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Gonadal and reproductive patterns in *Tilapia leucosticta* (Teleostei: Cichlidae) in an equatorial lake, Lake Naivasha (Kenya)

MOHAMED HYDER

Department of Zoology, University College, Nairobi, Kenya

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(With 2 plates and 3 figures in the text)

The cichlid fish *T. leucosticta* (Trewavas) was studied by fortnightly seining an area of an equatorial lake (Lake Naivasha) in Kenya to study their reproductive and gonadal patterns. The study lasted 16 months during which period temperature, rainfall and (for the last 11 months) sunlight patterns were obtained and analysed. Testicular and ovarian development was lowest in the months of July-August. No evidence of breeding was detected during this period. This period is also marked by the lowest rainfall, the lowest temperatures and least sunlight. Slight but fluctuating breeding activity and gonadal development is resumed in October following increased sunlight and temperatures from September. The period December to February is marked by sustained high temperatures, high sustained maximal sunlight and low rainfall. It is also the period of rising gonadal development in most mature males and females reaching a peak in both sexes in February. This is followed shortly after by a sharp peak in reproductive activity. It is concluded that sunlight and temperature are the most important factors influencing gonadal development and subsequent breeding in *Tilapia* even under equatorial conditions. When preceded by conditions of sustained high temperatures and good sunlight which are conducive to the maximal development of the gonads of both sexes, the onset of rainfall seems to stimulate the initiation of the peak breeding activity. Sustained heavy rainfall on the other hand seems to check breeding.

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Introduction

Peak annual reproductive activity in temperate fishes has been repeatedly demonstrated (see reviews by Pickford & Atz, 1957; Hoar, 1957; Dodd, 1960; Atz & Pickford, 1963;

and a brief survey by Hyder, 1969*a*). The principal external factors which are associated with synchronous reproductive activity have been shown to be daylength and temperate (see above reviews as well as Amoroso & Marshall, 1960).

In the tropics daylength has also been shown to be an important factor in the reproduction of some higher vertebrates (Marshall & Corbet, 1959). Tropical fishes have by and large been little studied from the point of view of their annual reproductive activity and the relationship this might have with external environmental changes. The few people who have made detailed studies on the gonadal changes of tropical fishes are Ghosh & Kar (1952) on the common Indian catfish, *Heteropneustes fossilis*; Nair (1959) on the Indian shad, *Hilsa ilisha*; Sathyanesan (1961) on *Barbus stigma*; Rai (1965) on *Barbus* (= *Tor*) *tor* and Chan & Philips (1967) on the synbranchid eel, *Monopterus albus*.

If the zone is narrowed to the equator, then there are almost no comprehensive studies although observations have been made at different times on different fishes in different bodies of water.

Several such observations have been made particularly with respect to perhaps the most economically important fish of tropical African freshwaters—the cichlid fishes of the genus *Tilapia*. *Tilapia* have been much studied from the point of view of their reproductive behaviour because of their extraordinary mouth-breeding activity (see reviews by Aronson, 1957; Baerends, 1957; Lowe, 1959; Breder & Rosen, 1966; Hyder, 1966) and in recent years this has been particularly studied by Wickler's and Peter's schools in Germany. *Tilapia* has also been most intensively studied from the taxonomic point of view and this aspect has been particularly enriched by the long series of studies by Trewavas. As yet, however, such information as we have on their annual reproductive patterns has been only in the form of several observations (see review by Lowe, 1959). Lowe has probably undertaken most of the field observations on different species of *Tilapia* in different parts of Africa—particularly East and Central Africa—and these are documented in several publications (mostly reviewed by Lowe, 1959). Her own conclusions have been that rainfall is probably the major external factor in stimulating breeding activity in *Tilapia*. Fryer (1961) finds no correlation between rainfall and the reproductive activity of *T. variabilis* (one of the two endemic species of *Tilapia* in Lake Victoria) although an earlier study on both species by Lowe (1956) was inconclusive with respect to the breeding of this species. Aronson (1957) came to opposite conclusions to those of Lowe on the relationship of rainfall to the reproductive patterns of the West African species, *T. macrocephala*—namely, that it showed a marked drop in spawning frequency during the period of heavy rains. He is inclined to the view that light is probably the critical factor in inducing both gonadal development and breeding activity and noted the breeding intensity increasing in *T. macrocephala* specimens in a greenhouse in New York at the autumnal and vernal equinoxes.

Suggestions that light is an important factor in the reproduction of *Tilapia* have also been made by Pickford & Atz (1957) and these have been supported by a study of the histology of the testes of pond specimens of *T. nigra* (Hyder, 1970). Hyder (1970) also suggested that temperature is probably a relevant factor.

The problem to date has been that no systematic annual study of gonadal patterns has been made in *Tilapia* supported by data on gonad weight, gonad histology and an assessment of the impact of external factors (particularly light) on these gonadal and reproductive patterns. The earlier study by Hyder (1969*a*) was primarily a detailed background study of the histology of the *Tilapia* testis. The specimens obtained for this previous study were neither regularly obtained nor did they provide a useful enough cross-section of the female population to permit acquisition of sufficient evidence of any seasonal reproductive activity and the possible impact that external factors might have on it. In late 1967, however, a site on Lake Naivasha was identified where seining recovered both sexes and practically all age groups of *T. leucosticta* and this permitted a more accurate assessment of their reproductive patterns. Hence the present study which was mounted in January 1968, and lasted 16 months till the end of April, 1969.

Materials and methods

An area of Lake Naivasha shore which yielded a range of size and sex of *T. leucosticta* was seined at fortnightly intervals throughout the present study using a 25 yard long seine net of 1 inch mesh in a standard uniform way. The whole catch was then taken back to the laboratory in Nairobi where the fish were put into 5 cm length groups (total length) thus: below 5 cm; 5–10 cm; 10–15 cm; 15–20 cm; 25 cm and over. Thirty fish (if available) from each length group were randomly selected for detailed measurements of total length, standard length, body weight and gonad weight. The rest of the fish were measured for total length only to get an idea of the length group distribution. Gonad samples were taken from each length group. These were fixed in Bouin, embedded, sectioned at 4–10 μm and stained with haematoxylin and eosin.

The numbers of brooding females (with eggs or young in the mouth) were recorded for each catch—i.e. all the fish in each catch were examined to see if they were bearing young or eggs. The ovary of one brooding female (when available) was additionally preserved for histological examination.

Mean daily maximum and minimum air temperature and rainfall records of Naivasha were kindly supplied by the E.A. Meteorological Organization of the East African Community.

Total radiation at the lake site where the regular fishing was being done, was also recorded for the eleven months from June 1968 to April 1969, using a Casella bimetallic actinograph. I am grateful to Mr C. Dunford of the Marina Club (Lake Naivasha) for making this possible.

Results

Maturation size

Males

From the histological examination of the gonads and milt production, maturity in the *Tilapia leucosticta* of Lake Naivasha appears to be reached in fish of approximately 18–20 cm total length. No fish of below 15 cm has been found to produce a free flow of milt or to show fully developed gonads or any histological signs of having spermiated. Nor have any fish of below this size been seen to have a well-developed interstitial tissue, sign of immediate spermiation in *Tilapia* (Hyder, 1970). In evaluating the reproductive patterns of the *Tilapia leucosticta* of this lake therefore, only these fish of above 15 cm total length are taken into consideration.

Females

The best guide to the maturation size of female mouthbrooding *Tilapia* is the identification of the minimum size of fish brooding young or eggs. Lowe (1955) has remarked on an observation that at times *Tilapia* fry may take shelter in the mouths of other than parent fish and in some cases of young fish. This investigation has yielded no evidence of this happening in the *Tilapia leucosticta* of Lake Naivasha. The tenacity with which this fish seems to hang on to eggs and young is quite remarkable as individual fish have been carefully observed during transportation to the laboratory and have shown no evidence of parting with the eggs or fry in the mouth. This is in agreement with the observations of Welcomme (1967) who found the same thing in the specimens of the same species that he studied in Lake Victoria.

It must be assumed thus that the fish caught with young or eggs in their mouth are actual parents and not foster parents.

From these observations, the smallest size of brooding fish was found to be 17·0 cm total length and 13·5 cm standard length. The majority however lay between 18·0 and 22·0 cm total length. It appears that the minimum maturation size of the female of *Tilapia leucosticta* under the specific conditions of Lake Naivasha would not be below 15·0 cm. No fish below this size has been found by macroscopic or microscopic observation to have mature gonads.

Patterns of testicular changes

As Fig. 1 shows the mean testis weight is not constant throughout the year. There are periods of high and low mean testicular weight even allowing for the variance about this mean. The mean G.S.I. (gonosomatic index = gonad weight/body weight × 100) patterns are almost exactly like those of mean testicular weight.

In male fish of 15 cm and over (total length), the highest mean testicular weight and mean G.S.I. throughout this study was noticed in mid-February 1968. This was followed by a sharp overall drop in mean testicular weight and mean G.S.I. both of which never recovered to the peak value observed in mid-February 1968. Eventually the mean testis weight and G.S.I. fell sharply in early June and remained low for about four months till late September 1968. Thereafter two short-lived peaks in early November and early December are seen before the main February peak reappeared in 1969. This was again followed by a prolonged fall in the mean testis weight and the mean G.S.I. and a further slow rise to another peak about three months later in late April when the study ended.

Histologically the changes in the testis may be conveniently divided into three principal phases according to the period of the year. These are from January to June, from July to September and from October to December.

January to June

This period may be described as the period of maximum maturity with a peak about early to mid-February (Plate I(a),(b),(f)). Depending upon general climatic conditions, another peak may come in late April-early May. The testes are most enlarged and the majority are in various phases of reproductive activity. The lobules show evidence of spermiation or else are full of sperm. The interstitial tissue is unquestionably maximally developed during this period. Individual fish, it must be remembered, can be at different phases of the reproductive cycle. It would appear quite certain that the area where the seining has been carried out was primarily a brooding area for the females which was also being used by males that are either about to establish territory or else are recovering from spermiation possibly before breeding yet again or moving out into the main body of the lake. Towards the end of this period most of the mature male fish are in a state of near exhaustion with most of the central lobules being completely devoid of sperm and the interstitial tissue showing signs of virtually complete breakdown (Plate I(c),(d)). Regeneration of spermatogenesis follows almost immediately after a series of spermiations by any

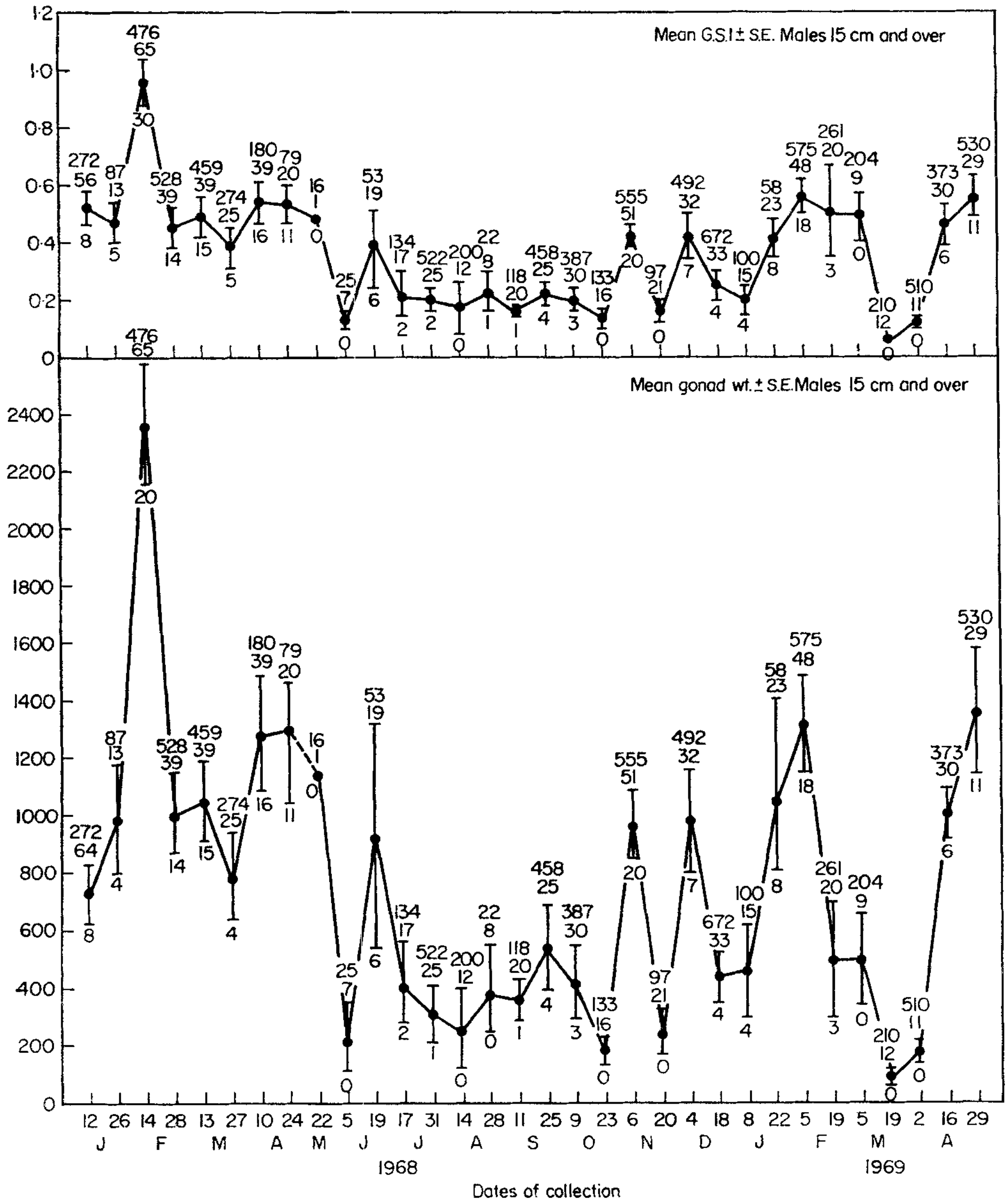

FIG. 1. Showing seasonal changes in the mean G.S.I. (±S.E.) and mean testis weight (±S.E.) of male *T. leucosticta* of 15 cm and over. The top figure at each point is the total catch for that date of collection. The figure below that is the number of males of 15 cm and over within that total catch. The bottom figure at each point is the number of males of 25 cm and over.

single male and it is probable that those males that had their spermiation earlier in the period would regenerate sufficiently for them to spermiate yet again should conditions continue to be favourable. No individual histories are known, however, and it is difficult to give any direct supporting evidence of this happening.

July to September

This period is, on the whole, marked by very quiescent fish that are recovering or else freshly maturing. The testes are on the whole of low weight and showing signs of retarded development. The number of males of 25 cm and above decreased considerably. They very probably move into the deeper parts of the lake where they feed and grow. Figure 1 implies that most of the males caught in the seine area during this period are just attaining maturity. The testes are not only of low weight but also of lower diameter with relatively small lobules generally in various phases of spermatogenesis. There are lots of primary germ cells and spermatogonia and most of the other early phases of spermatogenesis are represented during this period. The interstitial tissue is poorly developed if at all and in most cases it is barely detectable.

October to December

This period is on the whole marked by more speedy recovery of testicular development (Plate I(e)). The testes are at diverse histological phases and some spermiation is resumed during this period. The mean testicular weight increased slowly. This is reflected histologically by the increase in testis diameter and more and more lobules being filled with spermatozoa. Towards the end of this period, more and more testes show signs of having started to spermiate and the interstitial tissue is greatly developed. It is quite clear thus that some minimal spermiation is in progress during this period and that the individual fish show a great deal of variation in their sexual state since the individual sexual state will vary considerably.

To summarize, therefore, February and (depending upon the climatic conditions) the end of April, appear to be the months of maximum testicular development and activity in *T. leucosticta* of Lake Naivasha. July, August and September are months of the least gonadal development and activity. October sees the resumption of spermatogenetic activity and breeding and this goes on (with interruptions in November) to January.

Patterns of ovarian changes

Figure 2 shows the mean ovarian weight and the female G.S.I. patterns of *T. leucosticta* for the 16 months of this study. Both show a considerable variation as can be expected from the relatively higher gonadal weight of females in comparison to males. Like the testes, the mean ovarian weight showed peaks in February and November 1968 and in February and April 1969 when the study ended. The peak in November in both males and females was sharp and unsustained. The peak in February was, again as in the males, progressive. If we look at these patterns in terms of periods similar to those which categorize the testes, some broad observations can be made.

January to June

The period January to June has a variable but high mean ovarian weight with the most consistently high peak in February. This peak in February is followed by a slow fall in the

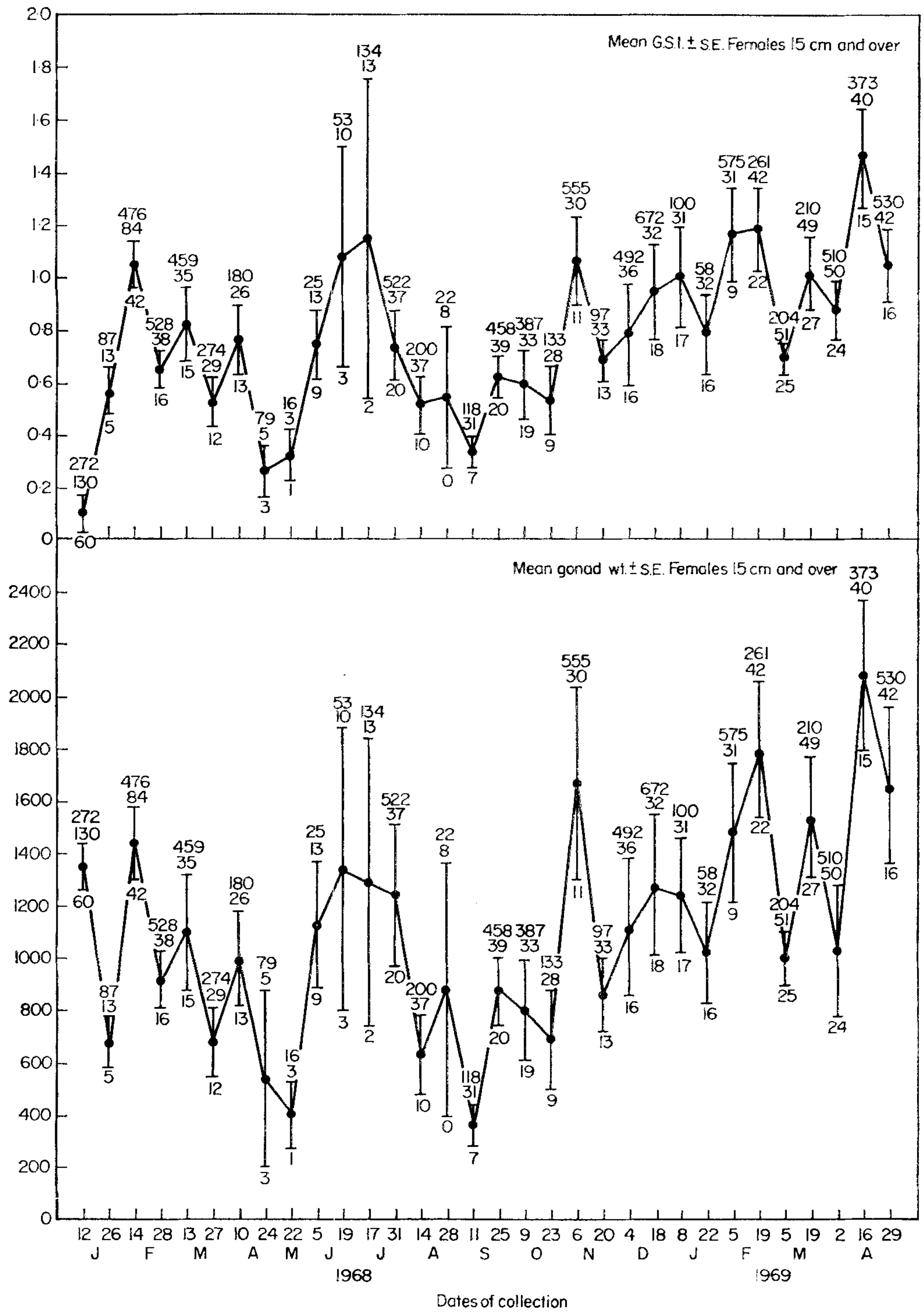

FIG. 2. Showing the comparable female mean G.S.I. (±S.E.) and ovarian weight (±S.E.) patterns.

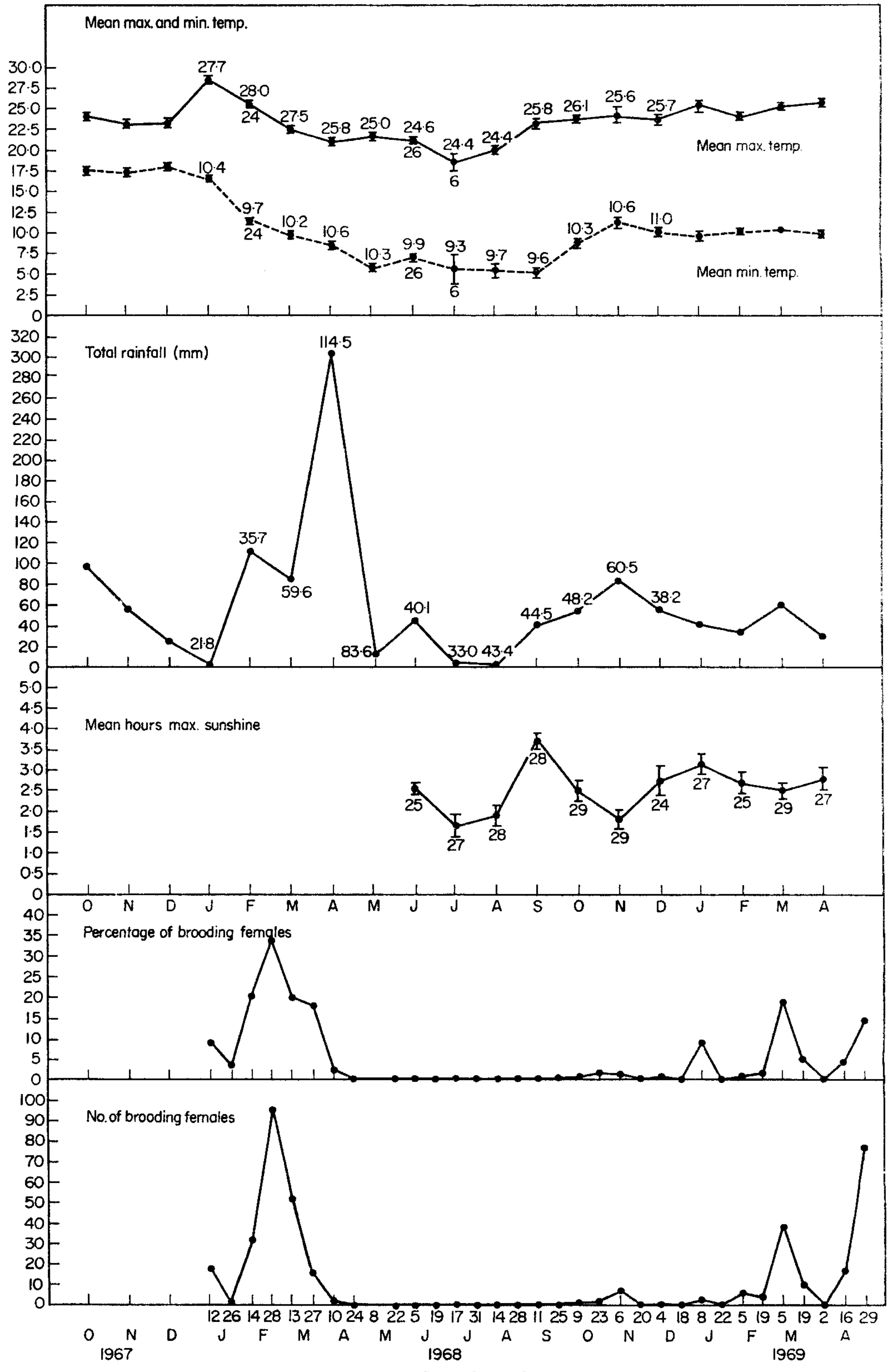

FIG. 3—See caption opposite.

mean ovarian weight and reaches its minimum in May 1969. In 1969, the February peak recurred but there was an additional peak in April 1969. June 1968 showed a rise in mean ovarian weight with a great amount of variation.

July to September

This is the period of the lowest ovarian development as judged by the mean ovarian weight. The great variability noted in June continues into July. But August is the month of least ovarian development. This can be seen from both the patterns of mean ovarian weight and that of G.S.I. It is not until late September that recovery takes place.

October to December

October sees a slight fall in the mean ovarian weight and this is followed by a second peak mean ovarian weight of 1968 in early November though this was very short-lived. Thereafter December had a slow rise.

January to April

Once again an increased development of the ovaries similar to the previous year was noticeable in 1969 with a peak in February followed by a sharp fall in mean ovarian weight more or less coincident with the peak reproduction as gauged by the recovery of brooding females. This fall in mean ovarian weight is also coincident with that of the mean testis weight. It is also relevant to note that the number of females in the higher length group (20 cm and over) is considerable and the fall in mean ovarian weight is *not* due to smaller fish being caught. This combined with the relatively small variation in the ovarian weight (again as in late February 1969) is indicative of massive ovulation at this time. The sharp rises and falls which continue in March and April with a second peak in the later month, is largely indicative of intense breeding activity during this period.

Histologically, despite the wide individual variation, the picture is consistent with that derived from the patterns of mean ovarian weight. Evidence of ovulation can be seen in the period January to April with the most intense ovulation taking place in February-March of both years and April of 1969 (Plate II(a),(b),(f)). Thus the histological picture confirms the general observation noted above. Apart from the exceptional cases of fish with large ovaries. most of the others have poor ovarian development in May and June (Plate II(c)). July and August show the most retarded ovaries particularly the latter month. The exceptional large ones found in June and July are probably of a previous development rather than a fresh development (Plate II(d)). Maturation appears to resume in late September and in October there is evidence of fresh ovulation. November shows much less indication of ovulation than October (Plate II(e)). However, ovulation and maturation are in progress during the whole of the period October to December.

FIG. 3. Showing the mean monthly temperature, rainfall and sunshine patterns and the fortnightly recoveries of brooding females (as a percentage of the total catch) or in total numbers. The number above each point in the temperature graph is the monthly mean for 22 years. The number below each point indicates the number of days with complete records where records were not obtained for the whole month. The number at each point on the rainfall graph indicates the monthly mean for 54 years. The number at each point on the sunshine graph indicates the number of days of the month with valid sunshine records.

Patterns of brooding female numbers

The pattern of changes in the numbers of brooding females recovered during the catches is interesting and is shown in Fig. 3. Figure 3 shows the actual numbers recovered per catch. But as the total number of fish caught varied from catch to catch, it is perhaps useful to relate the numbers of brooding females caught to the total catch of the collection and this is shown separately in Fig. 3.

If this pattern is representative of the breeding patterns of *T. leucosticta* in Lake Naivasha as I believe it is, then there *is* a peak breeding extending from early February to May. From June to September there is no reproduction noticed. Reproduction begins again in October and continues sporadically at a low level from then to a peak in late February—early March. A possible peak might be achieved in late April depending upon the general climatic conditions.

Changes in the external factors

The principal external factors that were followed during this period were temperature, rainfall and light. The temperature was the maximum and minimum daily air temperature recorded by the Meteorological Department of the East African Community. Records of temperature are not available for one month from 26 June to July 1968 as there was a breakdown in the recording equipment at this period. Apart, however, from this break, the temperature records are almost complete. The rainfall records were also supplied by the same Meteorological Department of the East African Community. Both the temperature and rainfall were taken at stations very close to the lake and are probably a fairly accurate reflection of the conditions operational on the surface of most of the lake. Due allowance has however to be made for the fact that the temperature was that of the air and not of the water, determinations of which were not possible during this study.

The light was recorded from early June 1968 when eventually the Casella bimetallic actinograph was functioning reliably. Thus although records of the light pattern were not available for the first five months of the study, reliable records were available for at least 24 days of each of the remaining 11 months.

Temperature changes

The mean monthly maximum and minimum temperatures for the period October 1967 to April 1969 inclusive are shown in Fig. 3. Several features of this pattern need commenting upon. The first is that the months of October 1967 to January 1968 enjoyed high temperatures. Both the mean maximum and the mean minimum temperatures for these months were high. Although the mean maximum temperatures for October–December 1967 were about the same as those of October–December 1968, the mean minimum temperatures for the former year were significantly higher than they were for the latter year. January 1968 however enjoyed considerably higher mean maximum as well as mean minimum temperatures in comparison to January 1969. February 1968 was also warmer than February 1969. However March and April, 1969 were warmer months in 1969 than they were in 1968.

The coolest months of the year 1968 was August. July was also probably cool although records were obtainable for only six days of this month for 1968. September 1968 saw a rise in maximum but not minimum temperature. October however enjoyed warm weather as seen earlier.

The significance of temperature on gonadal development and reproductive activity will be discussed later.

Rainfall changes

The total monthly rainfalls from October 1967 to April 1969 inclusive are shown in Fig. 3. Above each point the mean rainfall for the month from 1914 to 1968, is shown. This helps to define not only divergence or similarity of the study period from the "normal" pattern but also of each month from the norm for that month.

The first feature deserving comment here is that December 1967 had less than half the rainfall December 1968 had. Furthermore, this was little more than half the mean for the month. January 1968 had virtually no rainfall while January 1969 had more than twice its normal rainfall. February, March and April 1968 on the other hand had considerably more rainfall than either the corresponding months in 1969 as well as the average for these months. While May 1968 was virtually dry and well below its normal rainfall, June 1968 was quite normal. July and August however, were almost completely dry and well below normal. September, October and November 1968 had quite normal rainfall patterns.

The significance of this rainfall patterns during the 16 months of the present study on the gonadal and reproductive patterns will be discussed later.

Sunshine changes

Figure 3 shows the sunlight pattern from the beginning of June 1968 to the end of April 1969 in terms of mean hours of maximum sunshine and mean maximum continuous hours of sunshine per day for each month.

September stands out as the month with the greatest number of hours of maximum sunshine (103 hours). The month with the lowest amount of total hours of sunshine was July (44 hours). As the number of days in every month which had valid recordings varied, it was thought best to express the light patterns in terms of mean hours of maximum sunshine per day for every month. This gives an interesting pointer to the kind of influences sunshine might have on the gonadal and reproductive patterns. Thus it becomes clear that the months of July, August and November had the least sunlight. September was the brightest month, and October had good average sunshine. Sustained bright sunshine was really encountered from December to April.

The respective relevance of the various external factors on the gonadal development and reproductive patterns of *T. leucosticta* in an equatorial lake such as Lake Naivasha will be assessed in the discussion.

Discussion

Lake Naivasha in Kenya is less than a degree south of the equator at an altitude of 6230 feet and lies in the Great Rift Valley. It occupies an area of 80 sq. miles and has a maximum depth of 20–25 m. This investigation was undertaken to supplement the histological studies previously carried out (Hyder, 1969*a*) on the testis of *Tilapia* and to discover patterns of reproduction of *Tilapia leucosticta*, the principal species of *Tilapia* found in this lake. Like the other two species of *Tilapia* found in this lake, *T. leucosticta* is not endemic to Lake Naivasha; they were introduced at various times (Elder & Garrod, 1961).

Such information as we have with reference to the reproductive patterns of the cichlid fishes of the genus *Tilapia* has been relatively scanty and sporadic. Even less is known of the influence of external factors on such patterns. Lowe in her various studies of *Tilapia* (see Lowe, 1959) has come to the conclusion that their *breeding* is largely stimulated by rainfall although she conceded that Aronson (1957) found otherwise in the case of *T. macrocephala*. Her specific communication on *T. leucosticta* (Lowe, 1957), however, is inconclusive on the natural breeding patterns of this species due probably to rather scanty data she had. Equally Welcomme's study (Welcomme, 1967) fails to throw sufficient light on the annual reproductive patterns of *T. leucosticta* found in Lake Victoria.

This study of *T. leucosticta* in an equatorial lake has revealed several interesting features of the reproductive patterns of this fish and the possible role that the external factors might play on the reproduction of *Tilapia*. Looking at the gonadal patterns and brooding females as a whole, the major point that emerges is that *T. leucosticta* appears to go into a quiescent phase (as far as reproduction is concerned) during certain months of the year—notably July to September. During this period both males and females have about the lowest gonad weight of the year and histologically they mostly look to be in a retarded proliferative phase. There are no brooding females recovered during this period and in general the number of mature fishes that visit the shore where breeding and brooding is undertaken, is low. There is no histological evidence of even partial ovulation being in progress. Neither brooding females nor testicular or ovarian development start to reappear until some time in October to November. Sporadic reproductive activity was restored in October–November but the incidence is extremely low until suddenly in late February early March a peak of reproductive activity is noticed as reflected by the sudden rise in the numbers of brooding females. Thus although it is possible to recover (as we did in this investigation), sporadic, individual ripe males and females throughout the year, this of itself does not, of course, in any way mean either that reproduction is necessarily continuous nor a lack of peak reproductive activity at certain times of the year.

Two further interesting points in the gonadal pattern might be noted here. One is that there is little doubt that in February, a peak overall development of the gonads in most mature males and most mature females, is encountered. The second point is that this is shortly after followed by, to all intents and purposes, a synchronous fall in the overall gonad weight of both males and females. Both of these features are probably extremely significant in that soon after this peak gonadal development is reached, there is a sudden appearance of large numbers of brooding females.

It is evident that a synchronous maximal development of males and females is probably an essential prerequisite to the onset of the peak breeding activity noted after the gonadal development. In this connection, the mere presence of sporadic ripe males or females does not of itself imply reproductive activity. Besides, a fish with as complex a breeding behaviour as *Tilapia* many important factors will probably have to be satisfied to induce even a ripe fish to breed (Aronson, 1949).

An examination of the sunlight and temperature patterns reveals a strong pointer as to the effects of their changes on the reproductive patterns of *T. leucosticta*. The peak gonadal development in February 1968 was certainly preceded by periods of nearly three months high temperature and practically no rainfall and probably sustained maximal illumination if the sunlight patterns of late 1968 to early 1969 are anything to go by. It is highly probable that the high peak gonadal development in February 1968 in comparison to February 1969 was primarily due to the high temperatures and presumed good light operating from November 1967 to mid-February 1968, conditions which were not repeated in November 1968–February 1969. Where rainfall is preceded by high temperatures and intense solar radiation, it is of course quite easy to overlook the effect these two factors might have had on the gonads and the subsequent reproductive activity. In most tropical countries such intense illumination and high temperatures are well-known to precede rainfall. Where they do not persist for a long enough period (witness September and October 1968) there is, interestingly, poor reproductive activity. June to August is not just the "dry" period but, more important, the period of lowest temperature and illumination as Fig. 3 very clearly shows. It is not the lack of rain so much as the depression of the temperature and sunlight that probably accounts for the relatively poor development of the testes and the overall lack of any noticeable reproductive activity as reflected by the lack of brooding females and/or fry. The high illumination in September was not, it would seem, sustained for long enough nor backed up by a sufficient temperature rise to permit a maximal development of the gonads before the intervention of the rains in late October and most of November. But apparently they were sufficient to induce an initiation of some reproductive activity from October as indicated by the reappearance of the brooding females and the overall increase in gonadal weight. The sustained relatively high illumination of December 1968 and January–February 1969 produced a marked effect as witnessed by the subsequent peak of gonadal development in March. These conditions continued in March and April 1969 and were probably responsible for the subsequent peak in the brooding females at the end of April and the general rise of gonadal development.

That both light and temperature are important in gonadal development of *Tilapia* has been noted by Pickford & Atz (1957) and by Aronson (1957). Under equatorial pond conditions, Hyder (1970) found a gross stimulation of the testes of *T. nigra* at very small sizes of down to 5 cm total length. Here the temperature was high and the light intensity in the shallow ponds considerable. Thus, potentially, given good illumination and high temperature, *Tilapia* can probably breed all the year round. Such observations as were made by Baerends & Baerends van-Roon (Baerends, 1957) and by Lowe (1957) are probably due to these two factors. It seems highly improbable, however, that *T. leucosticta* breed continuously in Lake Naivasha since the females start to mature about 16–17 cm total length and yet continue to grow over 25 cm. It is well known that conditions of continuous breeding such as these encountered in ponds have severe repercussions on the subsequent growth of *Tilapia* after the attainment of maturity (Hyder, 1966).

As indicated earlier, Lowe concludes from her many field observations of different species of *Tilapia* that breeding takes place during the rainy season. Thus Lowe (1956) states: "Breeding in *T. esculenta* coincides with months of most rain and the quiescent non-breeding season with months of least rain." Lowe (1958) states: "Both *T. esculenta* and *T. nilotica* appear to show greatest breeding activity in the months of most rain." So her conclusion (Lowe, 1959) is: "Among many *Tilapia* most ripe fish are found in the rainy season. . . ." What is not very helpful however is that Lowe does not distinguish clearly between gonadal development and breeding activity. Our own findings suggest that the stimulation of gonadal development correlated best not with rain but with good sunlight and high temperatures. Thus the peak gonadal development in February of both years was much more likely to be the result of sustained good sunlight and relatively high temperatures preceding this period. This is a dry period without question. So the maturation of the gonads does not appear to be significantly correlated with rainfall. There is on the other hand some correlation between the onset of peak breeding and the onset of rainfall. But this is not to say, as is implied by Lowe (1956, 1958) that there is a quantitative proportionality between the rainfall and the breeding. Indeed, prolonged heavy rains if anything appear to check rather than stimulate breeding. Thus April 1968 with the most rainfall had very poor recoveries of brooding females while late February and early March of the same year had substantially lower rainfall but nevertheless had the greatest recoveries while March and April 1969 with substantially less rainfall, had once again peak breeding female recoveries. Furthermore, breeding activity certainly can and does proceed without rainfall. It is the onset of rainfall that appears to trigger the peak breeding in February-March and in April. In this sense, therefore, these findings do not support Lowe's implied correlation between the intensity of rainfall and of breeding while supporting that there is some coincidence in the onset of the rainfall and that of peak reproductive activity. Fryer (1961) found no correlation between rainfall and breeding intensity in the case of *T. variabilis*—one of the two endemic species of *Tilapia* found in Lake Victoria, East Africa. He does, however, concede that this was based on inadequate data. Aronson (1957) found that the period of heavy rains had reduced spawning frequency and caused gonadal regression in the West African species *T. macrocephala*. Here, however, a totally new factor to be considered would be the effect of rainfall on the salinity of the waters as this species is known to inhabit lagoons with somewhat higher salinity than in a genuinely freshwater lake.

How the onset of the rainfall could influence peak reproduction is not clear. The observation that I have made at different times with tank specimens of *Tilapia* kept in the open air that during warm sunny days, most reproductive activity seems to take place in late afternoon to dusk, could be a pointer. Could it be that after the good sunlight and high temperature of December to February, the sudden reduction in the sunlight, and temperature at the beginning of March is the precipitating factor? It is clear, however, that the rainfall is only associated with peak reproduction in *T. leucosticta* when conditions prior to those of rainfall were ones of sustained high temperature and good sunlight to permit the development of the gonads. Alternatively, it could be that the synchronous maximal development of the testes and the ovaries after these conditions is in itself the precipitating cause. Should this be the case, the recurring coincidence of the peak breeding activity with the onset of rainfall would still demand an explanation.

It seems then that in this equatorial lake, the overall development of the gonads of *T. leucosticta* (and particularly the development of the testes), is largely under the influence of light and temperature and that such synchronous peak development of gonads in both sexes is an essential prerequisite to the precipitation of massive reproductive activity. It also appears that rainfall as such has no bearing on the development of the gonads though its onset relates closely to the initiation of synchronous reproductive activity. It is not clear if this is a result of sharp temperature and light changes associated with the onset of the rains or is a result of the rainfall itself. Nor is it clear what adaptive function this might have in relation to food availability for the adults and for the young. The role of food on the reproductive patterns of *Tilapia* has yet to be clarified. Sustained heavy rainfall, on the other hand, appears to effect the cessation of reproductive activity. The mechanism whereby sustained heavy rainfall can do this is not clear either. It could be through the direct effect of cloud cover on illumination (Aronson, 1957) or through the subsequent increase in murky run-off. Such run-off could not only affect the penetration of light into the water but could also deny the requisite visibility or effect changes in breeding substrata, both being necessary for the breeding act.

It is seen from this study, therefore, that despite a constant daylength within the equatorial belt, the pattern of sunshine intensity is variable. As far as this equatorial lake (Lake Naivasha) is concerned, the period of observed sustained maximum sunshine is usually in the months of December, January and February. Depending upon the rains, this can extend to April or even May. These months (December–February) are also the months of the highest temperature. It is concluded that it is not by coincidence that there is a gradual increase in the gonad development of most mature females during this period culminating in a peak reproductive activity in late February–March. This peak could probably change depending upon patterns of sustained maximal sunlight and high temperature. It is also concluded that a subsequent peak would probably arise should these favourable two external factors continue (see Hyder, 1969*b*). Thus although *T. leucosticta* shares with other cichlids of the genus *Tilapia*, the capacity for continuous reproduction within a population, this is only so if the conditions of sunlight and temperature are sustained at an adequate level as they are in equatorial ponds. The onset of rainfall, when preceded by conditions of high temperature and sunlight, both of which are conducive to gonadal development, seems to initiate peak breeding. Heavy sustained rainfall, on the other hand, is probably more of a limiting than a stimulatory factor.

Summary

T. leucosticta in Lake Naivasha (Kenya) lying 50 seconds south of the equator at an altitude of 6230 feet were studied over a period of 16 months to find out their reproductive patterns. Fortnightly regular seines were made at an area previously identified as a brooding site which also had representative samples of all ages of both sexes. Body length and weight and gonad weights were determined for a representative sample of the catch and samples were taken from all age groups of both sexes for histological examination. Patterns of temperature, rainfall and (for the last 11 months of the study) sunlight, were studied to discover the factors influencing the reproductive patterns. Gonadal development and G.S.I. of both sexes reached a peak in most fishes about February to March each year. This period is followed by a sharp increase in the numbers of brooding females. The period of December to March generally enjoys sustained high temperatures and maximum sunshine. It is concluded that these two factors are probably the most important in stimulating the maximal gonadal development in February. It is suggested that rainfall as such is probably unrelated to gonadal development except in initiating and (if heavy and sustained) in checking, breeding. This agrees with the finding that in shallow equatorial ponds enjoying high sunshine penetration and high temperature, breeding of *Tilapia* is continuous. The altitude of Lake Naivasha and its relative shallowness probably accounts for the pronounced effects of low temperatures on gonadal development in the months of July and August. September though a bright month, has medium temperatures but the combination appears sufficient to initiate minor reproductive activity in October interrupted by the rains and poor light in November.

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