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Observations on the biology of the cichlid fish *Tilapia variabilis* Boulenger in the northern waters of Lake Victoria (East Africa)

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INTRODUCTION

Two species of the genus *Tilapia* occur naturally in Lake Victoria. Of these the most abundant and therefore the most important economically, is *T. esculenta* GRAHAM, and it is for these reasons that more information is available concerning this species than the related *T. variabilis* BOULENGER. Thus LOWE (MCCONNELL) (1956) who was the first to make a serious study of the *Tilapia* species of the lake since the pioneering survey of GRAHAM (1929), dealt in considerable detail with *T. esculenta* but treated *T. variabilis* much less fully. Later studies (GARROD 1959) have also been concentrated on *T. esculenta*. Because of a relaxation in certain areas of net-size regulations (discussed below) *T. variabilis* has recently assumed greater economic importance than was the case when restrictions were imposed, and this has called for further study of its general biology and the possible effects of commercial exploitation. The following account represents a preliminary contribution to the information required, and deals almost entirely with observations made in the northern waters of the lake and particularly in the vicinity of Jinja (Uganda).

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HABITAT PREFERENCES THROUGHOUT LIFE

It is generally agreed that, in contrast to *T. esculenta,* which, while widespread in Lake Victoria, shows a preference for land-locked gulfs with soft bottoms, *T. variabilis* is a frequenter of more exposed shores. This statement, however, requires qualification, for, in the Jinja area at least, habitat preferences differ at different phases of the life cycle. These preferences are summarised briefly below. They refer to the most usual state of affairs in the Jinja area but are not absolutely rigid, for *T. variabilis* is a very adaptable species capable of existing under a variety of conditions.

The habitat preferences of *Tilapia variabilis* at different stages of development.

— c 15 mm.	Brooded in mouth of female parent, off-shore in more than 1 metre of water over predominantly rocky bottoms.
15-30 mm.	Very shallow water (usually less than 5 cm and frequently less than 2 cm deep) at extreme margin of lake, almost invariably over solid rock bottom.
30-45 mm.	Usually in water deeper than 5 cm but less than 0.5 metre, predominantly over solid rock bottom : i.e. in similar situations but further off shore than the smaller specimens; but occasionally in reed beds, either sparse or dense, and (rarely) weed beds.
4.5-8.0 cm.	In a variety of littoral habitats, often similar to those frequented by preceding size group, but in deeper water : frequently in sparse reeds, but also among dense bottom vegetation and on exposed shores.
8.0-17.0 cm.	In a variety of habitats, but predominantly inshore on rather exposed shores. Move around in shoals, probably over considerable distances.
17.0-20.0 cm.	As previous size group but with tendency to show less marked shoaling behaviour.
20.0-28.0+ cm.	In a variety of habitats, particularly, but by no means exclusively, on exposed shores, but with specific requirements both for spawning (on sandy bottoms) and brooding (on rocky bottoms).

As the fishes change their habitat so do they change their food. As noted in greater detail below, the smallest individuals permanently released by the parent collect food of both plant and animal origin from the rock surfaces over which they live. Older fishes gradually change to the adult diet which, as already known (GRAHAM 1929, FISH 1955), consists almost exclusively of algae of planktonic origin which may be collected either while it is in suspension or after it has settled on the bottom. While it is not denied that at times *T. variabilis* may collect phytoplankton, in the Jinja area at least it appears to be essentially a deposit feeder and collects little food directly from the plankton. This statement is based on the appearance of the food and on the almost invariable presence of sand grains, often in considerable amounts, in the stomach, and which can only have been collected from the bottom and have presumably been taken in inadvertently as the fish collected sedimented algae. This also suggests that, in this area at least, feeding takes place on hard and not soft bottoms, thus giving a further clue to habitat preferences. In the affluent rivers of Lake Victoria, in some of which *T. variabilis* is found, food must be collected from the bottom as there must be little suspended plankton.

THE BROODING GROUNDS AND NURSERIES, AND THE BEHAVIOUR OF VERY YOUNG FISHES

The Brooding grounds and nurseries.

In the Jinja area habitat preferences of the very early stages of *T. variabilis* can be defined with considerable precision. LOWE (MCCONNELL) (1956a) has described the breeding behaviour of this species, which involves the making of a sandscrape nest by the male, at which, after a period of courtship, the eggs of the female are fertilised and taken up into the mouth of the female parent. This behaviour, of necessity, takes place over a suitable substratum — usually sandy. After taking up the eggs the brooding female moves from the breeding ground to a distinct brooding ground. That this takes place shortly after the fertilisation of the eggs is shown by the presence of egg-carrying, as well as young-brooding females on the brooding grounds. Brooding grounds are at times apparently located quite close to breeding grounds, for ripe males in breeding dress and with fully developed genital tassels were captured from time to time at both those most regularly fished. Conditions were such, however, that these suspected breeding grounds could not be seen.

Brooding grounds in the Jinja area are, perhaps always, of a readily defined type. They consist of inshore regions where the shore-line is composed of slabs of flat rock which tilt very gently to the lakeward side. Often such areas are of distinctly limited extent and may have a shore-line length of no more than about 15 metres. Such beaches must, however, be somewhat sheltered. If exposed to the full force of regular wave action they are apparently unsuited to the needs of the young fishes. One such exposed beach, considerably larger than some of those which are regularly frequented by large numbers of juvenile fishes has been searched without revealing a single brood of young. It is in the deeper water, but close inshore, off sheltered beaches of this type that brooding females congregate, and it is here that the young are released.

Whether, as seems most likely, the brooding females swim into as shallow water as possible before finally releasing their broods, or the young move inshore themselves after release, has not been ascertained, but certainly these newly released fishes congregate in the very shallowest water at the extreme margin of the lake. Such areas can conveniently be termed nurseries. These nurseries must be among the most stable of the littoral habitats of Lake Victoria inasmuch as they are not greatly, and only temporarily, affected by lake-level fluctuations. Bare rock slabs often extend for considerable distances both above and below the water-line, and even when a thin layer of soil covers the exposed parts a persistent rise in lake-level would soon result in its removal.

Steeply sloping rocky shores are apparently unsuitable as nurseries, presumably because of the lack of very shallow water at the extreme margin. Although such beaches sometimes occur in close proximity to nurseries where young *T. variabilis* are abundant, they themselves are completely deserted.

Nurseries of this type offer several advantages to the young fishes. Because of the extreme shallowness of the marginal waters predacious fishes are unable to enter the domain of the young *T. variabilis* and the same factor will also prevent the pied kingfisher [*Ceryle rudis rudis* (L.)] which feeds on small fishes, from feeding there. This bird, which is very common on the lake shore, feeds by hovering until it sights its prey then plummeting almost vertically downwards into the water. Such behaviour is inhibited by water only a few centimetres deep. Virtual freedom from predators is therefore ensured during the very early stages of independent existence. The only evidence of predation on these early stages obtained is a single observation of a malachite crested kingfisher [*Corythornis cristata cristata* (PALL.)], which feeds by skimming fishes from near the surface, systematically taking small fishes, presumed to be *T. variabilis,* from a nursery. In addition, one buff-backed heron was seen wading in a nursery but what it was collecting could not be ascertained. One reason why more steeply shelving rocky shores are not utilised as nurseries may be because no such protection from predators is afforded.

Another advantage of such habitats is that the young fishes live over a carpet of food (see below). No such carpet is provided by sandy shores of similar configuration and, although such beaches are not common in the Jinja area, those which do occur are not utilised as nurseries by *T. variabilis.* A single brood, believed to be *T. variabilis,* was seen on such a beach in the early part of the investigation but is so unusual that I now suspect that it may have been a brood of the introduced *T. zillii* GERVAIS which was at that time just beginning to establish itself in the area.

While some evidence of mortality in the nurseries has been obtained, all available information indicates that it is extremely low, and losses during this period of development are probably much lower than in most other fishes. Possible losses sustained during the brooding period are mentioned on p. 18.

Behaviour of the very young fishes.

During early larval life respiration is probably in part cutaneous. The tail region has a rich blood supply and the integument is thin. Such respiration would be advantageous in the cramped environment frequented at this stage.

Feeding commences before the young fishes leave the parental mouth for the last time, and before the yolk sac is completely absorbed. Examination of the gut contents of fishes still being brooded by the mother revealed that these feed selectively and ingest planktonic organisms among which the diatom *Melosira* usually predominates. Other algae, such as *Pediastrum,* are also eaten, and so to a much smaller extent are cyclopoid copepods.

It is now well known that fishes, including *Tilapia* spp., often ingest algae which they are incapable of digesting (VELASQUEZ 1939; LOWE 1952; FISH 1950, 1955; VAAS and HOFSTEDE 1952) etc., but diatoms are apparently invariably digested by adult fishes. In the case of very young *T. variabilis,* however, even diatoms are not always digested for specimens of *Melosira* whose contents were quite green have been seen in the rectal region.

The size at which the young fishes are released from the parent's mouth is somewhat variable. Specimens only 14.5 mm in length have been collected in the nurseries, while others as long as 17.5 mm have been found in the mouth of a brooding female.

After leaving the parental mouth the behaviour of the young fishes changes. At first they occur in the most inshore waters of the nurseries where the depth of water is often less than 2 cm. The members of a brood remain in a distinct shoal, in this way differing from certain other cichlids in which the shoaling instinct breaks down when the parent/young relationship ceases. Populations of these small fishes are sometimes extremely dense, many shoals occuring in quite small nurseries.

On arrival in the nurseries the young fishes terminate the very brief period during which they feed on plankton and begin to feed largely on bottom material. This, as revealed by the examination of numerous gut contents, consists largely of the algae which grows on the rock surface, but includes also a certain amount of animal matter, particularly minute chironomid larvae, rotifers, and occasional chydorid cladocerans, collected from the same source. A few individuals contain quantities of planktonic algae and occasionally cyclopoid and diaptomid copepods. The algae could either be taken while in suspension or after settling on the bottom, and it is suspected that the diaptomid copepods may have been individuals driven inshore by waves as this is not their typical habitat. However, the amount of food derived from the plankton is negligible. Members of a shoal can always be seen actively browsing on the bottom.

Among the organisms ingested are certain bdelloid rotifers. These contract and are able to resist the action of the digestive juices of the fish and pass out with the faeces alive. Many living specimens have been seen to emerge and move away from faecal ribbons produced by fishes up to 7 cm in length.

An important feature of the shallowest waters of the nurseries is that, until the recent introduction of *T. zillii* (dealt with below), the early stages of *T. variabilis* occured there alone. No other indigenous fish has apparently exploided this niche. In the somewhat deeper water frequented as they increase in size, other species are encountered, particularly species of *Haplochromis,* but their numbers in the vicinity of the nurseries are small in comparison with those of *T. variabilis.*

DISPERSAL

As the young fishes increase in size they gradually move into deeper water, thus vacating their original habitat for incoming young. They remain in the nurseries until they are about 6 to 8 cm in length and then disperse to other habitats.

Individuals from about 8 to 17 cm in length move around in large shoals. From time to time such shoals were caught during seining operations at the brooding grounds, presumably as they were passing those regions, and they have also been encountered on sandy beaches. LOWE (MCCONNELL) (1956) also met with such shoals.

Circumstantial evidence that these shoals remain together was obtained. A group of African seine netters operating on a sandy beach apparently encountered a shoal of *T. variabilis* which included several marked fishes (20 to 25 was the estimated number), Unfortunately, as a result of some dispute, no tags were returned! As it seems extremely unlikely that so many fishes could be caught together had they been marked at different times, the chances are high that the shoal was one or other of the two of which a considerable number had been marked five miles away 6 and 8 months previously.

After shedding their young the former brooding females also disperse. Some information on the movements of these fishes has been obtained from marking experiments. Fishes captured by seine netting were marked by means of the small plastic tags described by VAN SOMEREN and WHITEHEAD (1959). Preliminary results of marking experiments carried out by the Lake Victoria Fisheries Service had already shown that individuals of this species may at times move over considerable distances (LOWE (MCCONNELL) 1956). Further data have now been obtained.

While fishes leaving the brooding grounds in the Jinja area have been found to travel for distances of more than 60 miles, most disperse over an area which is relatively small in comparison with the size of the lake, and returns of marked fish offer little evidence of a regular pattern of movement (Fig. 1). Most recaptures have been made within 15 miles of the point of release and in most cases the distance was less than 5 miles. Although this may in part reflect the activities of the local fishermen and a lack of knowledge of the reward system by those living further afield, it seems probable that the pattern of dispersal shown in the figure does correspond to a large extent with the main area of dispersal. Thus no fish, marked in the Kisumu area to the East, where marking has gone on for several years, nor from the Entebbe area to the West where other specimens of the species have been marked, have been found in the Jinja area and only one Jinja-marked fish has been caught near Entebbe and none near Kisumu. This, coupled with the evidence of homing given below, points to the existence of relatively localised populations.

That individual fishes leaving the brooding grounds may very quickly leave the area is shown by the capture near Entebbe 28 days after marking of a fish which must have covered at least 60 miles at a rate exceeding 2 miles/day. Other fishes, however, have been found to move much smaller distances from the brooding grounds in comparable periods.

Cases indicating either prolonged association or re-encounter after a long interval have been recorded. A brooding female and a ripe male

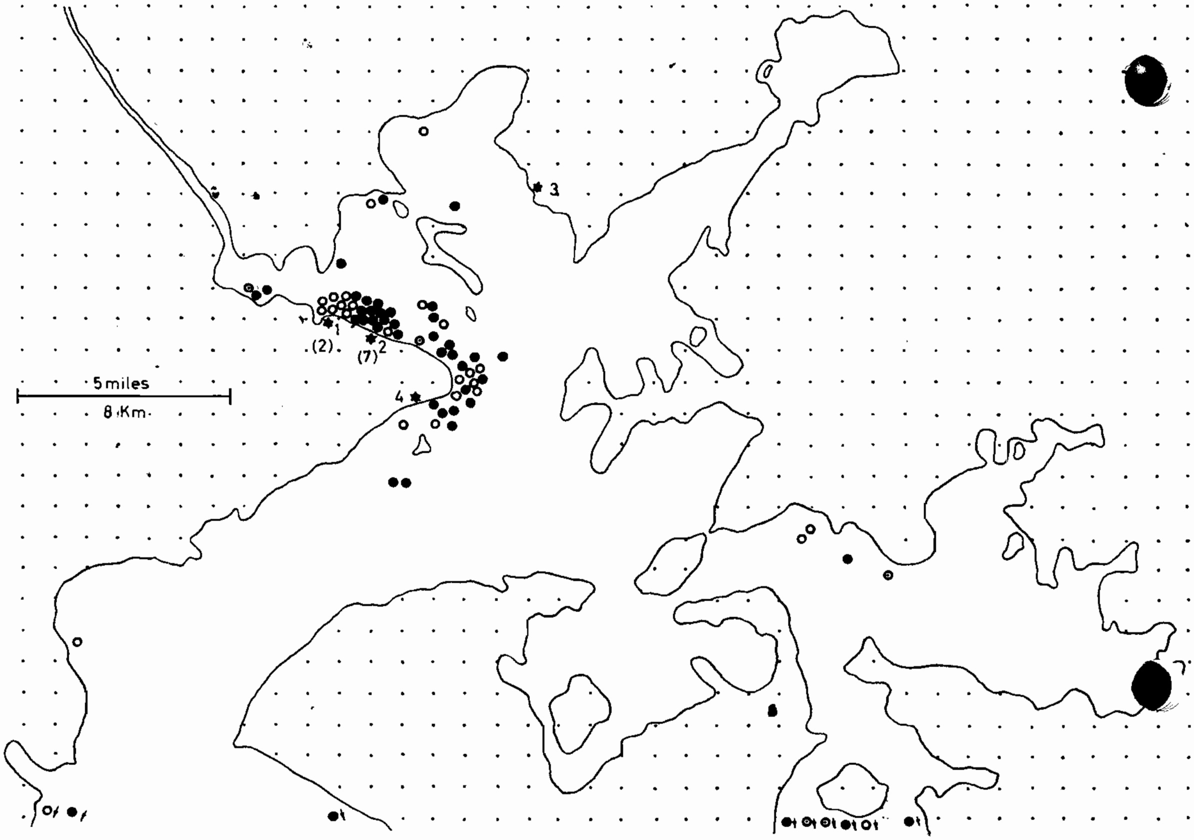

Fig. 1. - Dispersal patterns of *T. variabilis* in the Jinja area. Fishes were marked at stations 1 to 4 and recaptured at the points shown. Arrowed circles indicate recaptures made outside the area covered by the map. Numbers in brackets at stations 1 and 2 indicate fishes marked and recaptured there and which are not indicated by circles. Symbols : O :- marked at station 1. ● :- marked at station 2. ◐ :- marked at station 3. ⊙ :- marked at station 4 which is not a brooding ground.

marked together at a brooding ground were recaptured together at the same place 232 days later. More significantly, two females marked together were caught together in a single fleet of nets some five miles away 255 days later. Non-breeding adult males may also associate together, for Mr D. J. Garrod informs me that he has evidence from commercial catches that almost monosex male shoals with quiet gonads are to be encountered at certain times.

HOMING

Definite evidence of homing behaviour in connexion with breeding activities has been obtained in the Jinja area. The two brooding grounds at which most fishes were marked were very restricted in size. Considering the area over which these fishes were shown to disperse, the chances of recapturing one on the same beach would be extremely remote unless homing took place. In fact seven fishes were recaptured at one beach and two at the other after intervals of from 73 to 395 days, and eight fishes were recaptured, within or extremely close to the area covered by the seine net at the first beach, by fishermen who took to setting their gill nets there. These latter fishes had been free for periods ranging from 45 to 805 days. The sexual condition of these fishes was often such as to indicate that they had returned to brood young in the same restricted area as that in which they had previously done so, and three cases concern females carrying young on both occasions.

This is apparently the first recorded case of homing in the family Cichlidae and is an addition to the short list (nine species) given by Gerking (1959) of lake and pond fishes in which this phenomenon is known. The distances involved, incidentally, are considerably greater than those in several of the previously recorded cases.

A number of individuals of *T. variabilis* have also been recaptured at Kisumu by members of the Lake Victoria Fisheries Service on the beach at which they were marked, but unfortunately the sexual condition of these fishes was seldom recorded so in these cases it is not known whether homing was connected with breeding activities.

ECOLOGICAL RELATIONSHIPS WITH OTHER SPECIES OF *TILAPIA*

Apart from *T. variabilis* only *T. esculenta* is indigenous to Lake Victoria. However, several other species of the genus have recently been introduced into the lake, and of these *T. zillii* Gervais is now well established. The ecological relationships of *T. variabilis* to *T. esculenta* and *T. zillii* are considered in this section.

T. variabilis and *T. esculenta.*

As might be expected of two old established species which have evolved in the same lake *T. variabilis* and *T. esculenta* show marked ecological differences at certain periods of their lives. As GRAHAM (1929) and LOWE (MCCONNELL) (1956) have already pointed out, *T. esculenta* predominates in gulfs and bays with soft bottoms and which are rich in phytoplankton, while *T. variabilis* is more frequently encountered on exposed shores. Non-breeding adults of both species are, however, regularly taken together in commercial catches and, on some beaches in Kenya, brooding females of *T. variabilis* can apparently be caught with adults of *T. esculenta* (L. V. F. S. 1953). From results obtained in the Jinja area it is suspected that the reason for this is that the seine net used was one of the very large type which can be used in the Kavirondo Gulf, and which enclosed a large area, only part of which was a brooding ground of *T. variabilis.* Very sharp ecological separation at times of breeding prevails in the Jinja area. Here the brooding grounds frequented by *T. variabilis* appear to be the exclusive province of this species (*T. zillii* being for the moment ignored) and, during the whole of the period of investigation, no specimen of *T. esculenta* was ever taken in such a situation, even though, as shown both by catches made in experimentally set gill nets and by fishermen, this species was quite plentiful in the immediate vicinity. Similar separation probably occurs also on breeding grounds for, while nests of *T. variabilis* are now well known, the exact breeding sites of *T. esculenta* remain undiscovered.

The ecological separation of these two species was also found to be very clear cut in the earliest stages of existence for, while tens of thousands of juvenile *T. variabilis* have been seen in the nurseries, no specimen of *T. esculenta* was ever seen there. LOWE (MCCONNELL) (1956) however, records young *T. variabilis* « 1-6 cm long » in swamp channels at the margin of the lake in company with more numerous individuals of young *T. esculenta.* While this indicates that separation may not always be so definite as the present study indicates, it appears that LOWE's fishes were usually more than 2.5 cm long, by which time some dispersal from the nurseries could have taken place.

These two species often differ strikingly in their relative abundance in commercial catches at different seasons, a feature which has become much more apparent since the introduction of 4½ in. mesh gill nets which collect adequate samples of *T. variabilis.* Sometimes, particularly in June and July, a decline in the landings of *T. esculenta* (which predominates in most areas), is accompanied by a marked increase in the landings of *T. variabilis.* While this may partially reflect changes in the habits of the fishermen it is also suggestive of either temporary ecological replacement or reciprocal changes in the activity of the two species. The figures from different landings however give such a confused picture that the most that can be said is that from time to time and over periods of several weeks the behaviour of the two species differs sufficiently to influence, often markedly, their relative abundance in commercial catches in any given area.

T. variabilis and *T. zillii.*

Adults of *T. zillii* feed on higher plants and therefore do not compete for food with the microphagous *T. variabilis.* The two species do, however, make similar claims for certain environmental resources. When the present investigation began late in 1957 the nurseries of *T. variabilis* were tenanted only by this member of the genus. However, early in 1959, young specimens of *T. zillii,* adults of which first began to appear in gill net catches in the area in mid 1958, began to appear there, and by the end of April juveniles were quite plentiful in the very shallow water at the margin where they accompanied *T. variabilis* of similar size. From then on these two species shared this environment and behaved in a similar manner in that the smallest individuals occurred in the shallowest marginal waters while larger specimens frequented deeper water, there being, in general, an obvious, though unmeasured, correlation between fish size and water depth. On several occasions, however, specimens of *T. zillii* considerably larger than any of the *T. variabilis* found under such circumstances, were seen in very shallow water near the margin. *T. zillii* became so plentiful in the nurseries that, during the periods in 1959 when *T. variabilis* was present only in small numbers (see p. 14) visual examination and captures with a mosquito-gauze seine net suggested that it was the most abundant species. Its presence did not, however, prevent the influx of large numbers of *T. variabilis* later.

Unlike the adults, small individuals of both species feed to a large extent on the same kind of food, and in fact the gut contents of some of the smallest specimens of *T. zillii* are indistinguishable from those of *T. variabilis* of similar size. At this stage of development members of both species can be seen browsing on the bottom in a very similar manner. While this great similarity should not be minimised there are sometimes differences in the food taken, particularly in specimens above about 3 cm in length. Such individuals of *T. zillii,* besides taking the bottom algae and its associated fauna, which constitutes the major part of the food, also collect recognisable fragments of higher plants which often accumulate as debris along the water line as a result of wave action. Such food is not taken by *T. variabilis.* Sometimes too the gut contents of specimens of *T. zillii* as small as 3 cm in length differ from those of *T. variabilis* of similar size by the inclusion of detritus, which gives the gut contents a « coarser » texture than those of *T. variabilis.* Whether this is a true difference or merely means that the fine pharyngeal dentition of *T. variabilis* enables it to grind such detritus into fine unrecognisable particles in a way not possible to the coarser toothed *T. zillii* is not certain. As not all guts of *T. zillii* of this size have this appearance, however, the indications are that it is a true difference.

This means that, from a very early age, *T. zillii* utilises the same food as *T. variabilis,* but is less rigorously restricted to one food source than is that species. Under conditions of food scarcity in very shallow water such as may well occur during periods when the lake is rising rapidly and large areas of bare rock are inundated, *T. zillii,* by its ability to feed on detritus and fragments of higher plants, may well be at an advantage. Again, pools of water only two or three centimetres deep sometimes form at the lake margin in hollows in the rock. In these the type of food which *T. zillii* is able to utilise often accumulates, and when these pools are connected to the lake *T. zillii* is more plentiful in them than is *T. variabilis,* particularly if the detritus is thick, and the pool is turbid. On one occasion too a rise in lake level flooded some marginal vegetation. This was colonised by specimens of *T. zillii* up to about 9 cm in length while the individuals of *T. variabilis* which entered these areas were much smaller. On one occasion some young specimens of *T. zillii* were seen feeding on a dead juvenile of *T. variabilis.* This habit could conceivably be of value in times of food scarcity.

T. zillii may also be at an advantage if and when competition in its most literal sense takes place. Aquarium observations show why this is so. *T. zillii* may be more aggressive than *T. variabilis* but the observations, made on a tank containing young of both species, were insufficiently critical to demonstrate this conclusively. What did become apparent, however, was that a hierarchy based on size was set up and that larger fishes (in this case *T. zillii*) tended very definitely to monopolise the available food (in this case chopped worms dropped into one part of the tank) and to drive off smaller fishes irrespective of species. In nature, therefore, the specimens of *T. zillii* which not infrequently co-exist in shallow water with smaller specimens of *T. variabilis,* will be at a marked advantage if there is a definite scramble for food.

Another important point is that *T. zillii* has a much greater fecundity than *T. variabilis.* In most habitats heavy losses of young are to be expected in non-mouth-brooding fishes but, by colonising the nurseries of *T. variabilis,* the young *T. zillii* have exploited what is perhaps the safest habitat in the lake for juvenile fishes and therefore enjoy all the advantages of great fecundity and, in this habitat, few of its disadvantages. This greater fecundity may well be advantageous to *T. zillii* in any competition with *T. variabilis.* A comparable case concerns the British freshwater amphipods among which, of three species with very similar ecological requirements, *Gammarus pulex* (L) has a greater biotic potential than either *G. duebeni* LILLJEBORG or *G. lacustris* SARS, a fact which led HYNES (1955) to suggest that this « accounts at least in part for its ecological dominance » over the other two species, one at least of which in fact it may well have ousted from certain areas (HYNES 1954).

It seems, therefore, that in the juvenile stage of development *T. zillii* is likely to become a serious competitor of *T. variabilis* and possibly even a serious threat to its survival.

Competition among adults on the brooding grounds is also a possibility. The first adult of *T. zillii* to be captured on a brooding ground of *T. variabilis* was taken in May 1959, and since that time several specimens have been taken at both the best sampled brooding grounds, but as yet they comprise but a small proportion of the catch. There is little vegetation on the brooding grounds so there is little likelihood of *T. zillii* being attracted to them as feeding grounds, but the bare rock may well provide suitable conditions for the attachment of eggs and it is not inconceivable that this species may begin to use them as breeding grounds. It may or may not be significant that some of the adults caught in these areas were ripe females.

Of competition in other habitats there is as yet little evidence, but certainly *T. zillii* is increasing at a great rate and is now common in habitats formerly dominated by *T. variabilis.* At the Masese landing, near Jinja, the number of *T. zillii* brought in by fishermen has gradually increased and in some months, when catches of *T. variabilis* were low, the number of *T. zillii* caught has totalled as much as 34 % of the number of *T. variabilis.* In one habitat off some weed beds in the Napoleon Gulf where *T. variabilis* was always more abundant than *T. esculenta,* seven settings of gill nets by Mr H. Y. ELDER in January and February 1960 produced 77 *T. zillii,* 52 *T. variabilis,* and 18 *T. escu-*

lenta, indicating the colonisation by *T. zillii* of a former stronghold of *T. variabilis.*

In its competitive relationship to *T. variabilis, T. zillii* may be assisted by its more rapid growth rate which, by reducing the period necessary to achieve sexual maturity, certainly increases its relative fecundity, but other implications of this biological difference are not yet understood.

BREEDING FREQUENCY AND SEASONAL CHANGES IN BREEDING INTENSITY

Breeding takes place throughout the year but its intensity varies. The gonadial condition of fishes caught commercially is not a good guide to temporal changes in reproductive activity as brooding individuals segregate and the composition of catches is therefore markedly in-

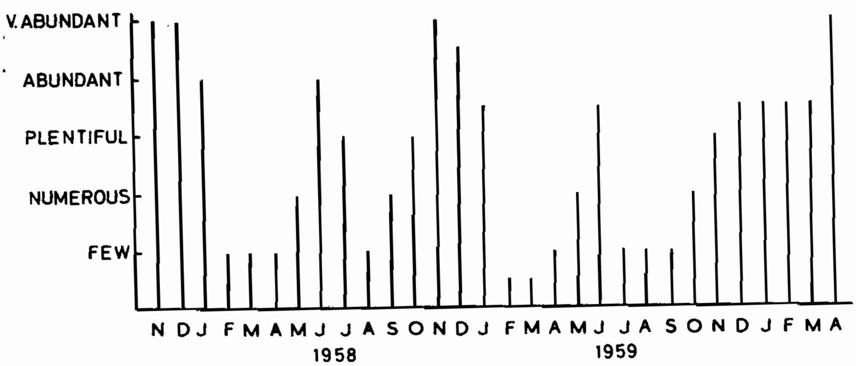

Fig. 2. - Seasonal changes in abundance of young fishes in the nurseries. For comments see text.

fluenced by the site in which nets are set. The changing pattern can, however, be followed at the brooding grounds and nurseries. Because it was difficult to pull a seine net at the brooding grounds most regularly sampled (snags being frequent) a comparison of catches from visit to visit is not valid, and the best guide is undoubtedly the changing density of the shoals of small fishes in the nurseries. Even here strictly quantitative data are almost impossible to obtain as to count the constantly moving shoals of young is virtually impossible. Nevertheless one can get an overall impression. Such is shown in fig. 2 which is *not* based on counts and which is only a substitute for an equally imprecise statement in words. The pattern is somewhat irregular. Events from November 1957 to about October 1959 did follow a rough pattern with a peak of reproductive activity around November and December, a smaller peak around July, and relatively little activity from February to April and around August, but although numbers increased towards the end of 1959 they did not achieve the density found in November-December of the two previous years, nor did they diminish after about February. In fact they maintained their fairly high concentration until March and then became greatly abundant in April after which observations had to be discontinued. No apparent correlation exists between these changes in breeding intensity and the seasonal variation in catch per net of fishermen operating in the same vicinity, nor is there any apparent correlation between rainfall and breeding intensity, though in several species of *Tilapia,* including *T. esculenta* in L. Victoria (GARROD 1959), rain appears to act a stimulus to reproductive activities.

Marking experiments have yielded information on breeding frequency. Of the females marked at the brooding ground one can recognise those which are brooding eggs or young, and also those which have just released a brood. These latter are readily and unmistakably recognisable by the enlarged mouth whose floor is depressed by an outward bulging of the hyoid apparatus and attached tissues, a condition which persists for at least a few days after release of the brood. In this region is quite frequently a sore patch, resulting apparently from a scraping of the « chin » on the bottom. This suggests that, during brooding, the females tend to keep near the bottom. By relating the gonadial condition of recaptured females to this known state it is possible to obtain some information about breeding frequency. Of brooding or recently brooded females marked, 23 have so far been recaptured in a fit condition to yield information. So little is known of the periodicity of breeding of these economically important cichlids of equatorial lakes that this information is worth recording in full as is done in fig. 3 where information relating to 4 males is also recorded.

While no well defined pattern emerged, certain interesting facts are revealed. The minimum period recorded between broods is 131 days (fish no. 6) and a very similar period is indicated for no. 15. Eggs in the ovaries of fish no. 6 were already beginning to ripen in readiness for the production of the next brood, indicating that at least three broods can follow in succession. Unfortunately it is not proven that 130 days or thereabouts in the *minimum* period between broods, though this may be the case, and it does seem improbable that more than one brood could have intervened between those carried at marking and recapture. Should the latter conditions hold then a period of 60 to 65 days is indicated as necessary to produce a brood. Similar or even shorter periods have been recorded between broods in mouth-brooding species of

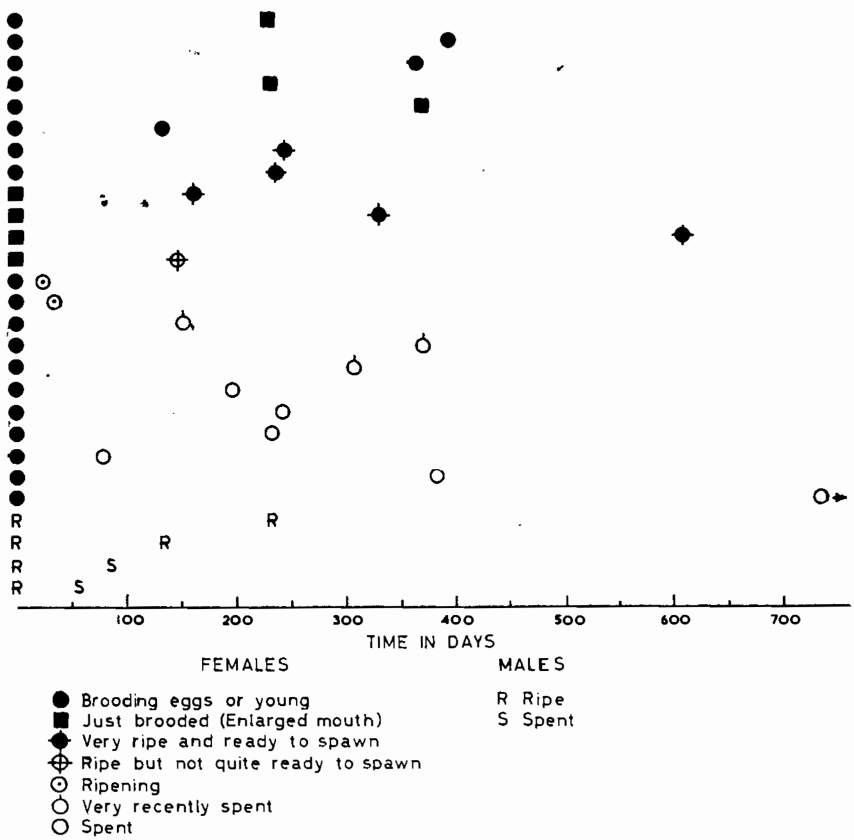

Fig. 3. - The sexual condition of individuals of *T. variabilis* marked when brooding or just after brooding (females) or ripe (males) and subsequently recaptured after different intervals of time. The condition at marking is shown on the extreme left.

Tilapia [not less than two months in *T. esculenta* (personal information from Mr C. C. CRIDLAND) : 30-40 days in *T. mossambica* PETERS (VAAS and VAN HOFSTEDE 1952)] but these records refer to aquarium or pond kept fishes whose metabolism often differs strikingly from that obtaining in fishes in nature, and in fact in both the cases cited the fishes concerned were markedly stunted. *T. variabilis* itself behaves very strangely in ponds where it begins to breed at a very small size and when less than 7 months old (LOWE 1955).

In nature the energy required to produce a brood of eggs is considerable, and involves a period of probably not less than three weeks starvation. The gonad weight has to be built up from as little as about 0.6 % of the total weight in « spent starting » females, with which we are here concerned (less in « spent quiet » fishes), to at least 2 %. (The percentage weight of very ripe gonads varies very considerably from fish to fish, the range recorded being from 1.97 to 4.62 %, most being between 3 and 4 %. The heaviest ovaries noticed weighed 11.5 gm, this being some 3.93 % of the total weight of a 23.7 cm fish).

If a brood can be produced in rather less than 130 days, then fishes nos. 1 and 4 may well have just produced their second brood since marking and no. 5 its third successive brood. Even if about 130 days are required to produce a brood then fishes nos. 7 and 8 were probably about to produce their second brood, nos. 2 and 3 could have been brooding for the third time since marking, and no. 16 could have just done so. The evidence indicates that *T. variabilis* is at least capable of producing three (and conceivably five) broods within the space of 8 months. The very slow growth of mature fishes (see below) suggests that, after reaching sexual maturity, these fishes devote much of their energy to breeding so, allowing for periods of rest, of whose existence sexually inactive adults testify, the production of three (or five) broods per year seems not at all improbable.

BROOD SIZE

To estimate true fecundity it is essential to know the number of young produced per brood. This is difficult to ascertain as brooding females usually discharge at least some eggs or young during capture. Also it was not deemed desirable to sacrifice many brooding females during the marking experiments. In fact only two of the fishes obtained can be regarded as absolutely reliable as indicators of brood size. One, with a total length of 25.1 cm carried 513 eggs. Probably very few eggs had been lost and the mouth appeared crammed to capacity. (The fact that the maximum number of eggs found in the mouth of this species by LOWE (MCCONNELL) (1955) — in a 25 cm fish as it happens — was 286, indicates how readily these are lost when the fish is disturbed). This number, when compared with the counts of ovarian eggs given by LOWE

(McCONNELL) (1955), suggests that most of those produced can be safely gathered into the mouth. That losses take place during brooding is indicated by the reliable record of 228 advanced young in the closed mouth of a 25.5 cm female.

The number of young per brood probably varies somewhat with the size of the adult, but as a first approximation 200 per brood successfully reared to the time of release seems a reasonable estimate.

As to conditions within the parental mouth, although SHAW and ARONSON (1954) went to considerable trouble to test the importance of ionic and osmotic factors involved and the bactericidal and fungicidal properties of the mouth of *T. macrocephala* (BLEEKER), as well as the importance of mechanical churning, no difficulty was experienced in rearing eggs of *T. variabilis* placed in a beaker under a running tap.

LENGTH FREQUENCY OF BREEDING FEMALES AND ITS RELATIONSHIP TO COMMERCIAL CATCHES

The size distribution of brooding females captured at the brooding grounds gives useful information about the size at which *T. variabilis* become sexually mature and on the composition of the population of breeding females. The smallest fishes recorded brooding were two which were 18.5 and 18.7 cm in length, but such precocious individuals are definitely rare and in general breeding does not commence until the female has reached a length of at least 20 cm. With the two exceptions mentioned the next smallest brooding females were all over 20 cm in length.

Fig. 4 shows the length frequency of the 373 brooding or just brooded females caught by non-selective gear (a seine net) on the brooding grounds, and reveals clearly that the majority (more than 63 %) have a length of between 23.0 and 25.4 cm. This suggests either that some females do not begin to breed until they attain this size or that until they do they breed less frequently. That a smaller proportion of the breeding population is made up by larger fishes may be in part attributed to cropping or other forms of mortality, but is probably indicative of a decline in fertility with increasing age.

The same figure shows also the length frequency distribution of a sample of 1122 specimens of *T. variabilis* caught in the usually employed commercial gear (gill nets almost exclusively of 4½ inch mesh) in March 1959. One reason why this curve is pushed to the right in comparison with that for breeding females is that when the sample was taken the population of *T. variabilis* in the Jinja area included a preponderance of males among the larger fishes (see below). Also the population structure at that time was such that more large fishes were available than will be the case when 4½ inch mesh nets have been used for some time. Again this is a catch curve and not a true retention curve, but BEVERTON's (1959) calculations showed that the retention range of *T. variabilis* is about a centimetre lower than that of *T. esculenta* in gill

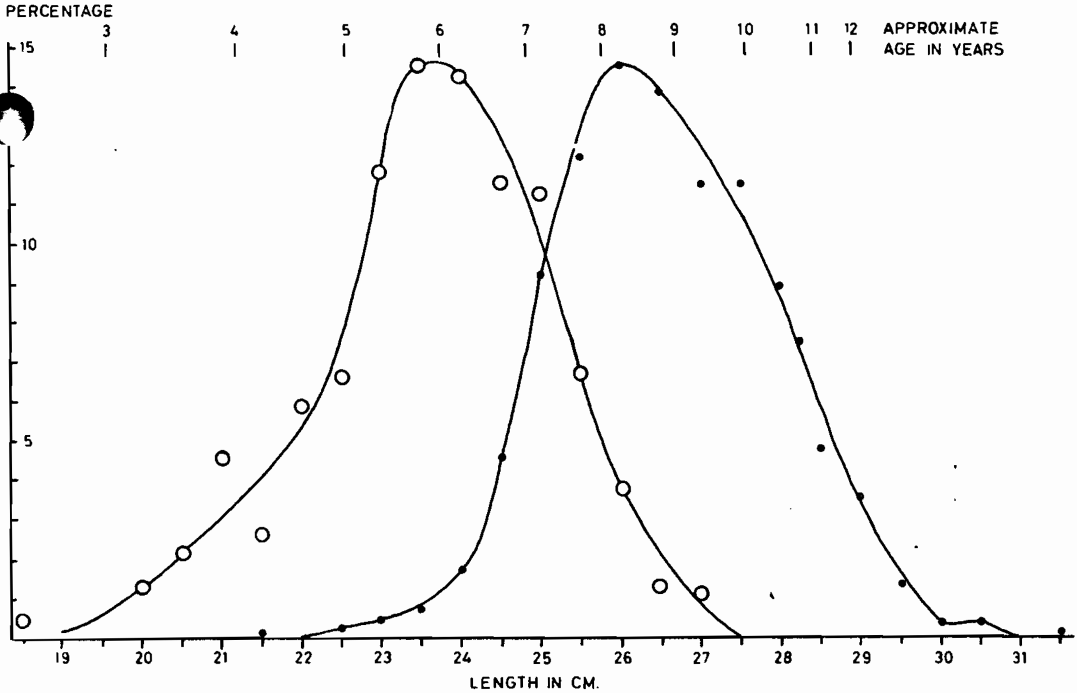

Fig. 4. - Length frequency of 373 brooding or just-brooded females of *T. variabilis* caught by non-selective gear at brooding grounds (open circles), and of 1122 specimens from commercial catches (solid circles).

nets of any given mesh, which means that the peak length for 4½ inch nets is about 27.5 cm. It is therefore apparent that breeding females below about 24 cm. in length are cropped to only a small extent in the gill nets currently employed by African fishermen. The significance of this is mentioned in a subsequent section.

POPULATION STRUCTURE IN RELATION TO SEX AND SIZE

The sex ratio of specimens of *T. variabilis* caught in gill nets varies considerably according to the size of the fishes concerned. This is shown in table 1 which is prepared from information collected during routine sampling by the East African Fisheries Research Organisation during 1956-58.

While movements of females to breeding and brooding grounds are likely to influence these figures this may be partially offset by similar movements of ripe males to breeding grounds, and the figures probably give a reasonably accurate picture of the sex ratio of different segments of the population. Males preponderate in all size groups sampled, i.e. from about 22 cm upwards, and the proportion of males increases as the average length of the fishes in the sample increases.

Mesh size (inches)	Total number of fishes	No. of males	No. of females	Percentage of males
4	1630	1042	588	64
4½	272	204	68	75
5	57	45	12	79

Table 1. - Sex ratios of *T. variabilis* according to size (1956-58) as shown by gill net catches.

As until recently the population of *T. variabilis* has been relatively unfished in the Jinja area this may indicate that males grow faster than females and certainly indicates that they attain a larger size. With one or both of these two factors operating an accumulation of males should build up at the upper end of the length range and males should therefore be better represented than females in catches made with the larger meshed gill nets. This being so population structure with regard to sex may be expected to change in the future as a result of exploitation, and this may have unpredictable repercussions; though as one male can fertilise the eggs of several females (LOWE (McCONNELL) 1956a) the results are likely to be a diminution of intraspecific sexual selection and its possible consequences, rather than an actual shortage of males.

GROWTH RATE

Difficulties attendant on the estimation of growth rates of tropical fishes are well known and stem largely from the fact that seasonal climatic changes are ill defined. Thus « annual rings » are not, as a rule, laid down on scales, otoliths or other structures. This difficulty is particularly acute in Lake Victoria which stradles the equator and in which seasonal changes are very small. Ill-defined marks on the scales of *T. variabilis,* termed « rings » by Holden (1955) are most prevalent in mature fishes but also occur in small specimens and can obviously result from one or more of several causes. Even if they represent « spawning marks » which result from a period of breeding they are valueless as indices of growth, partly because it is not known whether breeding frequency is constant in all individuals (and the indications are that it is not), but mainly because *T. variabilis* grows extremely slowly after achieving sexual maturity (see below). In fact, to quote one case, a marked fish which had been absent for more than two years, during which it could have bred several times, had not grown at all. Obviously this fish could leave no record on its scales of any breeding which may have taken place during this period as the scales had not increased in size.

Information on growth rate has, however, been obtained from marked fishes. Early experiments carried out by the Lake Victoria Fisheries Service using clip-on opercular tags indicated that *T. variabilis* grew very slowly. These results were, however, suspect because of damage caused by the tags. More recently, experiments employing small plastic tags attached by silver wire to the dorsal musculature of the fish have been carried out both by the L.V.F.S. and the writer. These tags have no effect on the growth rate or survival of fishes more than 13 cm in length (van Someren and Whitehead, 1961). Unfortunately the fishes dealt with by the L. V. F. S. were measured only to the nearest quarter of a centimetre which means that, because growth is often very slow, only fishes which have been free for long periods are of much value in assessing growth rate. Nevertheless, from the considerable number of returns of such fishes marked in the Kisumu area it has been possible to select 140 which had been free for a minimum period of 60 days (the greater majority for over one hundred days and the longest for 784 days) and which were in a suitable condition to yield information. To these were added 67 marked in the Jinja area and for which accurate data were available. These were put into length groups and the average time taken to grow 1 cm. was calculated in each case. From this the slope of six different parts of the growth curve was obtained, and a graph drawn in. Refinements such as differential growth rates of the sexes or of fishes in different areas have had to be ignored at this stage, though there was a suggestion from the figures that growth was more rapid in the Kisumu area (Kavirondo Gulf) than near Jinja. The result, which is no more than a crude first approximation, is shown in fig. 5. The slope of the graph has been continued below the 12 cm. level and indicates that *T. variabilis* will attain this length at an age of about one year, which seems reasonable.

T. variabilis grows very slowly, particularly after maturity. Some individuals in fact appear to cease growth for long periods and even cases

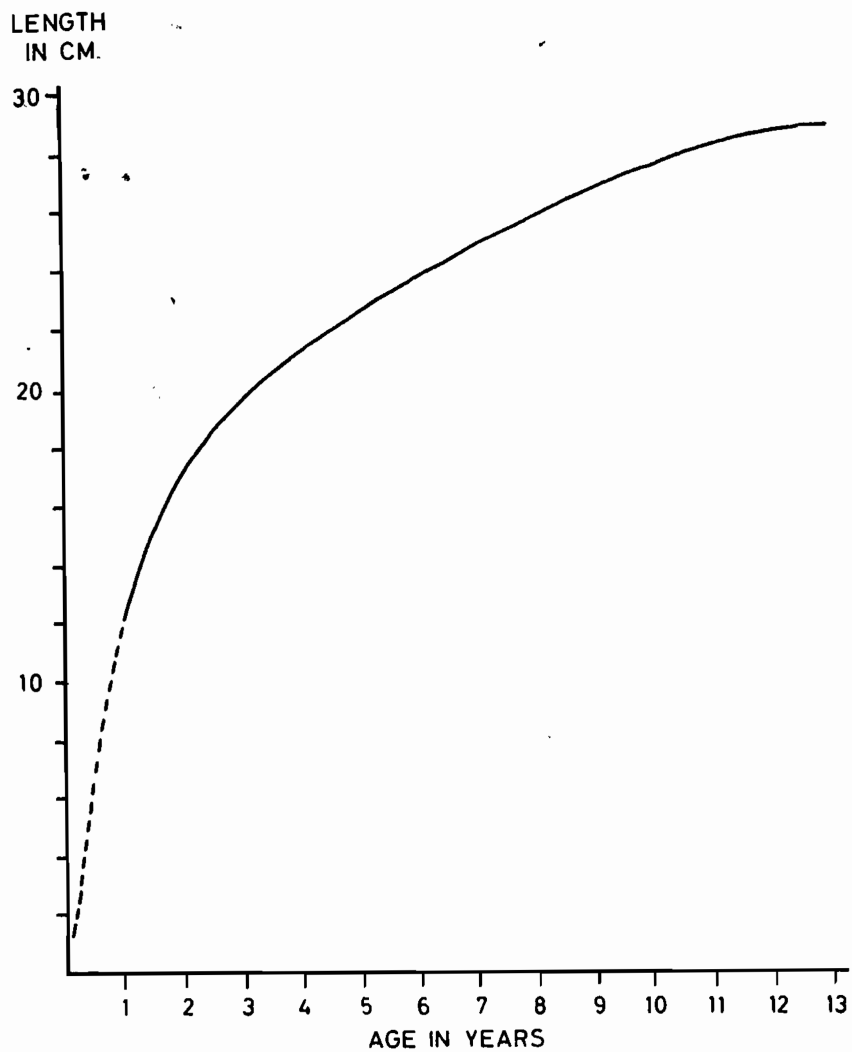

Fig. 5. - The growth rate of *T. variabilis*.

of shrinkage are recorded. A striking example of slow growth in the Jinja area was a female 23.3 cm in length when marked, and which was exactly the same length when recaptured after 805 days. Of shrinkage several cases were recorded in the L. V. F. S. records but these are suspect because of the none too accurate methods of measurement employed, but two cases, involving decreases in length of 1 mm and 3 mm were recorded at Jinja. The former is too small to be of significance but the latter (in 369 days) does indicate that shrinkage can take place in this species in nature.

IMPLICATIONS OF SLOW GROWTH

That *T. variabilis* grows slowly has practical and biological implications. Exceptionally precocious females may begin to breed when about 2½ years old but only a small proportion of the breeding stock of females is made up of fishes less than 4 years old and those comprising its bulk are from 4½ to 7½ years old. Almost all the fishes caught commercially are 7 or more years old. At present an accumulated stock is being fished, for 4½ inch mesh gill nets (the most commonly used gear) only came into general usage in 1956, before which *T. variabilis* was scarcely fished in the Jinja area. With intensive fishing this stock will eventually be depleted, and the process is in fact already in progress. This depletion is in itself not unduly alarming for the fishes removed comprise but a small proportion of the breeding stock and it is apparent that many of them would never reach a size at which they could be caught in 5 inch mesh gill nets and would therefore be largely wasted from the point of view of human food if not caught. After depletion, however, recruitment of catchable individuals will be slow. This is discussed further in the final section of this paper.

Such slow growth as is shown in *T. variabilis* is surprising in a tropical fish which can grow throughout the year. It is slower than that of its associate *T. esculenta* (Garrod 1959, L. V. F. S. 1958, 1959) and apparently very much slower than the introduced *T. zillii, T. nilotica* (L) and *T. leucosticta* Trewavas for which growth data from marked fishes in Lake Victoria are now available (L. V. F. S. 1958, 1959). What is perhaps more remarkable is that *T. variabilis* is potentially capable of more rapid growth than is achieved in nature. In fish ponds individuals introduced when less than 2 cm in length have been recorded as attaining a length of 13 to 19 cm in just under 7 months — at which size they were apparently breeding (Lowe 1955). This is an outstanding example of the widely divergent growth patterns shown by species of *Tilapia* under the influence of different environmental conditions.

It would appear that, after reaching maturity, *T. variabilis* directs its energies to reproduction rather than growth, but the reasons for this are obscure. Reproduction itself which, as shown, may involve the production of at least three successive broods, may be in part responsible. The production of a brood imposes strains other than those associated with the production of eggs or sperm. In the female a period of starvation (when brooding) is involved, and this may apply in part also to males which devote much energy to the construction of a nest and defence of a territory. That these cannot be more than contributory factors, however, is shown by the more rapid growth of other species with similar habits. Looked at another way, the present growth pattern may be advantageous in making but a small demand on the energies of fishes engaged primarily in reproduction, but why a slow growth rate and long life span should be more advantageous in this respect than a more rapid growth rate and a shorter life span is obscure.

As noted, growth rates may differ somewhat in different areas, and absolute size attained may also vary. In the Jinja area specimens longer than 31 cm are exceptional and very few exceed 30 cm, but specimens at least 38 cm in length are known from the Kenya waters of the lake.

PREDATORS, PARASITES AND OTHER HAZARDS

Man is undoubtedly the most important predator of adults of *T. variabilis*. Losses of adults to other predators appear to be small and doubtless include sickly and slow moving individuals. Depredations of fish-eating birds (GRAHAM 1929, E.A.F.R.O. 1952) are probably very small as are those of crocodiles and otters. CORBET's (1961) extensive data on the food of the non-cichlid fishes of the lake, which include the main predators capable of feeding on *Tilapia,* show that members of this genus are eaten to only a small extent.

Freedom from predation in the very early stages of existence has already been emphasised, but it is not known whether any young are lost to larval-fish-eating species of *Haplochromis* whose food can seldom be specifically identified (GREENWOOD 1959). Apart from this the most vulnerable stage is probably from about 3 to 9 or 10 cm when individuals are sufficiently small to be eaten by predatory species of *Haplochromis,* though data on any such mortality are lacking. Predatory *Haplochromis* spp. are common off the nurseries, but though specimens have been opened on several occasions no evidence of feeding on *T. variabilis* has been obtained.

LOWE (MCCONNELL) (1956) stated that the *Tilapia* species of Lake Victoria are « remarkably free from parasites ». Recent experience has not confirmed this. Even casual examination has revealed the following parasites. Protozoan infections are common. One or more species of *Trichodina* occur ectoparasitically on *T. variabilis* and infection of young in the parent's mouth has been noticed. The habit of brooding young must facilitate transmission of parasites such as this. Sporozoan infections are common. Unidentified microsporidians not infrequently form conspicuous cysts on the fins and other superficial tissues of young

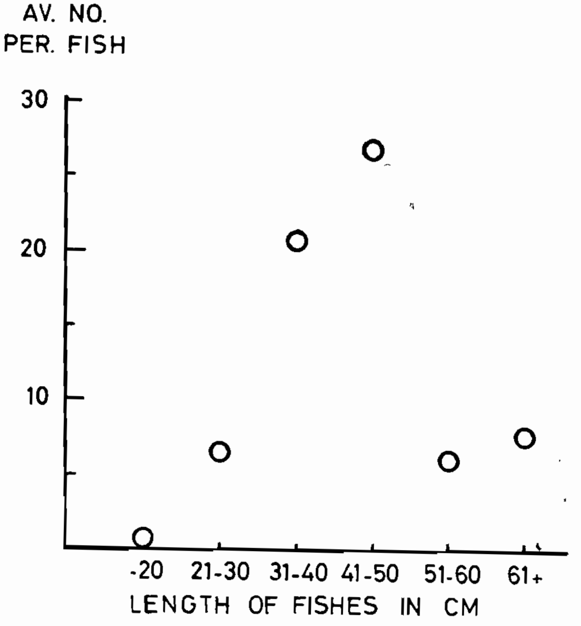

Fig. 6. - Infestation rate of young *T. variabilis* by a strigeid trematode according to length.

fishes and BAKER (1958) found spores of a *Myxobolus*-like myxosporidian in the liver and spleen of adult fishes. BAKER (1958, 1960) also found two forms of trypanosomes in more than 50 % of the *T. variabilis* which he examined, and showed that more than 70 % of the individuals harboured the unpigmented intra-erythrocytic parasite *Dactylosoma mariae* HOARE.

Occasional individuals harbour encysted *Clinostomum*-like trematodes in the buccal cavity, and other unidentified trematodes have been seen on the fins. Young fishes are frequently and sometimes heavily infected with the black metacercarial cysts of a strigeid trematode. It was noted that fishes from about 30 to 50 mm tended to be most heavily infected with these parasites and random samples collected over about 7 weeks (a period believed to be sufficiently short to be little influenced by any seasonal periodicity) totalling 209 fishes gave the kind of distribution shown in fig. 6. This is suggestive of mortality of heavily infected fishes. (Up to 184 cysts were counted on one specimen). Young fishes have obviously been exposed for an insufficient length of time to get heavy infestations, but the decline in numbers on larger fishes can only be explained by mortality — either death as a direct result of parasitism or predation on weak and therefore more easily captured individuals. No evidence of the latter possibility was obtained though the fact that this fish is parasitised at all presumes some predation. Fishes over about 10 cm in length seem to be virtually free from this parasite. While insufficient to yield definite figures the data indicate that mortality from this cause may at times be high.

Crustacean parasites are frequent. The branchiurans *Argulus africanus* Thiele and *Dolops ranarum* (Stuhlmann) occur, particularly in the mouth, but are not numerous. They averaged only 0.63 and 0.28 parasites per fish respectively in gill net catches examined in the Jinja area. The copepod *Lamproglena monodi* Capart is common on the gills but is seldom present in numbers. More important are infections of a form of *Lernaea cyprinacea* L. which, although averaging only 0.35 parasites per fish, is sometimes present in quantity and causes damage to the lips. *L. barnimiana* (Hartmann), although larger, is very rarely found on *T. variabilis* in Lake Victoria and is probably unimportant.

Although obtained in Lake Kioga, the only other lake from which *T. variabilis* is recorded, a fibrous cyst merits mention. This somewhat ovoid structure had axes measuring about 5.5 and 4.0 cm and weighed about 36 gm. This was seen only after imperfect preservation and for this reason examination in a cancer research laboratory unfortunately threw no light on its detailed structure.

One undoubted cause of mortality is the stranding of young in « pools » which remain in depressions in the rock surface as the lake level falls and which eventually dry out. Fishes in this predicament have been seen several times, particularly when they have colonised areas of considerable size which occasionally become flooded for short periods and then dry out. In such cases mortality may be high, involving hundreds of fishes on occasion, but still affects only a small proportion of the young in a nursery.

A NOTE ON COLOUR POLYMORPHISM

The occurrence of occasional individuals, usually females, of *T. variabilis* which exhibit an aberrant orange and black colour pattern (the « maradadi » pattern of the fishermen) is well known. The typical maradadi pattern consists of blotches of black pigment dorsally on a pale orange background, but every gradation between this and the normal form seems to exist. There is also a true piebald pattern which, in the Jinja area, is very rare and which is very much like the piebald pattern found in some species of *Haplochromis* in the lake and in *Pseudotropheus zebra* (BOULENGER) in Lake Nyasa. There also occur, but again they are rare, individuals which are virtually pure white in colour, and others approach this condition.

While the maradadi pattern is largely sex linked this is not invariably so and maradadi males do occur, but they are sufficiently rare for LOWE (MCCONNELL) (1956) not to have seen a ripe individual. Such males do become ripe and presumably breed, for they have been seen, complete with genital tassel, during the present study.

The percentage of maradadi individuals in the population differs in different areas, for this form was seen more commonly in an area east of Buvuma Island than in the vicinity of Jinja. These areas were some 20 miles apart and within the range of dispersal of which *T. variabilis* is capable, but beyond its most usual limits. Of almost 700 adult females marked at brooding grounds near Jinja (within about 5 miles and almost all within less than one mile of each other), only 11 (about 1.6 %) exhibited a maradadi coloration to some degree, while of 22 adult females marked on the eastern shore of Buvuma no fewer than 13 (about 59 %) showed this pattern, and the impression gained from immature fishes was that the same state of affairs prevailed. On one occasion seven, or possibly eight, maradadi individuals were seen together among rocks in the second-mentioned locality unaccompanied by any normal individuals. The percentage occurrence of maradadi fishes differs from that quoted by LOWE (MCCONNELL) (1956) whose material came from three bays to the east of the area sampled near Jinja and north of that in which the incidence of this form was so high. These facts support the idea that, in spite of dispersal, relatively localised populations exist. That this should be the case in a fish which is so eurytopic is of interest from the point of view of evolution and merits comparison with the state of affairs prevailing in another African cichlid fish *Pseudotropheus zebra* of Lake Nyasa which also exhibits colour polymorphism and of which the relative frequency of the different forms varies from area to area (FRYER 1959). On the one hand this state of affairs is presumably achieved as a result of homing to breed and on the other as a result of intense specialisation and consequent stenotopy.

THE *TILAPIA VARIABILIS* FISHERY

The present study has been concerned largely with the natural history of *T. variabilis,* of which however certain features are of great relevance to its commercial exploitation and are discussed briefly here. The remarks apply particularly to the Jinja area as the possible differences in the maximum size achieved by this species may slightly alter the picture in different parts of the lake.

Prior to 1956 the stock of *T. variabilis* was but little fished. Some large individuals of the population were removed before this time but the effects of fishing on the stock must have been small. In 1956 gill nets of 4½ inch mesh came into use, at first illegally, later with official approval. The effect of this on the catches can be seen in fig. 7. As noted earlier the accumulated stock provided good catches when first cropped. Since then numbers, and consequently catches, have fallen. The very marked decline during 1959 and 1960 (the catch per net in 1960 was considerably less than half that of 1958) indicates that already the accumulated stock has been drastically reduced, and the steepness of the decline suggests that the yield will diminish still more in the future.

It has been pointed out in an earlier section that the use of 4½ inch gill nets does not greatly affect the stock of breeding females of *T. variabilis.* Provided, therefore, that nets smaller than this are not used, the breeding stock should be reasonably well preserved and a steady yield obtained. On account of the slow growth rate, however, this yield will be small, certainly no more than 0.3 fishes per net in the Jinja area if fishing continues at its present intensity.

The present tagging experiment was of necessity not designed to give an estimate of population size or degree of exploitation, but, bearing in mind the fact that most of the individuals marked belong to a segment of the population which is not fished as intensively as are somewhat larger individuals, and taking into account that some recaptures were made in 4 inch mesh gill nets, the indications from returns brought in by fishermen are that the population is being heavily fished at present. This conclusion is borne out by the decline in commercial catches. The decline could conceivably entice the fishermen to use 4 inch mesh gill nets, which would have serious consequences for, while it would result initially in an upsurge in the number of fishes caught, these would be considerably smaller in size than those caught at present and the breeding stock of females would become exposed to serious exploitation.

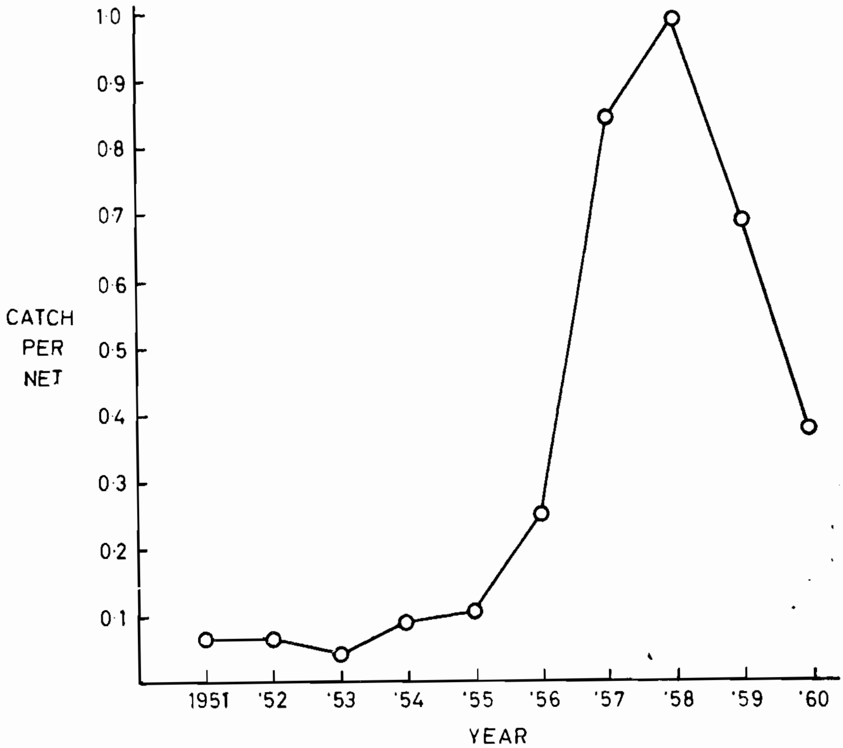

Fig. 7. - Yelds of *T. variabilis*, expressed as catch per net, at the Masese landing (near Jinja) over 10 years, to show the effect of the replacement of gill nets of 5 inch mesh by those of 4 1/2 inch mesh during 1956, their more widespread adoption in 1957 and 1958, and the subsequent decline in numbers in 1959 and 1960.

Note. — The system of recording was changed early in 1959 from that of total enumeration to one of random sampling. While this may to some extent affect the absolute figures it in no way affects the well-marked trends shown here.

It may, therefore, be recommended that the use of gill nets of mesh size less than 4½ inches should be discouraged.

Seine netting is also uneconomical in the long run as on sandy beaches it tends to produce immature fishes and may disturb breeding grounds.

As conditions on brooding grounds in the Jinja area are such that seine netting can only be practised at the expense of much damage to gear, disturbance of brooding females and consequent loss of eggs or young is not likely to prove a serious problem.

For purposes of legislation one cannot consider this species alone as the nets which catch it catch other species, often in greater numbers. In the Jinja area at least the beneficial effects on the yield of *T. variabilis* (largely temporary) accruing from the introduction of 4½ inch mesh gill nets is not sufficient to offset the damage done to the stocks of *T. esculenta* which could give better yields if cropped exclusively with 5 inch mesh nets. Similarly the use of seine nets should not be considered with this species alone in mind for on some beaches they crop species of *Haplochromis* which could not be collected satisfactorily by other means.

Bearing these things in mind the outlook for *T. variabilis* may be summed up as follows. On the credit side a large segment of the breeding stock appears to be safe from the gear at present in use. Recruitment of young to this stock is probably satisfactory, as natural mortality of immature individuals is apparently low, though more information on the effects of the strigeid trematode mentioned earlier is required. To offset this, however, is the very slow growth and probably future competition with *T. zillii* which could influence survival of the young (and possibly other) stages with a consequent diminution in numbers of *T. variabilis*. The large scale replacement of *T. variabilis* by *T. zillii*, which may well occur, could conceivably be beneficial to the fishery, though the eventual effect of *T. zillii* which, as a result of its weed-eating-habits may modify the environment of other species, is purely conjectural. What is salutory to remember is that the possibility of competition with *T. variabilis* was quite unforeseen when the decision to introduce this species was made. The lesson to would-be introducers is plain to see.

ACKNOWLEDGMENTS

I am very grateful to Dr. V. D. VAN SOMEREN and my former colleagues Mr H. Y. ELDER and Mr D. J. GARROD for reading and criticising my manuscript, for supplying me with catch data collected at the commercial landing, and for information relating to marked fishes recaptured after my departure from Africa.

SUMMARY

An account is given of the general biology of *Tilapia variabilis* in Lake Victoria. Its habitat preferences are geared to its special requirements at different phases of the life cycle. Very distinct and different habitats are frequented by breeding pairs, brooding females, and juveniles. Post-juvenile fishes and non-breeding adults, on the other hand, frequent a variety of habitats. Particulars are given of the brooding grounds and of the nurseries frequented by the young fishes, and the general behaviour and feeding habits of the early stages are described.

Evidence both of dispersal and of homing to very circumscribed areas for brooding the young is presented.

Ecologically *T. variabilis* and *T. esculenta* appear to be complementary species, and there is probably little or no competition between them. With the introduced *T. zillii*, however, competition seems more probable. Although adults differ markedly in feeding and breeding habits, young of both species frequent the same habitats and make similar demands on available environmental resources. This situation and the possible effects of the greater fecundity of *T. zillii* are discussed.

Quantitative data on breeding frequency and brood size are difficult to obtain, but information so far available shows that at least three broods can be produced within about eight months and that the average number of young per brood reared to a size at which they become independent is probably about two hundred. Breeding takes place throughout the year but varies in intensity. Correlations between breeding intensity and environmental variables are still obscure.

Occasional precocious females breed before they attain a length of 19 cm., but most are more than 20 cm. in length; peak numbers of brooding females are found among fishes of 23 to 24 cm., and only a small proportion of breeding females exceed 26 cm. in length. Present day commercial catches (in 4 1/2 inch mesh gill nets) do little damage to this breeding stock as few of the fishes caught are less than 24 cm. in length.

As the mean length of any sample increases, the proportion of males in the sample increases, and males preponderate in all adequate samples above about 22 cm. in length.

Growth rate is remarkably slow for a tropical fish. Data are still far from adequate but the indications are that to reach a length of 20 cm., takes about 3 years, after which growth becomes very slow, a 26 cm. fish being about 8 years old. Implications of this are discussed.

Predation appears to be slight, but parasitism is frequent and may result in some mortality, possibly serious in one case. Other hazards are mentioned.

Brief reference is made to colour polymorphism.

The change-over in the commercial fishery from gill nets of 5 inch to those of 4 1/2 inch mesh led initially to greatly increased catches of *T. variabilis*. Following the removal of accumulated stocks catches rapidly declined. The decline will probably continue but, provided the mesh size is not reduced further, and unless competition from *T. zillii* becomes severe, a sustained yield should eventually be obtained. This yield will, however, be very low.

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