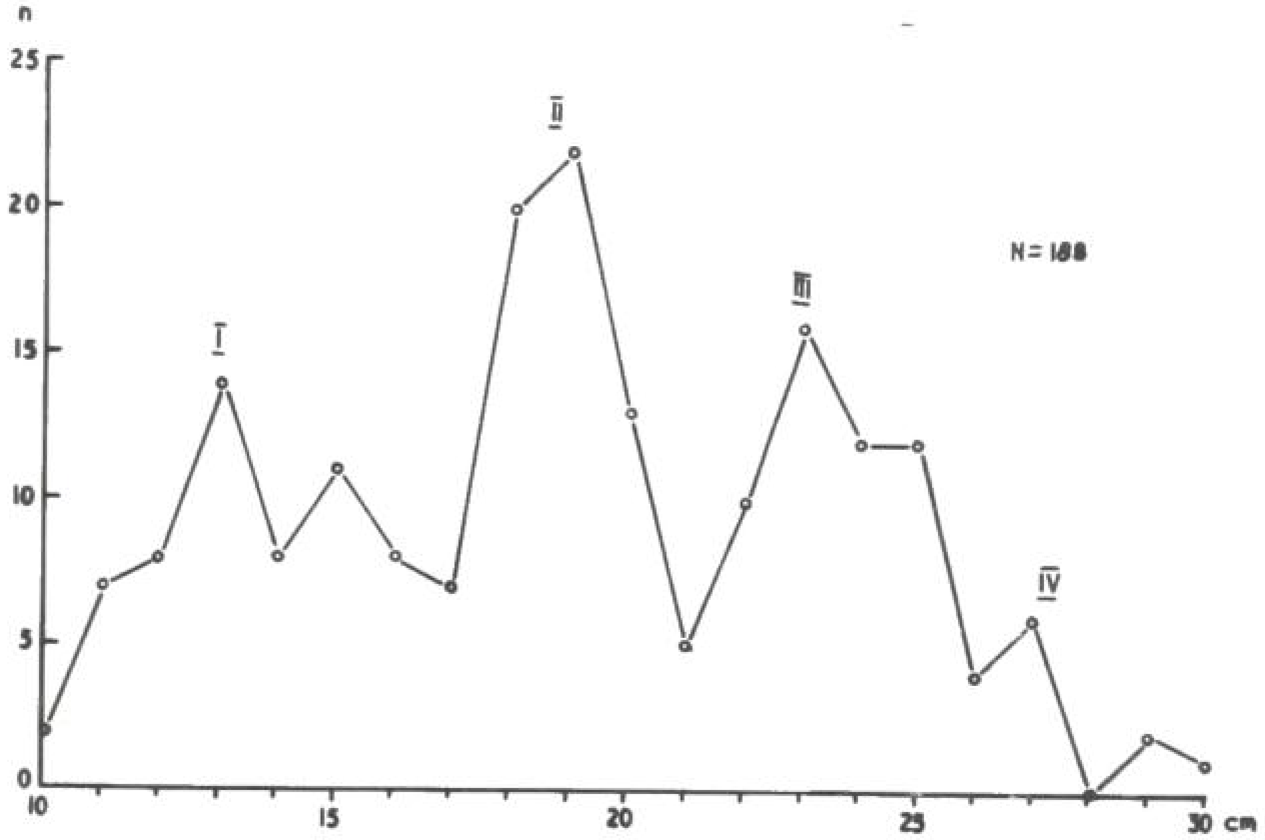


Fig.13

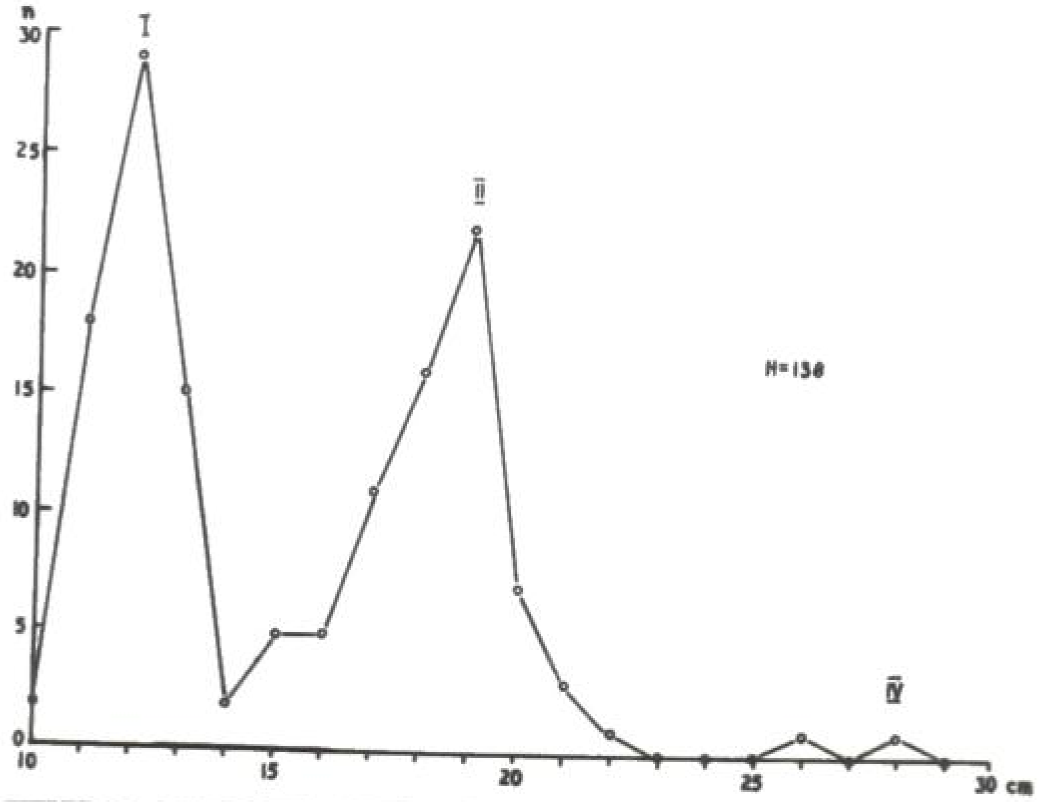


Fig.14

Length-frequency distribution of
Fig.12. T. galilaea (Both sexes).
Fig.13. T. nilotica " "
Fig.14. T. zilli/melanopleura ".

in the population. The modal lengths of these admittedly arbitrary size classes are shown in Table 7 below:

All lengths are in cms.

Table 7: Modal lengths of arbitrary size classes of Tilapia species.

	SPECIES		
Size Class	T.nilotica	T.galilaea	T.zilli/melan
I	13.0	12.0	12.0
II	19.0	19.0	19.0
III	23.0	25.0	-
IV	27.0	29.0	27.0

These values show a striking consistency from species to species and raise immediately the question of whether the size classes are reflections of the sampling procedure rather than the structure of the population. Unfortunately, scale reading of Tilapia was not possible for Lake Volta population. Some vague formation of crowded circuli observed were much too faint for providing reliable indication (plate 1). The breeding seasons are so ill-defined that attempts to trace length-frequency modes are generally unsuccessful. Any scale rings present appear to be spawning rings.

An attempt has been made to assess the effect of net selection upon two model populations of contrasting characteristics. In this, certain assumptions have been made to simplify the processes of calculation. These are discussed below:

1. That the catch of any net is distributed in a "normal" manner

PLATE 1.

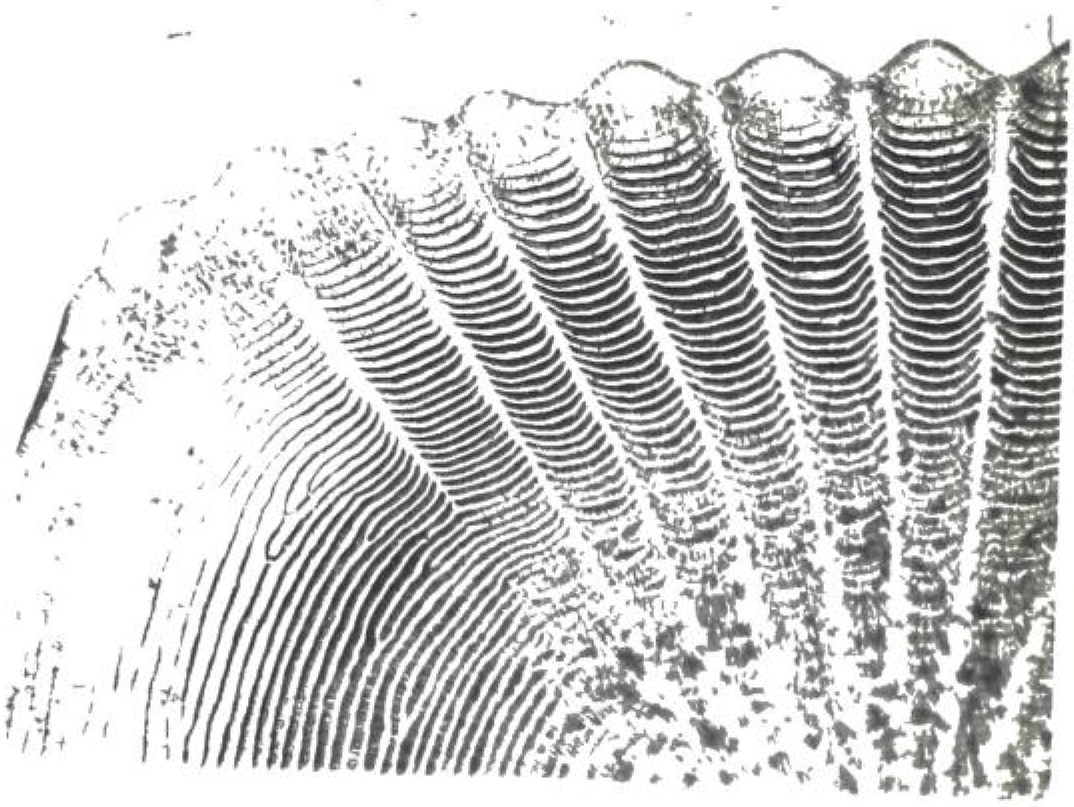


Fig. 1. T.galilaea (female) scale. 10 x. 12 cm total length.

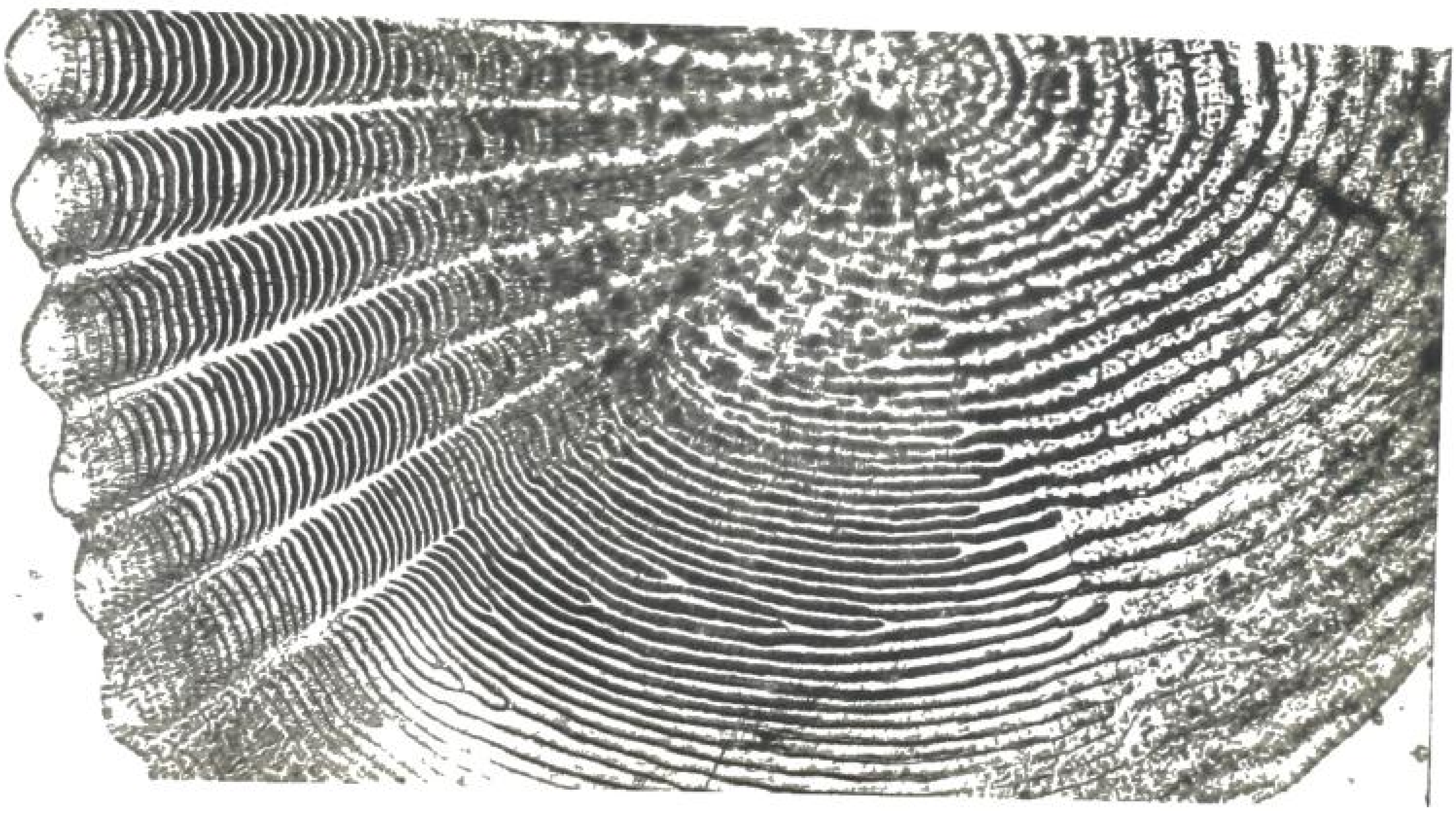


Fig. 2. T.galilaea (female) scale. 10x. 20.2 cm total length.

about the mode. The validity of this has been tested using data for T. galilaea, the species most commonly taken, and the 3 inch net, which was the most effective. Fig.15 shows the observed catches from the net, together with a curve of expectation of catch assuming the same mean length and standard deviation. It is immediately clear that the practical curve is skewed to the right (β_1 = +0.99; p= $>$ 0.02); the curve also shows that the distribution is clearly leptokurtic (β_2 = 4.64 ; p= $<$ 0.01) and when tested by χ^2 the practical curve is significantly different from expectation ($p < 0.01$). Nevertheless it was considered that the assumption was, to a first approximation, acceptable since what was sought was the general character of the catch characteristic of the fleet of nets and not accurate quantitative values.

2. It is further assumed that the behaviour of the fish towards nets of different mesh size is identical and that, say, small mesh nets are not avoided to a greater extent than large mesh nets.

3. The characterisation of the five nets required a knowledge of the modal length of fish caught by each mesh size as well as the range of sizes of fish taken. Table 8 shows the practical values of the range of sizes taken; these data are plotted on fig.16.

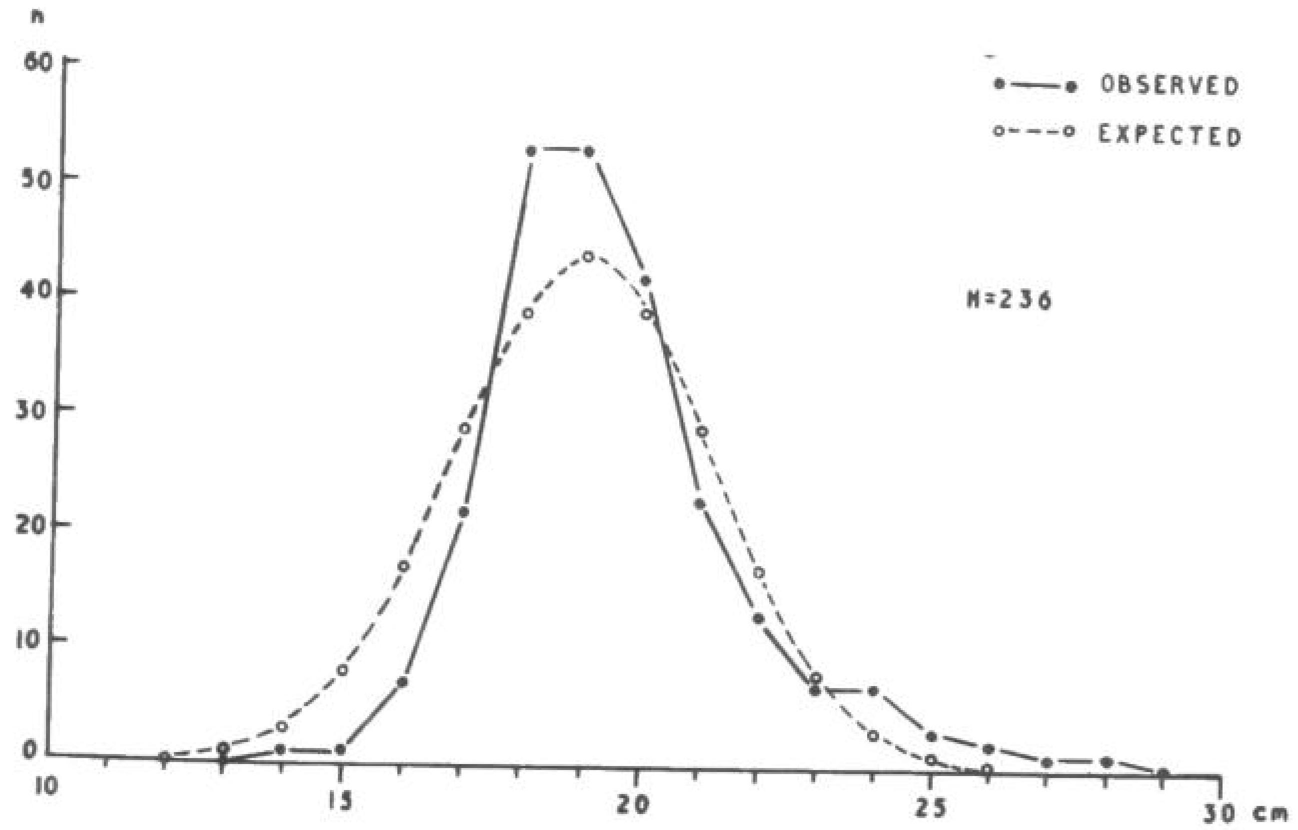


Fig. 15. Length-frequency distribution of <u>T. galilaea</u> caught in 3" net.

TABLE 8.

Size range of *Tilapia* spp. caught in $1\frac{1}{2}$, 2, 3, 4 and 5 ins. experimental gill nets.

Species	Mesh size in inches.				
Range in cms.	$1\frac{1}{2}$"	2"	3"	4"	5
T. galilaea	10 - 12	11 - 14	14 - 28	17 - 34	23 - 33
T. nilotica	12 - 19	12 - 13	16 - 26	20 - 29	-
T. zilli/melan.	11 - 19	12 - 17	13 - 21	21 - 25	-
N	37	53	362	81	9

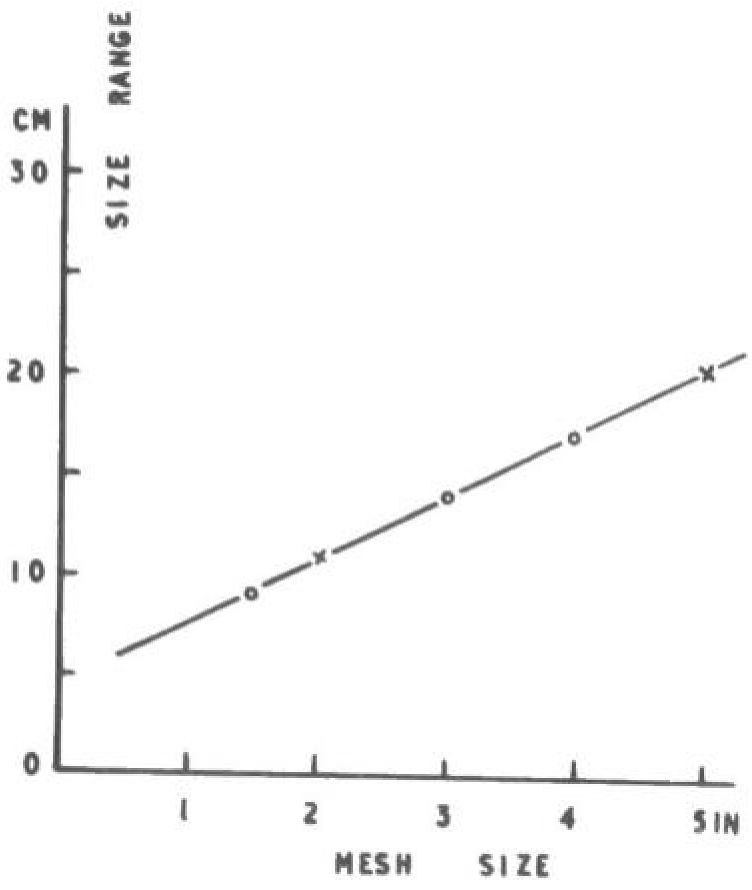


Fig. 16.

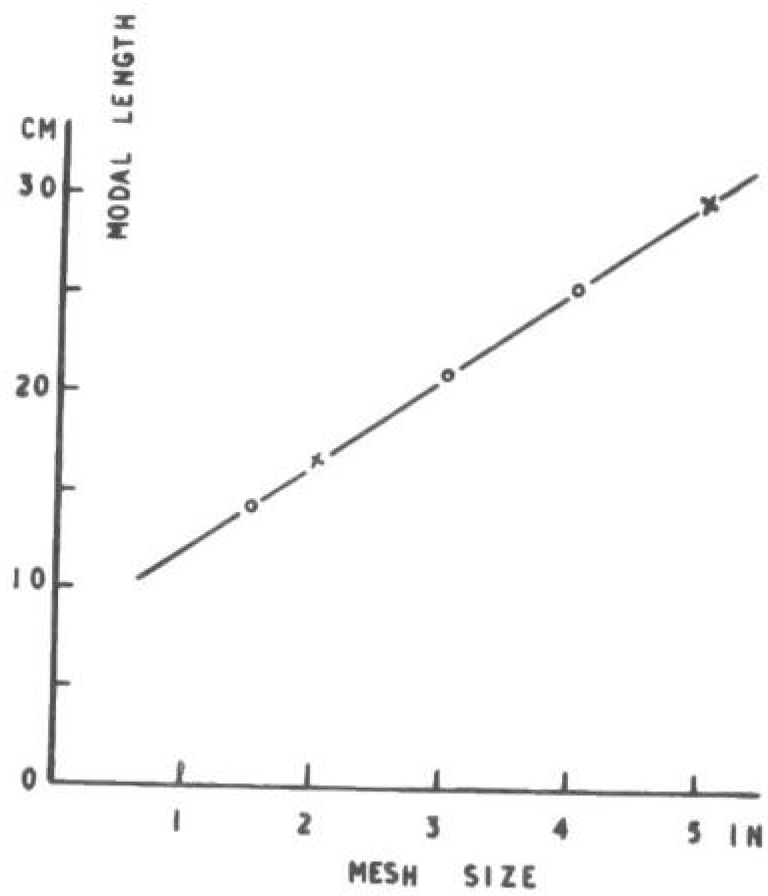


Fig. 17.

Relation between size range of fish, modal length and different mesh sizes.

It will be seen that the values for three of the nets fall upon a straight line and it has been assumed that the correct values for the 2-inch and 5-inch nets may be obtained by assuming a linear relation between catch-range and mesh size.

The modal length of fish caught by each net was determined in a similar fashion by assuming that the mode would lie at half the range above the minimal recorded size (fig.17). Thus for example if the smallest fish caught in a net was 10 cm. and the estimated range was 8 cm., the mode was taken as 14 cm.

With these assumptions the characteristics of the fleet of nets could be approximately described. Two cases were now studied. In the one it was assumed that all lengths were equally abundant in the population and that the fishing intensity of all nets was equal so that the same number of fish were taken at the relevant modal length by each net. This seems a more reasonable assumption than the alternative that an equal number of fish were caught by each net, if it is assumed that all fish have an equal opportunity of being caught.

The other case was one in which there is a single population with length normally distributed around a mean determined from the total calculated range. It was here assumed that any net catches individuals to an extent determined by their abundance in the population and the catch characteristics of that net.

The composition of the catch, expressed as length-frequency diagrams, for these two extreme conditions are shown in figs.18 and

19. It will be seen that the expected catch characteristic of the normally distributed population reflects the structure of the stock, but that the form of the curve is very markedly leptokurtic. With a population randomly distributed in size the catch characteristic does not reflect the structure of the population nearly so closely. As might be expected, it shows a rapid uprising at the shortest lengths caught, a trough due to insufficient coverage between the two inch and three inch mesh size and a long tail at the greater lengths.

With these results it is possible to draw certain tentative conclusions about the structure of the naturally occurring populations. The catch characteristics for the three groups have been standardised in fig.20 by reducing each length frequency to a percentage of the total catch. It is clear that the catch for T.galilaea resembles to a certain extent the catch characteristic in fig.18. This should not be interpreted as implying that the fish present are a single population with a considerable variation of length within the population. This may be the case. It is also possible that the peak around 19 cm. length reflects the product of an exceptionally favourable spawning period, a period in which, assuming almost equal growth rates, all three species enjoyed highly productive spawning.

The curve for T.zilli/melanopleura differs from the other two in showing a marked peak around 12 cm. From the results of the model represented in fig.18, it appears reasonable to conclude, not only

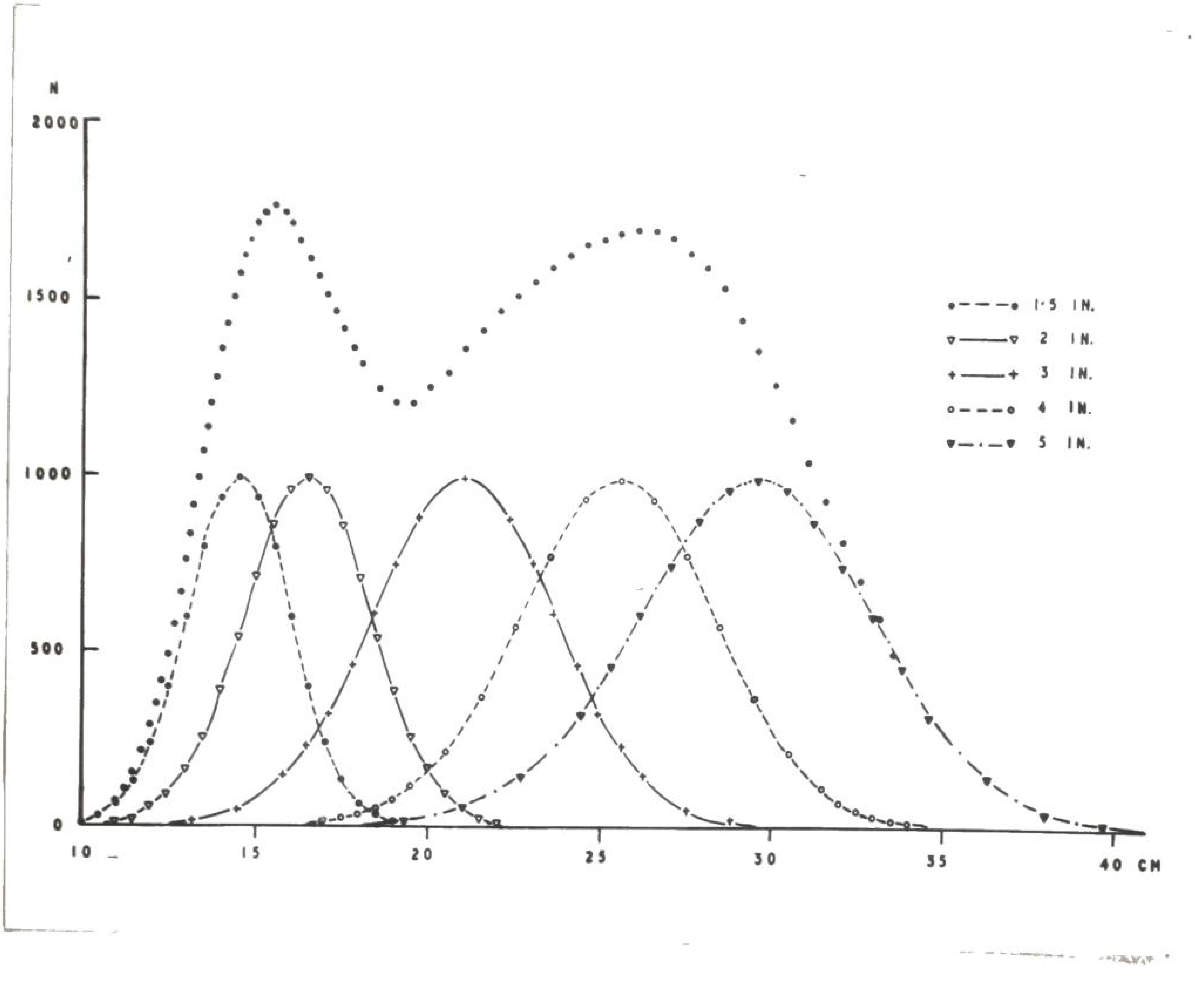


Fig. 18. Catch characteristic of randomly distributed population.

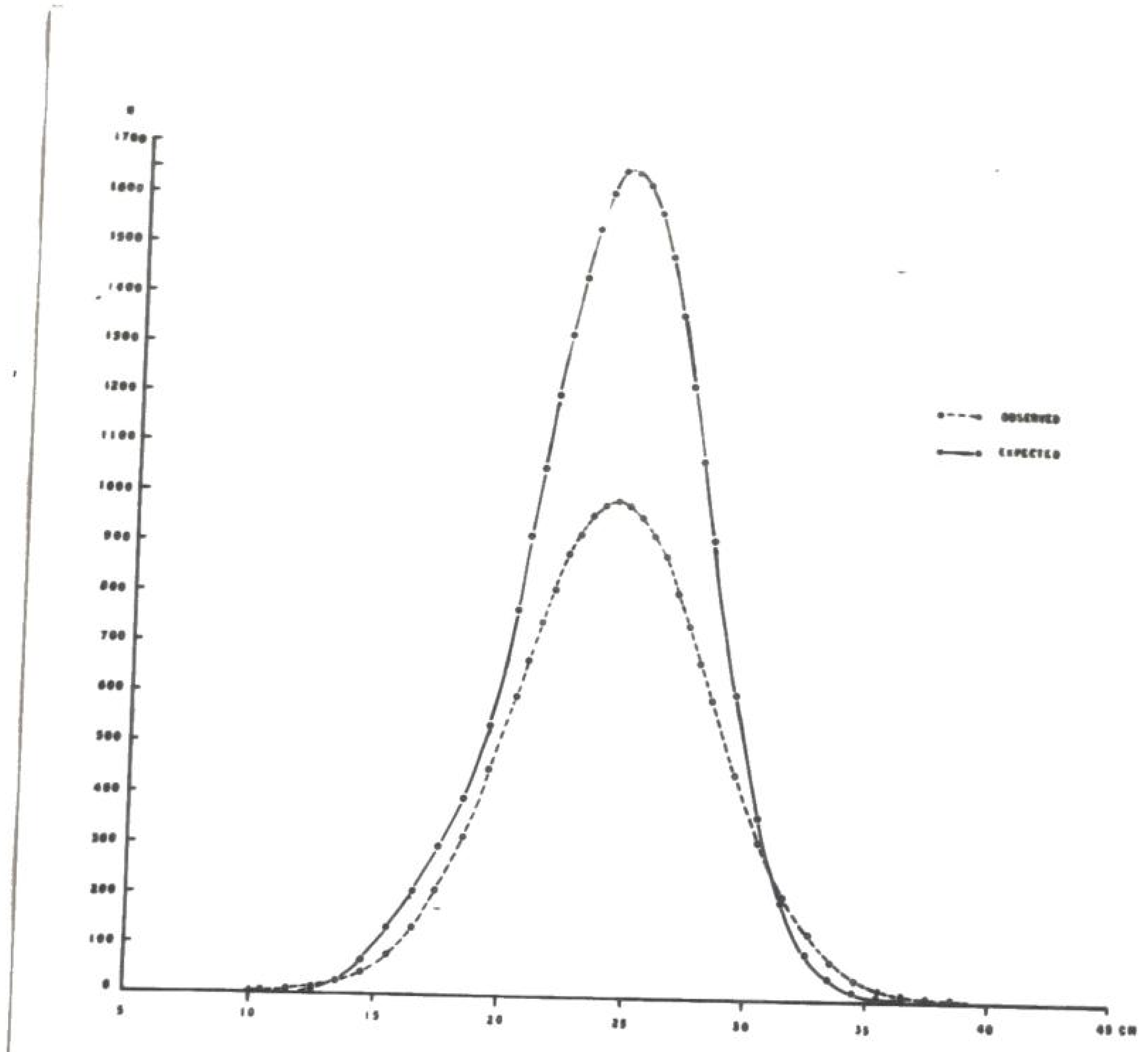


Fig. 19. Catch characteristic of normally distributed population.

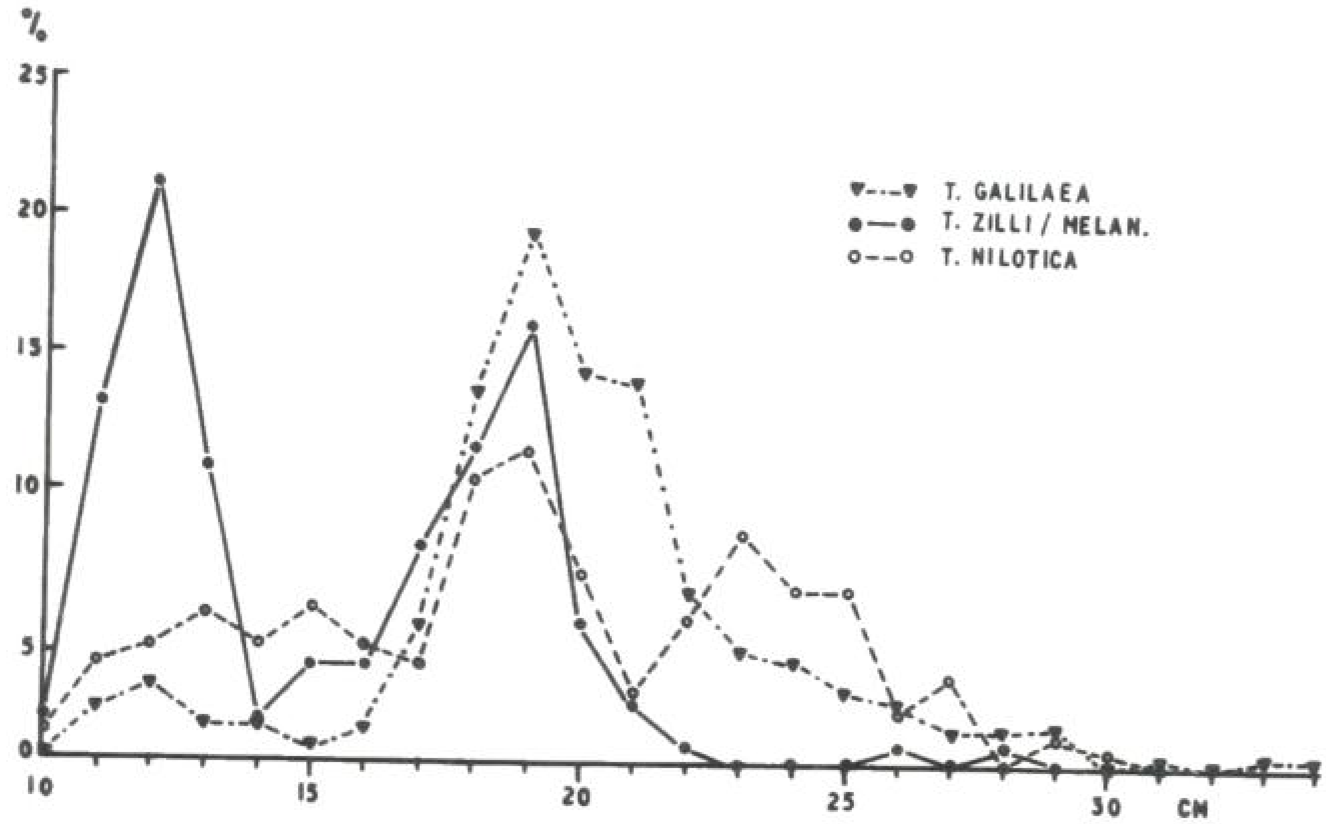


Fig. 20. Length-frequency distribution of _Tilapia_ species expressed as a percentage of the total catch.

that this difference is real, but that it reflects a second population or successful spawning time which was missed by T.galilaea and T.nilotica. It is possible that the small peak on either side of 27 cm. in the curve for T.zilli/melanopleura may represent a third successful spawning period, but this conclusion is very inadequately supported by the evidence.

From the model catch characteristics it seems likely that the wide mesh nets sampled fish up to the maximal size occurring and that T.galilaea reached, in this locality, significantly greater lengths than T.zilli/melanopleura.

The curve for T.nilotica is not easy to interpret. The trough around 21 cm. might well be due to the small size of the total sample and no safe conclusion can be drawn here.

These data were also broken down into catches during the dry and wet seasons in the hope that information upon the growth rate might be obtained. Inspection of these results figs.21-24 suggested that when the data were further subdivided in this manner they were too sparse to allow any valid conclusions to be drawn.

To sum up, the length-frequency diagrams suggest either that the variation in size within any age group is considerable or that there are times when spawning is more successful than others. The former interpretation applied to the case of T.zilli/melanopleura would imply that a considerable interval occurred between spawnings as the two supposed age categories differ in mean length by about 7 cm. and that T.zilli/melanopleura also perhaps spawns more frequently than T.nilotica

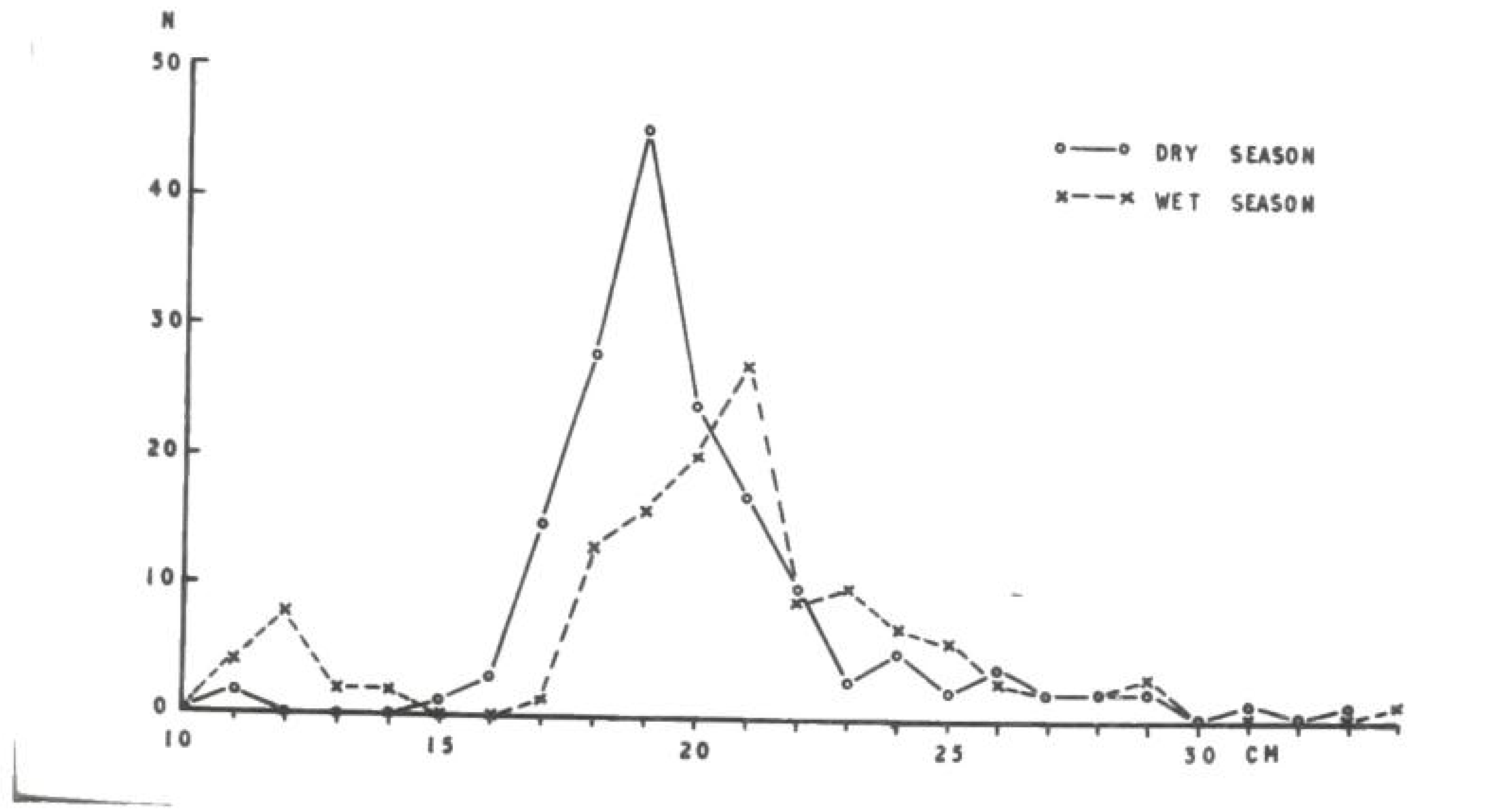


Fig. 21. Length-frequency distribution of T. galilaea in Dry and Wet Seasons.

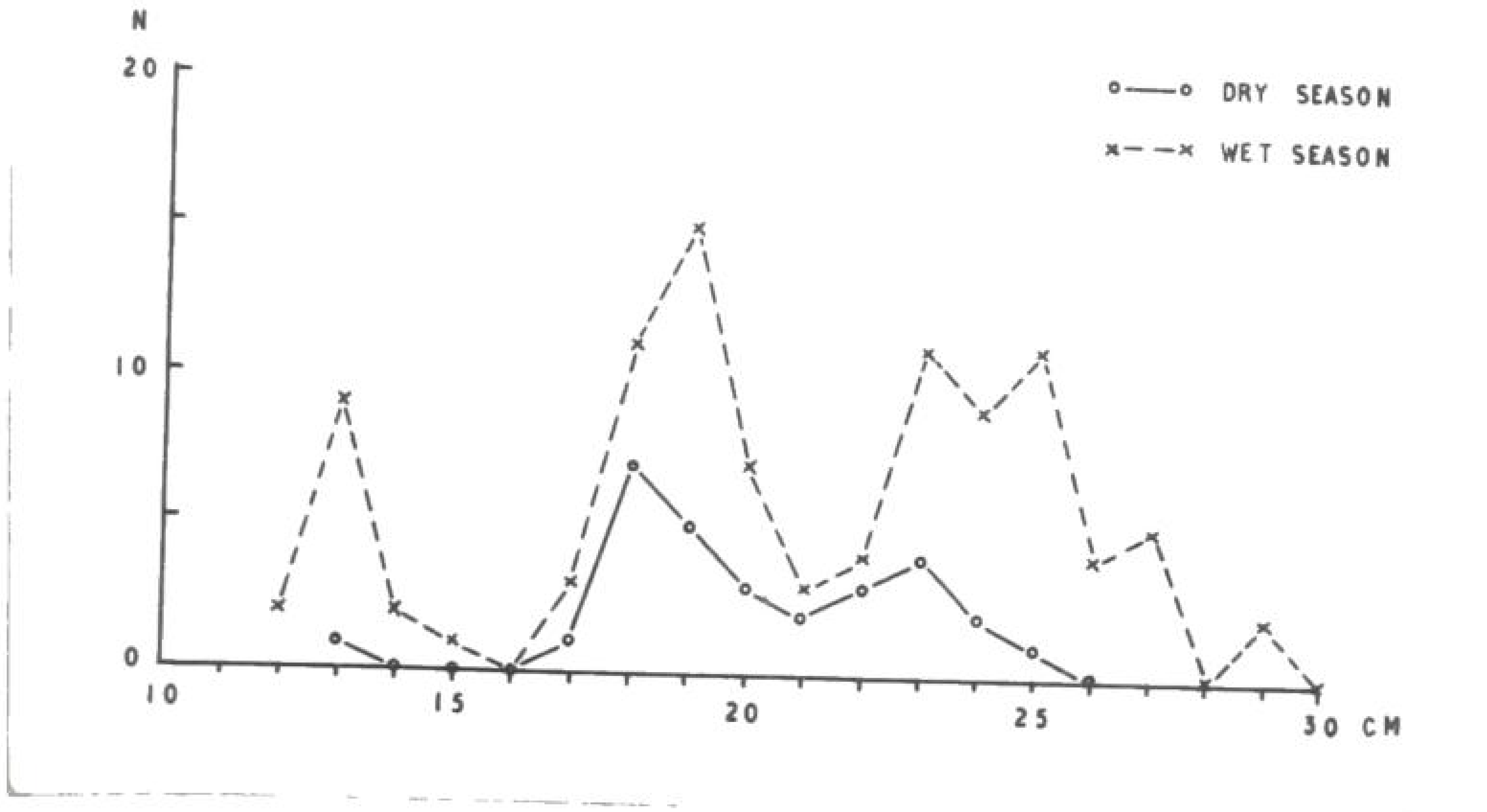


Fig. 22. Length-frequency distribution of T. nilotica in Dry and Wet Seasons.

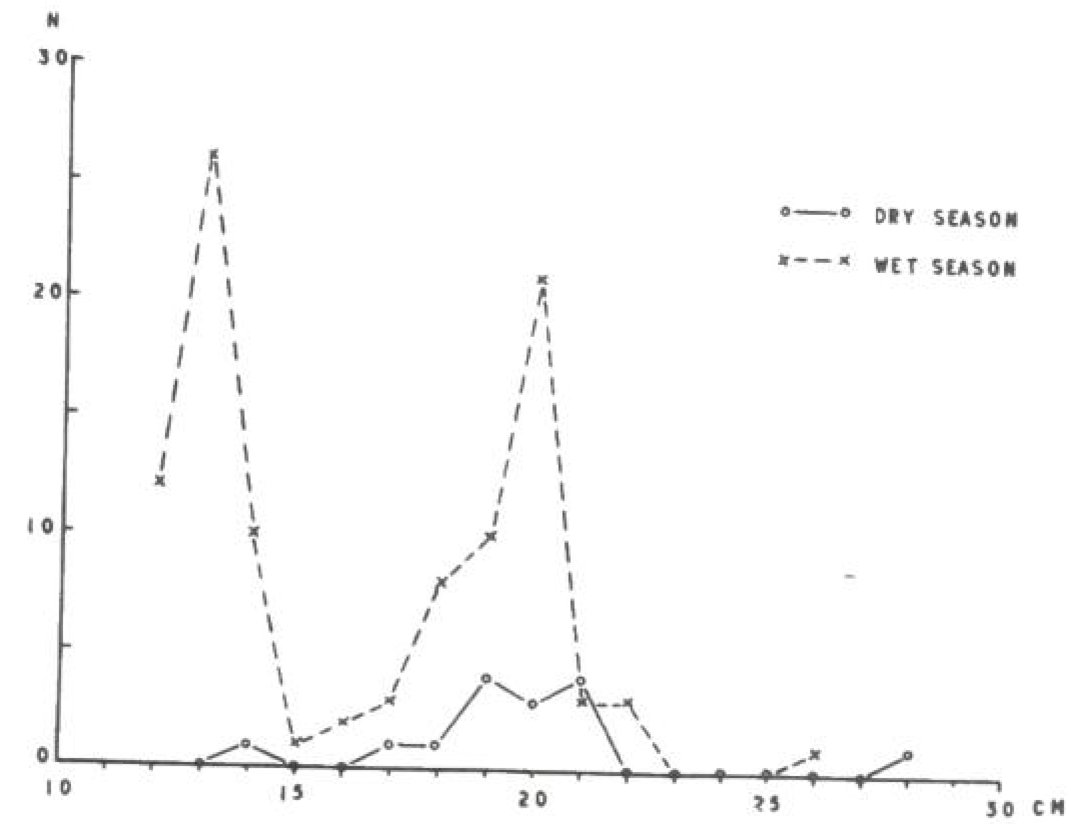


Fig. 23. Length-frequency distribution of T. zilli/melanop. in Dry and Wet Seasons.

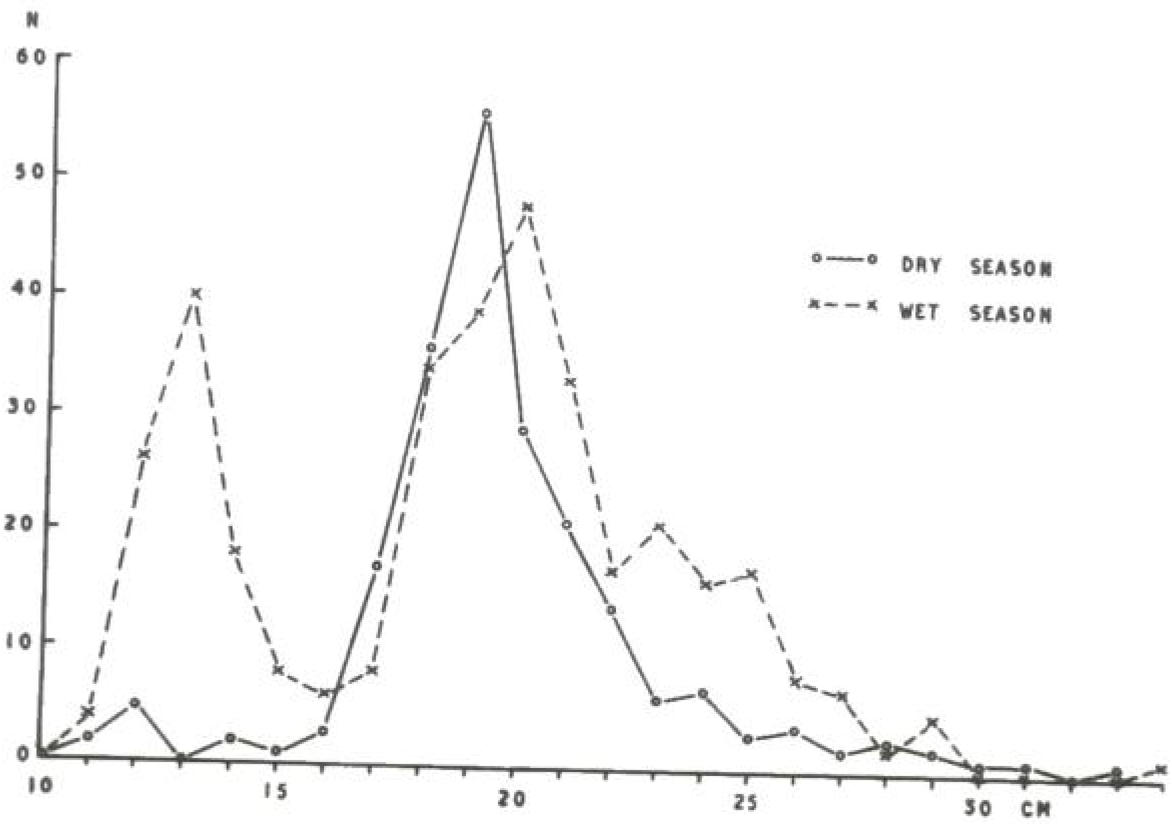


Fig. 24. Length-frequency distribution of Tilapia spp. in Dry and Wet Seasons.

and *T.galilaea* which showed no significant peak in the lower range of distribution. The latter interpretation assumes that there is no specific spawning season but that spawning may continue possibly throughout the year although it may be more productive at certain particular times.

A study of the reproductive biology of the species may assist in deciding between these alternative interpretations and this matter is now considered.

VI. SEX RATIO IN TILAPIA SPECIES.

In considering the reproductive biology of *Tilapia* it is convenient, before considering problems concerned with sexual maturation and fecundity, to examine the sex ratio.

Sex ratio is the number of males to females, expressed as a percentage of the total fish of the same species in the sample. At first sight, it seems that the sex ratio is constant and unchanged, but closer analysis shows that the sex ratio may vary with time, age and habitat.

Krizenecký (1914) writing from a general point of view states that ".... the determination of the sex is reflecting the metabolic changes in organisms, the sex is a result and a consequence of a particular metabolic rate." More recently, Hoar (1957) writes that the mechanisms determining sexuality in fishes are unstable and it is therefore not surprising that the proportions of sexes in different broods of fishes may be modified artificially. Alm (1946) has been concerned mainly with studies on ecological influences affecting the sex ratio and he, together with others, has demonstrated the lability of sex ratio in different ecological conditions. These conditions may affect the number of females in a sample, in a month, in the season of the year, in a length group or in the total catch of all species combined, or considered separately.

Sex ratio may be divided according to Krizenecký (1953) as follows:

(a) Primary sex ratio at the time of fusion of the gametes when the zygote, the new individual of the new generation, is created,

(b) Secondary sex ratio which is expressed by the number of females at hatching and

(c) Tertiary, which is the sex ratio in adult specimens which are capable of taking part in sexual reproduction.

Many factors may influence the sex ratio of a species at birth. In Gambusia holbrooki (Grd) there may be great fluctuation from the 1 : 1 average not correlated with water temperature or season (Dulzetto, 1935 ex Noble, 1938). In a cichlid closely related to the jewel fish, Thumm (1908 ex Noble, 1938) has shown that old females mated with young males gave progeny which was predominantly male. On the other hand, the same males mated later with a young female, gave about 400 young, of which 300 were females. Fertilization of the eggs of trout (Huxley, 1923) immediately on shedding resulted in a preponderance of females, while a considerable delay in fertilization after stripping resulted in a preponderance of males. Rearing temperatures, food supply and available space (Eberhardt, 1943 ex Hoar, 1957) have been shown to alter sex ratios.

In this investigation, the determination of the sex ratio was limited to adult specimens only.

The sex ratios of the Tilapia caught over the period of study is summarised in Table 9. From this it will be seen that apparent differences occur. Females are predominant in T.galilaea and T. zilli/mel. but the average sex ratio of all the specimens together is 1:1.

Table 9. Sex Ratio of *Tilapia* species.

Species	No. of ♂s	No. of ♀s	Total	% ♂s	% ♀s	Sex Ratio	P
T.galilaea	144	170	314	45.9	54.1	1:1.18	.10
T.nilotica	107	81	188	56.9	43.1	1.32:1	.05
T.zilli/melan.	66	72	138	47.8	52.2	1:1.09	.70
All species	317	323	640	49.5	50.5	1:1.02	.80

My effort was thus to discover where and under what conditions males predominate, females predominate or when the sex ratio is equal.

Fig.25 and Table 10 shows the sex ratio (expressed in % females) of T.galilaea in different months of the year. It is obvious that except in March, May, June and August, females were the predominant sex. There was a decline in the number of females from January (68.7%) to June when no females were collected. Females again predominated in July (66.7%) decreasing in August to a value of 37.5%. Except in January and June these differences are, however not statistically significant, p being $>.5$. In January p is $<.001$ suggesting that T. galilaea females predominated at this time. The total catch in June was so small as to make impossible any assessment of the sex ratio.

The pattern was different in T.nilotica. Fig.26 indicates this. Over 64% of the catch in January was made up of females whilst males predominated from February till July ranging from 55.2% to 80.0% with

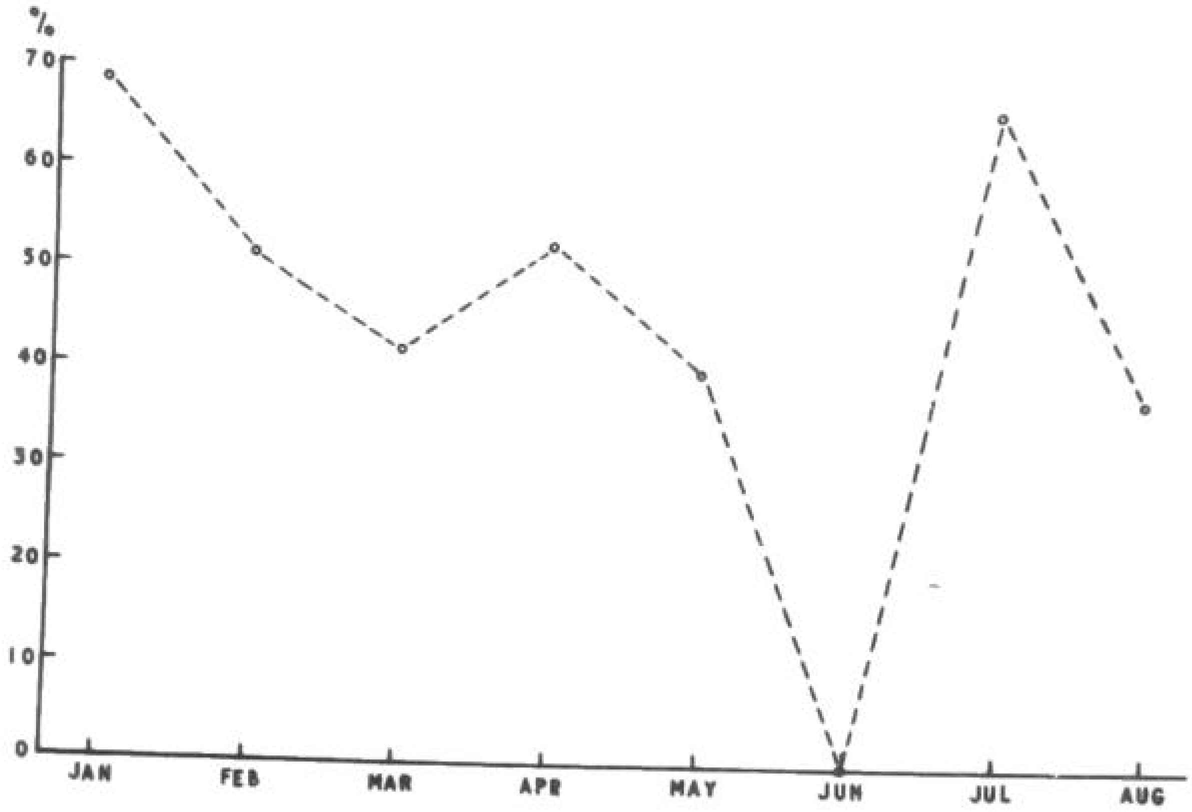


Fig. 25. Sex Ratio of T. galilaea.

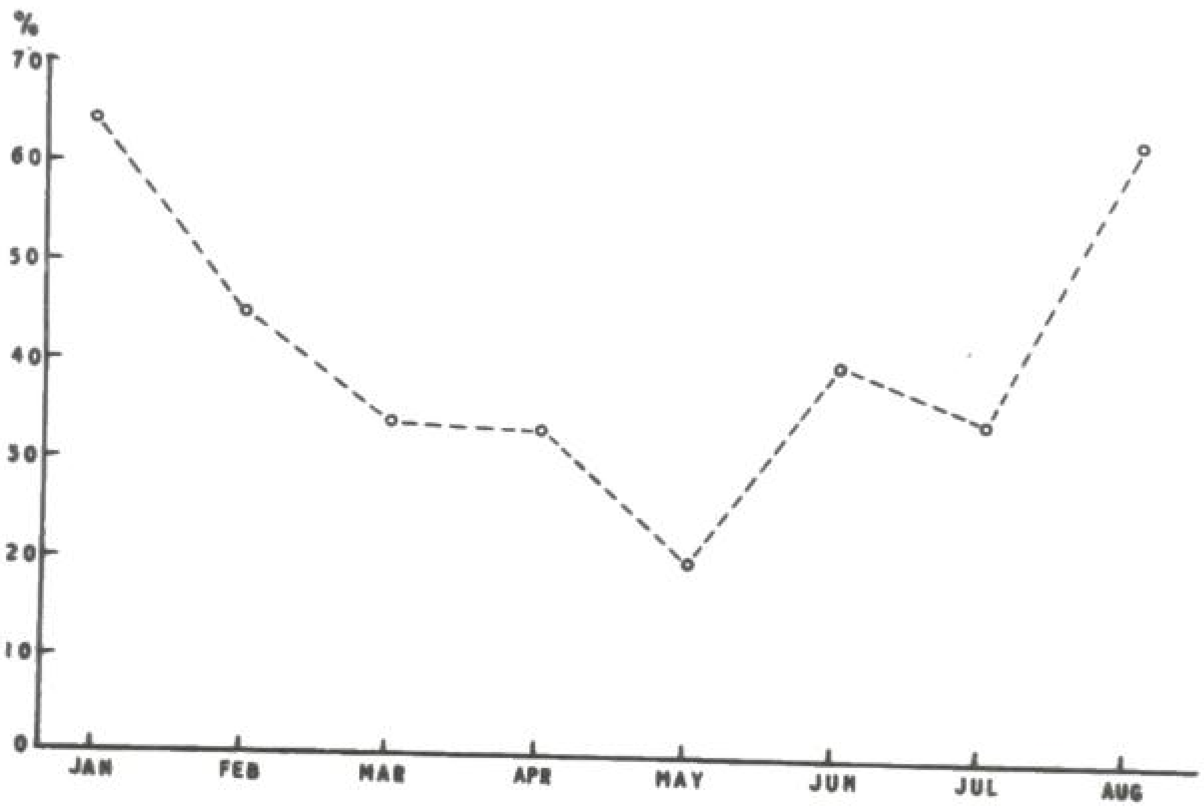


Fig. 26. Sex Ratio of T. nilotica

a maximum in May. Females had again become abundant in August (63.2%). Examination of the data in Table 11 shows that during the period from March to July males constituted nearly 68% of all catches. Many of these monthly figures were however so small as to make statistical treatment of the results from individual months valueless. When the total catch over the period of five months is summed the probability that the ratio observed is significantly different from 1:1 is $> .001$. There seems little doubt that during this period males predominated in the population being sampled.

In the first four months of the year, female T. *zilli/melanopleura* were abundant in the catch, p being $< .10$ (see fig.27 and Table 12). There was a decline afterwards in May and June, $p > .10$, with a minimum of 27.3% in May but on both occasions the total catch was small. The number of females increased again in July (71.4%) but fell to 33.3% in August when again the total catch was small, p being $> .10$. The ratio observed is not significantly different from 1:1, males thus predominating in May and June and again in August.

In the combined *Tilapia* species (fig.28 and Table 13), the general trend of affairs was comparable to that found in the species taken separately. There was a preponderance of females in January (67.5%), $p < .001$ with a progressive decline to a minimum of 33.3% in May and June. In February, $p > .80$, in April $p > .80$ and in July and August $p > .80$ which suggests that there was an equal number of

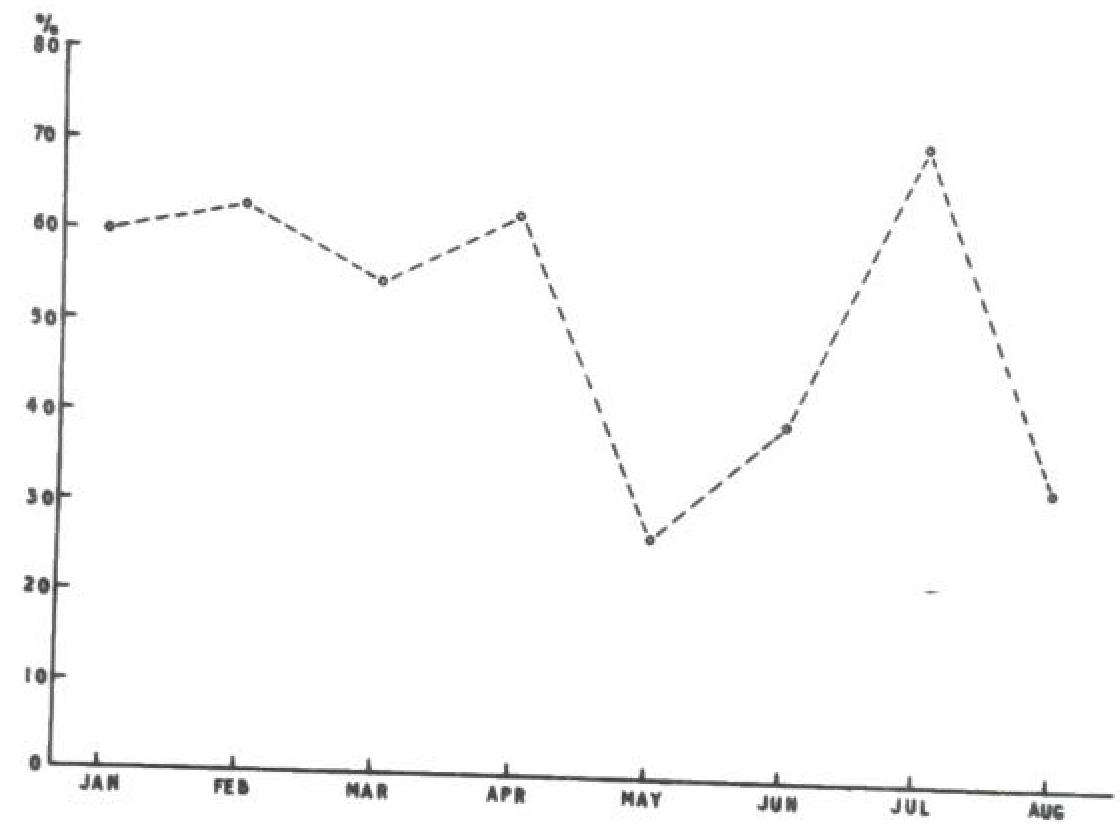


Fig. 27. Sex Ratio of T. zilli/melanopleura.

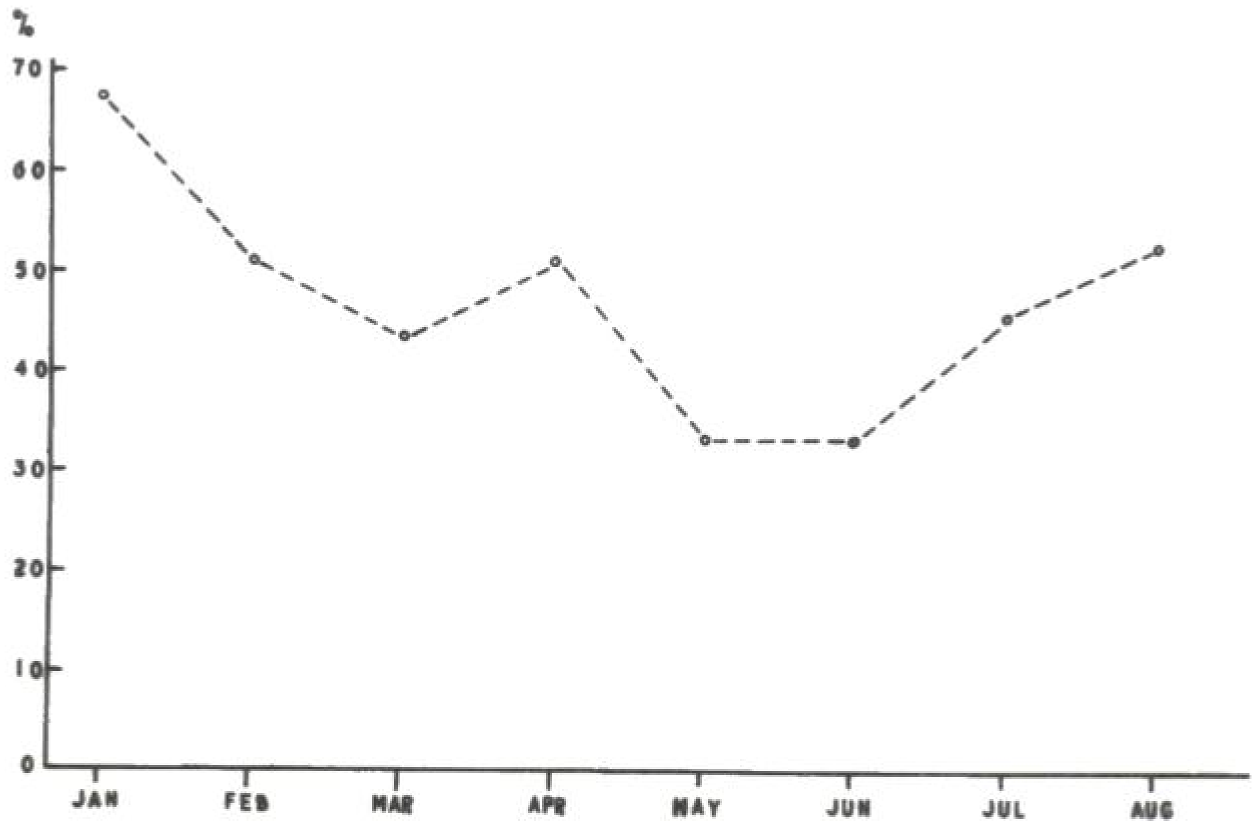


Fig. 28. Sex Ratio of Tilapia species.

Table 10: Sex Ratio of *T. galilaea* in different months.

Month	No. of ♂	No. of ♀	Total	% ♂	% ♀
Jan.	31	68	99	31.3	68.7
Feb.	35	37	72	48.6	51.4
Mar.	29	21	50	58.0	42.0
Apr.	26	29	55	47.3	52.7
May	12	8	20	60.0	40.0
June	4	-	4	100.0	-
July	2	4	6	33.3	66.7
Aug.	5	3	8	62.5	37.5
	144	170	314		

$p = > .05$

Table 11: Sex Ratio of *T. nilotica* in different months

Month	No. of ♂	No. of ♀	Total	% ♂	% ♀
Jan.	6	11	17	35.3	64.7
Feb.	32	26	58	55.2	44.8
Mar.	27	14	41	65.9	34.1
Apr.	6	3	9	66.7	33.3
May	4	1	5	80.0	20.0
June	6	4	10	60.0	40.0
July	19	10	29	65.5	34.5
Aug.	7	12	19	36.8	63.2
	107	81	188		

$p = > .05$

Table 12: Sex Ratio of *T. zilli/melanopleura* in different months.

Month	No. of ♂	No. of ♀	Total	% ♂	% ♀
Jan.	4	6	10	40.0	60.0
Feb.	10	17	27	37.0	63.0
Mar.	20	22	42	47.6	52.4
Apr.	6	10	16	37.5	62.5
May	8	3	11	72.7	27.3
June	6	4	10	60.0	40.0
July	2	5	7	28.6	71.4
Aug.	10	5	15	66.7	33.3
	66	72	138		

$p = > .05$

Table 13: Sex Ratio of Tilapia species in different months

Month	No. of ♂	No. of ♀	Total	% ♂	% ♀
Jan.	41	85	126	32.5	67.5
Feb.	79	78	157	50.3	49.7
Mar.	75	58	133	56.4	43.6
Apr.	39	41	80	48.8	51.2
May	24	12	36	66.7	33.3
June	16	8	24	66.7	33.3
July	23	19	42	54.8	45.2
Aug.	20	22	42	47.6	52.4
	317	323	640		

$p = > .05$

males to females in these months. In March, $p < .20$, in May $p < .05$ and in June $p < .10$. These ratios are however not significantly different from 1:1, but suggest that there was an excess of males in May though this requires confirmation.

Nothing conclusive can be deduced from these apparent variations in the sex ratio throughout the period of study except to say that the ratio is 1:1 month after month.

Lowe (1952, 1956 a & b) has shown that in Lakes Victoria and Nyasa ripe Tilapia generally congregate in the spawning areas and are rarely caught in other parts of these lakes. A preponderance of males in catches is found in a spawning area as the ripe males move to and remain in these areas for considerable periods, whereas the females pick up the eggs into the mouth as soon as they have spawned and move off to the "brooding grounds". This results in segregation of the sexes immediately after spawning. It also means that seasonal variations in the abundance of ripe fish can only be estimated by fishing in the spawning areas. For this reason it is difficult to collect samples which represent the sex ratio in the lake as a whole.

Observations in shallow, clear water near Akosombo indicated that breeding males established breeding territories close to the shore in the spawning grounds, where a nest is prepared below about two feet of water. A male moves out to meet a female and, when she is in an active breeding condition, leads her into the territory where spawning activities start. After spawning, the female moves away and the male keeps a close watch for other passing females. This happens in the mouth-brooders, T. galilaea and T. nilotica but in T. zilli/melanopleura which are substrate brooders, both males and females guard the eggs together. On many occasions, the water was too opaque to allow such nests and breeding habits to be observed.

The area sampled by the gill nettings was not however a spawning ground and, with the exception of T. nilotica the sex ratios over the period examined do not differ significantly from 1:1. In the case of T. nilotica there is fairly clear-cut evidence of a movement of females away from the fishing ground between March and May. The reason for this may become clear when the state of sexual maturity of the fish has been considered.

VII. MATURITY AND FECUNDITY

In studying the fecundity of fish it is necessary to know the stage of growth at which maturity is first achieved and also whether there are distinct well separated spawnings or spawnings recurring at frequent intervals. Clearly, a fish which has to grow to a considerable size or age before reaching sexual maturity is likely to have a lower reproductive potential than one which reaches sexual maturity rapidly, unless this should be offset by very copious egg production. Again, fish which spawn repeatedly at short intervals might be expected to have a higher reproductive potential than those which show a limited breeding season, although this difference may again be affected by the total number of eggs laid at each spawning.

The habits of the fish in these connections are, from a practical viewpoint, of importance in terms of management since clearly the protection of the breeding grounds, eggs and fry of a seasonally spawning fish provide different problems from those of a fish which breeds almost continuously. Similarly any consideration of mesh size limitation will be influenced by the size at which the species concerned first reaches sexual maturity.

To arrive at a picture of the breeding habits of fish, examination must be made of the state of the gonads, and especially the ovary, of individuals of different size and at different seasons of the year. In the present study attention was concentrated upon the ovary and observations in some cases were limited to <u>T.galilaea</u>

as the techniques involved were time consuming and it was possible only to examine a limited quantity of material. The usual methods employed may involve both gross and histological examination of the ovary.

THE OVARY:

The ovary of Tilapia is elongated and tapers anteriorly. It is suspended in the body cavity along its entire length by the mesovarium. Blood vessels enter the ovary along the length of the mesovarium and ramify through the mediodorsal portion. The ovaries of small, middle and large-size Tilapia are longitudinally paired structures and fusion is only evident in the oviducts at their junctions with the ovaries. Chacko and Krishnamurthi, (1954) have reported that the left ovary of T.mossambica Peters in Madras is slightly longer than the right. This is true also of the three species studied here.

The texture of the ovary ranges from floccular, almost testis-like in the young, through microscopically granular in juveniles, to grossly granular, varying with the size of the individual eggs, in the adult. During the breeding season the surface of the ovary assumes a beaded appearance as it becomes distended with maturing oocytes. Frequently also the organ undergoes striking colour changes, ranging from whitish in the young female to greenish or yellow in ripe adults owing to the deposition primarily of yolk and secondarily of pigment within the enlarging oocytes. Just before being laid, the eggs become enlarged.

The proportion of the body cavity occupied by the ovary varies with the stage of sexual maturity of the female. When ripe, the ovaries may comprise quite a large portion of the body weight. At the height of the breeding season they expand and may distend the body wall of the female.

Zuckerman (1962) states that, in fish, oocytes undergoing growth and maturation occur in the more ventral portions of the ovary. In many teleosts, eggs are shed into an ovarian cavity on the ventro-lateral wall of the ovary and pass to the exterior through a duct which joins the caudal portion of the organ. The ovarian wall is lined with folds or lamellae each consisting of a central layer of spongy connective tissue and an outer layer of germinal epithelium from which eggs develop. "In some teleosts, the ovarian cavity is formed only when mature follicles rupture by a hollowing-out of the internal tissues (e.g. Tilapia, Aronson and Holz-Tucker, 1949)".

My observations show that in Tilapia species the ovarian capsule is continuous with the oviduct - the cystovarian condition. The ovary develops a highly complex system of ovigerous lamellae from the ovarian wall in which young and mature follicles are randomly distributed. Each lamella consists of a central layer of spongy connective tissue and an outer layer of germinal epithelium. The eggs develop from cells of this germinal layer, and as they grow they fill the lamella. At the time of spawning, eggs are released into the central cavity of the organ, not through

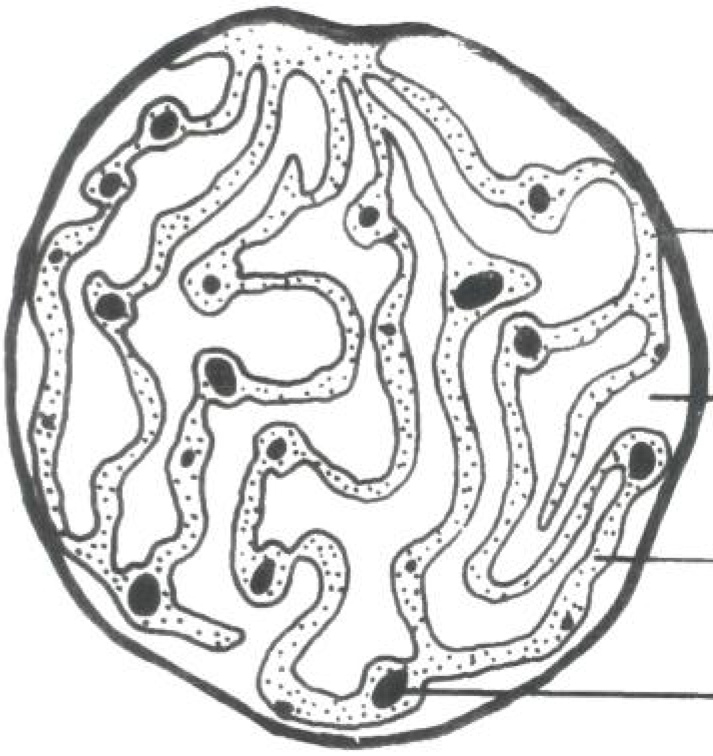


Fig. 29. Diagrammatic transverse section of the ovary of *Tilapia*.

the body cavity (fig. 29) and pass down the common oviduct. From the oviduct the egg is extruded through the genital papilla, which lies im ediately behind the anus. In the female the papilla is broader and the oviduct opens from this as a transverse slit (McConnell, 1955 b) (fig. 3).

THE ONSET OF SEXUAL MATURITY

The onset of sexual maturity may be ascertained either by histological examination and measurement of the developing oocytes or by dissection of the ovary followed by a sorting of the eggs into different size categories and differential counting. The two methods may be expected to give the same result. The histological procedure is laborious and has been here used only as a check upon the validity of the results obtained from dissection.

In adopting the histological procedure, measurements were made upon the sizes of the oocytes and from an examination of the data thus obtained the oocytes were divided into five classes. It further appeared important to determine whether there was a uniform distribution of oocyte size throughout the ovary or whether oocytes of different sizes were concentrated in different regions. To determine this sections were cut through the anterior, middle and posterior ends of the ovaries and oocyte measurements made in the different regions.

In classifying the oocytes the scale proposed by Reingardt and Trudova (1962) for carp in a lake in the southern U.S.S.R. was adopted. In this the cytology of the oocytes is the factor used in assigning the oocytes to the various categories. These are:

Stage α -) immature follicles with no cellular details; the only
Stage β -) difference being in the egg diameters.

Stage γ - outermost layer composed of one layer of cells and called a 'one layer oocyte'; clearly defined nucleus which is rounded.

Stage δ - cover of oocytes (radial shell) is translucent; zona radiata appears.

Stage ε - Four layers of cells create the 'shell' of oocyte; nucleus is losing rounded shape to become oval.

Stage ζ - very mature egg ready for spawning; clear nucleus surrounded by yolk granules.

Because there were no cellular details to differentiate Stage α from β, these stages have been put together, and for the classification of oocytes in T.galilaea the Stage A includes Stages α & β in Reingardt and Trudova's classfication.

The diameters of the developing oocytes corresponding to these stages are tabulated below:

Stage	Diameter Range in mm.
A	0.02 to 0.22
B	0.23 to 0.58
C	0.59 to 1.00
D	1.01 to 1.43
E	1.44 and above

Comparison of the distribution of different oocyte stages in different regions of the ovary suggested that there was no localisation of eggs of particular sizes. The data from which this conclusion is drawn are shown in Table 14. The data show the number of oocytes counted along a standard length of ovarian epithelium, together with these values expressed as percentages of total oocytes counted in each fish. The length of ovarian epithelium selected for measurement was, in each case, characterised by the fact that a continuous row of oocytes lined the edge of the epithelium. This is illustrated by photomicrographs of typical fields. In these conditions a mass of small oocytes will give a high count, a mass of large oocytes a low count (Plate. 2). Thus if there were localisation of oocytes of different sizes in different regions of the ovary, the observed percentage value would deviate from 33.3%. Examination of the data shows that the observed values lie within the range of 23.5 - 41.3% with an overall average of 33.3% and mean values for the three regions of 33.3%, 34.8% and 31.9%. From these results, and visual observation, it is concluded that oocytes of different sizes are randomly distributed within the ovary.

Table 15 shows the distribution of oocyte size categories in specimens of T. galilaea collected between January and August 1966.

Ovaries containing eggs at stage C are commencing to mature. Within the present limited sample the smallest individual in this

PLATE 2.

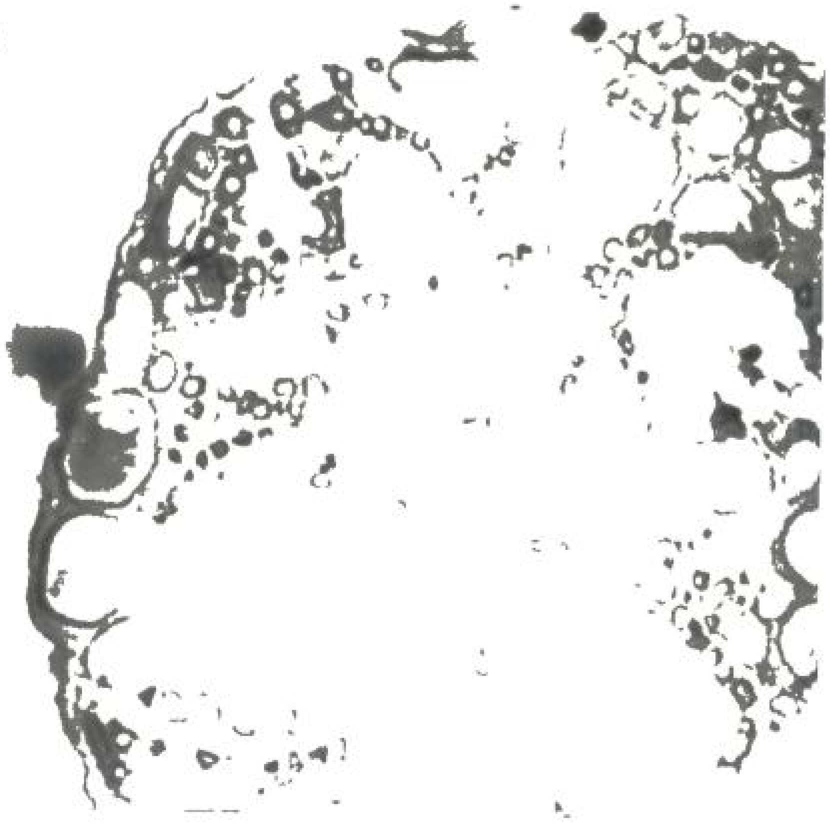


Fig. 1.
18.2 cm total length. Specimen caught in March 1966.

Fig. 2.
15.0 cm total length. Specimen caught in August 1966.

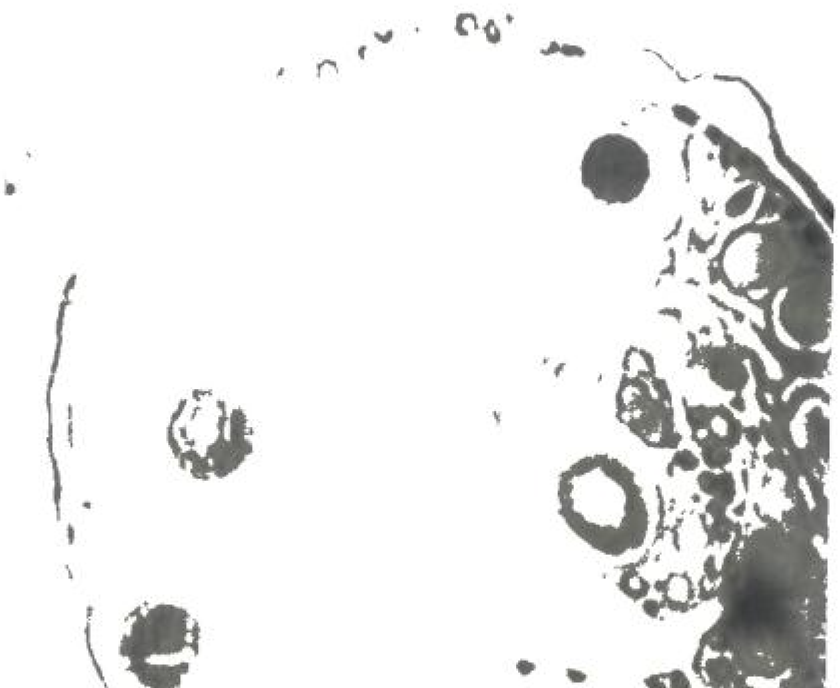


Fig. 3.
19.5 cm total length. Specimen caught in February 1966.

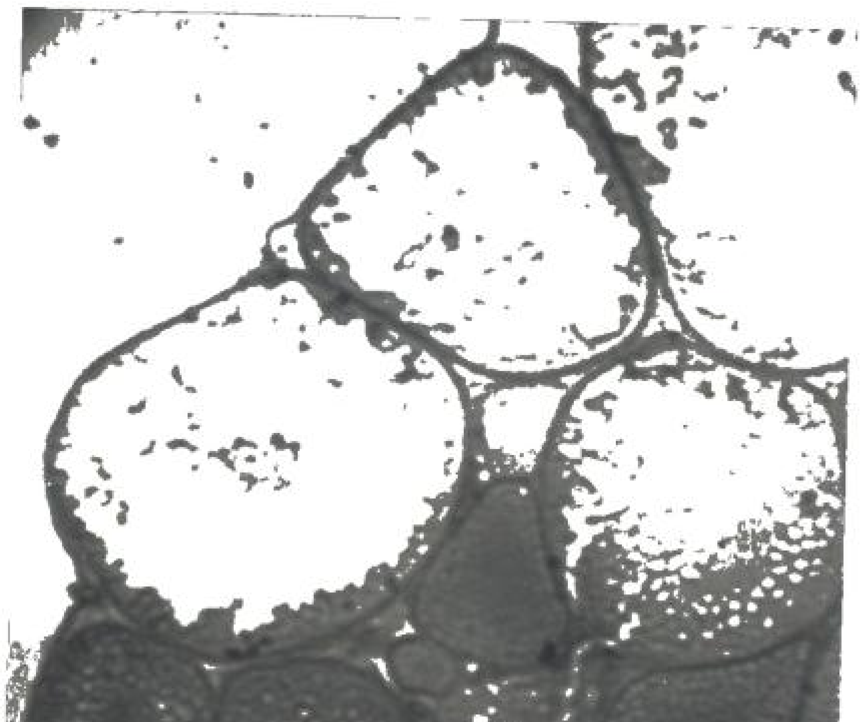


Fig. 4.
25.5 cm total length. Specimen caught in July 1966.

Figs. 1 - 4. Transverse Sections of the ovary or portions of the ovary of T. galilaea. 10 x.

TABLE 14.

No. of eggs of different diameters counted along a standard length (T.galilaea). Data according to LENGTH and WEIGHT OF fish.

Length (cms.)	Weight (g)	Posterior		Middle		Anterior		Total	Date of collection
		No.	%	No.	%	No.	%		
10.7	25	58	33.9	49	28.7	64	37.4	171	January
10.8	20	32	34.4	36	38.7	25	26.9	93	April
11.2	20	48	37.8	40	31.5	39	30.7	127	May
12.5	30	38	33.3	46	40.4	30	26.3	114	April
13.0	40	32	30.5	35	33.3	38	36.2	105	August
15.0	70	42	37.8	43	38.7	26	23.5	111	August
17.5	110	43	36.1	32	26.9	44	37.0	119	May
17.5	120	40	38.4	32	30.8	32	30.8	104	March
18.2	110	20	30.3	27	40.9	19	28.8	66	March
19.0	140	48	32.4	48	32.4	52	35.2	148	January
19.5	150	24	33.8	22	31.0	25	35.2	71	February
20.0	150	11	28.9	14	36.8	13	34.3	38	August
21.0	440	18	38.3	17	36.8	12	25.5	47	July
21.0	450	10	31.4	12	37.2	10	31.4	32	July
22.0	580	8	25.8	11	35.5	12	38.7	31	July
22.0	230	34	28.1	50	41.3	37	30.6	121	April
24.5	370	18	36.0	16	32.0	16	32.0	50	April
24.6	330	91	35.1	64	24.7	104	40.2	259	May
25.0	380	26	28.3	38	41.3	28	30.4	92	May
28.2	500	20	34.5	22	37.9	16	27.6	58	February

Mean % 33.3 34.8 31.9

Overall % 33.3

TABLE 15.

Nos. of eggs per standard length in each egg-group
of <u>T. galilaea</u>

Index No.	Length (cms.)	Weight (g)	Gp.A	Gp.B	Gp.C	Gp.D	Gp.E	Date
1	10.7	25	171	-	-	-	-	Jan.
2	19.0	140	148	-	-	-	-	"
3	19.5	150	65	-	6	-	-	Feb.
4	28.2	500	34	4	18	2	-	"
5	17.5	120	104	-	-	-	-	Mar.
6	18.2	110	53	1	12	-	-	"
7	10.8	20	93	-	-	-	-	Apr.
8	12.5	30	106	2	6	-	-	"
9	22.0	230	96	19	-	-	-	"
10	24.5	370	26	4	11	7	2	"
11	24.6	330	258	-	-	-	-	May
12	25.0	380	66	18	8	-	-	"
13	11.2	20	120	3	4	-	-	"
14	17.5	110	117	2	-	-	-	"
15	21.0	440	22	10	15	-	-	Jul
16	21.0	450	10	3	9	10	-	"
17	22.0	580	14	7	4	9	2	"
18	20.0	150	11	8	13	5	1	Aug.
19	15.0	70	108	2	1	-	-	"
20	13.0	40	104	1	-	-	-	"

condition was 11.2 cm. in total length, but larger specimens which appeared to be immature were also found. It is possible that the wide range of sizes of immature fish comprising 10.7 to 24.6 cm total length is misleading as it is not certain whether at least some of the larger specimens may not have been 'spent' rather than 'immature'.

An alternative procedure for determining the onset of maturity is to make direct observations upon the state of the ovary by disection. The smallest individuals which contain mature oocytes may thus be determined. While this procedure may be applicable to other species, in the present case this technique was found to give misleading results. Thus, for example, a specimen of <u>T.galilaea</u> of 10.7 cm total length was initially assessed on the basis of dissection as containing mature oocytes, but subsequent histological examination of portions of this ovary showed that none were in fact present.

Another technique introduced by Wallace (1909) and later employed by Coulter (1963/64) on <u>Lates mariae</u> Steind is to determine the "total" length at which 50% of the fish contain developing oocytes. These may readily be recognised in dissection. This technique also proved inapplicable in the present study since all specimens collected, even the smallest, contained developing oocytes.

A third, but less precise, criterion for determining the onset of maturity is the length at which the fish assume their breeding colours. Among the specimens examined the smallest female <u>T.galilaea</u>

showing breeding colours was 15.0 cm total length, and of T.zilli/melanopleura 12.0 cm. In none of these species were males in breeding colours collected. Corresponding figures for T.nilotica were 12.3 cm for males and 13.2 cm. for females.

When these results, using breeding colour, are compared with those obtained from histological examination of the ovaries of T.galilaea, it appears that the onset of maturity occurs before the assumption of breeding colours.

Two specimens, one of 11.2 cm. total length and one of 12.5 cm. total length were found in which ovarian histological maturation had started. These are both smaller than the smallest specimen recorded as showing breeding colours, although the specimen of 12.5 cm. length showed slight indications of the onset of colouration. That ovarian maturation should preceed changes in pigmentation is not surprising since Aronson (quoted by Hoar, 1955) has shown that ovariectomy of female Tilapia results in the opercular colouration reverting to that of immature individuals.

It seems clear that from a practical viewpoint the assumption of breeding colours provides a realistic assessment of the minimal size of mature fish since mating will not occur until the nuptial dress is assumed.

Table 16 shows data from other authorities on the minimal breeding size of different Tilapia species from other water bodies. It will be seen that there is a great variation in the values recorded, varying from 8 - 9 cm. for T.mossambica in Indonesia to

39.0 cm. for T.nilotica in Lake Rudolf.

There are, moreover, often marked differences in the results obtained for the same species in different localities. Thus, of the species which occur in the Volta Lake, values from other localities vary from 11.6 to 24.0 cm. for T.zilli, from 12.0 to 39.0 cm. for T.nilotica and 15.2 to 22.0 cm. for T.melanopleura. It is noteworthy that the values recorded in the present investtigation agree fairly closely with the lower value reported in each case.

It is well known that sexual maturity may occur at very different lengths in the same species collected from different localities. The physiological basis of this has been the subject of only limited study. It is clear, however, that in temperate waters photoperiod probably plays a very important part in the onset of sexual maturity. Thus, for example, Craig-Bennett (1931), reports that the males of Gasterosteus aculeatus Linn., from a variety of habitats such as rivers, ponds and canals at the same latitude, all start to mature at the same time. Other factors unquestionably enter. Thus Frost (1943) has shown that in Phoxinus phoxinus L, relatively few individuals became sexually mature in their first year and Bullough (1939 & 1940 a) has shown that in Phoxinus laevis Linn. there is a complex interaction of day-length and environmental temperature determining the onset of sexual maturity. Similarly in T.mossambica, Jubb (1952) reports that breeding will not occur at low water temperatures encountered

TABLE 16.

MINIMUM BREEDING SIZE OF TILAPIA SPECIES
OBSERVED IN DIFFERENT WATERS.

SPP.	Length (cms)	Locality	Age	Author
T. zilli	16.0	Niger (Backwater)	-	Welman (1948)
"	13.5	" (Swamp)	-	"
"	17.0(♂)	L.Albert (Butiaba Lagoon)	-	McConnell (1953)
"	24.0	Dedo Dam (Kidetok)	-	"
"	21.0	" " (Arabaka)	-	"
T. esculenta	13.0	Malya Fishponds	-	"
T. variabilis	15-17.0	Korogua Fishponds	-	"
T. leucosticta	18.0(♀)	Lake Edward	-	"
"	20.0(♀)	Teso Dams (Kidetok)		"
"	22.0(♂)	" "	-	"
"	21.0(♂)	Lake Albert	-	"
"	18.0(♀)	"	-	"
T. nilotica	12.0(♀)	L.Albert (Buhuku Lagoon)	-	McConnel (1958)
"	14.0(♂)	"	-	"
"	39.0	Lake Rudolf	-	"
T. zilli	11.6(♂)	Niger	1+	Daget (1956)
"	12.3(♀)	"	"	"
T.galilaea	18.0(♀)	Lake Albert	-	McConnell (1949)
T.esculenta	20.0	"	-	"
T.zilli	17.0	"	-	"
T.nilotica	22.0	"	-	"

TABLE 16 (CONTD.)

MINIMUM BREEDING SIZE OF *TILAPIA* SPECIES
OBSERVED IN DIFFERENT WATERS.

SPP.	Length (cms)	Locality	Age	Author
T. melanop.	15.2(♀)	Lake Kariba		Soulsby (1963)
"	18.6(♂)	"	-	"
"	22.0	Congo		De Bont (1950)
T. mossambica	8-9 cms.	Indonesia	2-3 mths.	Vaas & Hofstede (1952)
"	12-14 cms	Nicaragua (America)	5-6 "	Reidel (1965)
"	16.9 (♂)	Lake Kariba	-	Soulsby (1963)
"	12.5 (♀)	"	-	"
T. macrochir	20.3	"	-	"
T. mariae	10.0	Osse River	-	Whitehead (1962)
T. mossambica	9-10 cm	Madras	3 mths.	Chacko & Krishnamurthi (1954)

during the winter of the Rhodesian High Veld.

In the tropics there is little seasonal variation in either water temperature or day-length (see fig.30) and it may be that such factors do not play any part in determining the onset of sexual maturity. It must, however, be recognised that certain fish such as *Lates*, *Alestes*, *Heterotis*, *Labeo*, *Distichodus* and the Mormyrids breed during the flood seasons following rains and the possibility cannot be excluded that changes in photoperiod have indeed been significant in bringing these fish to maturity so that they can reproduce during the floods.

It seems possible, however, that in some tropical fish which lack definite breeding seasons the onset of sexual maturity may be determined by growth rate and that this in turn will be affected by food supply and, when population densities are high, by indirect effects arising from crowding. Such considerations may perhaps apply to *Tilapia* and the relative small size at which the *Tilapia* have become mature in the Volta Lake may be a reflection of the good feeding conditions which have probably prevailed following the first flooding. If this is correct, then the length at which these fish became sexually mature may well change as the Lake itself matures. Such a suggestion is, however, speculative and the need for experimental studies upon the question using tropical non-viviparous fish is obvious.

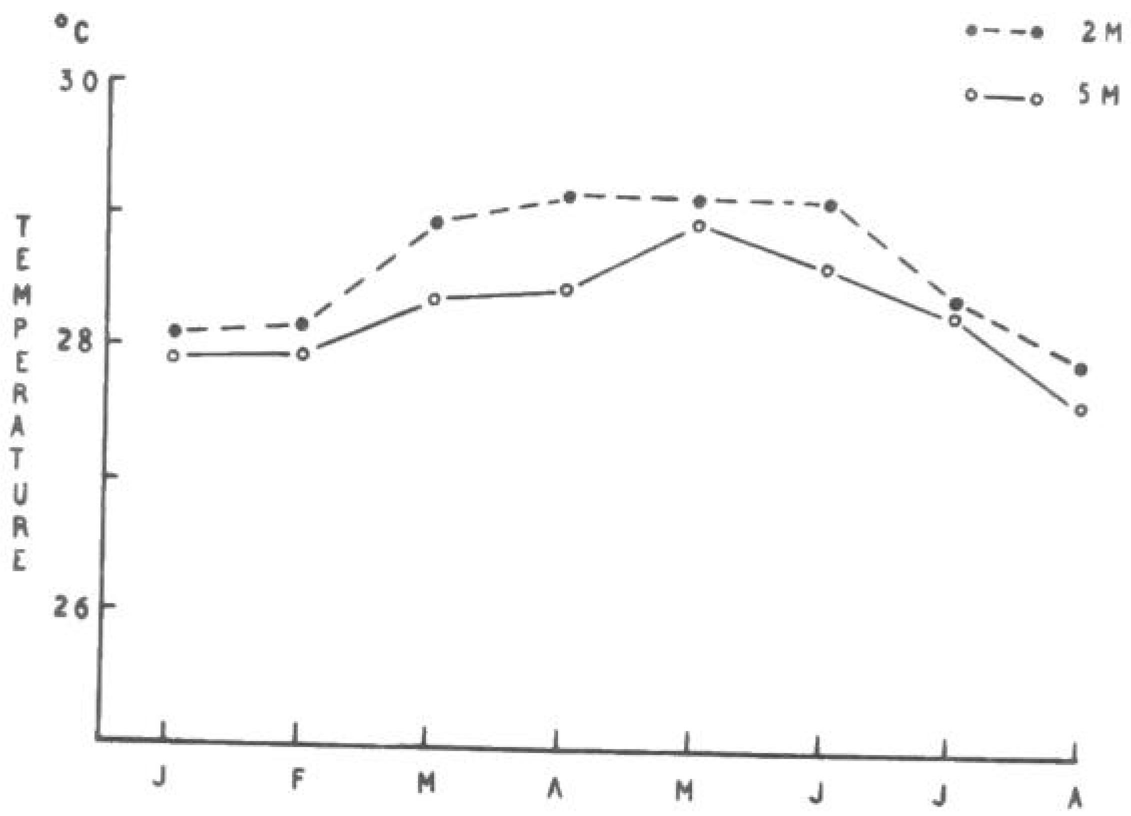


Fig. 30. Mean monthly variation in water temperature.

VIII. SPAWNING

The spawning behaviour of the fish may be assessed in various ways. In a fish which has a limited spawning season it may be expected as Hickling & Rutenberg (1936) have pointed out that all the oocytes within the ovary will be in very similar stages of maturation and that samples of ovaries taken at different times will show markedly different modal stages of maturation. If, however, a fish has either a long spawning period or spawns continuously, then no particular pattern of oocyte development will be observed.

An examination of the results obtained from the histological study of the ovaries summarised in Table 15 p 73 shows that there is, in this sample, no particular pattern. Fish with maturing oocytes were collected in all months except January and June for which months data on only two fish are available.

A check on this conclusion was made by direct dissection of the ovaries of a larger sample of 60 fish, 20 of which were used in the histological examination previously described.

In counting the number of eggs, a subsample of about 0.1 g was taken from the weighed ovary. The eggs in the subsample were counted under a lens and the number in the subsample was multiplied up to the weight of the ovary.

It was found that the eggs fell by appearance into four categories which are characterised as follows:

Group 1 - eggs are very small and difficult to separate from the ovigerous tissue. Average diameter was less than 0.19 mm.

Group 2 - Average diameter ranges from 0.19 to 0.44 mm.

Group 3 - Eggs easily detach from each other and from ovigerous tissue. Average diameter from 0.45 to 0.90 mm.

Group 4 - Ripe eggs with an average diameter of 0.90 mm. or more, the greatest recorded being 1.70 mm for a 28.5 cm. female.

The number of eggs in each egg-group except 1 was counted. Eggs in Group 1 because of their small size and large number (See Table 17). were not counted.

From the histograms in fig.31 which show the mean percentage proportion of each egg-group calculated for the different months, and Table 18,it will be seen that eggs of all groups are present in the ovaries in all months. It will be noted that in May eggs of the largest group are absent which might be taken to imply that there had been a heavy spawning during the previous month. Such a conclusion must however be treated with reserve owing to the small size of the sample. In general the data are in agreement with those obtained by the more critical histological technique and certainly do not contradict the opinion that spawning probably occurs in all months over the period studied.

TABLE 17. No. of eggs in each egg-group of <u>Tilapia galilaea</u>

Sample No.	Length (cms)	Weight (gms)	No. of Eggs				TOTAL	Date of collection
			Group I	Group 2	Group 3	Group 4		
1	10.7	25	+++	-	-	-		January
2	17.5	110	+	1575	-	-	1575	"
3	18.0	120	+	1306	-	-	1306	"
4	19.0	140	++	463	-	-	463	"
5	19.5	150	++	236	1074	881	2191	"
6	21.0	180	+++	78	1821	1103	3002	"
7	21.5	200	+	2899	188	-	3087	"
8	21.5	200	+	4325	-	-	4325	"
9	22.0	215	+	330	989	1601	2920	"
10	22.0	215	+	3063	1437	-	4500	"
11	22.5	230	+	1686	1142	-	2828	"
12	23.0	240	+	2467	1644	-	4111	"
13	23.5	265	+	3193	-	-	3193	"
14	23.5	265	+	1729	1183	-	2912	"
15	24.0	275	+	2168	1475	-	3643	"
16	16.5	95	+	1834	1276	-	3110	February
17	17.5	110	+	1502	1038	-	2540	"
18	17.5	110	+	2256	800	-	3056	"
19	18.0	120	+	1042	-	-	1042	"
20	18.0	120	++	896	1394	-	2290	"
21	18.0	120	+	1230	-	-	1230	"

TABLE 17 (CONTD.) No. of eggs in each egg-group of *Tilapia galilaea*

Sample No.	Length (cms)	Weight (gms)	Group I	Group 2	Group 3	Group 4	TOTAL	Date of collection
22	18.0	120	+	1128	-	-	1128	February
23	18.8	140	++	676	358	333	1367	"
24	19.0	140	++	-	2619	-	2619	"
25	19.0	140	+	2513	-	-	2513	"
26	19.0	140	+	2372	-	-	2372	"
27	19.5	150	+	1985	2778	-	4763	"
28	19.7	150	++	898	2513	-	3411	"
29	20.0	160	+	1663	2215	-	3878	"
30	20.5	175	+	2404	937	-	3341	"
31	20.8	175	+	2113	2433	-	4546	"
32	28.2	500	++	683	1881	1467	4031	"
33	17.5	120	+	4712	-	-	4712	March
34	18.2	110	+	3826	1707	-	5533	"
35	20.0	180	+	+	1999	1374	3373	"
36	20.5	180	++	610	829	-	1439	"
37	20.5	180	+	1369	-	-	1369	"
38	22.5	250	+	-	1365	2249	3614	"
39	10.8	20	+++	790	-	-	790	April
40	12.5	30	+++	729	-	-	729	"
41	18.0	130	+	2132	-	-	2132	"
42	19.8	180	++	613	1751	-	2364	"

TABLE 17 CONTD.) No. of eggs in each egg-group of *Tilapia galilaea*

Sample No.	Length (cms)	Weight (gms)	Group I	Group 2	Group 3	Group 4	TOTAL	Date of collection
43	20.0	150	+++	845	-	-	845	April
44	20.5	190	+	3347	-	-	3347	"
45	20.5	190	+++	965	-	-	965	"
46	20.5	190	+	1596	978	-	2574	"
47	20.5	190	+	1720	-	-	1720	"
48	22.0	230	+	1912	2102	-	4014	"
49	24.5	370	++	562	1065	830	2457	"
50	11.2	20	+++	382	-	-	382	May
51	17.5	110	+	2381	-	-	2381	"
52	21.0	200	+	1752	-	-	1752	"
53	22.0	230	+	2690	-	-	2690	"
54	24.6	330	+	4270	-	-	4270	"
55	25.0	380	+	1936	1416	-	3352	"
56	25.5	450	+	307	2197	2854	5358	July
57	26.5	440	+	740	2791	3248	6779	"
58	28.5	580	+	767	2941	2749	6457	"
59	13.0	40	++	1241	-	-	1241	Aug.
60	15.0	70	++	1885	-	-	1885	"
61	20.0	150	+	1060	603	890	2553	"

+++ Very abundant

++ Abundant

\+ Few

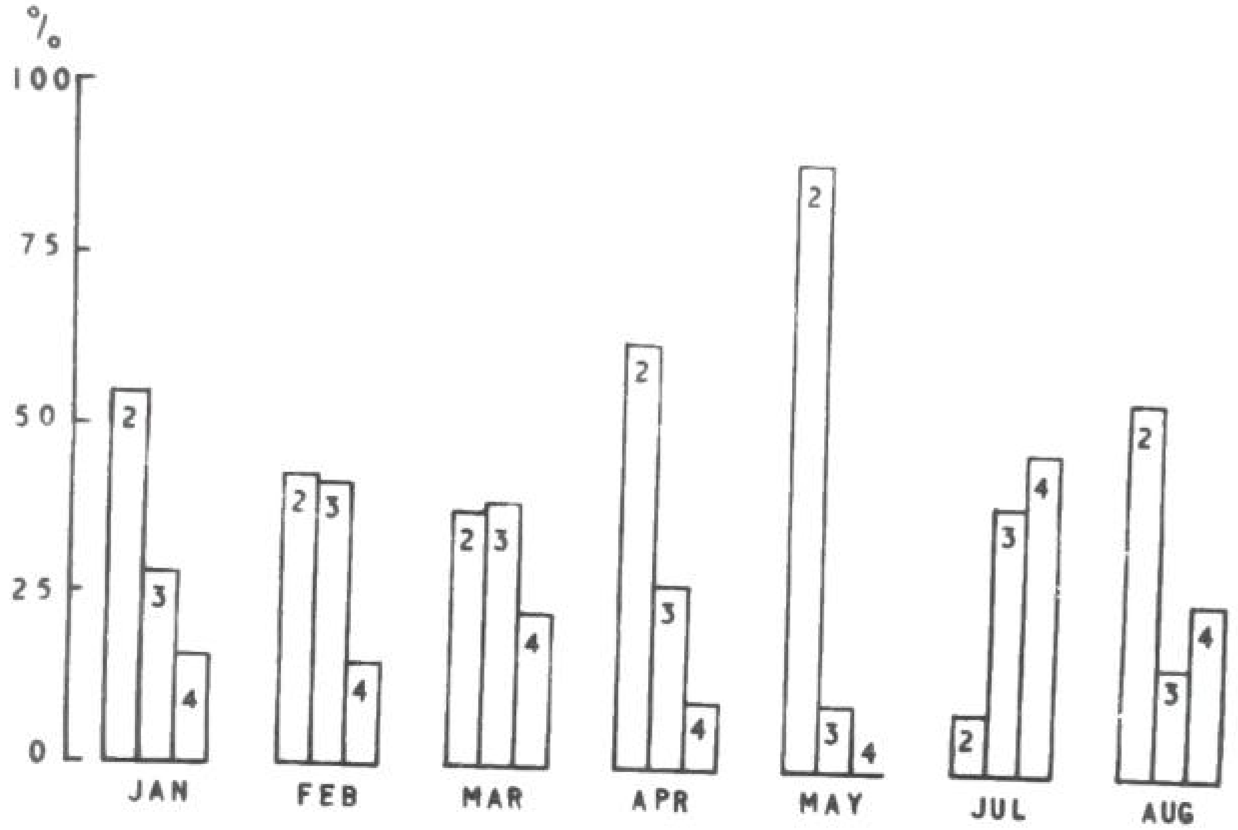


Fig. 31. Monthly mean percentage proportion of each egg group.

TABLE 18. Mean % Proportion of Egg Groups in T. gal.

Month	% Group 1	% Group 2	% Group 3	% Group 4	N
January	++	55.1	29.1	15.8	14
February	+	42.9	42.6	14.5	17
March	+	37.5	39.1	23.4	6
April	+	63.4	26.6	10.0	11
May	++	89.8	10.2	-	6
June	-	-	-	-	-
July	+	9.4	42.4	48.2	3
August	++	56.5	17.5	26.0	3
					60

THE COEFFICIENT OF MATURITY:

An alternative procedure for assessing the sexual condition of fish is provided by the weight of the gonads. Since weight is likely to be affected by absolute size a maturation coefficient or gonado-somatic ratio has been adopted. The former is the same as the latter but expressed as a percentage. It has been used by Cadwalladr (1962/63) in a study of Labeo victorianus Boulenger. Clearly the more mature the fish, the greater will be the maturation coefficient.

Maturation coefficients have been determined for a large number of specimens and the monthly average maturation coefficients calculated. The results of such an analysis are shown in figs.32-34 and Table 19. It will be seen that there are seeming variations in the maturation coefficient with time. The individual samples which constitute the peaks are however based on samples so small as to make their validity doubtful. There is nevertheless a suggestion that the maturation coefficient of all three species is low in the earlier months of the year.

To test this the data obtained from the different species were lumped. fig.35. This procedure, by itself, is not however satisfactory as the maturation coefficients of T.zilli are strikingly greater than those for the other two species. To eliminate this uneven weighting the following procedure was used. The maturation coefficients of the individual fish were expressed as percentages of the maximal maturation coefficient recorded for the species.

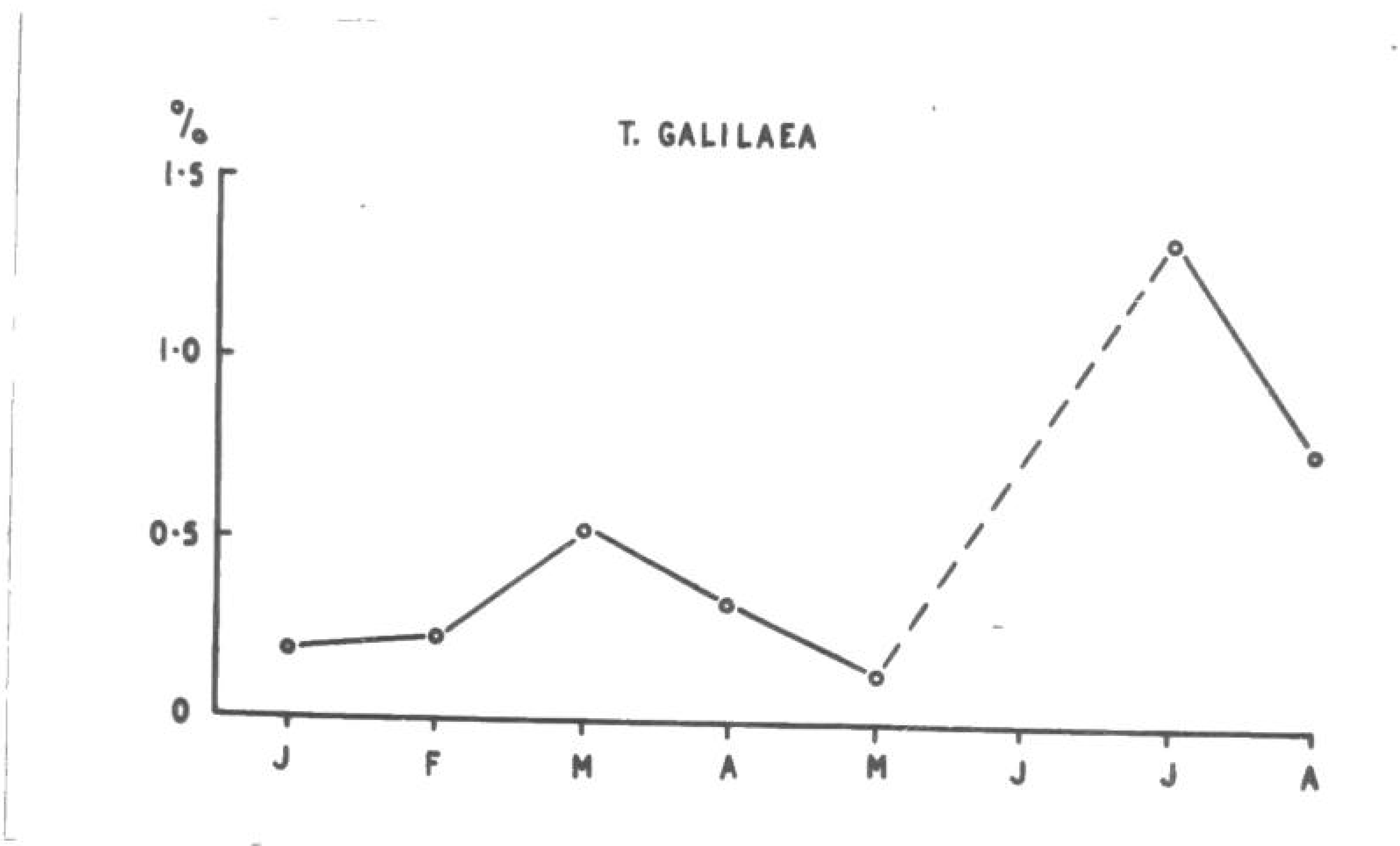


Fig. 32. Seasonal variation of Maturation Coefficient of *T. galilaea* (monthly average values).

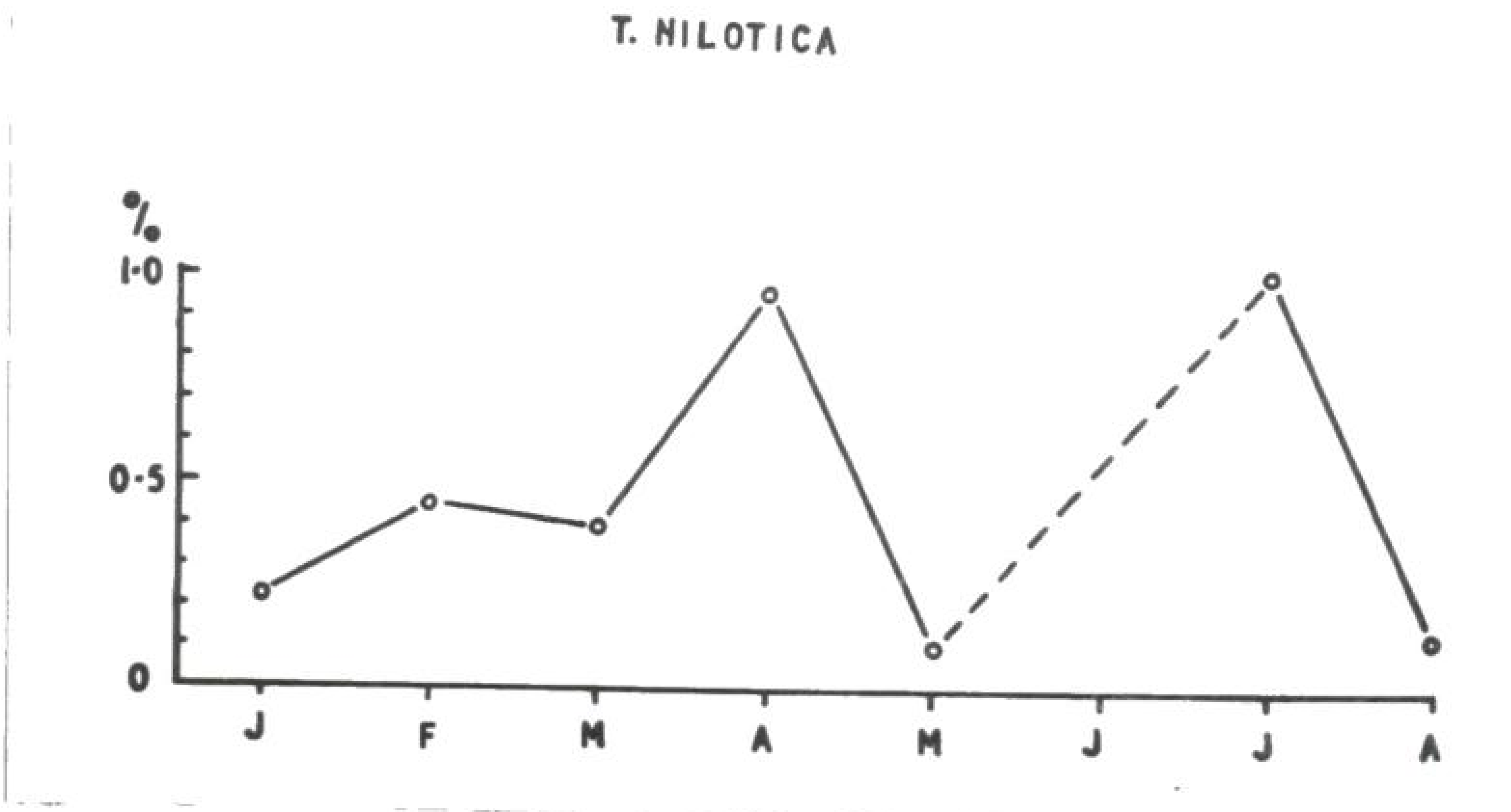


Fig. 33. Seasonal variation of Maturation Coefficient of *T. nilotica* (monthly average values).

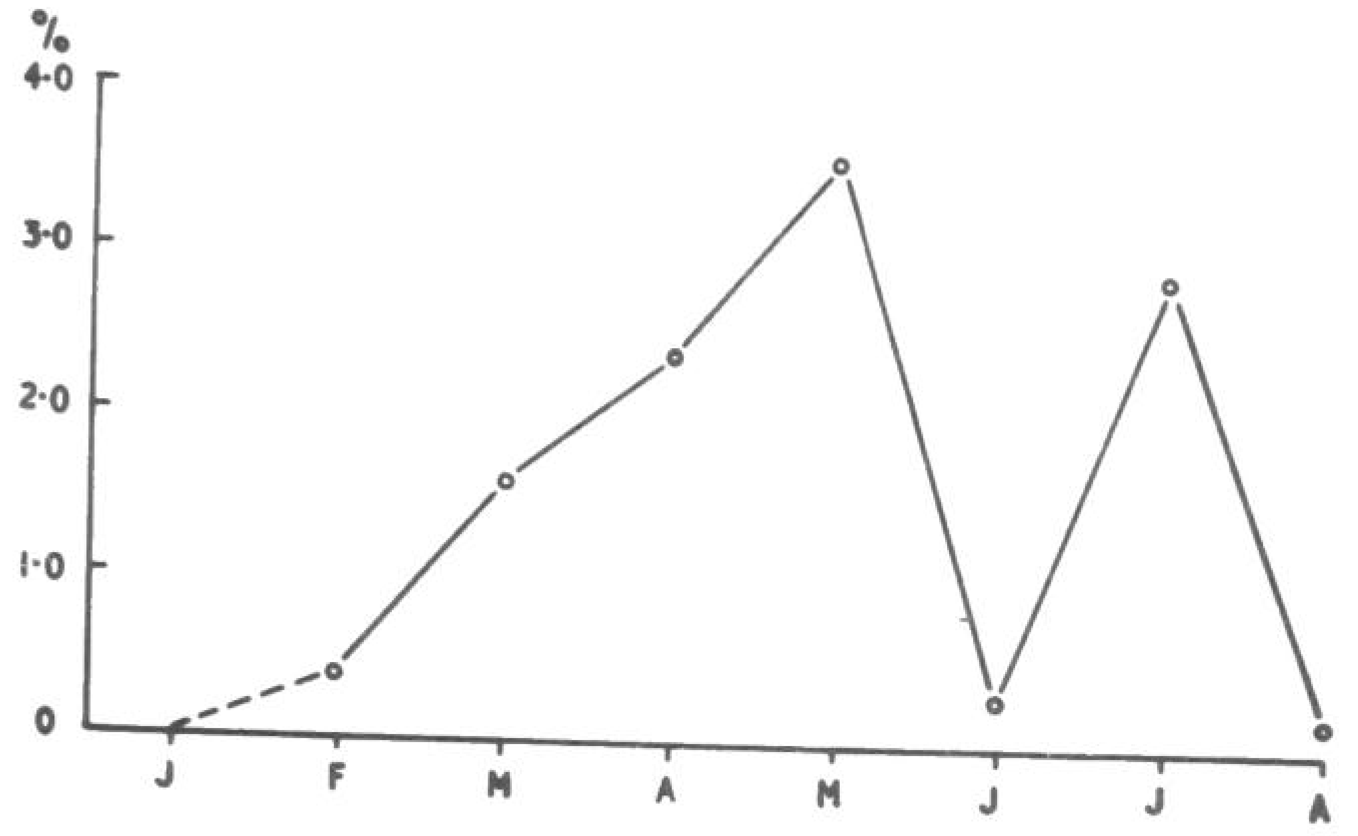


Fig. 34. Seasonal variation of Maturation Coefficient of T. zilli/melanopleura (monthly mean values).

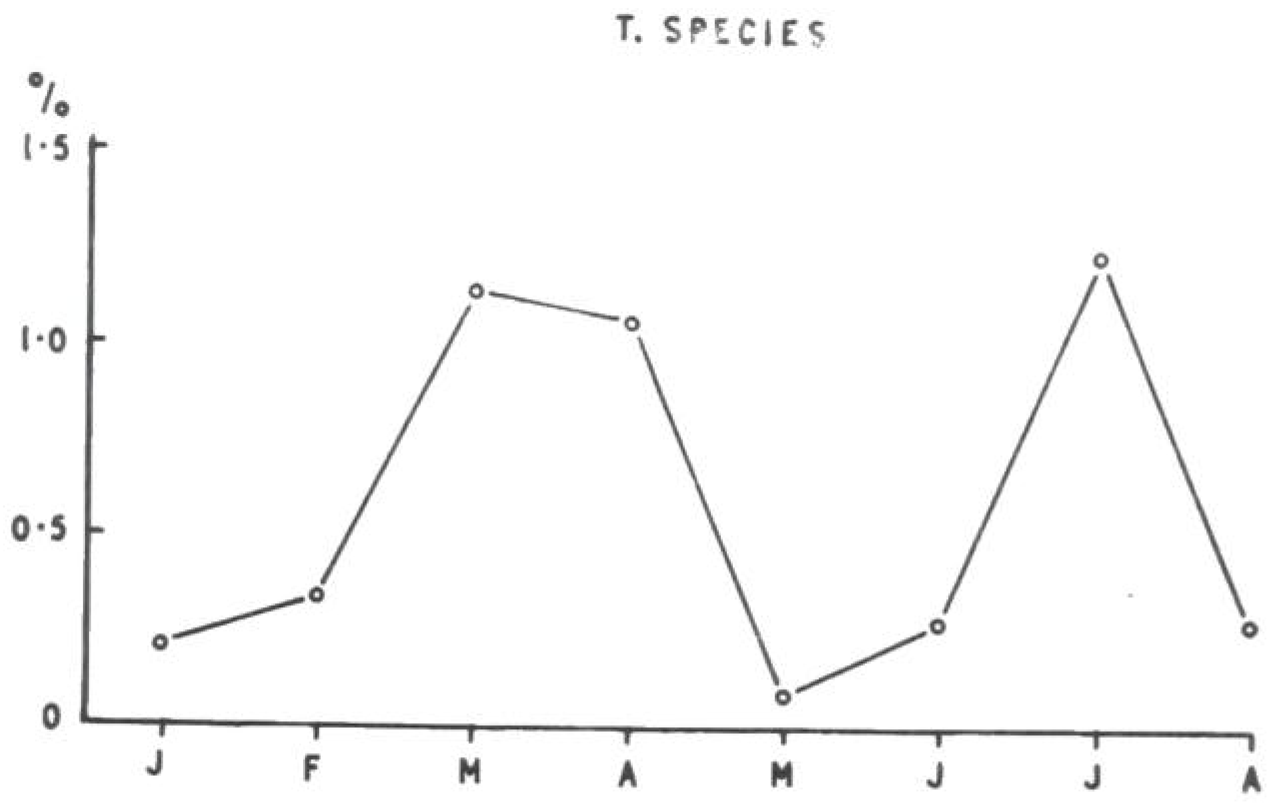


Fig. 35. Seasonal variation of Maturation Coefficient of Tilapia species (monthly mean values).

TABLE 19. MEAN MATURITY COEFFICIENT OF T. NILOTICA

Months	Male	No. of fish	Female	No. of fish
January	0.02170	2	0.22070	3
February	0.05543	18	0.43886	14
March	0.11148	9	0.39222	6
April	0.09510	3	0.96085	2
May	0.01550	1	0.09760	1
June	0.06660	1	-	-
July	0.05360	8	1.01428	10
August	-	-	0.13560	9

MEAN MATURITY COEFFICIENT OF T.ZILLI/MELANOPLEURA

Month	Male	No. of fish	Female	No. of fish
January	0.01060	1	-	-
February	0.16107	7	0.43959	11
March	0.14899	15	1.56534	20
April	0.05500	1	2.39040	6
May	0.11405	2	3.62780	2
June	0.04930	1	0.28610	2
July	-	-	2.93750	1
August	-	-	0.23340	4

TABLE 19 (CONTD.) MEAN MATURITY COEFFICIENT OF T. GALILAEA

Month	Male	No. of fish	Female	No. of fish
January	0.02520	19	0.20600	31
February	0.02945	15	0.21531	21
March	0.03769	15	0.52576	7
April	0.01720	2	0.33435	11
May	0.02902	5	0.14470	6
June	0.01030	1	-	-
July	0.07580	1	1.36040	3
August	0.03670	1	0.78720	3

MEAN MATURITY COEFFICIENT OF TILAPIA SPP.

Month	Male	No. of fish	Female	No. of fish
January	0.02421	22	0.20730	34
February	0.06418	40	0.33698	46
March	0.09752	39	1.13153	33
April	0.06245	6	1.04958	19
May	0.04859	8	0.09135	9
June	0.04203	3	0.28610	2
July	0.05606	9	1.22581	14
August	0.03670	1	0.28220	16

Clearly this procedure is somewhat arbitary, but, in view of the small sample size, it appeared to be the only method which would allow some assessment of a possible change of maturation coefficient with the season.

The results of this, together with the standard errors of these means are shown in figs.36 and 37 and Table 20. It will be seen that as far as the males are concerned there is no significant change in the maturation coefficient during the period studied. With the females, however, the position is different. The maturity coefficient does not differ significantly from January to May while the low value reported for June depends upon a sample of only two fish. The results for July are however very significantly greater (a comparison of January and July shows that $t=2.56$, $p=> .01$) than for the preceeding months. The value obtained for August does not differ from that observed in the earlier months of the year.

When these results are examined by species, it is clear from inspection that this high level of the maturity coefficient in July is true of <u>T.nilotica</u> and probably, despite the small sample, of <u>T.galilaea</u>. No conclusion can be drawn from the single specimen of <u>T.zilli</u> caught during this month.

The high value of the maturation coefficient of <u>T.galilaea</u> in July is reflected in the fecundity figures summarised in Table 17. It will be seen there that the individuals examined from the July catch had a markedly higher percentage of eggs in group 4 than did the rest, a high percentage of group 3 eggs and the lowest percentage of group 2 eggs.

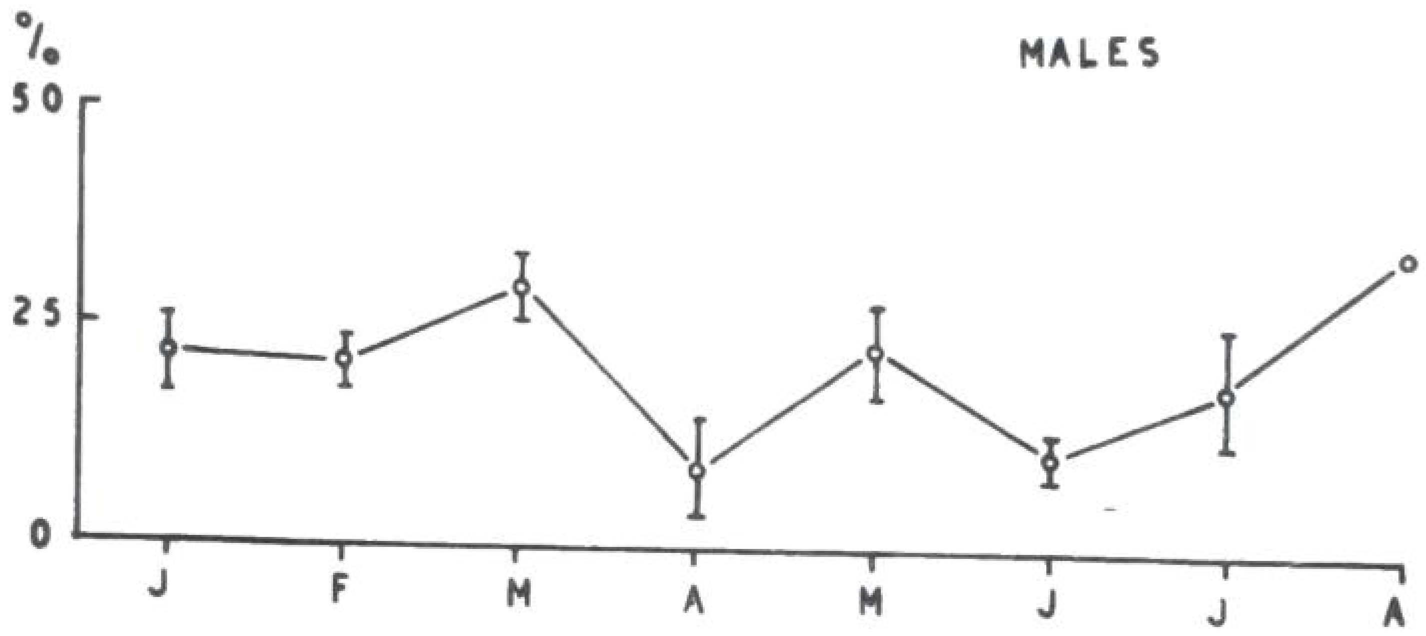


Fig. 36. Mean monthly Maturation Coefficient expressed as a % of the maximal Maturation Coefficient. (T. species - males).

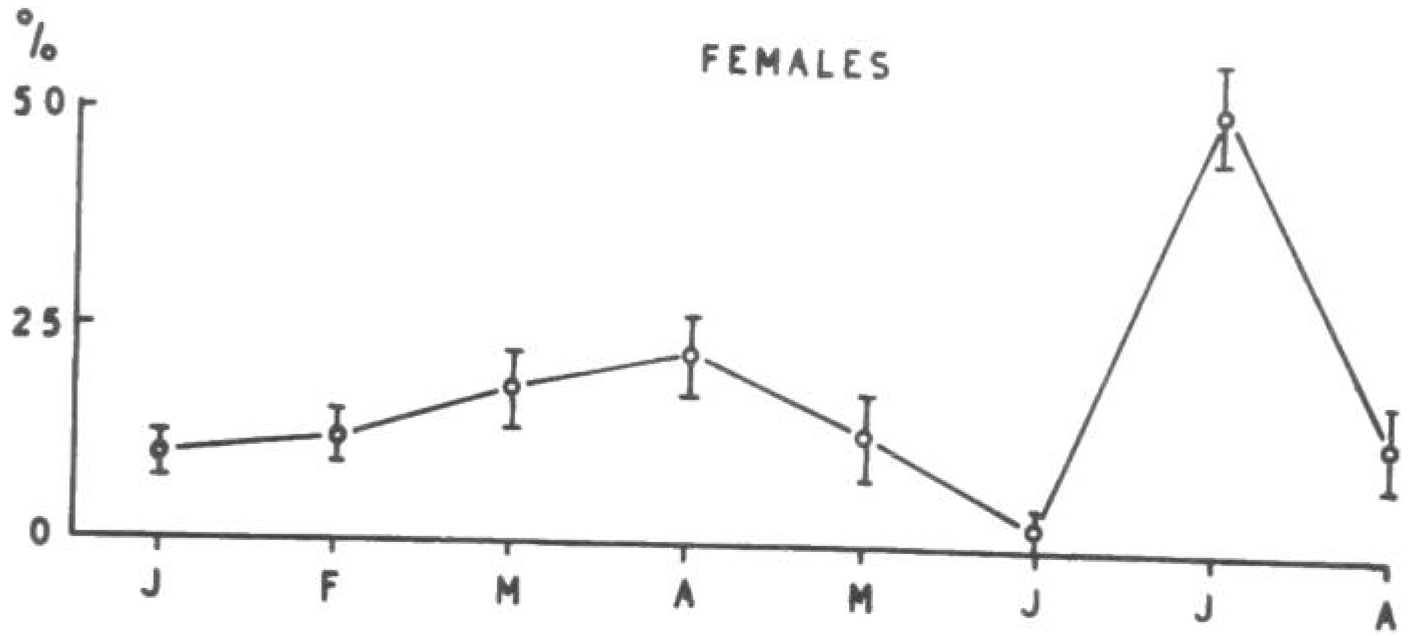


Fig. 37. Mean monthly Maturation Coefficient expressed as a % of the maximal Maturation Coefficient. (T. species - females).

TABLE 20 MEAN MATURATION COEFFICIENT EXPRESSED AS % MAXIMAL MATURATION COEFFICIENT (TILAPIA SPECIES).

Females

Month	N	Mean	σm	p
January	34	10.1	1.92	0.001
February	46	12.2	2.65	0.10
March	33	17.9	4.06	0.80
April	19	21.6	4.66	0.30
May	9	12.9	4.76	0.40
June	3	2.0	0.94	0.001
July	14	50.5	6.00	0.001
August	16	11.6	5.78	0.40

popn. $\bar{x}$ = 16.76

Males

Month	N	Mean	σm	p
January	22	21.5	4.05	0.70
February	40	21.1	2.77	0.50
March	39	29.6	3.85	0.10
April	6	9.3	5.37	0.05
May	8	22.7	5.46	0.90
June	3	11.2	2.10	0.01
July	9	19.0	6.66	0.50
August	1	35.3		

popn. $\bar{x}$ = 23.17

A comparison of the present data with those shown in fig.26 is of interest. In the figure it can be seen that over the period from March to May there was a significant excess of males in the specimens of T.nilotica caught. In August the sex ratio significantly exceeded 50%. At the same time the total catch in July was nearly three times that in June. This strongly suggests that the fishing grounds were invaded at this time by new individuals which included females in an advanced stage of sexual maturity. It seems further possible that this event may correlate with the increase in Lake level which started in June. It is suggested that the rise in Lake level established new potential spawning grounds which attracted individuals of both sexes, that this movement continued in August but that a major spawning of T.nilotica (and possibly T.galilaea) occurred towards the end of July.

SEXUAL MATURITY AND SIZE OF FISH:

In the preceeding discussion emphasis has been placed upon possible seasonal variation in sexual maturity and also upon the minimal size at which females of the different species become sexually mature.

It is now necessary to examine the data more closely to study the effect of size upon maturity. This is most easily effected by a comparison of the maturity coefficient with size in the different species. The results of such analysis can be seen in figs. 38-40. Despite the relative paucity of specimens it seems clear that a high maturation coefficient is shown only by large fish. This may

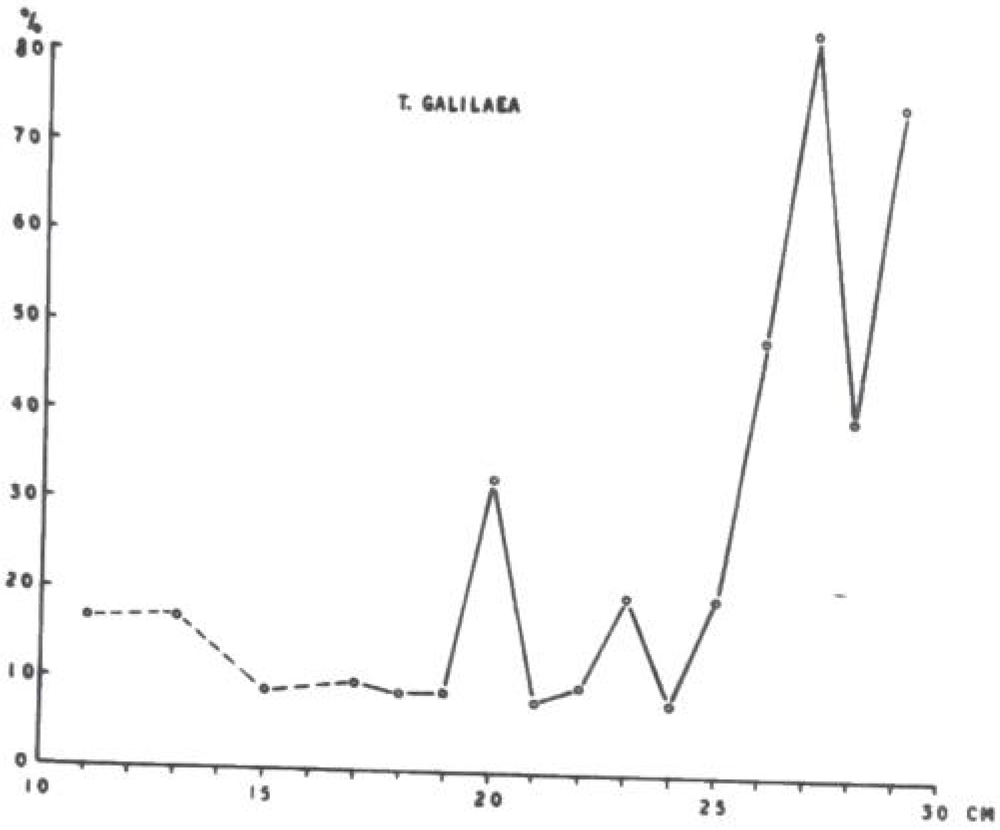


Fig. 38. Effect of size on Maturation Coefficient. (T. galilaea).

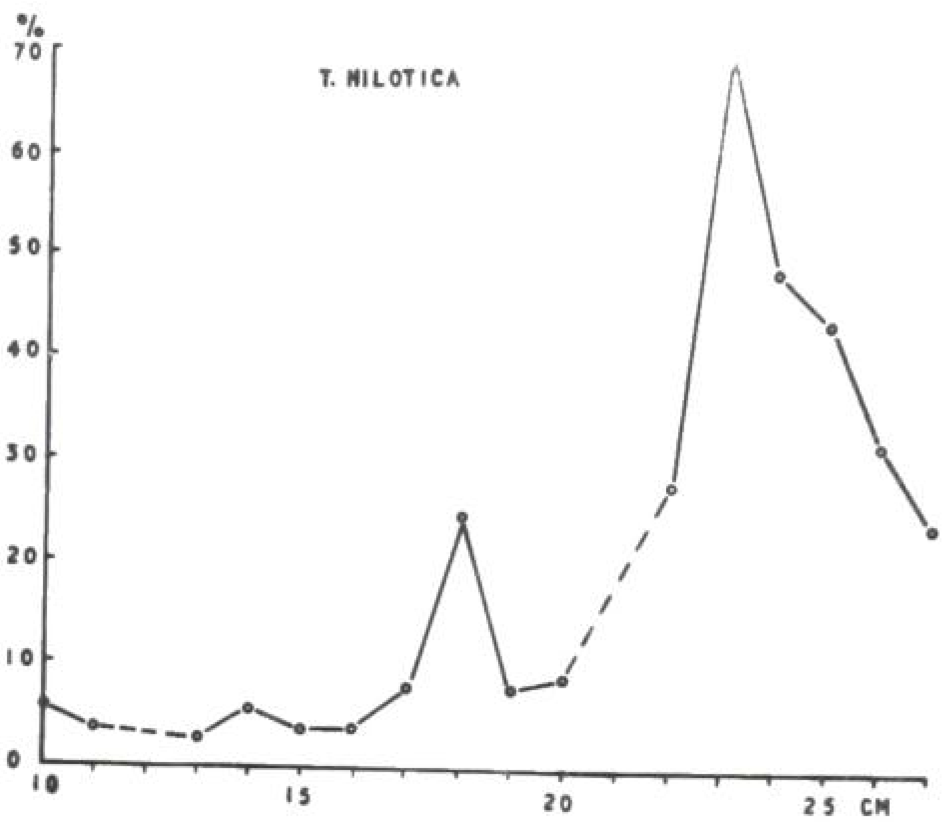


Fig. 39. Effect of size on Maturation Coefficient. (T. nilotica).

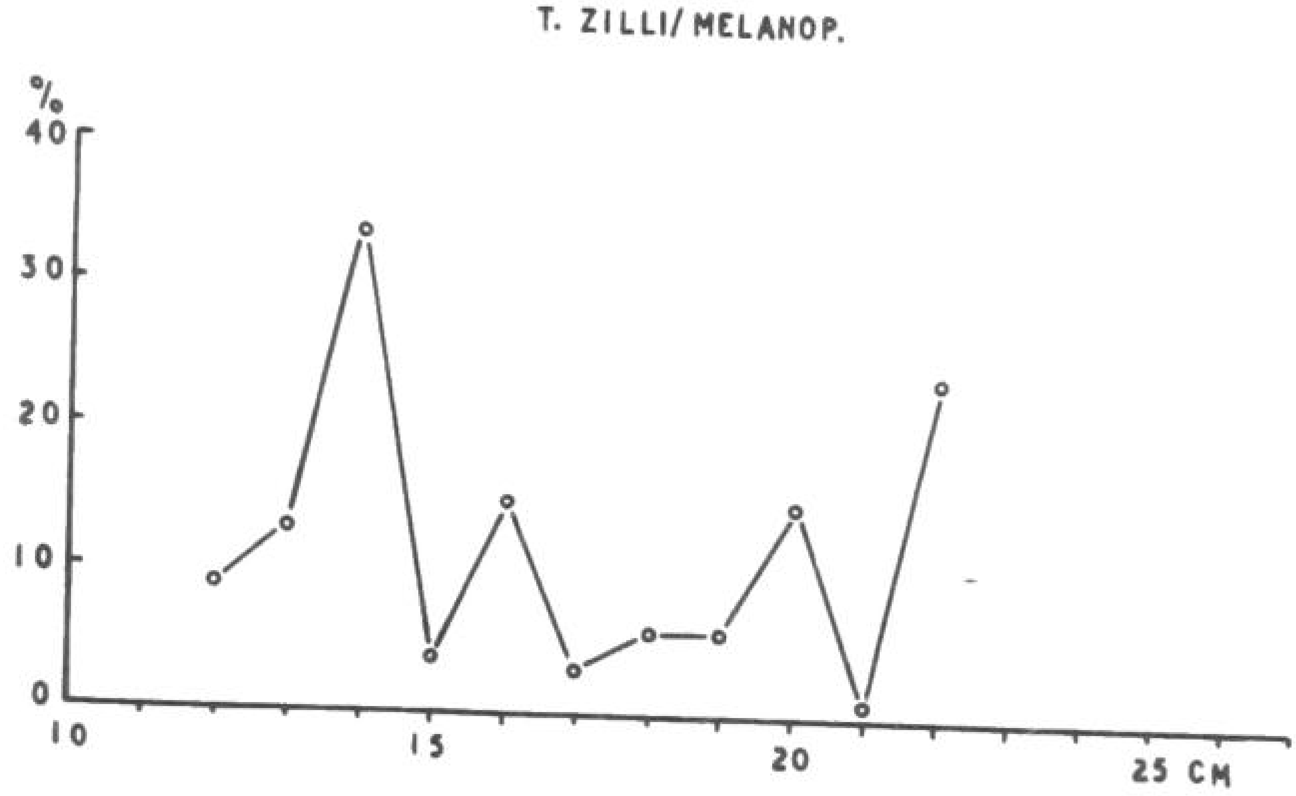


Fig. 40. Effect of size on Maturation Coefficient.
(*T. zilli/melanopleura*).

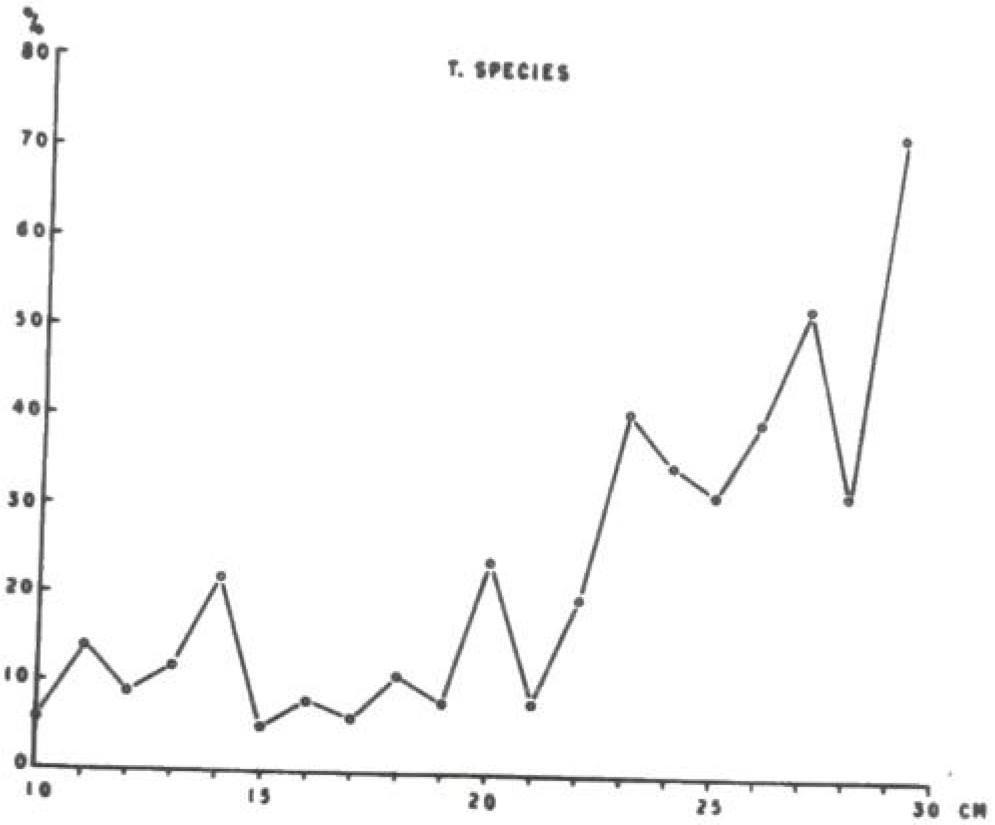


Fig. 41. Effect of size on Maturation Coefficient.
(*Tilapia* species).

imply that the fish only reach full sexual maturity once they have achieved a certain size. Fig.41 shows the lumped data for all three species. From these data it is clear that there is a relatively great increase in the size of the ovary in fish greater than 22 cm. length. A study of the results for individual species is broadly in keeping with this conclusion.

Such a result might be taken to imply that the fish will only spawn once they have exceeded this critical length. On the other hand the results may simply reflect a heterogenic growth effect in which the ovary shows a marked positive heterauxis beyond a particular size and, if this be the case, the maturation coefficient throws no particular light upon the size at which spawning can occur.

It appeared therefore necessary to reanalyse the data in Table 17 to see whether the abundance of eggs in different stages of maturation was also related to size. The mean lengths of fish showing group 2 eggs only, of fish showing group 3 but not group 4 eggs and fish having group 4 eggs were determined. The results are set out in Table 21 below.

Table 21. Mean length of fish of each egg-group.

Groups	No. of fish	Mean length cms	σ	σ_m
2	26	18.3	3.4	0.7
3	22	20.5	7.0	1.5
4	12	23.1	3.3	1.0

These also strongly suggest that there is a close correlation between maturity, as judged by a detailed analysis of the contents of the ovary, and size. The result may be expressed also as the smallest size at which eggs of different groups appear. The data in Table 17 give the following values:

Group 2	10.8 cm.
Group 3	16.5 cm.
Group 4	18.8 cm.

leading again to the conclusion that a definite size must be attained in this population before mature eggs start to develop in the ovary.

This analysis may be carried further by examining the relation between the numbers of eggs in different groups for specimens of different lengths. The results of such an analysis are shown in fig. 42. It will be seen that there is no correlation between size and the abundance of young oocytes, but that the number of more mature oocytes increases significantly with size.

These results are open to two interpretations. It is clear that fully mature oocytes do not occur in specimens of <u>T.galilaea</u> less than 18.0 cm length and that their number increases with the size of the fish. Similarly the maturity coefficient starts to increase sharply at about the same length.

If it be assumed that fully mature oocytes are retained for only a short period in the ovary before ovulation, then it follows that the size of successive broods will become greater as the fish

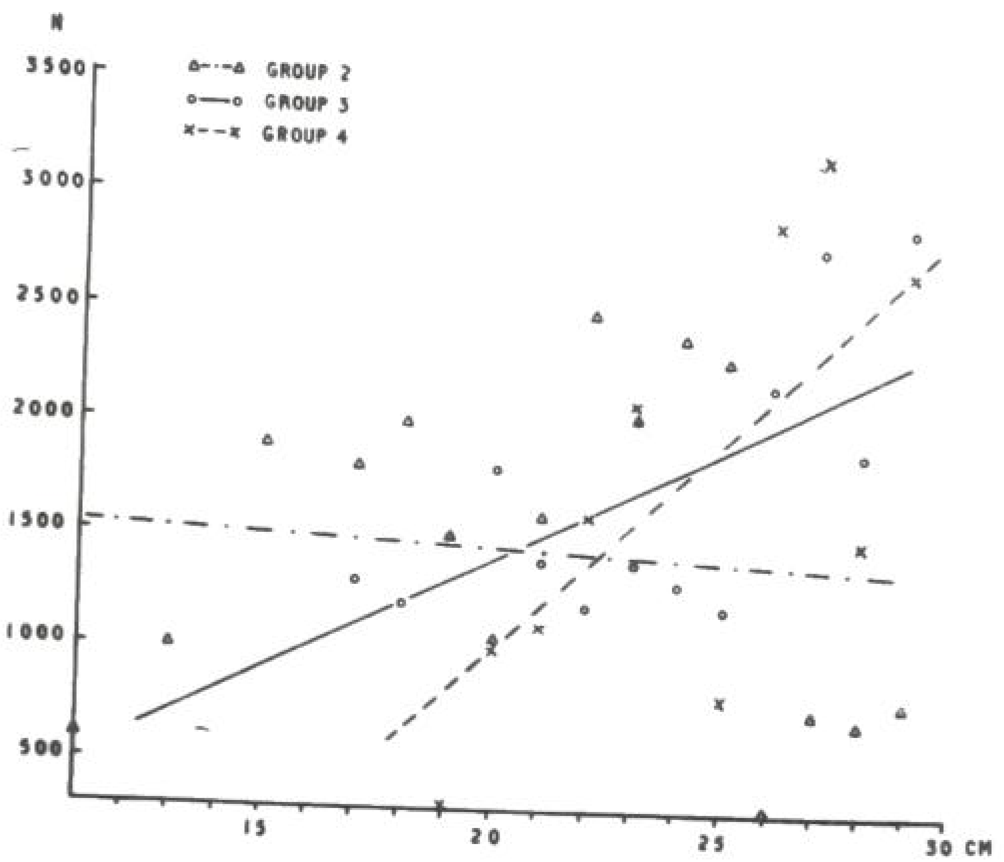


Fig. 42. Relation between the size of female and the number of eggs in different groups.

grow and, further, an explanation is provided as to why some fish of greater length than 20.0 cms do not contain mature oocytes. A limited number of field observations support this view. Thus McConnell (1955) reports that a 16 cm specimen of T.galilaea from Lake Victoria had a brood of 538 ripe eggs, a 23 cm. specimen 1000 and a 30 cm. specimen 1560 ripe eggs.

Thus there is the possibility that the oocytes develop at different rates and that spawning does not occur until a certain number of mature oocytes have accumulated in the ovary. As an alternative postulate it might be assumed that spawning occurs, not when some critical volume of eggs have accumulated in the ovary, but rather when some external circumstance triggers spawning.

The former hypothesis might lead us to expect the presence in the ovaries of groups of oocytes of different sizes representing succeeding generations, the latter a more uniform distribution. An attempt was made to clarify this by determining the frequency of oocytes of different sizes in ovaries from specimens of different maturation coefficients. All oocytes greater than 0.25 mm. in diameter in one ovary were measured. The results are shown in figs.43 and 44. In specimen A which had a maturity coefficient of 0.0092%, only small oocytes less than 0.25 mm were found. In specimen B with maturity coefficient 0.9603%, oocytes of a very wide variety of diameters occured, while in specimen C of maturity coefficient 1.9710%, an essentially similar distribution was encountered, the only real difference being one of absolute numbers. In no case is

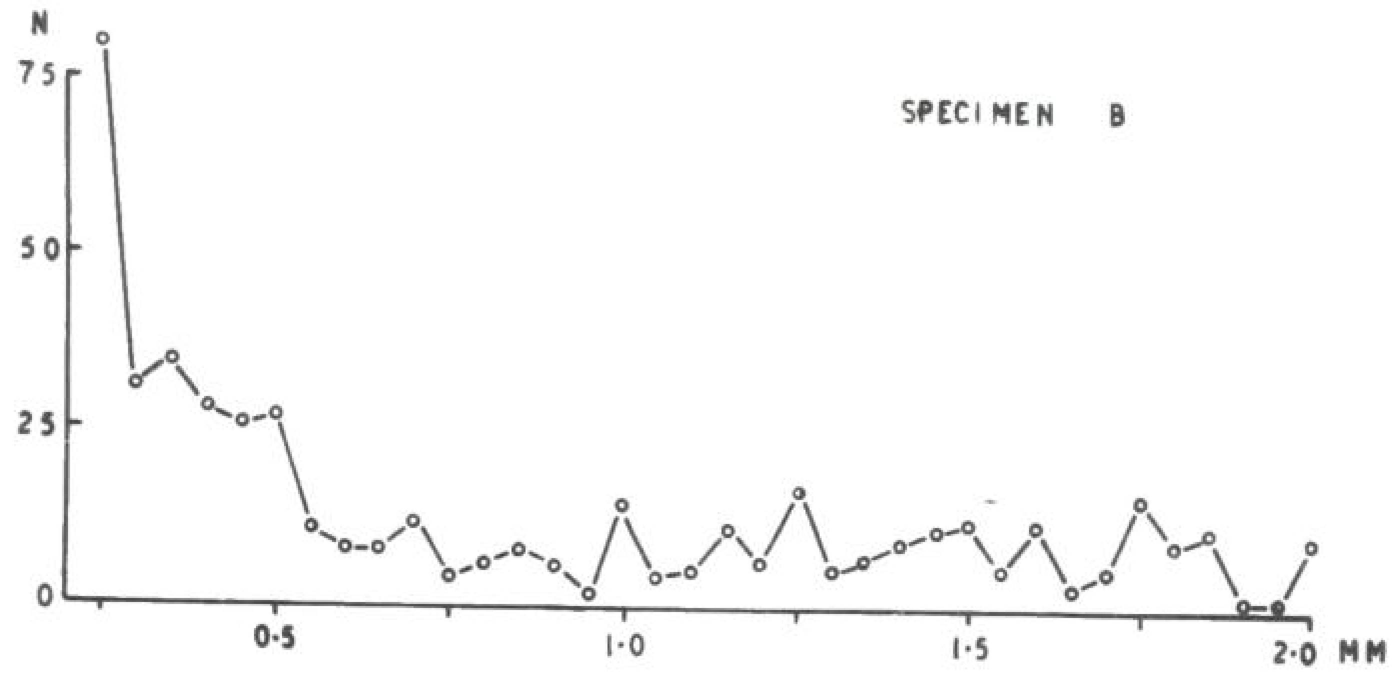


Fig. 43. Frequency of different sizes of oocytes in ovaries with different maturation coefficient.

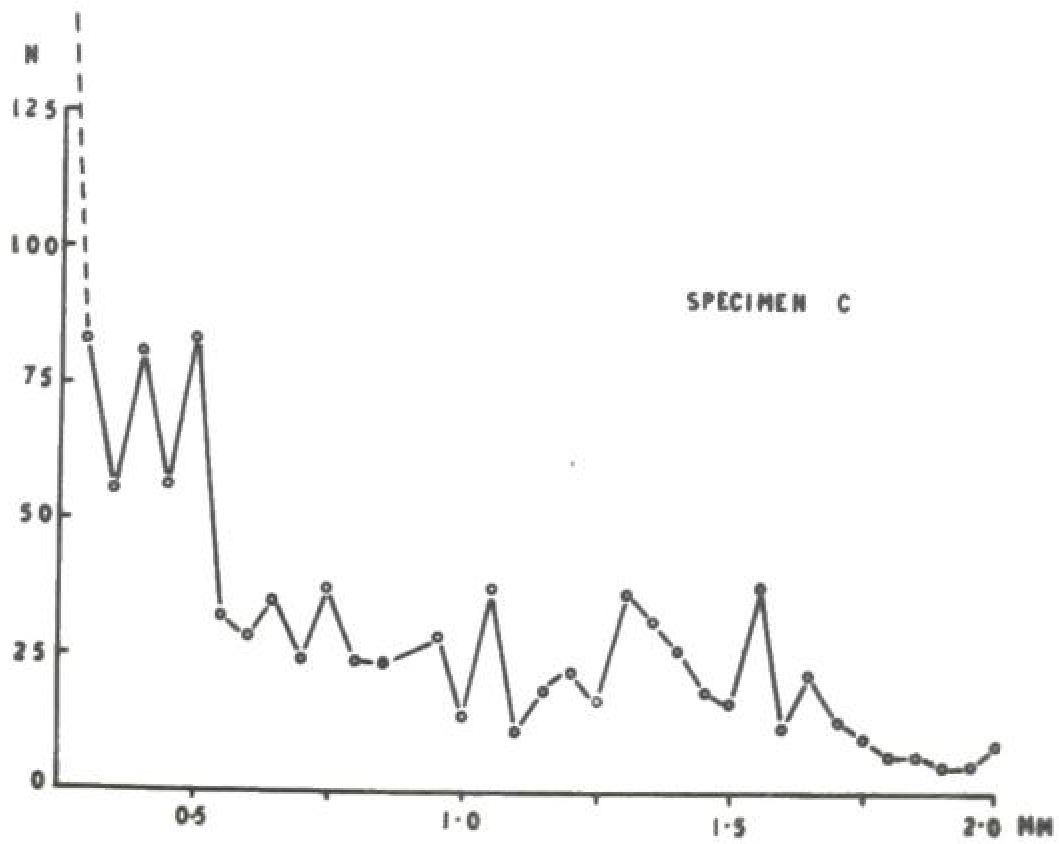


Fig. 44. Frequency of different sizes of oocytes in ovaries with different maturation coefficient.

there any clear indication of distinct classes of oocytes. Such a result might thus lead to the conclusion that oocytes of all stages of maturity occur in the ovary. There is, moreover, no indication that the largest oocytes constitute a class which is accumulating in the ovary.

This result might thus be interpreted as meaning that once a critical level of maturity is reached, spawning is triggered by some external factor and that eggs of a variety of diameters but all capable of development will be shed. This idea receives some support from the results of Lowe (1955) who found variations in the size of the ripe ova of different species of *Tilapia*. Thus values ranging from 2.8 x 2.5 mm to 4.3 x 3.7 mm were found for *T.nilotica* and 1.1 x 0.8 mm to 2.0 x 1.4 mm for *T.zilli*.

However as soon as the assumption is made that eggs of a variety of sizes may be shed, it no longer becomes possible to recognise a distinct size class as representing mature oocytes. Indeed all oocytes greater than 0.25 mm are yolk laden and if distinct generations of oocytes are to be found they must be sought in the earlier stages of development.

As a further test the histological composition of individual ovaries was examined and the presence or absence of different histological stages of early oocyte development noted. The results of this analysis are shown in Table 22. It will be seen that in almost all fish all histologically recognisable stages occur. If the smallest oocytes are neglected, it will also be seen

TABLE 22 The occurrence of different histological stages of development in the ovary of T.galilaea

Index No.	Length in cms	Dense Cyto-plasm I	Medium Dense Cytoplasm II	Granular bordered nucleus III	Shrunken oocyte IV	Early Yolk V	Full Yolk VI	Date of Collection
1	19.0	++	+	+	++	+	-	Jan
2	10.7	++	+	+	++	-	-	"
3	19.5	+	+	+	+	++	-	Feb.
4	28.2	++	+	+	+	+	++	"
5	17.5	+	+	+	+	+	-	Mar.
6	18.2	++	+	+	+	+	-	"
7	10.8	+	+	+	-	+	-	Apr.
8	12.5	+	+	+	+	+	-	"
9	22.0	+	+	+	+	+	-	"
10	24.5	+	+	+	+	+	++	"
11	11.2	++	+	+	++	+	-	May
12	17.5	+	+	+	+	-	-	"
13	24.6	+	+	++	+	+	-	"
14	25.0	++	+	+	+	++	+	"
15	21.0	++	++	+	+	+	++	Jul.
16	21.0	++	+	+	+	+	++	"
17	22.0	++	+	-	+	+	++	"
18	13.0	++	+	+	+	+	-	Aug.
19	15.0	+	+	+	+	++	-	"
20	20.0	+	+	+	+	+	++	"

++ Abundant

\+ Present

\- Absent

that out of the 20 individual ovaries examined, 13 showed one subsequent stage of ovarian development to be relatively more abundant than the rest. This might perhaps reflect the results of sequencial waves of development following a spawning and be taken as evidence that ovulation occurs when a certain number of mature oocytes have accumulated in the ovary.

However, the argument here developed is recognised as being dependent upon very uncertain interpretations of the available data and no firm conclusion can reasonably be drawn as to whether the stimulus for ovulation is inherent in the processes of ovarian growth or dependent upon some extraneous environmental factor. The actual act of spawning is in these species released by the courtship ritual and is not the matter under consideration.

IX. DISCUSSION

The present investigation must be accepted as a preliminary exercise designed to see whether the technique of sampling by gill net fishing could aid in clarifying problems concerning the biology of Tilapia in the Volta Lake. The results cover only a limited period of time and the samples studied are small. Nevertheless they allow certain conclusions, though mostly of a negative character, to be drawn.

The first problem which has to be considered is that of sampling. It has been shown that the fleet of nets employed probably provided samples which, above a certain size range, reflected with some accuracy the composition of the population in such parameters as size and sex and probably also in abundance. It is clear, however, that the method is grossly inefficient in providing information about generations, reproduction and growth. This is partly due to the fact that, to obtain samples of any size, a single fleet of nets is completely inadequate. A rough calculation shows that, throughout the period of study, each net was, on the average, collecting only one specimen per fishing day. If the method is to be employed further, it is obvious that several fleets of nets must be used at the same time so that samples of a size adequate for proper statistical analysis may be obtained.

The second major criticism of the method is that there seems every reason to believe that the different species of Tilapia move freely and that at different times what might be regarded as different populations were collected in the nets. This is most clearly indicated by two cases. Firstly during the months of March to July the sex ratio for T.nilotica fell below 40%. There was a significant excess of males in the samples at this time. (See fig. 26 and Table 11). It is to be presumed that the females of this species had, during that time migrated elsewhere. Again in a consideration of the maturation coefficients it was found that during July the specimens of T.nilotica caught showed a significantly greater coefficient than those taken in other months of the year. This also probably reflects some movement of the stock.

To form a complete picture of the breeding behaviour of these fishes it is clear that the limited gill netting here employed is insufficient unless it is supplemented by nets set in a number of different localities together with some type of tagging proceedure which would allow it to be ascertained as to whether any movements of the fish from one area to another occur. Tagging would further have the advantage of allowing direct observations upon growth rates to be made.

Finally it is obvious that the value of gill netting, as practised here, is limited by the fact that the young stages of the species are not sampled and that an investigation using cast-nets or young fish traps should be instituted to extend any data acquired from gill nets.

When all these limitations are accepted, it is nevertheless possible to recognise, though not answer, certain questions. The first of these concerns the reproductive habits of the fish. The present data do set reasonable limits to the minimal size at which the females of these three Tilapia species start to come to maturity in the Volta Lake. In this connection it is to be noted that the smaller mesh gill nets which are in current use upon the Lake will in fact capture individuals before they have had an opportunity to breed. But the results fail to throw any critical light upon whether there is seasonal spawning, at what size or age spawning commences, what factors may determine spawning and so forth.

Eggs and nests of an unidentified Tilapia were observed inshore in March and during June and July eggs of T.zilli/melanopleura were found. However during the period April and May the water was too opaque to allow observations to be made. The length-frequency diagrams (figs. 12-14) might be interpreted as implying that there are certain times at which major spawnings occur, thus leading to the unimodal peak of size found in T.galilaea and T.nilotica and the double peak shown by T.zilli. Riedel (1965) says that spawning in T.mossambica does not start prior to the onset of the rainy season as indicated by the absence of fry at the end of the dry season. It must however be emphasised again that the structure of an adult population is determined not only by the time of spawning, but by the subsequent fate of the progeny; that is to say the chances of survival of the young stock may be far greater at certain times or in certain conditions than others and thus lead to the presence of dominant size groups in the population. The familiar case of the North Sea herring of the year class 1904 will illustrate this point.

The present data could indeed imply that there are certain major spawning times. It has been shown that the coefficient of maturity increases markedly with length. But fish of all lengths appear in the catch in all months and, in general the maturation coefficient does not vary greatly from month to month. If however it be assumed that some environmental factor can cause a sudden rapid increase in the rate of oocyte maturation leading to spawning, the present results might have been obtained. Those individuals which had grown faster or were older would be more mature and waiting, in a sort of reproductive diapause, for the necessary environmental signal while the younger or smaller fish were still maturing. If such a steady process of maturation continues until the spawning season, the larger fish will also be the more fecund and the correlation between size of fish and size of brood noted by McConnell (1955) will still occur.

It is clear, however, that more data and of a different character will have to be obtained before the question can be decisively answered and that the field studies will have to be supplemented ultimately by laboratory investigations if a complete analysis is to be made.

A. SUMMARY

1. This thesis describes and collates observations on the occurrence, the maturity and fecundity of *Tilapia* species in the Volta Lake around Akosombo from January to August 1966.

2. The position of *Tilapia* species among the general fish population is determined.

3. The absolute size of the fish population tended to decrease during the latter part of the period of study.

4. Factors affecting the change in the composition of the fish catch are discussed; rainfall, turbidity, increase in lake level and hence availability of food appear to be of major importance.

5. The length-frequency distribution of both sexes as caught in gill nets was very similar.

6. Without regard to sex, the length-frequency distribution of *T. nilotica* suggested the occurrence of four distinct size classes in the population. The same tendency was recognised in *T. galilaea*. It was, however, possible to recognise only three distinct size classes in *T. zilli/melanopleura*.

7. The length-frequency diagrams suggest either that the variation in size within any age group was considerable or that there were times when spawning was more successful than others.

8. With the exception of *T. nilotica*, the sex ratio of the other two species over the period examined did not differ significantly from 1 : 1.

9. Methods for determing the minimum size of fish at which sexual maturity is attained were studied, among which were determination by breeding colours and examination of the ovaries.

10. From a practical viewpoint, breeding colours are considered to provide a realistic assessment of the minimum size of mature fish since it appeared that the onset of maturity occurred before the assumption of breeding colours.

11. On the basis of breeding colours, T. galilaea was found to reach maturity at a length of 15.0 cm, T. zilli/melanopleura at 12.0 cm and T. nilotica at 13.2 cm total length. in the Volta Lake.

12. These results are compared with the minimum breeding size of different Tilapia species from other water bodies.

13. Factors determining the onset of maturity are discussed among which were photoperiod, environmental temperature, available food and overcrowding. The last three factors might perhaps apply to Tilapia species in the Volta Lake.

14. The small size at which these species become mature at the present time might be correlated with the exceptionally good feeding conditions prevailing during this period of high productivity.

15. T.galilaea belongs to the type "plurimodal" i.e. the ovaries contain more than only one portion (batch) of ovarian eggs which are distinguished from each other by size, stage of

development and appearance. There was also no localization of oocytes of different sizes in different regions of the ovary.

16. *Tilapia* species in the Volta Lake either have a long spawning period or spawn continuously but there are indications that there are times when exceptionally successful spawnings occur.

17. There was no correlation between size and the abundance of young oocytes but the number of more mature oocytes increased significantly with size.

18. Oocytes of all stages of maturity occurred in the ovary, but there was no indication that the largest oocytes constituted a class which was accumulating in the ovary.

19. It is suggested that spawning is triggered by some external factor and eggs of a variety of diameters but all capable of development are shed.

XI. ACKNOWLEDGEMENTS

I am gratefully indebted to Mr. A. Titiati of the Zoology Department and the staff of the Fisheries Division, Akosombo for their continued help in collecting the material on which this study is based.

I express my gratitude to Mr. F. Denyoh of the Fisheries Division, Akosombo and to Mr. T. Petr who co-operated at all times in my quest for information and also for granting permission to use some of their data from their published works.

To Mr. R. Attionu and Dr. S. Biswas, I acknowledge my gratitude for allowing me to publish some of their hydrological data in this thesis and to the State Construction Corporation for providing me with meteorological data.

I would also like to express my thanks to Mr. K.Y. Dabri for his technical assistance in preparing the histological sections and to Mr. R. Foli for his excellent photography.

My special thanks are due to Dr. A. Lelek as a source of advice and information and for his continued co-operation, cordial help and supervision of this work.

To Dr. M. Edmunds I tender my warmest thanks for his helpful discussions and for correcting the script.

I express my thanks to Professor D.W. Ewer who generously gave me the benefit of his specialised knowledge, read the script and gave much constructive and helpful criticism.

Thanks are also due to Mr. T.K. Quartey for typing the final draft of this thesis.

My final indebtedness to the Zoology Department for providing the necessary equipment and to the Volta Basin Research Project for the facilities extended to me throughout the period of study.

And with great pleasure I record my gratitude to all those who have assisted directly or indirectly in the writing of this thesis on the studies of the biology of the species of *Tilapia* in the Volta Lake.

XII. REFERENCES

Alm, G. (1946). Reasons for the occurrence of stunted fish populations with special regard to the perch. Rept. Inst. Freshwater Res. Drottningholm., 25 : 1 - 146.

Aronson, L.R. (1948) ex Hoar, W.S. (1955). Reproduction in Teleosts. Mem. Soc. Endocrin. No.4, Physiology of Reproduction. Cambridge University Press, Cambridge.

Aronson, L.R. & Holz-Tucker, A.M. (1949). Ovulation in the mouth-breeding cichlid fish, Tilapia macrocephala (Bleeker). Anat. Rec., 105 : 568 - 569.

Biswas, S. (1966). Oxygen and phytoplankton changes in the newly forming Volta Lake in Ghana. Nature, Lond., 209 : 218 - 219.

Blache, J. (1964). Les poissons du Bassin du Tchad et du Bassin adjacent du Mayo Kebbi. Etude Systematique et Biologique. O.R.S.T.O.M., Paris.

Brown, J.M. & Van Someren, V.D. (1953). New Fish Culture Methods for Tilapia in East Africa. Nature, Lond., 172 : 330.

Brown, M.E. (1957). Physiology of Fishes. Academic Press, N.Y.

Bullough, W.S. (1939). A study of the reproductive cycle of the minnow in relation to the environment. Proc. zool. Soc. Lond., A, 109 : 79-102.

______ (1940 a). The effect of the reduction of light in spring on the breeding season of the minnow (Phoxinus laevis Linn.). Proc. zool. Soc. Lond., A, 110 : 149 - 157.

Coulter, G.W. (1963/64). Research Report, Fisheries Research Bulletin. Zambia.

Chacko, P.I. & Krishnamurthi, B. (1954). Observations on Tilapia mossambica in Madras. J. Bombay nat. Hist. Soc., 52 : 349 - 353.

Craig-Bennett, A (1931). The reproductive cycle of the three-spined stickleback, Gasterosteus aculeatus Linn. Phil. Trans. B. 219 : 197.

Daget, J. (1954). Les poissons du Niger Superieur. Inst. fr. Afr. noire. Dakar, No.36.

______ (1956). Memoires sur la biologie des Poissons du Niger Moyen. 11. Reserches sur T.zilli (Gerv.). Bull. Inst. fr. Afr. noire, 18 : 165 - 223.

De Bont, A.F. (1950). La reproduction en etanges des Tilapia melanopleura (Dum) et macrochir (Blgr.). Comptes Rendus de la Conference Piscicole Anglo - Belge, 1949. Commun. 8 : 303 - 12.

Dulzetto, F. (1935). "Ulterori osservazioni sulla vita sessuale della Gambusia holbrookii Grd." Boll. Zool., 6 : 159 - 62.

Eberhardt, K. (1943). Geschlects - bestimmung und - Differenzierung bei Betta splendes Regan 1. Z. indukt. Abstamm. -u. Vererbleher, 81 : 363 - 373.

Ewer, D.W. (1965). Biological investigations on the Volta Lake. May 1964 - May 1965. Man-Made Lakes. Institute of Biology, Academic Press, London and New York : 21 - 31.

Frost, W.E. (1943). The natural history of the minnow, Phoxinus phoxinus. J. Anim. Ecol., 12 : 139 - 162.

Guyer, M.F. (1953). Animal Microbiology - Practical Exercises in Zoological Micro-Technique. Univ. of Chicago Press, Chicago.

Hickling, C.E. & Rutenberg, E. (1936). The ovary as an indicator of the spawning period in fishes. J. mar. biol. Ass. U.K., 21 : 311-17.

Hoar, W.S. (1957). The Gonads and Reproduction. (ex Brown, M.E. (1957)). "The Physiology of Fishes" Vol.I. Academic Press, N.Y.

Huxley, J.S. (1923). "Late fertilization and sex ratio in Trout". Science, 58 : 291-292.

Irvine, F.R. (1947). "The Fish and Fisheries of the Gold Coast". London, Crown Agents for the Colonies.

Jubb, R.A. (1952). Some notes on freshwater fishes in Southern Rhodesia. Family Cichlidae. Rhodesia agric. J., 49 : 69 - 73.

Krizenecký, J. (1914). Problem urcení pohlaví. (The problem of sex determination). Casop. Lek. ceských, No.46-52.

Krizenecký, J. & Krizenecka-Pulankova, A. (1953). Notes on growth determination, age determination and sex ratio in the Perch (Perca fluviatilis L.). Vest. Král. ces. spol. nauk, Mat. prir. 15: 1-26

Lowe (McConnell), R.H. (1949). Annual Rep. East African Inland Fisheries Res. Org. (1949).

Lowe (McConnell), R.H. (1952). Report of the Tilapia and other fish and fisheries of Lake Nyasa 1945-47. H.M.S.O., London.

_____ (1953). Notes on the ecology and evolution of Nyasa fishes of the genus Tilapia, with a description of T. saka (Lwe). Proc. zool. Soc. Lond., 122. 1035-1041.

_____ (1955 b). Species of Tilapia in East African dams, with a key for their identification.

E. Afr. agric. J. 10 : 256-262.

_____ (1955 c). The fecundity of Tilapia species. E. Afr. agric. J. 21 : 45-52.

_____ (1956 a). The breeding behaviour of Tilapia species (Pisces-Cichlidae) in natural waters; observations on T. karomo (Poll) and T. variabilis (Blgr.) - Behaviour. 9: 140-163.

_____ (1956 b). Observations on the biology of Tilapia (Pisces-Ciclidae) in L. Victoria. East African Fish. Res. Org., Jinga, Uganda. Suppl. publ. 1: 1-72.

_____ (1958). Observations on the biology of Tilapia nilotica (Linne) in East African waters (Pisces-Cichlidae). Rev. Zool. Bot. Afr. 57: 129-170.

Mackereth, F.J.H. (1963). Some methods of Water Analysis for Limnologists. Freshwater Biol. Assoc. Scientific Publication No.21.

Nikolsky, G.V. (1963). Ecology of Fishes. Academic Press. London and New York.

Noble, G.K. (1938). Sexual Selection among Fishes. Biol. Rev. 13 : 133-158.

Petr, T. (1967). Fish Population Changes in the Volta Lake in Ghana during its First Sixteen Months (Hydrobiologia in press).

Reidel, D. (1965). Some Remarks on the Fecundity of Tilapia (T. mossambica Peters) and its introduction into Middle Central America (Nicaragua) together with a first contribution towards the Limnology of Nicaragua. Hydrobiologia 25 : 357-388.

Reingardt, J.V. & Trudova, T.K. (1962). The annual cycle of gonad development in carp of Lake Lenin. Collected papers of TRUDY ZONALNOGO SOUSCANA PO TIPOLOGII I BIOLOGICESKOMU OBOSNOVANIJU RYBOCHOZJAJSTVENNYCH ISPOLZOVANIJA UNUTRENNYCH VODOJEMOV of the southern part of U.S.S.R. pp. 359-362.

Soulsby, J.J. (1963). Fishing Survey at Kariba. Rhodesia. agric. J. Vol.60. No.5, Sept.-Oct. 1963.

Thumm, J. (1908). Cited in WOLTERECK, R. "Geschlechtsbestimmung bei Warm wasser- Fischen. (Nach einer Zuschrift von Joh. Thumm). Int. Rev. Hydrobiol. 1: 519-521.

Vaas, K.F. & Hofstede, A.E. (1952). Studies on T.mossambica (Peters) in Indonesia. Contr. Inl. Fish. Res. Sta. Bogor, Indonesia. No. 1 : 1-88.

Viner, A.B. (1967). Exploratory Investigations into the Hydrobiology of Lake Volta, Ghana. Jan. 1965 to Apr. 1966. (in press).

Wallace, E. (1909). Onset of first maturity in *Lates mariae.* Marine Biol. Assoc. Internat. Fish. Invest. Southern Area. 2 : 51.

Welman, J.B. (1948). Preliminary Survey of the freshwater fisheries of Nigeria. Lagos, 1948.

Whitehead, R.A. (1962). The life history and breeding habits of the West African Cichlid fish *Tilapia mariae* and the status of *T.meeki*. Proc. zool. Soc. Lond., 139: 535-543.

Worthington, E.B. (1929). A report on the fishing survey of Lakes Albert and Kyoga. Crown Agents for the Colonies, London.

Worthington, E.B. & Ricardo, C.K. (1936). Scientific results of the Cambridge expedition to the East African Lakes 1930-31. No.15. The fish of Lake Rudolf and L. Baringo. J. Linn. Soc. Lond; Zool., 39 : 353-389.

REPORTS

1965 Fisheries Report, Fisheries Division, Accra

1966 " " " " "

1953 Annual Report, E.A.F.R.O., Jinja, Uganda.