Zeitschrift: Acta Tropica
Band: 23 (1966)
Heft: 2

Artikel: The biology of "Tilapia grahami" boulenger in Lake Magadi, Kenya

Autor: Coe, Malcolm J.

DOI: https://doi.org/10.5169/seals-311342

Department of Zoology, University College Nairobi, Kenya.

The Biology of *Tilapia grahami* Boulenger in Lake Magadi, Kenya.

By MALCOLM J. COE

Introduction

A great deal has been written concerning the speciation of Cichlid species in the Great Inland Lakes of East and Central Africa. There are, however, several species of Tilapia isolated in the alkaline lakes of the Great Rift Valley, living in extreme conditions of temperature, salinity and pH which are still virtually unknown. This paper deals with one of these fish, *Tilapia grahami* Boulenger which lives in the lagoons and Soda springs of Lake Magadi in southern Kenya.

Lake Magadi is a highly alkaline lake which lies in the floor of the Rift Valley bounded by the Latitudes 1° 43′ S and 2° 00′ S and Longitudes 36° 13′ E and 36° 18′ E. It covers an area of approximately 42 square miles, and lies at an altitude of 1,987 feet above sea level. Lake Magadi is divided by a ridge of alkaline trachyte into a larger Southern element, Amagad and a smaller Northern element, Little Magadi or Lake Enegarami. The latter lies 52 feet above the average level of the former (i.e. 2,039 feet) (fig. 1).

The first European to visit the lake was A. FISCHER who passed along the foot of the Nguruman escarpment in April 1883, and described the general physiography of the region (FISCHER, 1884, pp. 58, 60, 75 and 76; 1885, p. 199). His geological collections were the first to be described from this part of the Rift Valley. Later KAISER (1898, p. 322) reported on geological phenomena to the West of the Lake.

Major F. Burnham surveyed the lake for the first time in 1904 and later in 1908. J. S. Coates carried out further survey work. A report based on the latter's studies was published in 1923 (anonymous, 1923) and gives analyses of Trona, lake liquors, spring waters and rocks.

J. W. GREGORY in his studies of the Rift Valley also visited the Nguruman escarpment and Lake Magadi (1921, pp. 178-183).

In 1914 PARKINSON published the then most detailed account of the geology of the area, and this was not superceded until BAKER (1958) carried out his detailed studies between April and October 1952 for the Geological Survey of Kenya. This latter work has been of inestimable value to the author in preparing the present paper.

Lake Magadi lies in the floor of the Rift Valley in a region much disturbed by tilting and faulting. The lake basin itself lies on a much faulted bed of lower Pleistocene Trachyte, which itself overlies Pliocene Olivine Basalts. Dotted around the lake are extensive recent patches of Alluvium, Loess, hill wash soils and middle Pleistocene Chert beds.

Except during periods of heavy rain most of the lakes surface is covered with a layer up to 15 feet thick of crystalline trona, composed largely of Na_2CO_3 and $NaHCO_3$ in combination with small variable quantities of NaF, NaCl and a trace of Na_2SO_4. BAKER (1958, pp. 41-48) carried out boring operations to study these Evaporite series and found down to 150 feet,

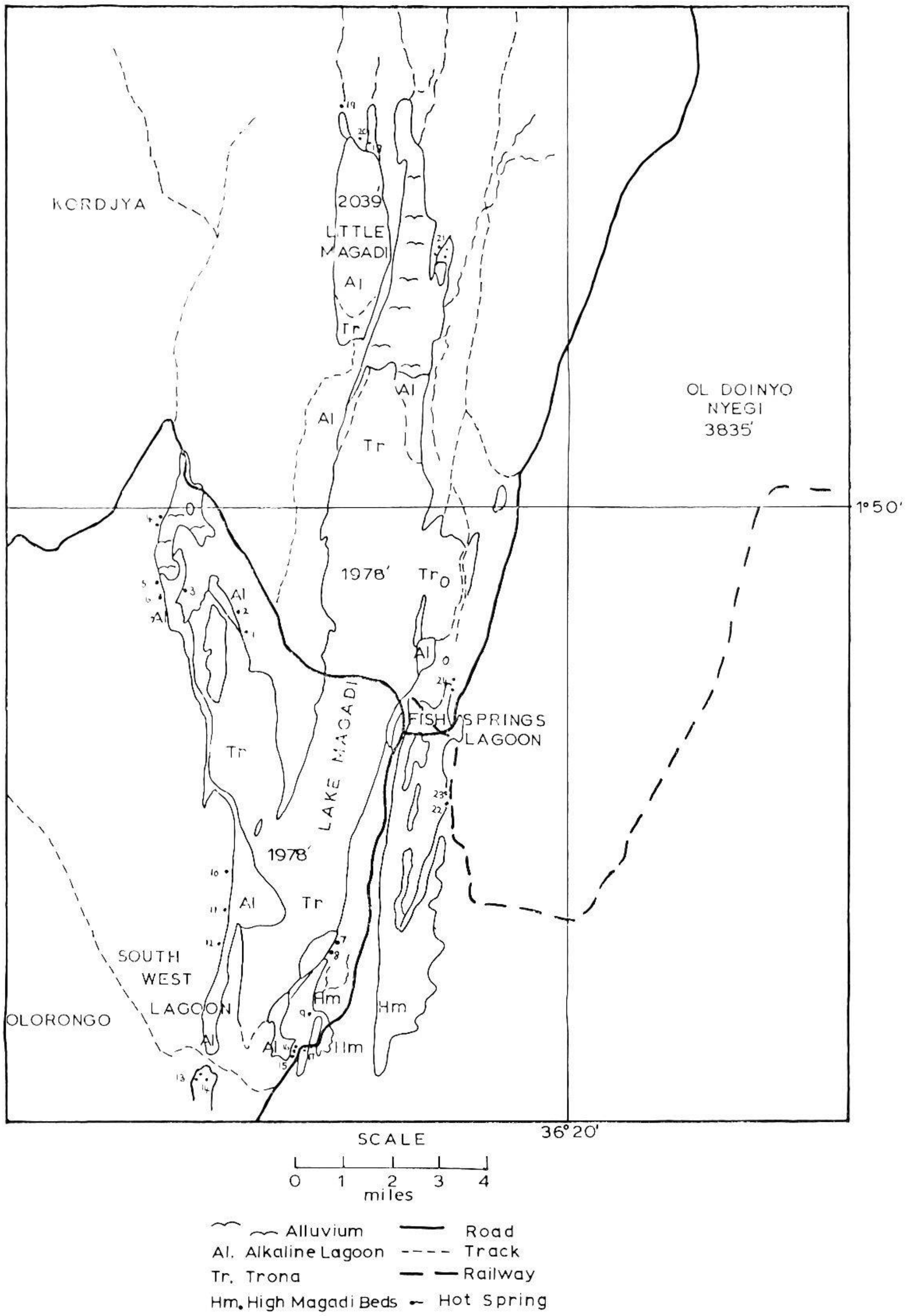

Fig. 1. Lake Magadi, general map.

evidence of alternate layers of trona and clay deposits. This discovery tends to support WHITE's contention that the lake has undergone periodic flooding and recrystallization (1953). Such a phenomenon he feels may well account for the unusual purity of the lakes soda deposits. The trona has been dredged and exploited commercially by the Magadi Soda Company since 1927. Analyses of trona show that Na_2CO_3 and $NaHCO_3$ make up 80.9% of the total with the remainder containing 0.9% NaF, 1.7% NaCl and 0.06% Na_2SO_4.

A number of alkaline volcanic springs flow into the lake around the margin, and it is in close association with these waters that the small Lake Magadi Tilapia are found.

Tilapia grahami was discovered by J. W. Graham und described by BOULENGER (1912) as *T. mossambica*, but on later examination it was recognized as a new species and called *T. grahami* in honour of its discoverer. Apart from a short paper by WOODHOUSE (1912), these interesting fish have received little attention. The present paper is the result of field and laboratory investigations carried out between 1957 and 1963.

Climate

Lying on the floor of the Rift Valley, Lake Magadi occurs in one of Kenya's semi arid regions, with low annual rainfall, high daily temperatures and extensive lava bed rock deposits.

Rainfall is concentrated in two "rainy" seasons, which occur in March to April, and in December. Frequently the rain falls as a result of powerful and isolated storms driven by strong winds from the East and North East. It will be later shown that flash floods caused by these storms are of great importance in allowing passage of fish from one isolated spring community to another over the surface of the flooded trona. The humidity of the region is low, varying between 27 and 50%, resulting in rapid evaporation of rain when it does fall. Table 1 shows rainfall and evaporation data recorded at the Magadi Soda Company's township offices between 1957 and 1964.

Average monthly rainfall recorded over the period 1925-1959 is shown in Fig. 2, demonstrating the predominantly wet periods in April and December with a very dry period from June to December. While undoubtedly rainfall must have some effect on the fish when the lagoons become flooded, at present there is no indication that breeding is influenced by precipitation.

Shade temperatures recorded at the township offices vary from 22°C in the rainy (cloudy) season and between 35°C and 40°C in the dry season. The highest temperature ever recorded here being 42.2°C which is one of the highest ever recorded in Kenya. Table 2 gives monthly average maximum and minimum figures from January 1957 to June 1964. These show an annual

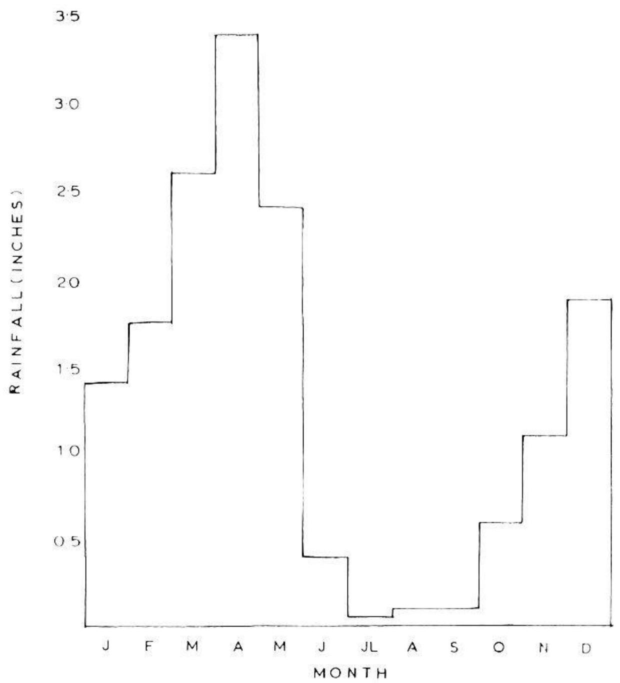

Fig. 2. Average monthly rainfall at Magadi Township Offices.

1

2

Plate 1. General view of the South West Lagoon. The "nursery" shallows are seen in the foreground, with the shallow lagoon in the middle ground and the rocky platform in the background. The temporary dam to observe diurnal migration can be seen to the right of the shallow lagoon.

Plate 2. Large numbers of fish moving en masse from the shallow lagoon in front of an observer.

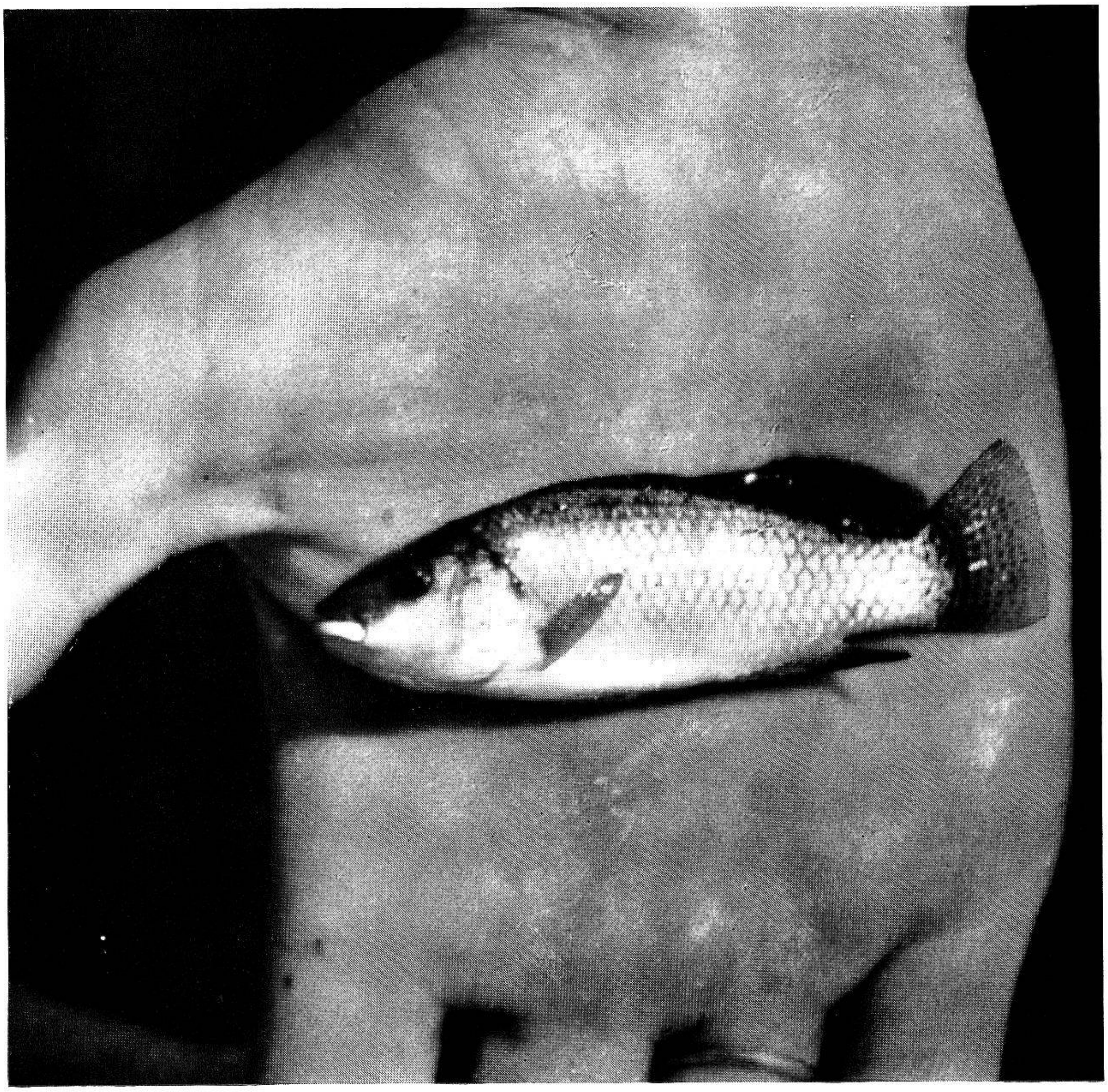

Plate 3. Adult male of *Tilapia grahami* from Fish Spring Lagoon. Plate shows prominent white lip, dark head and back, pale belly and mettled fins.

range of about 5°C and a remarkably even diurnal range of about 10°C. It should be remembered that all the foregoing climatic data were recorded at the slightly raised township offices, and that down at the lagoons temperature conditions would undoubtedly be more extreme. In any case the effect of day temperatures and the steady annual diurnal range must be expected to have a marked effect on the fish's habitat, particularly the shallower areas.

The Fish Habitat

It has already been stated that *T. grahami* are found in alkaline springs around the lake's margin. BAKER (1958) after considering numerous theories to account for these springs (PARKINSON, 1914, p. 45; GREGORY, 1921, p. 79; STEVENS, 1932, p. 39; TEMPERLEY, 1951, p. 6) considers "the greater part of the spring water is probably alkaline ground water, heated by contact with igneous rocks and forced to the surface as the result of pressures generated by

Plate 4. A small inlet in the shallow lagoon containing a large number of fish feeding on Algae encrusted gravel. The white lips of the male in breeding colour can clearly be seen in the centre of the picture.

boiling of the water that is in contact with hot rocks deeper in the earth's crust".

The physical properties of these alkaline springs is discussed fully in J. A. STEVENS' "Lake Magadi and its Alkaline Springs" (1932). This valuable paper was prepared when the author was working for the Magadi Soda Company. The most notable feature of the springs is the variation of the temperature of the water they produce. Around the lake, temperature differences of 33°C-86°C are found, and even in individual groups of springs temperatures may vary by as much as 10°C. There does not appear to be any correlation between the rate of flow individual or groups of springs and temperature. Spring liquor analyses carried out by STEVENS are given in BAKER (1958). The springs in which the author studied *T. grahami* were termed Spring No. 24 for those supplying the Fish Springs Lagoon and Spring Nos. 13 and 14 for those supplying the South West Lagoon. These two sets of springs showed rather different physical characteristics. The Fish Springs Lagoon water issues at 36°C and has a specific gravity of 1.015, while those of the South West Lagoon issue at between 42 and

TABLE 1.

Rainfall and evaporation at Magadi Township Offices.
(Inches.)

Year	1957		1958		1959		1960		1961		1962		1963		1964	
	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.	Rain	Evap.
	2.63	12.03	2.66	13.20	0.27	15.27	0.35	16.03	Nil	20.40	0.87	18.28	2.78	11.22	0.98	13.64
	0.84	13.60	2.90	8.10	3.24	13.96	1.56	18.12	0.22	18.28	0.72	15.08	0.90	13.26	1.90	13.22
	2.79	12.60	3.54	12.60	4.65	12.73	11.03	12.59	0.67	20.49	1.01	15.21	1.49	15.33	2.20	13.32
	4.37	9.00	3.22	11.00	1.63	11.15	3.06	10.10	1.47	14.67	2.88	12.08	9.70	11.66	5.54	8.70
	5.00	7.30	5.63	4.50	4.29	10.89	0.16	12.04	1.43	14.73	8.24	9.98	4.70	7.92	1.08	11.32
	1.23	11.50	1.51	9.75	Nil	12.28	0.41	12.47	0.37	16.63	0.40	10.12	0.18	9.30	0.07	11.27
	Nil	13.50	0.11	10.05	0.01	12.47	0.02	13.00	0.42	17.20	Nil	12.22	Nil	11.48		
	Nil	13.50	0.01	13.01	0.17	14.41	0.01	14.79	Nil	17.74	0.10	13.52	Nil	12.44		
	0.09	16.90	0.18	15.78	0.01	15.41	0.32	14.60	0.18	16.90	0.06	15.90	Nil	15.02		
	0.61	15.70	0.18	16.18	0.27	18.25	0.63	16.03	1.32	15.90	1.83	15.95	0.87	16.83		
	2.79	11.20	0.73	16.19	1.73	12.23	1.02	15.22	7.73	9.85	0.66	14.88	2.48	11.63		
	3.41	9.80	3.28	13.10	2.28	14.70	0.54	16.78	6.93	9.51	3.17	14.23	8.37	10.19		
Total rainfall	23.76		23.95		18.55		19.11		20.64		19.94		31.47			

TABLE 2.

Mean maximum and minimum temperatures.

	1957		1958		1959		1960		1961		1962		1963		1964	
	Mx.	Mn.	Mx.	Mn.	Mx.	Mn.	Mx.	Mn.	Mx.	Mn.	Mx.	Mn.	Mx.	Mn.	Mx.	Mn.
January	36.8	23.3	37.1	23.8	36.9	24.6	33.8	24.1	38.4	24.5	33.3	21.9	33.7	21.7	35.1	24.5
February	36.2	23.4	35.8	22.5	37.0	24.0	37.8	24.4	38.1	24.9	38.1	24.9	37.3	23.1	36.5	23.0
March	36.5	24.0	37.4	23.2	35.1	23.4	34.2	23.3	38.4	24.7	36.5	23.7	36.4	23.7	36.9	23.7
April	34.9	23.6	35.4	23.5	34.5	24.1	33.1	23.1	36.1	24.7	34.9	22.8	33.9	22.6	32.9	21.9
May	32.0	22.1	31.7	22.5	33.9	23.3	33.9	23.2	35.5	24.5	31.5	21.6	31.0	21.9	33.0	22.6
June	31.6	21.3	31.6	21.7	33.4	22.4	33.4	22.4	35.1	23.7	31.6	21.3	31.9	20.8	32.9	21.7
July	32.0	21.4	31.3	21.8	32.2	21.9	32.6	21.9	34.0	22.8	32.0	21.2	32.6	20.3		
August	33.0	22.3	33.2	22.3	34.1	22.3	33.7	21.9	33.8	23.6	33.3	22.3	32.9	21.2		
September	35.4	21.6	35.9	22.8	35.2	22.9	35.2	22.8	34.2	23.3	34.6	22.7	35.0	21.9		
October	36.9	24.1	36.7	24.3	35.0	23.0	35.9	23.7	35.4	24.1	35.4	23.4	37.5	24.1		
November	34.6	23.4	37.2	24.4	34.7	23.5	37.0	23.8	31.3	21.7	21.7	23.6	34.6	23.1		
December	34.7	23.3	34.6	27.0	35.6	23.1	37.1	23.8	31.4	21.7	35.1	23.2	32.1	21.3		

44°C and have a specific gravity of between 1.026 and 1.027. (*Note:* Individual springs within groups show a greater variation in temperature than is indicated in STEVENS' figures.)

All the alkaline springs, except those whose water is above 68°C are surrounded by thick multi-coloured Algal slime. The hottest springs do not contain fish and are situated at the North end of Little Magadi.

The output of these springs into their individual lagoons is considerable. STEVENS (1932, pp. 31-32) has calculated the total output per day of these springs and their relative effect in terms of input of Na_2CO_3 per day. These figures showed that the Fish Springs Lagoon had an inflow rate of 380,000 cubic feet per day, while those of the South West Lagoon were 2,490,000 cubic feet per day. This rate of flow would contribute an input of 106 tons of Na_2CO_3 in the former and 1,175 tons per day in the latter. The total estimated input of 4,300 tons per day from all the springs around the lake clearly shows the importance of the waters to stocks of soda in the main lake.

It is this large quantity of liquid being pushed into the edges of the lake that maintains the large series of lagoons free from crystallisation. In June 1963 when the South Western lagoons were visited at the end of a rainy spell, the lagoons were very large, but during a period of 9 days without further rain the surface was soon reduced by recrystallisation. During such periods of heavy rain individual lagoons become joined together and if it were not for the periodic gene flow allowed by these flood connections, between otherwise isolated fish communities, no doubt sub-specific differences might well have arisen in the area. On two occasions the author has found dead undamaged fish on the surface of the soda crust some distance from a lagoon, which seems to indicate that a flood movement of individuals does in fact take place.

Through the kind cooperation of Dr. Walter Rouse of the Magadi Soda Company it has been possible to obtain accurate data on how often the Trona has been flooded in recent years. During the companies dredging operations their equipment is supported on a raft which floats in an artificial paddock of cleared Trona. Fig. 3 shows the level of the lake relative to the surface of the Trona. It will be seen that since January 1961 the surface has been flooded on six occasions, so that at least over this period the length of lagoon community isolation has never been more than a few months.

In December 1960 it was noted that the edge of the Fish Springs lagoon was surrounded by an enormous number of dead fish. The fish were arranged in a line 2 feet wide and 6 inches deep around

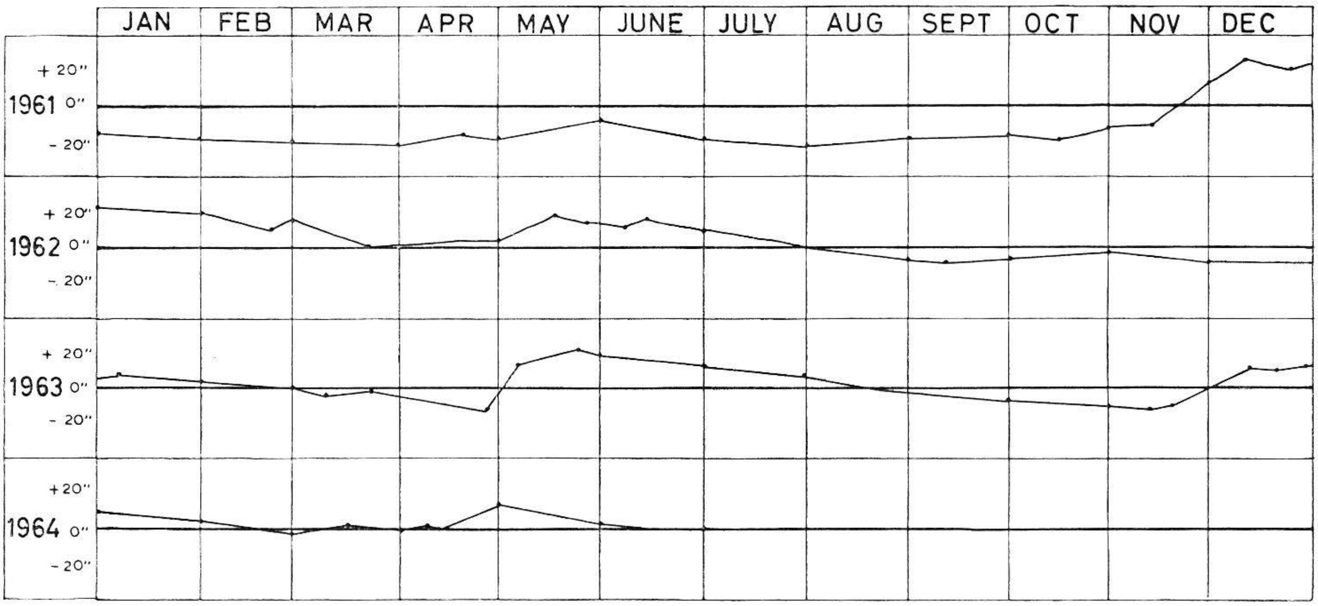

Fig. 3. Variation on lake levels relative to Trona surface.

a high water mark. On examining rainfall records it was found that this high water mark was produced in March of that year when 11 inches fell, much of it in one day. During this period of flooding the water became very turbid due to the presence of enormous numbers of the Blue Green Alga *Arthrospira sp.* It seems likely that the cause of death may well have been either the clogging of the fishes gills or the rapid deoxygenation of the water following an algal flush. Dr. HEINZ LOEFFLER has informed the author that he has encountered a sudden increase of pH following such flushes (1960, personal communication). Though this is possible, since the pH of these waters is normally c 10.3, a further increase sufficient to cause the death of the fish would seem unlikely.

In May 1962 Lake Natron which is another alkaline Rift Valley lake some 40 miles South of Magadi was visited and here again enormous numbers of dead fish were found around the shore. Their death had not long preceded the visit since large numbers of dying fish were still floating on the water close to the shore. The water along the margin of the lake was thick and dark with blue green algal slime, as had been reported at Magadi the previous year. Dying fish that were examined did not show signs of the gills having been clogged, nor was the pH abnormal, so that here deoxygenation following an algal flush would seem to be the most likely cause of mass fish mortality.

During field work at the lake the author has confined his detailed studies to the Eastern Fish Springs Lagoon and the South Western Lagoons. These two areas will therefore be described

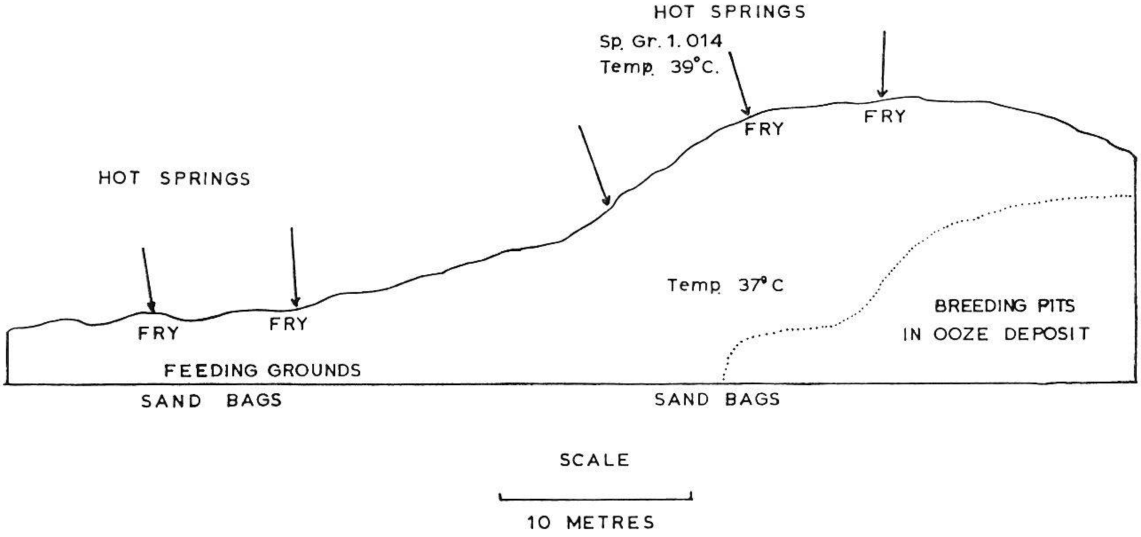

Fig. 4. Sketch map of Fish Spring Lagoon.

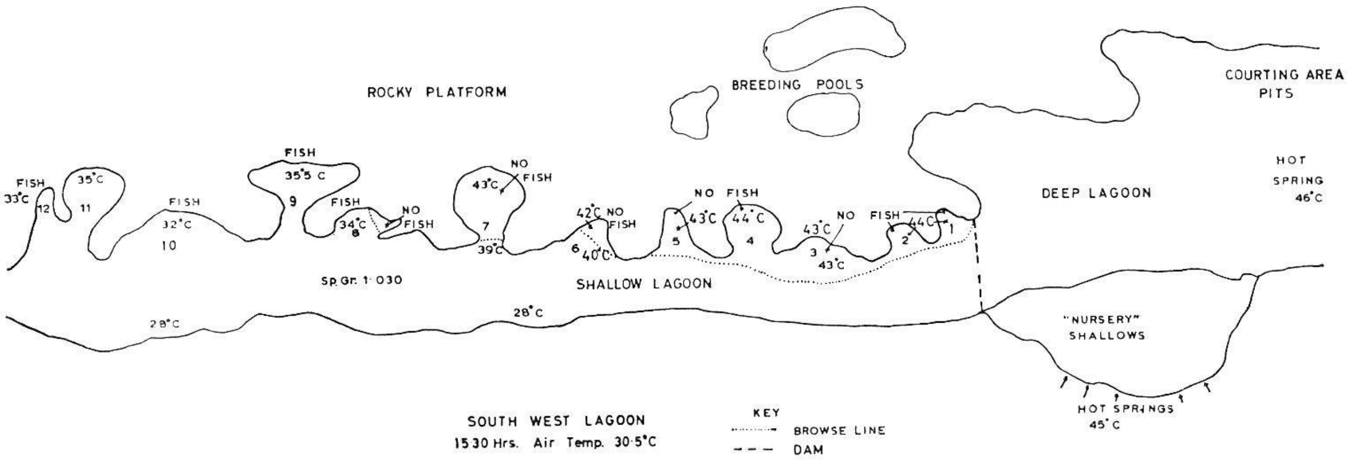

Fig. 5. Sketch map of South Western Lagoon.

before consideration is given to general biology and breeding behaviour.

Fish Springs Lagoon

This lagoon consists of a narrow band of water limited on its West side by a sand bag wall and shelving gently on the East to a volcanic gravel shoreline. The lagoon is fed by a number of small hot springs issuing at 36°C with a specific gravity of 1.016. Over its quite small area the lagoon is shallow (3″-6″), being deepest in the South West corner where algal sediment collects, and is utilized by male fish for nest building purposes. Figure 4 shows a sketch map of the area, which is marked with the main physical features together with the delimitation of courting, feeding and nursery areas.

South Western Lagoons (Plate 1).

This is a much larger area than the former, providing a much wider range of niches. In addition the fish in this lagoon are not artificially limited as they are in the Fish Springs Lagoon. The area studied which is shown in Figure 4 is but a small part of the total area of the lagoon, but was restricted since the whole margin is accessible and is nowhere too deep to observe the fish. The hot springs flowing into the lagoon vary from 36°C close to the Southern rocky platform, to 46°C in the centre of the deeper Northerly portion (Fig. 5).

The study area may be broadly divided into four habitats.

a) Shallow lagoon shelving from chert gravel to the wall of a rocky platform where hot springs issue at 36°-43°C.

b) Deep lagoon up to 2½ feet deep, edged with chert gravel and containing a large hot spring approximately at its centre (46°C).

c) Rocky platform limiting the width of the shallow lagoon in the East and the deep lagoon in the North. A number of hot springs issue from its surface and all rocks in the vicinity of hot springs are surrounded by thick deposits of algae. A number of deep pools distantly connected to hot springs contain fish. Large deposits of bird guano encrust the rock in places.

d) Shallow area of hot spring seepage in which a number of small pools are enclosed by chert ridges. This complicated pool system leads to eddies and great variations in temperature over short distances.

The specific gravity of the lagoon and spring is 1.030 and their pH 10.5 (the highest recorded at the lake).

Physical Environmental Factors and Their Influence on Behaviour

T. grahami lives in an extreme environment in which it must face both high alkalinity (pH c 10.5), high specific gravity (1.01 to 1.03) and high temperatures. The history of the lake and the development of its attendant fish fauna will be considered later, but it must be here mentioned that the present limitation of fish populations has been brought about by the gradual drying up of the lake since the last major pluvial period. At the present time the output of the hot springs do not appear to have appreciably decreased over the last 20-30 years (STEVENS, 1932).

The author has found no evidence of fluctuations in either pH or specific gravity although in certain South African Lakes sup-

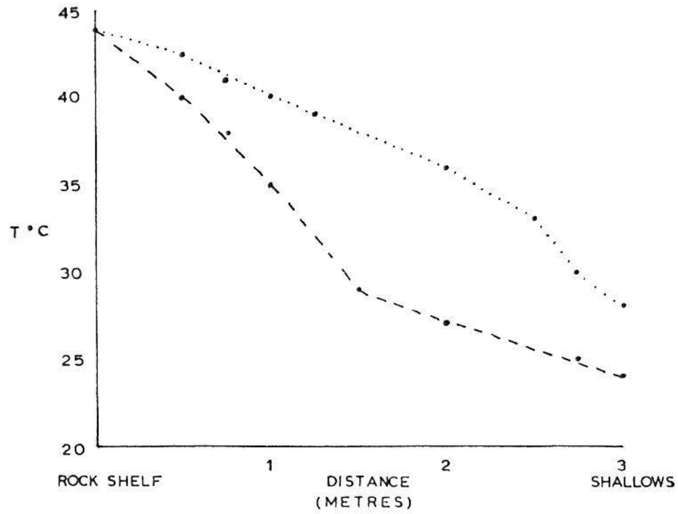

Fig. 6. Temperature gradient across South Western Lagoon. Broken line represents day and unbroken line evening temperatures.

porting rich blue green algal floras large diurnal pH changes have been reported (LIVINGSTONE, 1963). Hence it might be assumed that temperature, since this is variable, must be one of the most important influences on general and breeding behaviour. Although temperature recordings were made at the Fish Springs Lagoon, the most complete and significant figures were obtained at the South Western lagoons.

This area consists of a rocky platform from the edge of which hot springs issue into a narrow, shallow stretch of water. The temperature of the main springs remains constant day and night at c 43°C. During the day this water is crowded with vast numbers of feeding fish, and the water temperature falls across the 12 foot lagoon width from 43°C to 28°C. At this time it was felt that the hot water flowing into the lagoon was sufficient to maintain a fairly even temperature gradient across the water throughout the day and night. In June 1963, however, these waters were examined over 24 hours and it was found that at sunset the marginal water temperature fell sharply to 26°C and that the gradient across the lagoon became steeper. This diurnal temperature change is expressed in Figure 6. Thus the effect of insolation on the shallower parts of the lagoon during the day must be considerable, and when this effect is removed at sunset, radiation losses are rapid.

T. grahami is an extremely active fish occurring in all suitable situations in large numbers. When the water of any of these lagoons is approached, the shoals move en masse from the shallow to deeper water on a moving front, the dorsals of the larger fish (usually the males) cutting the surface of the water in a zigzag pattern as the shoal moves forwards. Occasionally if the fish are prevented from escaping by small rocky intrusions they will jump out of water to clear them, or even in many cases wriggle across them. This type of coordinated escape movement will last for two or three feet, after which the shoal moves towards the bottom where it disperses in no apparent order (Plate 2).

At the same time that these marked temperature variations were noted it was also found that at sunset (19.00 hrs.) the fish began to leave the shallow lagoon and swim to the deeper Northern waters. In fact this diurnal migration was so marked that by 20.00 hrs. the only fish to be found in the shallow water were close to the spring inlets. This sensitivity was more clearly demonstrated when a small dam was constructed across the mouth of the shallow lagoon where it connects with the deep lagoon. At 18.00 hours when the sun was already low on the western horizon, the water temperature began to fall, and at 18.15 fish began to slowly move out to deeper water in much the same way as they do when disturbed, except that here they all left by the narrow 18″ opening and did not attempt to jump the barrier as they do when disturbed. On entering the deep lagoon the shoals broke up, but by 20.00 hrs. most of them were concentrated around the large hot spring in the centre of this lagoon. In this situation the effect of insolation in the day must be much less and radiation losses at night also lower, so that water 3-6 feet from the spring remains constantly between 32 and 36°C.

This diurnal migration is a marked and important aspect of the fishes' behaviour. It should, however, be pointed out that this does not mean that no fish are present in the deep lagoon during the day, for it is only that part of the population that is under the influence of a strong feeding drive that are to be found in the shallows, and during the day there is a constant interchange of animals between the two areas.

The sensitivity of these fish to temperature can easily be observed in shallow water. *T. grahami* is a browser and its teeth which project slightly forwards are well adapted to this habit. The chert gravel in the shallow lagoon is thickly covered with blue green algae, and these plants form the main item of the fishes' diet. Stomach content analyses reveal a predominant fraction of algal material (90%) and the remainder is made up of Crustacea (Copepods), and Dipterous larvae. The presence of large numbers of fish during the day is almost wholly due to their habit of browsing on algae, and in these shallows the clear water kept free of ooze by water flow is a much better site for propagation of algae than the deep lagoon where deep faecal matter and plant ooze accumulate and cover the gravel bottom.

It has been observed that algae in the shallow lagoon are not evenly distributed on the bottom, but are fairly sparse in the outer waters and become thick near the hot spring inlets. When temperatures were measured across the lagoon, it was found that as the temperature increased so the algae became thicker, until at 40°C a dark browse line could be seen on the bottom. When feeding, the fish eat along the temperature gradient until they are close to the browse line, when they quickly turn round and swim back to feed in shallower water. In many hot spring inlets dead fish can be seen on the bottom, having succumbed to the temptation to cross the browse line in the course of feeding.

In 1962, in company with Professor LEONARD BEADLE, the author visited these lagoons and collected fish in order to study their breeding behaviour in the laboratory in Nairobi. Fish were removed from water at 36°C and placed in a large plastic bag of water that had inadvertently been removed from the proximity of a hot spring. In three minutes all the fish were dead and when the temperature was measured, it was found to be close to 41°C. Since this time this experiment has been repeated in the field and it has been found that fish that are behaving quite normally and feeding in water of 38°-39°C are rapidly killed when transferred to water at 42°C. In nature it is suspected that the fish often pass through water much closer to their lethal limit, which appears to lie between 41° and 42°C.

Limited experiments have been carried out in the laboratory in Nairobi where it has been found that a high water temperature is essential to the fishes normal high state of activity. If fish tank water prepared from crystalline trona with a specific gravity of about 1.02 and a pH of 10.3-10.5 was kept stocked with fish, providing the water temperature was maintained above 32°C, they were very active and soon assumed courting colouration and bred. If, however, the water temperature was allowed to fall to room temperature (20°-23°C), the fish became sluggish and rapidly lost their courting colours, both males and females becoming a rather dirty greenish brown. At this temperature the fish spent most of their time at the bottom of the tank and fed intermittently with a complete lack of their normal vigour. After 48 hours the water temperature was again raised, and the fish quickly responded with an increase in vigour. In 36 hours the males had reassumed their bright courting colours and started digging pits.

It would appear that the high water temperature and high metabolic rate associated with it have been important factors in the survival of this small fast-moving fish that lives in shallow water where large numbers of Avian predators are an ever present danger.

The fishes' tolerance to temperature is paralleled by its equally remarkable tolerance to changes in pH and Specific Gravity. COPLEY (1958) reported that he had kept *T. grahami* in fresh water and that they increased in size until they were indistinguishable from *T. nilotica*. Undoubtedly the fish can be transferred to fresh water but from the authors' experience with these fish they do not even when kept as monosex groups become very much larger than 3-4 inches. When transferred from soda water to tap water also maintained at a high temperature, the fish show a preliminary loss of vigour but soon adjust themselves, resume their activity and assume breeding colour. They have not, however, produced or reared eggs under these conditions. If the temperature of the tap water is allowed to fall to room temperature, the reaction is the same as that described in soda water, the fishes becoming sluggish and losing all breeding colour. The mortality rate in transferring fish from soda water to tap water is no higher than that associated with transporting the fish from Magadi to Nairobi (about 30%).

At present there is no evidence relating to the mode of osmoregulation employed by the fish when transferred in this way. Sections cut of the gills of young fish do not show an appreciably large number of secretory cells, but the hind gut is thickened and brownish in colour, which may indicate that this latter site is the main organ of salt balance. This important aspect of the fishes' biology is one that needs a series of long and carefully controlled experiments before the balance mechanism can be understood.

Breeding Behaviour

Apart from the original description of this species (BOULENGER, 1912) the only documented account of the fishes breeding habits is found in WOODHOUSE (1912) in which he gives a fairly detailed description of the fish digging pits, the females laying their eggs and leaving them to hatch. Since *T. grahami* is a "mouth" brooder, it is difficult to see how WOODHOUSE could have made such an error unless he watched the males digging pits and then later observing fry in the vicinity presumed that the eggs had been laid and left to hatch in the courting pits. *T. grahami,* like so many other members of this genus, is a "mouth" brooder. Even COPLEY (1958) comments somewhat ambiguously that "breeding is the same as in other *Tilapia*."

Other than in periods of flooding (WHITE, 1953) when the lagoons are considerably diluted, the physical conditions prevailing in these waters remain remarkably constant. It is not therefore surprising to find that breeding has been observed by the author in January, March, April, May, August, September and December. In the laboratory some males have remained in breeding colour almost continuously for a period of two years. It is possible though that under adverse conditions breeding may be slowed down or even stop altogether for short periods.

This suggestion is supported by observations made on *T. alcalica* in Lake Natron, which was visited in May 1962. At this time the shallows contained large numbers of fish concentrated in dense shoals. When trapped it was found that the shoals were made up of predominantly male fish, and of several hundred examined only a very small percentage displayed breeding colour. Since when these fish were collected there had been considerable flooding a short time before, the lack of breeding males is probably here again be related to sudden dilution of the water. At the same time when the depth of the water is suddenly increased it is possible that the temperature may also be lowered until insolation and hot springs can once more raise it to a level more suited to breeding.

The non breeding colour of a male *T. grahami* is a pale blue with dark fins. When, however, they enter their courtship drive, the male becomes very brightly coloured. (Plate 3).

Male Breeding Colours

The following are taken both from fish maintained in captivity and those caught in the wild.

Head: Lower lip broad, fleshy, and brilliant Chinese white. Upper lip and top of head grey-mauve. Sides of head to operculum pale irridescent blue. Black spot on posterior angle of operculum. Throat deep mauve. Eye with black stripe across pupil, white above and below. Iris edged with orange.

Body: Belly silvery white. Dorsal side of body black to dark grey. Pale black stripes down side of body between posterior edge of operculum and the base of the caudal fin. Stripes composed of black patches on the anterior edge of lateral body scales. Body between lateral stripes green-blue.

Fins: Pectoral fins colourless to yellowish, often edged with black. Pelvic fins black with black patch on chest between fin bases. Dorsal fin black along anterior and dorsal edge, ventral segment transparent with black diagonal stripes composed of black spots on inter ray membranes. Anal fin edged with black; black stripes composed as in the dorsal fin, along transparent segment. Caudal fin pale with black diagonal stripes composed as above. Either edged or wholly brilliant red-orange. The female is a much less colourful fish and during breeding the non-breeding colours are merely intensified.

Female Breeding Colours

Head: Lips grey-green. Outer edge of lower lip with a thin white pear shaped patch tapering from back to front. Top of head grey green. Sides of head grey green. Sides of head and operculum pale green-brownish. Faint black patch on posterior border of operculum. Eye stripe as in male but very indistinct. No white on eye.

Body: Belly white. Dorsally pale greenish brown lightening towards white belly. Seven faint black stripes laterally.

Fins: Pectoral fins colourless to yellow. Pelvic fins colourless, outer edge black. Dorsal fin, anterior edge dark grey. Diagonal stripes across posterior segment, composed as in the male. Anal fin colourless with pale grey border. Caudal fin colourless with faint grey diagonal stripes.

The initiation of the breeding drive is not clear but in the laboratory it has been found that it is possible to induce the production of breeding colouration by temperature changes. Fish caught in the South West lagoon and maintained in the laboratory in soda water at 36°-37°C produced breeding colour rapidly in all mature fish. Over a long period the majority (about 80%) would exhibit breeding colour while the remainder lost their colour for short periods. If, however, the heaters were turned off, the water would fall to room temperature (21°C) and in 24 hours all fish had lost their breeding colours. These could be reinduced by reheating the water to 37°C when in a further 24 hours most of the fish had resumed breeding colour.

In all male fish in full breeding colour seminal fluid could be squeezed from the genital opening. It will be seen that in the lagoons where the fish have a strictly segregated habitat the sex drive would seem to be predominant. When, however, this is in conflict with a feeding drive, the male will leave his courting pit and move off to the feeding grounds. Since large numbers of brightly coloured males can be seen browsing on the algae-covered gravel in the shallow lagoon, they do not lose their colour when they terminate their courtship activities to feed. In the laboratory the fish do not change colour when they leave their pits to feed, but since the area of the tanks is quite small (5.4 sq.ft.) they are never as far removed from their pits when feeding as they are in nature where the distance may be as much as 100 feet. There does not seem to be a proximity factor influencing the maintenance of colour even in the wild.

Breeding Pit Construction

When fish assume the breeding colour phase, the males immediately become aggressive and begin to construct their courting pits. This they do in areas of ooze or sediment, though in some cases where the water is flowing fast and no sediment collects, the males occupy a small area from which they remove gravel to create a shallow depression. If it is possible, the fish show a preference for constructing their pits against a solid object (a sand bag wall in the Fish Springs Lagoon or rocks in the South West Lagoon). In tanks in the laboratory except where a particularly large number of males are present pits were always constructed in the corners or along the side.

The first sign of pit construction activity is when the male swims around suitable localities rubbing his belly against the bottom and in this position lateral body movements create a small primary depression. After several such preliminary movements the fish will swim round the proposed site increasing the angle of his body to the horizontal until it is almost vertical. The tail is then vibrated from side to side so that the head is driven with some force against the bottom. At this moment the mouth is snapped open and shut thus filling it with gravel or ooze. Pectoral fin movements bring the animal back, head down at an angle of approximately 45° to the horizontal and the material held in the mouth is spat out by a sudden raising of the floor of the pharynx.

When pits are constructed in soft materials their average size is 6″ in diameter and 3″ deep. The edge is usually slightly raised though naturally this is always more distinct where the substrate is hard. In the softer sediments the wall usually take on a terraced appearance due to their collapse as the pit is constructed.

The male *T. grahami* is aggressively territorial at this time and will defend the pit against all other males who approach. The size of the territory varies according to the locality. In the South West Lagoon where the available breeding area is large the pits are about 2 feet apart, while in the Fish Springs Lagoon where the ooze shelf is quite small the pits are more closely packed, being often less than 1 foot apart.

Male Territorial Behaviour

While the male is constructing his pit, he will occasionally break away to half-heartedly pursue another male who approaches the area. On completion of the pit he becomes noticeably more aggressive. Here it must be remembered that the male will keep up a certain amount of clearing excavation until mating is completed. The pattern of behaviour here is very similar in its details to that described in general terms by BAERENDS (1950) for other Cichlids. For this reason only the main features of this activity will be described.

After completing the pit the male will swim backwards and forwards, occasionally swimming slowly away from the pit and then returning with a sudden dash to the centre of the pit where it hovers fanning the pectoral fins rapidly.

When another male approaches the pit, the resident fish swims backwards and forwards with increasing intensity in no specified directional pattern. The intensity of this agitated swimming increases until the intruder is less than 6″ from the edge of the pit, when the resident will turn and swim jerkily towards him, flicking the tail and erecting the dorsal fin erratically as he moves forwards. At the same time the pectorals are held laterally and moved backwards and forwards with a trembling motion.

When the two fishes are about an inch apart facing one another, the resident extends his pectorals and with a jerking motion of the tail moves forwards and snaps rapidly at the intruder's lips. This action is carried out by both fish but is initiated by the resident. Accompanying the snapping motion the resident male erects and collapses his dorsal fin rhythmically and at the same time expands the branchiostegal membrane which in frontal view increases the size of the head considerably. The black spots on the posterior angle of the operculum are by this movement brought into lateral view as large eye spots, in much the same way as recorded for the high intensity frontal display described for *Cichlosoma meeki* by BAERENDS (1950).

As in all recorded cases of such behaviour the intensity of the behaviour response may be related to the degree which the colour and aggressive behaviour of the intruder is developed. In cases where a young male not in breeding colour approaches a defended pit the resident male appears to be somewhat bewildered and "swimming on the spot" with pectorals and dorsals extended, the former trembling, it faces the intruder. Usually under these circumstance the intruder suddenly breaks away and flees, when the pursuit instinct in the resident is released, and he follows him butting at his belly. The only difference between this and the reaction of a resident male to a mature intruder fleeing is that the pursuit is quite short-lived and of obviously low intensity when immature males are involved.

In *T. grahami* there is little doubt that the degree of development of the fleshy white lower lip is the main indicator of sexual maturity, and this acts as the main, if not the only, releaser for aggressive behaviour in resident males.

A group of male fish maintained in the laboratory were tested for their reaction to a white lip, employing a green plasticene model fish with a strip of white plasticene fastened across the face horizontally. When the model was moved slowly on the end of a glass rod into a male's territory, the resident flew at it and carried out a violent frontal attack tearing large pieces of white plasticene away with his jaws. If the model was no removed after about two minutes, the resident male turned vertically and carried out displacement digging in front of the intruder. When the model was presented sideways with the white simulated lip patch placed laterally, the resident male attacked the patch in the same way as when the fish model was presented frontally.

This high intensity behaviour was only carried out when a white lip was present, for when the model was presented without a lip, the resident male nudged the model and snapped at it when it was brought within the pit bounds, but lacked the vigour and violence released by the presence of a white lip. The importance of the white lip as a sex-distinguishing character is well illustrated in Plate 4 where the mature males can easily be picked out. In fact in this case where the fish are observed from above the white lip is easily visible while the body outline is obscured.

Under normal circumstances, after frontal display the intruder will move slowly backwards to the edge of the territory when the resident male will carry out lateral display. This is initiated by a quick motion of the tail, which brings the male alongside his opponent. The two fishes will then direct blows against one another's sides with their caudal fins, and at the same time nudging movements are made against the opponent's belly. This action may be conducted with the two fishes remaining more or less stationary erecting and collapsing the dorsals rhythmically. Often though this stationary phase is followed by the fishes rapidly circling one another about a fixed point.

This latter circling movement is terminated by the intruder breaking away and being pursued with a fast jerky motion by the resident male. In nature pursuit will last for 1-2 feet and then be broken off by the resident male which will then return to his pit. In tanks though, since the area of potential pursuit is small, the action may continue for some time round the tanks' walls.

When on one occasion six mature males (2-2½) were kept in a tank 3′6″×1′6″, the whole bottom was covered with displacement pits so that no fish ever finished this first phase of courting behaviour. After seven days all the fish lost their breeding colours. When, however, four fish were removed from the tank, the remaining two quickly resumed breeding colour and completed pit building operations at opposite ends of the tank. Under these conditions the fish only came into contact and fought when they met in the course of their feeding operations.

It has already been explained that *T. grahami* shows a marked functional division of the lagoon into feeding, courting, maternity and nursery areas. In the South West lagoons some feeding will take place in most areas and is mainly carried out on algae-covered rocks along the edge of the rocky platform in the shallow lagoon. Hence when a male needs to feed he must leave his pit to do so. On such occasions they have been observed to swim out of their pit and then return to it; each time the fish leaves the pit it swims slightly further away before returning, until finally with a rapid dash it moves off to the feeding grounds. On such occasions another dispossessed male will often take over the pit, and when the resident returns, he will in turn be successfully repulsed as an intruder. In this way many of the pits change occupants several times during the course of digging and courting.

Courtship Behaviour

During the course of pit construction if a female approaches and enters a pit, the male will gently nudge her away with his nose. When, however, the pit is completed, the male will take up guard duties in the centre of his territory when his reaction to approaching females is quite different.

A female approaching the nest is faced by the male who will swim alongside her and nudge her belly. If the female is not gravid, the male will then ignore her, but if she has a swollen belly, she will often roll on her side as if to display its outline or the genital aperture to the male. After gentle nudging the female will swim fairly rapidly in and out of the pit. When this occurs, the male will follow her and swimming alongside will turn the female with shouldering movements back into the pit. This action is carried out with the pectoral fin closed on the side towards the female, and the opposite fin being rapidly fanned. In this way the male's body seems to be driven against the female so that she is turned back towards the nest.

Pointing and leading behaviour may go on for some time and in many cases the female will break off and leave the male to visit another pit in the vicinity. When the female remains with the male, she soon begins nudging him in the genital region. The response of the male to this action is to gently vibrate the hind end of the body, reminiscent of the action observed when at the end of courting the male ejaculates his sperm over the eggs. Males will carry out this trembling action when nudged by a young male, female or even when rubbed in the genital region with a fine rod.

The latter stages of courtship are observed when the female starts to swim rapidly in and out of the nest in the same manner as a guarding male. Latterly she will on entering the nest swim to the bottom and rub her belly, after which the male will join her and the two fish will carry out a gently circling movement nudging each other with their noses and flapping with their caudals. Though reminiscent of circling in rival males this action is not as intense.

The final phase of egg laying and fertilization has not been observed at the time of writing so it is not yet clear whether the eggs are fertilized on the bottom or whether after deposition the female picks them up and they are then fertilized in this situation. The time taken from courtship to egg laying varies with individuals, in some cases eggs have not been laid for 24 hours while in others observed in the laboratory fish that started courting at 10.00 hours have finished egg laying and the female has been driven from the nest by 13.00 hours.

Brooding

Once courtship and mating are completed the females move with their eggs in their mouths to what might be called the "brooding area" where they congregate with a number of feeding mature and non mature males. Brooding eggs in their mouths does not in any way seem to affect the female's capacity to feed. This is clearly demonstrated when females are caught and made to disgorge their young or eggs, which are always mixed with large quantities of newly browsed algae. Brooding females are found largely in shallow water and in the deeper pools held by the rocky platform.

The number of eggs lost due to the cannibalistic habits of males and non breeding females is high. Both in nature and in the laboratory fish can be observed swimming close to a brooding female and dashing to her mouth to snatch protruding eggs or fry. Thus during the brooding period the number of eggs or fry carried in the mouth is gradually diminished. It is of course possible that the mother herself occasionally swallows one of her own young though this is difficult to prove, and so far the stomach contents of brooding females have not demonstrated the presence of young fish.

When eggs are first laid, they are almost 2 mm in diameter, and the fry are released after brooding for 12-16 days when they are 8-10 mm long. It is inevitable that the number of young will in any case be reduced if the female is to carry them efficiently. This gradual reduction was demonstrated when fish were caught in a flat steel-framed net 1 metre square. All females caught were measured and the number of eggs or fry carried were recorded. In this investigation in which nearly 250 fish were examined it was

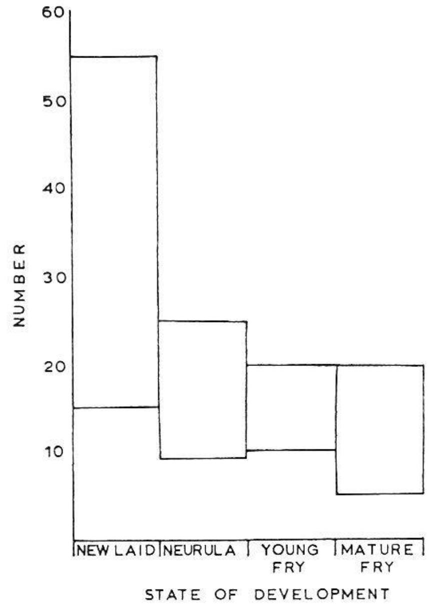

Fig. 7. Size range of eggs and fry removed from brooding females.

found that the shortest male found in breeding colour from which semen could be squeezed was 35 mm long, while the smallest brooding female was 25 mm long. The number of eggs carried at the outset was higher in the larger females. In a female 68 mm long 55 eggs were recorded while the largest number of eggs recorded in the smaller females (25-35 mm) was only 20. Such measurements are often made difficult in nature since when females are trapped they often disgorge some of their eggs or fry into the net before they can be examined.

The number of eggs or fry recorded (over the whole female size range) is shown in Figure 7.

Development of Eggs and Fry

When the first fish bred in the laboratory in February 1960 the eggs and fry were removed from the females and drawn. Since the appearance of eggs in this brood were noted it was possible to draw up a developmental sequence. This data is shown in Table 3 and Figure 8.

TABLE 3.

Development stage	Size	Age
New laid egg	1.8 mm diam.	0
Neurula	2.1 mm length	2 days
Small fry. Large yolk sac	4.0 mm	6 days
Medium fry. Yolk sac small	7.8 mm	11 days
New released fry	9.2 mm	14 days

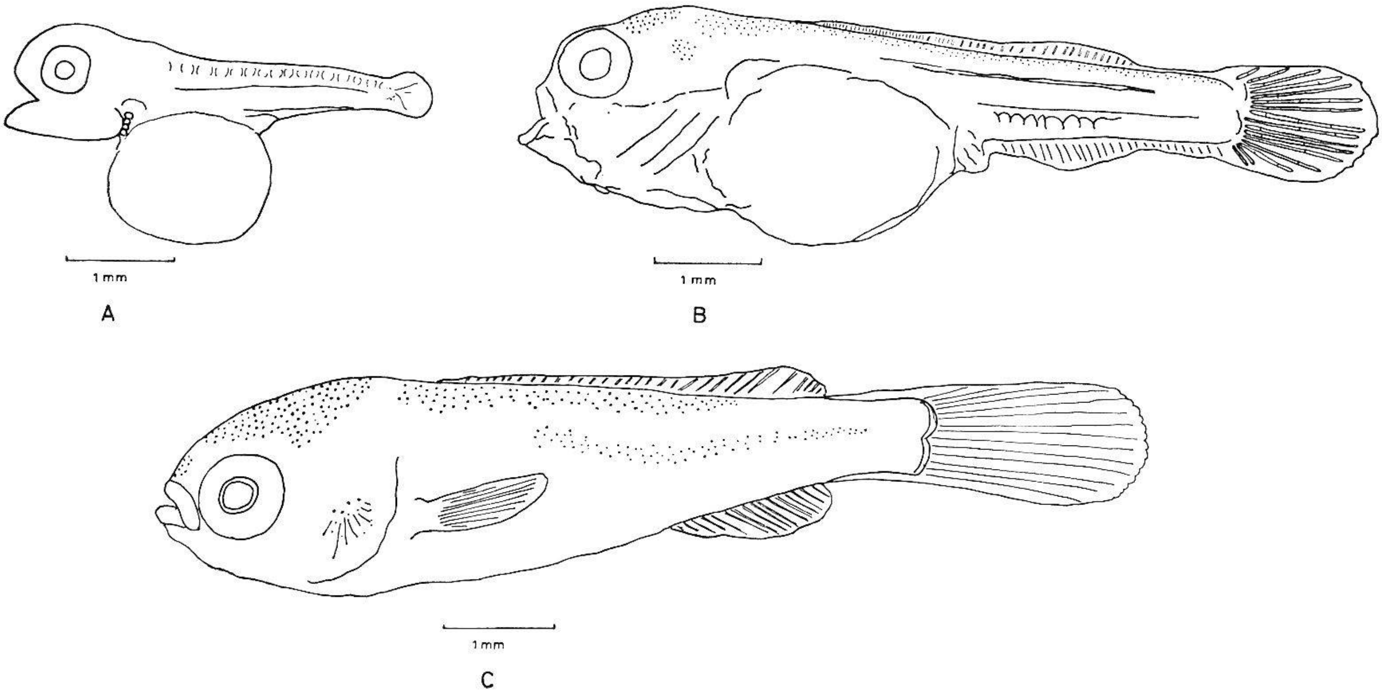

Fig. 8. Fry bred in the laboratory in Nairobi (A: 6 days, B: 11 days, C: 14 days).

Termination of Brooding

When the young fry are mature (8-9 mm), the females once more move to a new site where they are released. These are areas of shallow water either at the edge of the lagoon or along spring courses. At the Fish Springs Lagoon site the latter is the most usual situation, while in the South West Lagoon the fish have adapted an area of eroded cunker where a whole series of springs flow into the junction of the main and the shallow lagoon. This "nursery" area once more demonstrates grahami's remarkable tolerance to high water temperatures. In the main flow courses water temperatures may be as high as 41 °C while in small side cunker sheltered bays the water is only 37 °C. In order to reach these cool protected situations the female must swim through the hot spring courses, where often the water is so shallow that the fishes' back is completely exposed, in order to reach the cooler water where they will release their young. There is no evidence that once released the females show any maternal instinct towards their own young. The main features of a typical fry release site of this type is shown in Fig. 9.

Once released the young remain in this situation until they are about 15 mm long when they return to the main lagoon via the hot channels to join the large non breeding shoals.

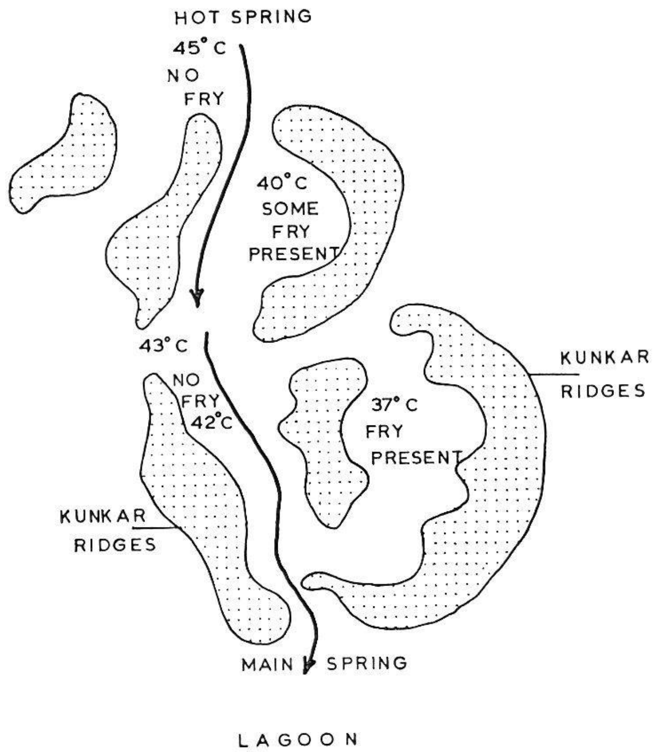

Fig. 9. Sketch map of a small sector of the "nursery" shallows.

Predation

Even though the young are free from the predatory attentions of adult fish in the shallows, they are constantly open to the danger of predation by birds. Black Winged stilt (*Himantopus himantopus* Lin.), Avocet (*Recurvirostra avosetta* Lin.), Blacksmith Plover (*Hoplopterus armatus* Burchell), Magadi Plover (*Charadrius venustus* Fischer and Reichenow), Little Egret (*Egretta garzetta* Lin.), Spoonbill (*Platalea alba* Scop.), and numerous waders have all been seen feeding in these "nursery" shallows. The Lesser Flamingo (*Phoeniconais minor* Geoff.), and Greater Flamingo (*Phoenicopterus ruber* Pallas) have also been seen feeding in the springs, and while their main food is zoo- and phytoplankton it seems likely that in this situation they also take, in the process of filtering their food a number of young fry.

In deeper water the adults are preyed upon by White and Pink Backed Pelicans (*Pelecanus onocrotalus* Lin. and *P. rufescens* Gmelin), Gull Billed Tern (*Gelochelidon nilotica* Gmel.), Cormorant (*Phalacrocorax lucidus* Licht.), Darter (*Anhinga rufa* Lace.), Wood Ibis (*Ibis ibis* Lin.), and Sacred Ibis (*Threskiornis aethiopicus* Lathum). The Pelicans appear to be particularly successfully paddling forwards through the water with their necks extended and snapping their bills rapidly open and shut close to the surface.

The Evolution of T. grahami

Fourty feet above the present lake level lie the High Magadi Beds, which were first described and thus named by TEMPERLEY (1951, pp. 15-16). These deposits represent remnants of old lake deposits which were almost certainly laid down as a result of periodic flooding of the lake's surface. WHITE (1953) has described the laminations in lake cores and has attributed them to this cause.

This has more recently been observed when we dug pits in the Southern lagoons and noted alternate layers of soda, black wind blown deposits and other evaporation detritus. The complete lack of faulting or tilting of this series suggests that this area of the Rift Valley has been comparatively stable since these deposits were laid down, and that they now give a fairly accurate picture of the area the lake must have covered in the past.

The beds examined when working at the lake lie in a small dry lagoon on the motor track from the Magadi township to the South West Lagoons. The deposits at this site have been laid down over lava and consist of faintly laminated pale brown silts. At the base of the silts is found a layer of dark brown laminated clay which contain a dense band of black fish fossils 5″ thick. These fish fossils were examined by COPLEY, then Kenya Fish Warden, who stated that they were *T. nilotica* (BAKER, 1958). Since the present study was started, PETER WHITEHEAD of the Department of Ichthyology, British Museum (Natural History) has examined the fossils and considers that they were not *T. nilotica,* but bore a superficial resemblance to the modern lake form *T. grahami* (WHITEHEAD 1959, personal communication). This aspect of the work is still continuing.

The fossil fish are large compared to their modern counterparts, being up to 8″ in length, and it has been suggested that since the last pluvial period when the lake began to dry up, the resulting dessication has led to a marked decrease in size (COPLEY, 1958).

While undoubtedly this has been a contributory factor to decrease in the fishes' size, there is in my mind little doubt that natural selection for a small fast-moving fish as the lake crystallized out and the fish were driven into the shallow water of the lagoons has been the most important factor in the evolution of this species. In addition the selection pressure for a small fast-moving fish must have been considerably accentuated by the presence of a large number of predatory birds in the shallow waters of the lagoons. At the present time except during periods of flood the fish have been slowly driven to extreme conditions of high alkalinity, temperature and pH, and although there is no evidence that the output of the springs is decreasing (STEVENS, 1932), should this happen in the future, the species will be wiped out.

At present it is difficult to say if the water was more dilute in the past when the High Magadi Beds were laid down than at present. There is, however, an indication from diatoms collected from the dry lake beds of Ollorgesaillie, some 20 miles NE of Magadi that at the time this lake contained fresh water (ISAAC, 1964, personal communication). Similar observations on diatoms from the High Magadi Beds should indicate the state of Magadi's water during the period of its maximum extent.

Fossils recovered from these deposits are at present being submitted to C 14 analysis, by which means it is hoped that it may be possible to gauge the speed at which the process of drying took place.

The problem of speciation in Lake Magadi is of greater interest when consideration is given to the other alkaline Rift Valley Lakes occurring to the South. Lake Natron which lies about 20 miles South of Magadi contains *T. alcalica* Hilgend a species which bears strong superficial resemblances to *T. grahami,* while still further south Lake Manyara contains another species *T. amphimelas* Boulenger.

T. alcalica was described as having been collected in the Nguruman Salt Lake, German East Africa. In fact this lake cannot be found on even the old German maps of Tanganyika, and since the Western shore of Natron is bordered by an extension of the Nguruman escarpment, there seems little doubt that the lake referred to was Lake Natron. This ambiguity in place names was repeated as recently as 1958 by COPLEY in his "Common Fresh Water Fishes of East Africa".

T. amphimelas occurs in small springs around the margin of Lake Manyara and was studied by the Makerere College Expedition to Lake Manyara in 1960 (KINOTI, 1961). Both this species and *alcalica* bear close superficial resemblance to *T. grahami,* and at least in *alcalica* their behaviour is also very similar.

Unfortunately this sector of the Rift Valley is poorly surveyed, so it is difficult to determine if there have been any connections between Magadi and Natron with perhaps an outflow during periods of flood to Manyara in the south. After travelling extensively in the intervening ground between Magadi and Natron it seems highly likely that at the time the High Magadi Beds were laid down that the two lakes were in some sort of connection by a route lying East of Shomboli.

In the last two years fossil deposits have been reported for Natron by Zaphiro and independently by ISAAC (1964, personal communication). While further south MORGAN-DAVIES has found fish fossils similar to those of the Magadi Beds East of Lake Manyara (personal communication 1963). It is to be hoped that all these deposits may be compared in the near future in order to determine if the present small species have a common ancestor. Together with Carbon dating it may be possible to obtain a time scale for their speciation.

Acknowledgements

I should like to thank the Magadi Soda Company for their help in supplying climatic data on Lake Magadi and for other facilities during field trips to the lake. Also the University College, Nairobi, for financial assistance towards this work.

For valuable discussions and suggestions I am particularly endebted to Brian Baker of the Kenya Mines and Geological Department, Peter Whitehead of the Department of Ichthyology, British Museum (Natural History) and to Professor Leonard Beadle of Makerere College, Uganda.

During field work at the lake I must thank my wife, Unity Coe und my many colleagues in the University College, Nairobi, who have suffered the blistering heat of the Soda Flats without complaint to assist in these investigations.

Bibliography

ANONYMOUS. (1923). The Soda deposits of Lake Magadi in Kenya.

BAERENDS, G. P. & BAERENDS-VAN ROON, J. M. (1950). An introduction to the ethology of cichlid fishes. — Behaviour, Supplement 1, 1-243.

BAKER, B. H. (1958). The geology of the Magadi area. Geolog. Survey of Kenya, Report No. 42. — Government Printer, Nairobi, pp. 1-81.

BEADLE, L. C. (1962). The evolution of species in the lakes of East Africa. — Uganda J. *26,* 44-54.

BOULENGER, G. A. (1912). Description of *Tilapia grahami*-Type. — Ann. Mag. Nat. Hist. (8) IX, 519.

BOULENGER, G. A. (1915). Catalogue of the fresh water fishes of Africa. Vol. II, pp. 211-212. — B. M. (Nat. Hist.), London.

COPLEY, H. (1958). Common fresh water fishes of East Africa, pp. 27-32, 116-129. — London.

FISCHER, G. A. (1884). Bericht über die im Auftrage der Geographischen Gesellschaft in Hamburg unternommene Reise in das Masai-Land. — Mitt. Geogr. Ges. Hamburg, 1882-1883, Pt. 1. Allgemeiner Bericht, pp. 36-99.

FISCHER, G. A. (1885). Ibid., Pt. 11, Begleitworte mit Original-Routenkarte, pp. 189-237.

GREGORY, J. W. (1921). The rift valleys and geology of East Africa, pp. 178-183. — London.

ISAAC, G. L. (1964). Personal communication.

KAISER, A. (1898). Die Schöllersche Expedition in Aequatorial-Ost-Afrika. — Bericht St. Gall. Naturwiss. Ges., 1896-1897, pp. 314-342.

Livingstone, L. A. (1963). Data of geochemistry, 6th Edition, Chapt. G. Geol. Surv. Prof. Paper 440 G. — U.S. Gov. Print. Off., Washington. p. Gg.

Loeffler, H. (1960). Personal communication.

Lyons, L. A. (1952). Magadi Soda, Mine and Qu. Eng., Vol. 18, pp. 249-251.

Morgan-Davies (1963). Personal communication.

Parkinson, J. (1914). The East African trough in the neighbourhood of the soda lakes. — Geogr. J., *44*, 33-49.

Stevens, J. A. (1932). Lake Magadi and its alkaline springs. Unpublished report to the Magadi Soda Co. Ltd., Kenya.

Temperley, B. N. (1951). Some geological and geophysical observations in the vicinity of Lake Magadi. Mines and Geological Dept., Nairobi. (Unpublished.)

White, T. H. (1953). Some speculations on the sudden occurrence of floods in the history of Lake Magadi. — Journn. E. A. Nat. Hist. Soc. Vol. XXII, No. 2 (94), pp. 69-71.

Woodhouse, G. W. (1912). The fish in Lake Magadi. — Journ. E. A. Nat. Hist. Soc. Vol. II, No. 4, pp. 95-97.

Zusammenfassung

1. Die allgemeine Physiographie der Region Magadi-See, Kenya, wird kurz beschrieben.

2. Das Klima ist hauptsächlich durch zwei Regenzeiten, eine von März bis April, die andere im Dezember, gekennzeichnet. Für 1957—1964 werden die Niederschlagsmengen angegeben und ihre Bedeutung für die Überflutung des Seespiegels diskutiert. Die Temperaturen, welche von den städtischen Stellen festgehalten wurden, schwanken zwischen 22° C bis zu 42,2° C.

3. Vulkanische Quellen liefern genügend heißes alkalisches Wasser für die *Tilapia grahami*-Schwärme. Die Beschaffenheit und Zusammensetzung der Quellwässer wird untersucht. Die Fische vermehren sich in der Regenzeit, wenn die Lagunen durch die Überflutung mit dem See verbunden sind.

4. Der Autor untersuchte vor allem die Fish Spring Lagoon und die South West Lagoon und zählt die wichtigsten Biotope auf.

5. Die Fische in den Lagunen können Wasser von hoher Temperatur (bis 39° C), alkalischer Reaktion (pH 10,5) und einem spezifischen Gewicht von 1,01—1,03 ertragen. Trotz der hohen Wassertemperatur ist die Abkühlung des seichten Wassers durch Strahlungsverlust in der Nacht groß und beeinflußt die lokalen Wanderungen der Fische beträchtlich.

6. Es wird angenommen, daß eine Wassertemperatur von ungefähr 41° C für die Fische tödlich ist. In den Lagunen halten sich die Fische während langer Zeit in einem Bereich von 2° C unter dieser Grenztemperatur auf.

7. Im Laboratorium konnte nachgewiesen werden, daß die Wassertemperatur die Aktivität der Fische und das Zustandekommen der Paarungsfarben (Hochzeitskleid) stark beeinflußt.

8. *T. grahami* ist ein Maulbrüter und dieses Verhalten wird unter natürlichen und unter Laborbedingungen beschrieben. Die Paarungsfarben des Männchens und des Weibchens werden zum erstenmal eingehend geschildert.

9. Das Männchen baut Gruben ähnlich wie es von andern Cichliden bekannt ist.

10. Männchen im Besitze einer Grube verteidigen aggressiv ihr Revier, und es hat sich gezeigt, daß die vorstehende weiße Lippe als Kampfsignal dient, wenn immer ein reifes Männchen versucht in eine besetzte Grube einzudringen.

11. Paarungsverhalten und der Beginn des Laichens werden kurz beschrieben.

12. Die Lagunen sind in Futter- und Paarungsterritorien aufgeteilt. Außerdem suchen die brütenden Weibchen zur Aufzucht der jungen Fische speziell seichte Stellen (nurseries) auf, sobald die Brut reif wird. Dabei müssen sie oft Stellen passieren, deren Wassertemperatur beinahe die letale Grenze erreicht.

13. Die Entwicklung der Eier und der Brut wird kurz geschildert und illustriert.

14. Zahlreiche Wasserraubvögel wirken als Kontrollfaktor für die Anzahl der Fische in den Lagunen.

15. Die Beziehung des fossilen *Tilapia,* welcher 40 Fuß oberhalb des heutigen Seespiegels gefunden wurde, zu den rezenten Formen wird kurz diskutiert.

16. Andere kleine *Tilapia*-Arten vom Manyara- und Natron-See zeigen ausgeprägte äußerliche Ähnlichkeit mit der Magadi-Art. Weitere Untersuchungen der heute lebenden und der datierten fossilen Formen können vielleicht zu einer Evolutionslinie für die Bewohner der Salzseen des Rift Valley führen.

Résumé

1o La physiographie de la région du lac Magadi (Kenya) est brièvement décrite.

2o Le climat montre 2 saisons des pluies dominantes, l'une de mars à avril, l'autre en décembre. Les quantités de pluies pour la période 1957–1964 ainsi que leur rôle dans l'inondation du bassin du lac sont discutées. Les températures enregistrées à la mairie varient de 22° C à 42,2° C.

3o Des sources volcaniques fournissent aux communautés de *Tilapia grahami* un approvisionnement abondant en eau chaude alcaline. La nature et la composition de ces eaux de sources sont décrites. L'isolement apparent des lagunes n'existe plus en période d'inondations, c'est-à-dire quand les poissons se reproduisent.

4o Les études principales ont été limitées à la lagune « Fish Spring » et la lagune « South West ». Les deux régions sont décrites et les habitats principaux sont énumérés.

5o Les poissons vivant dans les lagunes peuvent supporter des températures élevées (jusqu'à 39° C), une alcalinité de pH 10,5 et une densité spécifique de 1,01–1,03. Malgré les hautes températures, le refroidissement de l'eau peu profonde par rayonnement pendant la nuit est grande et a un profond effet sur la migration des poissons.

6o 41° C semble être la température létale. Le poisson des lagunes passe la majeure partie de son temps à une température de 2° inférieure à cette limite.

7o Au laboratoire, on a montré que la température influe sur l'activité des poissons et sur le développement de leurs couleurs nuptiales.

8o *T. grahami* incube les œufs dans sa cavité buccale et des observations sur cette habitude, faites au laboratoire et dans la nature, sont décrites. Les couleurs nuptiales du mâle et de la femelle sont décrites en détail pour la première fois.

9o Des trous sont construits par le mâle selon une technique révélant des similarités avec les autres espèces de Cichlidés.

10o Alors qu'il est en possession d'un trou, le mâle défend son territoire de manière agressive, et la lèvre blanche proéminente agit comme un signal de bataille lors de l'intrusion d'un autre mâle mûr.

11o Le jeu de la séduction et l'initiation au frai sont brièvement décrites.

12o Aux divisions de la lagune en un territoire de chasse et un territoire de parade s'ajoute un territoire pour les jeunes (nursery) au moment où les

femelles prêtes à frayer émigrent. Alors les poissons doivent de nouveau traverser des eaux où la température est proche de la limite létale.

13° Le développement des œufs et du frai est brièvement décrit.

14° Les grands oiseaux aquatiques prédateurs jouent un rôle important dans le contrôle du nombre des poissons de ces lagunes.

15° Les relations entre un *Tilapia* fossile, trouvé 40 pieds plus haut que le présent lac, et les *Tilapia* modernes sont discutées.

16° D'autres petites espèces de *Tilapia* des lacs Manyara et Natron montrent une étroite ressemblance, du moins de leur aspect extérieur, avec ceux du lac Magadi. Des études ultérieures sur les formes vivantes et fossiles permettront peut-être l'établissement d'une lignée évolutive valable pour les habitants des lacs alcalins de la Rift Valley.