THE FEEDING, DIET AND ECOLOGICAL RELATIONS OF

THREE SPECIES OF FISH OF ECONOMIC IMPORTANCE

IN SOUTHERN MALAWI.

This thesis is presented by D.M. Bourn to the Zoology Department of Edinburgh University for a Master of Science degree - spring 1972.
SUMMARY

The environment of Lake Chilwa (Malawi, Central Africa) is described with special reference to the foods available to the three fish species of economic importance: Barbus paludinosus Peters, Clarias mossambicus Peters and Tilapia shirana chilwae Trewavas. A semi-quantitative points method of analysis of their digestive tracts' contents - basically that of Hynes (1950) - is given with a computerised method of data analysis. The feeding patterns of each of the three species as a whole, with sex, maturity, length, area caught, time caught, presence or absence of vegetation, water conductivity and method of capture are described in terms of the relative percentage proportion and the percentage frequency of occurrence of thirteen food items.

B. paludinosus was found to feed during the day on zooplankton, non-filamentous green algae and some higher plant material; small fish fed predominately on zooplankton, but with increasing size the diet became more varied.

C. mossambicus was found to feed throughout the day and night and to have a highly varied diet; small fish fed predominately on zooplankton but with increased size fish became the major item.

T. shirana chilwae was found to feed mainly during the hours of daylight and to have a predominately, although not exclusively herbivorous diet, feeding on higher plant material, filamentous green algae and zooplankton. For small fish zooplankton was the major food item.

There were no major differences in the diet of any of the species with sex. The importance of environmental conditions, particularly the water conductivity and the presence or absence of vegetation, on the availability of food items and consequently on the diet of the fish is stressed.
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A word of explanation

The work described in this thesis was carried out during the period October 1969 to September 1971 while I was working on the Lake Chilwa Coordinated Research Project of the University of Malawi. I was recruited as a British volunteer by the United Nations Association International Service and worked under the auspices of the Food and Agricultural Organisation of the United Nations. My work in the project was divided about equally between routine collection, of background information on the changing physico-chemical environment which was of value in this thesis, and studying the feeding ecology of the three species of fish of economic importance.
INTRODUCTION

The continent of Africa provides an extraordinarily diverse range of environmental conditions and an equally diverse range of animal and plant life that has adapted to them. Over the past two decades there has been increasing emphasis on ecological understanding of those ecosystems that might provide more food for Africa's expanding human population.

The main purpose of this investigation was to study the ecological aspects of the feeding of three species of Lake Chilwa fish, which together form a very important, although rather unpredictable source of animal protein for the people of southern Malawi. The three species of fish Barbus paludinosus Peters, Clarias mossambicus Peters and Tilapia shirana chilwae Trewavas are the most abundant in Lake Chilwa in terms of landed tonnages per year. It was hoped that the data obtained would provide information, which, when considered with other work carried out by the Lake Chilwa Co-ordinated Research Project and the department of Fisheries of the Malawi Government would increase the understanding of the ecology of the fishery and rationalise its development and exploitation.

To achieve the stated objectives the work concentrated on an investigation of the kinds and amounts of food consumed by the three species, determined on a semi-quantitative basis; including the way in which feeding was influenced by habitat, water physicochemistry, and time of day, as well as the size, sex and maturity of the fish.
Research work on many inland waters has resulted in numerous papers reporting the findings of investigations into the biology and ecology of many species of fish found under various environmental conditions in widely separated areas of the continent. Of the more recent publications the following are the most comprehensive: Corbet (1961) described the food of twenty-six non-cichlid fish in the Lake Victoria Basin; Fryer (1959) described the trophic interrelationships of the littoral communities of Lake Nyasa (now Lake Malawi); Munro (1967) described the food of a community of East African freshwater fish in Lake McIlwaine, Rhodesia; Petr (1968) described the distribution, abundance and food of commercial fish in the Black Volta and the Volta man-made Lake in Ghana; Whitehead (1969) investigated the food habits of some juvenile fish in the Volta lake; Reynolds (1970) described the biology of the small pelagic fish in the new Volta Lake.

Valid and useful as these findings may be for the particular ecosystem, their relevance to other ecosystems is often doubtful because of intrinsic differences between ecosystems. Thus an attempt to review these disparate sources would be of little value. Where feeding information is available about the particular (or closely related) species under
study, it has been given in the appropriate subsection dealing with that species. In the discussion and conclusions this and other relevant information is dealt with in relation to the findings of this thesis.
LAKE CHILWA ENVIRONMENT
A. Abiotic

1. Geographical features.

Lake Chilwa (Shirwa, Chirwa) is a shallow, saline lake lying in a closed drainage basin, situated between longitudes 35°30'S and 36°S and latitudes 15°E and 15°30'E, at an altitude of 620 m above mean sea level (at Beira, Mozambique), in the Southern Region of the Republic of Malawi in Central Africa. During the period of study the area of open water was about 700 km² surrounded by an almost equal area of swamp. The average depth was about 2 m with a maximum of about 3 m and the catchment area was about 7,000 km² (Moss & Moss, 1969).

Because the lake lies in a closed drainage system, its depth and extent are entirely dependent on the water gained by rainfall, and water lost by evaporation and transpiration in the catchment area during any one year and the years immediately preceding. The yearly fluctuation in water-level, from a high after the rains to a low at the end of the dry season is usually in the region of 1 - 1.5 m. If rainfall is low in the catchment area for two or three years in succession and the water lost by transpiration and evaporation is not replaced, then there is, of course, a net drop in water level. Monthly depth measurements have been taken since 1949, by the Hydrology Department of the Ministry of Natural Resources. It has been suggested (R. McConnell - personal communication) that the lake level may
fluctuate cyclically with sun spot activity but as this has a periodicity of about 22 years it is not possible as yet to confirm her suggestion.

During periods of severe drought the lake may dry completely; such dry periods have occurred in 1882, 1920, 1922, 1934 and most recently in 1968. (McLachlan et al. - submitted to Arch. Hydrobiol.)

During flood conditions, the inflowing rivers deliver considerable quantities of dissolved and suspended matter, and throughout the year dissolved chemicals are brought in by the five perennial rivers. As water loss is only by transpiration and evaporation there is a net concentrating effect on the dissolved chemicals. During the period of investigation the water conductivity in the main body of the lake ranged from 500 - 2,500 $\mu$ho/cm depending on the area and the season. By contrast the conductivity of one of the main rivers - the Likangala - flowing into the lake ranged from 43 - 130 $\mu$ho/cm; that of Lake Malawi about 220 $\mu$ho/cm and that of Lake Windermere, England, about 60 $\mu$ho/cm.

2. Climatic features.

The area experiences a dry season from April to October; May to August are the coolest months, with average mean air temperatures of 20.5°C. The wet season is from November to April; October to February are the hottest months, with average mean air temperatures of 26.5°C. (1967 figures calculated from Morgan & Kalk, 1970). Although detailed records over a long period
are not available, it seems that the mean average rainfall in the catchment area varies from 80 cm/year on the plains to 125 cm/year on the mountains, and that evaporation over the lake is about 195 cm/year. Rainfall patterns differ from year to year and area to area. (Morgan & Kalk, 1970).


The Chilwa basin has been surveyed by the Malawi Geological Survey Department. The basin's geomorphic origin is a matter of some controversy, but it is related to the movements of the tectonic plates marginal to the great African Rift Valley. Underlying the area is ancient high-grade metamorphic rock, much of it covered by alluvium which on average is about 50 m in depth. The alluvium is predominately fine-grained, consisting mainly of dark clays and silts, with some sands. (Bloomfield, 1966)

Various terraces of ancient beaches, which ring the Chilwa-Chiuta depression at levels up to 33 m above the present lake level of Lake Chilwa, indicate that the lake, in the past, has been far more extensive than at the present. The contraction is probably due to a combination of long term climatic fluctuations. (McLachlan & McLachlan, 1969) It has also been suggested that a tilting or sinking of the southern end of the basin prevented drainage from this region to the north - through the present Lake Chiuta - and resulted in the formation of a closed drainage system in the southern section which now flows into Lake Chilwa. (Garson, 1960)

The geological history of the area is of importance because
of its bearing on the origins of the present fish fauna of Lake Chilwa, which will be discussed later in the Fish Fauna section. Dixey (1926) has suggested that at one time Lake Chilwa was connected to Lake Malawi, but this has been disputed by Bloomfield (1966) and Garson (1960). There has also been some debate over the route by which water drained from the Chilwa-Chiuta depression to the Indian Ocean, when the level was higher. Pike & Rimmington (1965) suggest that the area may have been drained at various times through one or other of two outlets, one to the south-east by the Ruo River to the Shire River and the Zambesi system, and the other to the North-east and the Lugenda River, forming part of the Ruvuma system.

Lake Chilwa has been without outlet and isolated from Lake Chiuta, to the north, since at least the middle of the nineteenth century (Moss & Moss, 1969) but the continuity of the ancient lacustrine terraces around both lakes shows that these lakes must themselves have been connected in the recent geological past. This is also confirmed by indications that the sand barrier, of 5 - 6 km in width and 16 m in height, which now separates them, is of geologically recent origin. (Garson, 1960)

4. Water physico-chemistry

The physico-chemical fluctuations of Lake Chilwa for the period 1966 - 68 have been reported by Moss & Moss (1969) and Morgan & Kalk (1970). However, their results represent conditions when the lake was in the final stages of decline before drying
in 1968 for almost a year. Table 1 summarises the results obtained during the period of this study, after the rebirth of the lake, when the water was considerably deeper, the water volume greater, and ionic concentrations lower. During the dry season, the lake level falls because of evaporation and transpiration (as already described) and the concentrations of the various ions build up, and the alkalinity, conductivity and pH increase. With the decrease in depth, the effect of surface wave action becomes more pronounced, and the water is more effectively mixed - especially in the open lake - and hence turbidity increases. The tendency towards deoxygenation of the bottom layers of the water is also reduced. With the onset of the rains, these trends over the whole lake are gradually reversed, until the end of the rains, when a new cycle is entered. Water temperatures are lowest from May to July and increase from August to January.

Unlike many deeper African lakes, Lake Chilwa has no permanent horizontal temperature stratification. During the day, surface temperatures are usually higher than bottom temperatures, but after a night of cooling, surface and bottom temperatures equilibrate, and because of the shallowness of the lake thorough mixing occurs.

During the 1969/70 rains, two tendencies were observed: 1) The formation of a freshwater ring around the periphery of the lake, leaving a central core of essentially undiluted water, which, after a few months, was mixed with the peripheral waters by wind-induced turbulence. (McLachlan
TABLE 1.

Ranges of various physico-chemical parameters in Chilwa waters and, for comparison, some results for the waters of the southern basin of Lake Windermere, England.  


<table>
<thead>
<tr>
<th></th>
<th>Lake Open Water</th>
<th>Kachulu Bay</th>
<th>Likangala Mouth</th>
<th>Likangala River</th>
<th>South Windermere</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Max</td>
<td>Min</td>
<td>Max</td>
<td>Max</td>
</tr>
<tr>
<td><strong>°C</strong></td>
<td>19</td>
<td>39</td>
<td>19</td>
<td>32</td>
<td>19</td>
</tr>
<tr>
<td>µmhos/cm</td>
<td>1400</td>
<td>2400</td>
<td>400</td>
<td>2500</td>
<td>80</td>
</tr>
<tr>
<td><strong>pH</strong></td>
<td>8.6</td>
<td>8.9</td>
<td>7.9</td>
<td>8.8</td>
<td>7.6</td>
</tr>
<tr>
<td><strong>Turbidity cm</strong></td>
<td>4.0</td>
<td>13.0</td>
<td>3.8</td>
<td>16.0</td>
<td>3.8</td>
</tr>
<tr>
<td><strong>Alkalinity me/1</strong></td>
<td>8.8</td>
<td>16.6</td>
<td>3.9</td>
<td>17.4</td>
<td>9</td>
</tr>
<tr>
<td><strong>O₂ mg/l</strong></td>
<td>5.7</td>
<td>9.3</td>
<td>3.6</td>
<td>8.5</td>
<td>3</td>
</tr>
<tr>
<td><strong>Na</strong></td>
<td>380</td>
<td>703</td>
<td>89</td>
<td>713</td>
<td>11</td>
</tr>
<tr>
<td><strong>K</strong></td>
<td>13.6</td>
<td>18.2</td>
<td>7.1</td>
<td>19.5</td>
<td>2.0</td>
</tr>
<tr>
<td><strong>Ca</strong></td>
<td>8.0</td>
<td>19.4</td>
<td>7.6</td>
<td>18.7</td>
<td>5.9</td>
</tr>
<tr>
<td><strong>Mg</strong></td>
<td>2.7</td>
<td>8.5</td>
<td>3.4</td>
<td>8.5</td>
<td>8</td>
</tr>
<tr>
<td><strong>Cl</strong></td>
<td>250</td>
<td>516</td>
<td>74</td>
<td>523</td>
<td>57</td>
</tr>
<tr>
<td><strong>PO₄</strong></td>
<td>3.1</td>
<td>6.7</td>
<td>6</td>
<td>7.6</td>
<td>1</td>
</tr>
<tr>
<td><strong>NO₃</strong></td>
<td>0.06</td>
<td>0.45</td>
<td>0.05</td>
<td>0.44</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>TDS</strong></td>
<td>986</td>
<td>2078</td>
<td>494</td>
<td>2266</td>
<td>232</td>
</tr>
</tbody>
</table>

* Macan (1970)

* Corlett (personal communication)

TDS = Total Dissolved Solids.
et al. (submitted to Arch. Hydrobiol.)

2) A more transient and localised effect, where less dense flowing water, containing low concentrations of dissolved material, tended to "float" on the surface, above denser water with greater quantities of dissolved material. (Personal observation).

The physical and chemical changes of the water prior to and after rebirth of the lake are extensively discussed in MacLachlan et al. (submitted to Arch. Hydrobiol.)

5. Economic factors

Estimation of the fish landings from Lake Chilwa was initiated in 1963. In 1965, when the fish production, in terms of estimated short tons landed, was the greatest so far, Lake Chilwa produced nearly 50% (9,800 short tons) of the total estimated catch in Malawi. This may very well be an exaggeration, because of acknowledged inaccuracies in the estimated landings in certain areas, notably Lake Malawi and the Lower Shire. Nevertheless, despite the relatively small size of Lake Chilwa, the fish yield in good years is relatively high, and forms a considerable proportion of the country's fish production. The production is, however, erratic because of the nature of the lake, but, even after a period when the lake had dried up, the rate of recovery of the fish population is high. It can be seen from Table 2
that in 1970, for example, only two years after the lake refilled, the estimated landings were already half those of the peak production of 1965, although the *Tilapia* fishery had not fully recovered.

The Southern Region of Malawi is a densely populated area. Fish production on Lake Chilwa plays an important part in the economy of the Region, and because of the lake's high yields and its proximity to the urban areas of Blantyre, Limbe and Zomba, it is an important source of protein for the population.

It is of interest in this connection that until recently there were no mechanised methods of fishing in use on Lake Chilwa, and only gill-nets, long-lines, seines, fish-traps, scoop nets and fish baskets were used (Mzumara, 1967). In 1970, however, the Extension Section of the Fisheries Department of the Malawi Government began testing various forms of miniature trawl nets, towed by two boats with low-power outboard engines (Ratcliffe 1971). The shallowness of the lake enabled the full depth from the bottom to the surface to be fished, in this way. This method has now been improved, and it is envisaged that a number of trawling units would be operated on the lake and substantially increase fish landings achieved in the future, particularly during the dry season when this method has proved most successful (Furse - Personal Communication).
TABLE 2

ESTIMATED LANDINGS OF FISH FROM LAKE CHILWA IN SHORT TONS,
(1963-1970)

<table>
<thead>
<tr>
<th>Year</th>
<th>Tilapia</th>
<th>Clarias</th>
<th>Barbus</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963</td>
<td>1012</td>
<td>2376</td>
<td>212</td>
<td>3600</td>
</tr>
<tr>
<td>1964</td>
<td>3351</td>
<td>2243</td>
<td>206</td>
<td>5800</td>
</tr>
<tr>
<td>1965</td>
<td>4720</td>
<td>2518</td>
<td>2562</td>
<td>9800</td>
</tr>
<tr>
<td>1966</td>
<td>1540</td>
<td>3345</td>
<td>3115</td>
<td>9800</td>
</tr>
<tr>
<td>1967</td>
<td>250</td>
<td>3140</td>
<td>210</td>
<td>3600</td>
</tr>
<tr>
<td>Drying</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>4</td>
<td>88</td>
<td>8</td>
<td>100</td>
</tr>
<tr>
<td>Rebirth</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td>5</td>
<td>3156</td>
<td>39</td>
<td>3200</td>
</tr>
<tr>
<td>1970</td>
<td>350(50)</td>
<td>2900(1500)</td>
<td>1650(600)</td>
<td>4900</td>
</tr>
</tbody>
</table>

2 - 1970 C. Ratcliffe (personal communication)
3 - Introduction of fine mesh beach seines. These were not in use in 1969 but were re-introduced in 1970.
4 - Figures in parentheses were of actual landings at Kachulu Bay.
B. Biotic

1. Fish Fauna.

Kirk (1967) listed twenty-three species of fish found in the Chilwa-Chiuta depression, of which thirteen were present in the water of Lake Chilwa, the remaining ten being found in the affluent streams and rivers and in Lake Chiuta. The distribution of some of the species in Lake Chilwa probably varies considerably with the volume of water flowing into the lake from the rivers, the physico-chemical nature of the water and the breeding habits of the fish. The three species in the lake, which predominate in the fish catches, and which are commercially most important, are: *Barbus paludinosus* Peters, *Clarias mossambicus* Peters and *Tilapia shirana chilwae* Trewawas. The other species and their actual distributions are given in Table 3. On the basis of a number of zoogeographical features, Kirk (1967) concluded that the affinities of the fish in the Chilwa-Chiuta depression were with the fish of the eastward-flowing rivers of Mozambique and Tanzania, and not with those of Lake Malawi. A comprehensive study of the distribution and population dynamics of the major fish species in Lake Chilwa is in progress. Preliminary analysis of the data gives some indication that, in the present conditions, when the populations are expanding after the 1968 dry period, *B. paludinosus*, *C. mossambicus* and *T. shirana chilwae* all have their highest biomass values in areas near the swamp and that away from vegetation *T. shirana chilwae* has the lowest biomass of the three.
<table>
<thead>
<tr>
<th>Fish Species</th>
<th>L. Chiuta</th>
<th>L. Chilwa</th>
<th>Chilwa stream</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alestes imberi Peters</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>B. innocens Pfeffer</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>B. manicensis Pellegrin</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>Barbus paludinosus Peters *</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>B. radiatus Peters</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>B. tangandensis Jubb</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>B. toppini</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>B. trimaculatus Peters</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>B. sp</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>Clarias mossambicus Peters *</td>
<td>*</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>C. theodorae Weber</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Cyphomyrus discorhyncus (Peters)</td>
<td>+</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>Gnathonomus macrolepidotus (Peters)</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Haplochromis callipterus (Gunther)</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hemihaplochromis philander (Weber)</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Labeo cylindricus Peters</td>
<td>0</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>L. sp</td>
<td>+</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nothobranchious kirkii Jubb ©</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>Parautropius longifilis (Steindachner)</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Paratracephalus catastoma (Gunther)</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>T. melanopleura Dumeril</td>
<td>+</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>T. shirana chilwae. Trewawas © *</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Tilapia sparrmanii A. Smith</td>
<td>+</td>
<td>+</td>
<td>0</td>
</tr>
</tbody>
</table>

* Of major economic importance + Present
© Endemic 0 Not recorded
(Furse, Personal Communication). The fact that fishing activity is greatest close to areas of vegetation provides some corroboration, although ease of access by the fishermen may also explain this observation.

2. Other fauna.
   1. Zooplankton.

   The species composition of the zooplankton has been observed to vary with the changes in the water conditions. Before the lake began to dry up in 1967-8, the smaller species of cladocerans predominated, mainly *Moina micrura* (de Guerre & Richard) and *Ceriodaphnia cornuta* (Sars). Rotifers were common throughout the year - the dominant species were of the genus *Brachionus*. The copepods *Tropodiaptomus kraepelini* (Poppe & Mrazek) and *Mesocyclops leuckarti* (Claus) were also present. (Kalk and Schulten 1970).

   On the rebirth of the lake in 1969, *Daphnia barbata* (Weltner) was the first cladoceran and *T. kraepelini* was the first recorded copepod. The larger *D. barbata* and *Diaphanosoma excisum* (Sars) became dominant, while the smaller cladocerans, which had been dominant before the decline of the lake, were present but not abundant. Rotifera also returned but generally did not appear to be as numerous as before, and were detected only intermittently during the year probably following algal blooms. (Kalk and Schulten (1970)).

   The main cladocerans were distributed throughout the
lake and swamp, but their density was much lower in the central part of the lake - possibly because of the generally higher ionic concentrations there. The highest concentrations of zooplankton appeared to be in the vicinity of vegetation.

ii. Insects and snails

As would be expected there have been marked changes in the composition and distribution of the non-planktonic invertebrate fauna with the decline and recovery of Lake Chilwa. These changes have been described by McLachlan and McLachlan (1969), McLachlan (1969) and McLachlan (1970) and are summarised here.

At the low lake level during drying, when water conductivity was 1,200 umhos/cm, only six species (three dipteran, two coleopteran and one hemipteran) of benthic fauna were found living on the mud, Corixidae being the vast majority. Biomass estimates ranged from 0-65 mg/m² dry weight. However skeletal remains containing fragments of soft material of eighteen species (eight dipteran, seven molluscan, two coleopteran and one hemipteran) were found, indicating that a much larger and richer fauna had existed not long before.

In early 1969, after the lake had begun to refill faunal biomass estimates up to 10,000 mg/m² dry weight were obtained. Thirteen species were recorded, including dipterans, molluscs, coleopterans and hemipterans, most of which had been recorded before from skeletal remains.
Later in 1969 when lake transects were possible it was found that bottom fauna was restricted to the periphery of the open water - the central part supporting virtually no fauna. This correlated with peripheral water conductivities of less than 500 μmhos/cm and central water conductivities of between 1000-2000 μmhos/cm.

In the 1969/70 rains a fresh-water ring was not re-established and no bottom fauna was observed in peripheral or central mud samples.

A rich periphytic faunal community of up to 2000 mg/m² dry weight was found associated with areas of vegetation. This appeared to exist throughout the year provided the water did not recede from the vegetation. The dominant species, here, was found to be the larval dipteran *Nilodorum brevipalpis* Keiffer. A more detailed account of the periphytic community and its distribution will be given by McLachlan (in preparation).

3. Flora
1. Macrophytes

The shallower peripheral areas of Lake Chilwa are composed almost entirely of dense swamp, occupying some 700 km². The most extensive swamp areas are located on the western side of the lake with as much as 10 km separating dry land from open water. A few isolated beaches occur where the swamp has been cleared.
No submerged aquatic plants are found in the open lake because of the high turbidity of the water, and in the swamp the vegetation is exclusively of the rooted emergent types. *Typha domingensis* Pers. (bullrush) is the dominant plant of the swamp area, whilst *Vossia cuspidate* (Roxb.) Griff. (hippo grass), *Panicum repens* L. and *Cyperus* spp. are common on the shallow landward sides of the swamp. *Cyperus papyrus* L. is confined to the Likangala and Domasi river-mouth areas.

On sandy, exposed shores and on the rocky shores of the lake islands, *Phragmites mauritianus* Kunth, *V. cuspidate* and *Sesbania goetzii* Harms are found. Small patches of the grass *Paspalidium guminatum* (Forsk.) Stapf occur in the open lake in water over 2 m deep.

An unusual feature in Kachulu Bay and to the north of Tongwe Island is the presence of reed "islands" of *Scirpus littoralis* Schrad. This is an estuarine species, not normally associated with inland waters.

Another unusual feature is that extensive areas in the South West of the lake have recently been colonised by the leguminous tree *Aeschynomene pfundii* Taub. This plant is normally found only on the landward edges of the swamp on seasonally flooded soils, but when the lake dried up in 1967-1968 seeds of this species were able to germinate on the exposed muds. When the lake refilled, the plants established themselves and were able to survive the relatively deep water of the open lake. Experiments have shown that regeneration by sexual reproduction is,
however, not possible in these conditions, so it is assumed that
this Aeschynomene zone is a temporary plant community in the lake
(C. Howard-Williams, Personal Communication).

A few free-floating species are found in the shelter of
the swamps. These include the duckweeds (Lemna perpusilla
Terr., Spirodela polyrhina L. and Wolffia spp.), the water cabbage,
Pistia stratiotes Linn. and a number of species of Utricularia.

Physical factors such as turbulence, water-depth and the
length of time the soil is dry each year appear to be the
important controls on the distribution of the lake vegetation.
Ionic concentrations in the lake waters seem to have little effect
on the distribution of the macrophytes (C. Howard-Williams, Personal
Communication).

ii. Algae

The turbidity of the main body of water in Lake Chilwa
is such that photosynthetic activity is only possible in surface
layers. Secchi discs normally disappeared well before 20 cm.
depth. However, the wind action which causes the turbidity
also results in water movements which distribute phytoplankton
to all depths, despite the lack of light penetration.
Epiphytic algae, on the other hand are only found on substrates
within the zone of light penetration, i.e. the top 20 cm. of the
water, and as, in the open water, few substrates are present in
this zone, these algae are much more common within the swamps
and the boundary areas between swamp and open water.
Although the swamp waters are relatively clear when compared with the waters of the open lake, light reaching the water surface in the swamps is very reduced and algal production is low in this area (Lenton, Personal Communication).

The algae of the period of study were quite different from those found in the drying phase 1967-68, when the water had much higher ionic concentrations. During the drying phase Cyanophyta (blue-green algae) predominated; the major phytoplankter in November 1967 (when the conductivity was 12,000 \( \mu \)mhos/cm) was *Arthrospira platensis*; *Anabaena* sp, *Spirulina* sp and *Oscillatoria* sp were also present but less common; the only non-blue-green present was the Chlorophyta *Scenedesmus quadricauda.* (Moss & Moss, 1969). In 1968, when the conductivity of the small body of water that remained was 17,000 \( \mu \)mhos/cm, the flora consisted entirely of the blue-green *Arthrospira platensis* and *Anabaenopsis circularis* and the diatoms *Nitzchia palea* and *Anomoeneis sphaerophora* (Mwanza, 1970).

By contrast, the algae found during the period of study, (i.e. after the lake had recovered) were characterised by much greater diversity with most of them belonging to the Chlorophyta (green) and Chrysophyta (yellow-green) species. *Planktosphaeria* and *Synura* spp. were the predominant phytoplankters and during calm periods of weather they sometimes formed extensive epineustic skins on the water surface. The most common epiphytic algae were *Spirogyra* spp. and the desmids *Pediastrum* sp and *Stauroastrum* sp; these were all found adhering to the stems of *Typha* and *Aeschynomene*
and other aquatic macrophytes. Some blue-green algae were present, mainly *Oscillatoria* sp., which was the first alga to be observed on the return of the lake, and *Anabaena torulosa*, which was found later (Mwanza, 1970).

In the initial period of the recovery of the lake, the open water regions had fewer species than the periphery, but gradually, perhaps because of decreasing ionic concentrations in the central area, algal species appeared in greater numbers throughout the lake waters.
Barbus paludinosus Peters.
The abundant minnow of Lake Chilwa.

(xl)
THE FISH STUDIED

A. Barbus paludinosus Peters 1852

**Family:** Cyprinidae; **Sub-order:** Cyprinoides

**English name:** Minnow

**Chichewa name:** Matemba (this is a general name for a number of species of fish that superficially resemble each other).

1. **Taxonomy and description**

Of the non-cichlid genera in Africa, *Barbus* has the largest number of species. However, the biology and ecology of the genus are poorly understood and little work has been carried out on its members. The genus may be divided into two groups on the basis of their scale patterns; one in which the striae are more or less parallel and the other in which the striae are radial (Jubb, 1967). *Barbus paludinosus* belongs to this latter group. It is a small fish; in Uganda, specimens have been recorded in Lake Victoria having a maximum length of 130 mm, and a modal length of 110 mm (Greenwood, 1966); in Malawi, specimens of 140 mm have been recorded from Lake Kazuni in the Northern Region. (Jackson, 1961b). The species has a pronounced, strong, serrated third spine in the dorsal fin, and no black pigment spots at the base of the caudal or anal fins; two pairs of barbels of variable length are present on the upper lip. It is silver-grey in coloration, but, when viewed from above, the dorsal surface is olive-green. Specimens from the swamp area of Lake Chilwa were generally darker than those from open water.
In a revision of the classification of certain Barbus species Greenwood (1962) concluded that Barbus paludinosus was the most variable member of the genus and was most closely related, at least on superficial characters to B. taitensis and B. amphigramma of East Africa.

2. Distribution and Habitat

B. paludinosus has an almost pan-African distribution from Ethiopia in the north, through east and central Africa, westwards to the Congo and Angola, and, as far south as the Orange and Uvongo rivers in the Republic of South Africa. There are thought to be a number of localised sub-species, that differ primarily in the length of the serrated dorsal spine, but also in the number of scales, and the length of the caudal peduncle (Greenwood, 1962). As its name implies, (paludinosus = of the marshes), the species is found mainly in marshes, small rivers and streams where plenty of cover from predators is available, but it is also present in the peripheral swamp areas of larger lakes, e.g. Malawi and Victoria. It is never found in the open water of Lake Malawi, which is deep, (Jackson, 1961b), but is present in the shallow areas of Lake Victoria, especially where the bottom is sandy, (Greenwood, 1966). It has a wide tolerance of water conditions, from very turbid marshy areas to the clear water of larger lakes, e.g. Bangwelu (Zambia), and Victoria, but is absent from high altitude streams, (Jackson, 1961a). It is found in all areas of Lake Chilwa, though apparently least commonly in the swamps.
13. Breeding

The breeding habits of *B. Paludinosus* are not well known, but Greenwood (1966) suggests that spawning occurs in streams and rivers during the rainy season. This is confirmed by studies of fish population dynamics being carried out on Lake Chilwa; gonads in a "ripe" or "ripe-running" condition being found most frequently from November to February. The sex ratio is not 1:1, the females considerably outnumbering the males. Both male and female fish mature at 5.0 cm and from preliminary growth-rate studies it is thought that these lengths would be attained during the first year of growth. The mean fecundity varies from 500 (5.0 cm) to over 5,000 (11.5 cm) (Furse, Personal Communication)

4. Food

Very few individuals of this species have been examined hitherto. In Lake Victoria Corbet (1961) found that they had a varied diet, including small snails and adult insects. Previous work on Lake Chilwa showed that *B. paludinosus* fed exclusively on zooplankton, (Kalk, 1969a & b), while Kirk (1967a) stated that the species fed mainly on zooplankton and some plant material.

5. Importance

*B. paludinosus* is very widely distributed throughout the African continent. It is, presumably, caught in many areas but only in Lake Chilwa does it form an important part of the fishery (Kalk, 1969b). See Fish-landing table, 2.
Clarias mossambicus Peters.
(Syn. C. gariepinus (Burchell).)
The common catfish of Lake Chilwa.
(x1/3)
B. *Clarias mossambicus* Peters 1852

**Family:** Claridae; **Sub-order:** Siluroidei

**English name:** Catfish  
**Chichewa name:** Mlamba

1. Taxonomy and description

The genus *Clarias* have flat and broad heads with small eyes and no scales. Their body is eel-like, elongate with a long, spineless dorsal fin, extending from slightly behind the head to the caudal fin from which it is narrowly separated. The anal fin is also long. Their hardiness is well-known, and they are able to survive in conditions which would be lethal to other fish. They possess an elaborate accessory breathing organ which allows them to utilise atmospheric oxygen. It is this capability which enables the fish to survive in deoxygenated water and to travel across land from one body of water to another. *Clarias mossambicus* in moist conditions can live out of water for at least eighteen hours. It is also reputed to burrow into the mud of drying rivers and marshes and aestivate. Around the mouth are four pairs of long, sensory barbels; the mouth is wide, allowing relatively large prey to be taken. The maximum size of the species varies considerably with environment. Fish 80-90 cm in length are often caught, although some specimens of 120 cm are occasionally taken in Lake Victoria. Individuals in Lake Kyoga, Uganda, are generally smaller, (Greenwood, 1966). Fish examined from Lake Chilwa during the period of study rarely exceeded 60 cm but a specimen of nearly 80 cm was recorded. In view of the
fact that only three years had elapsed since the rebirth of the lake, this length should not be taken as maximal. In coloration the fish is rather variable, but is generally grey-black dorsally, and creamy-white ventrally. But the fish can change colour in response to changes of habitat, and sometimes specimens have been found with the dorsal surface mottled grey-black-khaki.

There has been some controversy over the taxonomy of *Clarias mossambicus*, *Clarias gariepinus* (Burchell) 1822 and *Clarius lazera* Val 1840. Jackson (1961a) stated that *C. mossambicus* was the middle member of a cline covering the African continent, the most southerly member being *C. gariepinus* and the northern and western member being *C. lazera*. The boundaries between the three "species" are very indistinct because of their ubiquitous distribution in almost every piece of water and because of their terrestrial capacities. However, rather arbitrarily, the Zambesi system has been taken as the boundary between *C. mossambicus* and *C. gariepinus*; the former occurring in this system and to its north. Greenwood (1966) thought that until the taxonomy of the whole family *Claridae* was fully revised it was advisable to retain *C. mossambicus* as a separate species. Jubb (1967) maintained that *C. mossambicus* cannot be distinguished from *C. gariepinus* on the basis of the width of the vomerine and premaxillary bands of teeth (supposedly the main diagnostic feature) and so used the latter name, because of its earlier identification.
2. Distribution and Habitat

Subject to the taxonomic considerations set out in the previous paragraph, the distribution of *C. mossambicus* can be regarded as being limited to east and central Africa. It occurs in most bodies of water, whether permanent or temporary. In lakes it is generally found only in shallow inshore regions, near vegetation, but it is present in all areas of Lake Chilwa.

3. Breeding

The size at maturity depends upon the environment. In Lake Victoria, fish rarely mature under 50 cm; whereas in Lake Kyoga (Uganda), maturity is reached between 25-40 cm (Greenwood, 1966), and in Lake Chilwa maturity is reached at about 20 cm (Furse, personal communication). With the onset of the rains, migration occurs up rivers and streams (Jackson, 1961 and Greenwood, 1966) and across flood plains (Jubb, 1967) and spawning takes place in shallow water where vegetation is abundant. Greenwood (1966) suggested that the young spend about six weeks in these shallow hatching areas before returning to the parent body of water. The mean fecundity varies from 200 (20 cm) to 180,000 (78 cm) (Furse, personal communication).

4. Food

Greenwood (1966) described *C. mossambicus* as an omnivorous scavenger, but predominantly a predator of small fish (particularly of the genus *Haplochromis*). Amongst other food, insect larvae, molluscs and plants were also noted. Despite the fact that it
<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
<th>Date</th>
<th>Area</th>
<th>Feeding observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. mossambicus</td>
<td>Graham</td>
<td>1929</td>
<td>L. Victoria, Uganda</td>
<td>Fish, odonata, molluscs and plants</td>
</tr>
<tr>
<td></td>
<td>Worthington</td>
<td>1932</td>
<td>L. Kikoge, Uganda</td>
<td>Fish remains, water lily seeds and other plant material</td>
</tr>
<tr>
<td></td>
<td>Worthington &amp; Ricardo</td>
<td>1937</td>
<td>L. Tanganyika</td>
<td>Fish, molluscs, crustacea sand and mud</td>
</tr>
<tr>
<td></td>
<td>Hulot</td>
<td>1950</td>
<td>L. Malawi &amp; L. Tanganyika</td>
<td>Unidentifiable fish remains</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. gariepinus</td>
<td>Magis</td>
<td>1961</td>
<td>N. Katanga, Congo</td>
<td>Fibrous vegetable detritus, aquatic insects, fish remains and occasionally diatoms and rotifers</td>
</tr>
<tr>
<td></td>
<td>Corbet</td>
<td>1961</td>
<td>L. Victoria, Uganda</td>
<td>Up to 3 cm in length fed on Ostracoda and aquatic insects. With increasing length more fish taken. Adults fed on wide range of items including zooplankton, molluscs, termites and young birds, but principally fish - mainly Haplochromis sp. but also some Tilapia</td>
</tr>
<tr>
<td></td>
<td>Groenewold</td>
<td>1964</td>
<td>Transvaal, South Africa</td>
<td>General carnivorous feeder. Food consisted mainly of fish, terrestrial invertebrates, aquatic insects and zooplankton.</td>
</tr>
<tr>
<td></td>
<td>Greenwood</td>
<td>1966</td>
<td>Uganda</td>
<td>Omnivorous, predominately piscivorous - Haplochromis sp. Also insect larvae and plant material, very few fed on zooplankton.</td>
</tr>
<tr>
<td></td>
<td>Jubb</td>
<td>1967</td>
<td>South Africa</td>
<td>Omnivorous</td>
</tr>
<tr>
<td></td>
<td>Munro</td>
<td>1967</td>
<td>L. McIlwaine, Rhodesia</td>
<td>Small fish fed predominately on Chironomid larvae but this item decreased in importance in larger fish. Zooplankton of increased importance with size.</td>
</tr>
<tr>
<td></td>
<td>Kirk</td>
<td>1967</td>
<td>L. Chilwa, Malawi</td>
<td>Mainly piscivorous - B. paludinosus but few Cichlid species. Also larvae of aquatic insects, plant material and mud.</td>
</tr>
<tr>
<td></td>
<td>Schoonbee</td>
<td>1969</td>
<td>L. Barberspan, South Africa</td>
<td>Largely piscivorous but zooplankton could replace fish as dominant food item.</td>
</tr>
</tbody>
</table>
has very fine and numerous gill-rakers that would enable it to filter microscopic organisms from the environment. Few fish had been recorded as feeding exclusively on plankton. However, other workers have found that zooplankton may replace fish as the predominant food item (Schoonbee, 1969) particularly in larger fish (Mwase, 1967). For a more detailed breakdown of the evidence see Table 5.

5. Importance

In Uganda C. mossambicus is of little economic importance (Greenwood, 1966), but in Central Africa, particularly in areas with only small bodies of water, it forms an important part of the protein intake of the population (Jackson, 1961b; Kirk, 1967b). In Lake Chilwa, C. mossambicus forms a major proportion of the total fish landings, see Table 2.
Tilapia shirana chilwae Trewavas.
The endemic subspecies of 'bream'
found in lake Chilwa. (×2/3)
C. Tilapia shirana chilwae Trewavas 1966

Family: Cichlidae. Sub-order: Percoidel
English name: Bream (this is incorrect, but widely used)
Chichewa name: Makumba

1. Taxonomy and description

The many species within the genus have a wide distribution throughout Africa, and have adapted and evolved to be tolerant of many and varied environmental conditions. Tilapia shirana chilwae forms part of the Tilapia shirana - placida-ruvuma complex of the eastward-flowing rivers of Tanzania and Mozambique. Members of this group have four spines in their anal fins, are mouth brooders, and have affinities with T. karogwe of the Pangani river in Tanzania, which also have four anal spines. (Trewavas, 1941 and McConnell, 1959). Trewavas (1966a) states that T. mossambica has only three anal spines, but that this fact is not of sufficient significance to preclude a relationship with the group of 4-spined Tilapia species. The nominate subspecies, T. shirana shirana Boulenger is endemic to the Lake Malawi basin and Upper Shire River (Jackson, 1961a), while T. shirana chilwae is endemic to the Lake Chilwa-Chiuta depression (Trewavas, 1966a). The two sub-species differ in their breeding coloration and behaviour, egg-size, number of gill-rakers and blood protein chemistry. T. shirana chilwae is a relatively small member of the genus, growing to a maximum size of about 30 cm. In the first year of growth, individuals attain a length of about 10-11 cm but this varies with environmental conditions, (Kirk, 1970).
2. Distribution and Habitat

*Tilapia shirana chilwae* is endemic of the Chilwa-Chiuta depression. *T. shirana shirana* is endemic of the Lake Malawi basin and Upper Shire River. This latter sub-species is found mainly in the middle and lower reaches of rivers, estuaries and sheltered lake areas, whilst *T. shirana chilwae* occurs all over Lake Chilwa, but appears to be most abundant on the margin of the reed swamp and open water.

3. Breeding

Like many other *Tilapia* species in south and central Africa, *T. shirana chilwae* breeds during the warm weather from September until the beginning of June, spawning mainly occurring in the period December-January. Maturity is reached at about 12.5 cm in females and 15 cm in males. In this feature, it differs from *T. shirana shirana* which commences breeding at 18 cm for females and 22 cm for males (Lowe, 1952). It is probable that most females spawn twice each season, and between 100 and 400 eggs, depending on the size of the female, are shed on each occasion. After fertilization, the eggs are sucked into the mouth of the female, where they remain for the next three or four weeks, during which period the eggs hatch, and the young grow to a length of about 1 cm (Kirk, 1970).

4. Food

According to Kirk (1970), blue-green algae, diatoms and bottom deposits are ingested, but diatoms appeared not to be
<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
<th>Date</th>
<th>Area</th>
<th>Feeding Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. shirana</em></td>
<td>Ricardo, Borley &amp; Trewawas</td>
<td>1942</td>
<td>L. Malawi</td>
<td>Fed on higher plant material</td>
</tr>
<tr>
<td>(young)</td>
<td>Lowe</td>
<td>1952</td>
<td>&quot;</td>
<td>Vegetable detritus - probably picked up off the bottom. Also <em>Anabaena</em> sp. flagellates and ciliates.</td>
</tr>
<tr>
<td><em>T. mossambica</em></td>
<td>Vaas &amp; Hofstede</td>
<td>1952</td>
<td>Fish ponds</td>
<td>Mainly herbivorous. Small fish fed on diatoms unicellular algae and small crustaceae. Large fish fed on higher plant material, but also green and blue-green algae, diatoms and zooplankton.</td>
</tr>
<tr>
<td></td>
<td>Le Roux</td>
<td>1956</td>
<td>Fish ponds</td>
<td>Fish less than 5 cm fed on zooplankton. Adults fed on almost all available food but mainly phytoplankton</td>
</tr>
<tr>
<td><em>T. shirana</em></td>
<td>Jackson</td>
<td>1961a</td>
<td>L. Malawi</td>
<td>Bottom detritus and higher plant material</td>
</tr>
<tr>
<td><em>T. mortimeri</em></td>
<td>Matthes</td>
<td>1965</td>
<td>L. Kariba</td>
<td>Less than 7 cm in length predominately herbivorous but diet was more omnivorous than larger fish which generally fed on epiphytic algae.</td>
</tr>
<tr>
<td>(=T. mossambica)</td>
<td></td>
<td></td>
<td>Zambia</td>
<td></td>
</tr>
<tr>
<td><em>T. mossambica</em></td>
<td>Munro</td>
<td>1967</td>
<td>L. McIlwaine</td>
<td>Filamentous algae, diatoms and plant material were the main foods, but zooplankton was also important.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Rhodesia</td>
<td></td>
</tr>
<tr>
<td><em>T. shirana</em></td>
<td>Kirk</td>
<td>1970</td>
<td>L. Chilwa</td>
<td>Blue-green algae, diatoms and plant detritus ingested but appeared not to be digested. Possible that epiphytes, bacteria, crude protein and extracellular nitrogenous substances may be important.</td>
</tr>
<tr>
<td><em>chilwae</em></td>
<td></td>
<td></td>
<td>Malawi</td>
<td></td>
</tr>
</tbody>
</table>
digested, and blue-green algae only slightly so. See separate table for comparison of results of other workers on related species, Table 6.

5. Importance.

Commercially the genus is very important throughout Africa. Members have been introduced to South-East Asia and the American continent. There are large, natural fisheries, and certain members of the genus are used extensively in fish-pond culture. A large body of literature on their biology is available. In Lake Chilwa T. shirana chilwae is one of the three species of economic importance, but tonnages landed vary considerably with lake conditions from year to year. See Table 2.
A. Study of feeding

The fact that fish have an aquatic environment obviously makes it more difficult to study their feeding habits. Visual observation of their feeding and their foods ingested is generally not so easy, and in Lake Chilwa it is impossible, because of the high water turbidity. Faecal analysis which can be used to study terrestrial fauna is also much more difficult for fish study, for similar reasons. It is therefore necessary to catch fish and examine the contents of their digestive tracts. Particular problems encountered may be conveniently described under the following headings: sampling and collection, analysis of the food present in the digestive tract, and interpretation of results.

1. Sampling and Collection

Sampling should be unbiased and reflect the species, size, composition and sex ratios of the populations as a whole. Ideally, samples should be collected soon after feeding has taken place and before digestion has proceeded very far; the fish caught should not have had an opportunity to "fight" in attempting to escape, since in doing so they may regurgitate their stomach contents. For the same reasons they should be killed soon after initial capture.

Probably the best way to collect fish samples from a body of water is to use electrical methods. The use of such methods,
however, is limited by a number of factors. For example, the lack of suitable boundaries within a lake makes electrical fishing inefficient and difficult. Moreover, the intensity of current that must be used to stun fish is dependent on the conductivity of the water in which they live, and where conductivities are high, very high current intensities must be used. Hence in Lake Chilwa, with the prevailing water conditions, the method would be impracticable.

Another method is to use explosives and poisons. This was also contemplated for Lake Chilwa, but such methods would have set an inappropriate example to the local fishermen, and mainly for this reason it was not tried.

A third method is beach seineing. In Lake Chilwa, however, the extensive, peripheral reed swamp precluded the possibility of using it extensively. Use of this method on the few suitable, isolated beaches would have provided inadequate samples and it was therefore only occasionally used.

Fish baskets and scoops provide another method; but for Lake Chilwa they were thought to be too selective and inefficient to be used for regular sampling, although baskets were used for catching swamp specimens.

Another method is to use long lines with baited hooks, but this is primarily suitable for carnivorous fish. This method would clearly have provided artificial conditions for the study, and was therefore not used.

The most common method of catching fish used by the local
fishermen (Hornby, 1962) is to use gill-nets, and regular monthly samples were collected by this method. During the period of study this method was however found to have certain drawbacks, details of which are given in the following section.

Another common method of catching fish is to use a trawl-net. Unfortunately a suitable modification of this method for Lake Chilwa was only perfected by the Fisheries Department of the Malawi Government towards the end of the period of research. The method permits the collection of wide size ranges of fish, and obviously the fish can be killed soon after capture. One of the disadvantages of this method of sampling however was the possibility of artificial forced feeding of the fish when compressed at high density in the 'cod-end' of the trawl.

2. Examination and analysis

Excellent reviews of the methods that have been used in studying the food of fish have been given by Hynes (1950) and Windell (1966). Several methods of quantifying the food present in digestive tracts have been used by different workers and can be dealt with under the following headings:

i. Frequency of occurrence

Stomach contents are examined and the individual food organisms sorted and identified. The number of stomachs in which each item of food occurs is recorded and expressed as a percentage of the total number of stomachs examined. This method demonstrates that organisms are being ingested, but it gives no
information on the quantities or numbers, and does not take into consideration the accumulation of food items resistant to digestion.

ii. **Numerical method**

The number of individuals of each food type in each stomach are counted. These are summed up to give totals for each kind of food item in the whole sample, and then grand totals of all items are counted. The quotient of these gives the percentage representation, by number, of each type of food item.

iii. **Volumetric method**

This technique is reasonably simple and accurate when large volumes of food are present, and the number of items to be segregated is small (or can be grouped into not more than six to eight categories). The quantity of each larger food type in a stomach is measured by water displacement. If food volumes are small, direct measurement is impossible, and estimates are made. Studies by the volumetric method alone tend to mask the importance of the smaller items of food. Data may be much distorted by the occasional occurrence of an exceptionally bulky food item, which may be digested more slowly than the smaller items. Additional error can be introduced by the differential rates of digestion resulting from chitinisation and a tendency of the remains to accumulate.
iv. Gravimetric Method

The different food items are sorted, identified to species where possible, and the dry weight or the moist weight (at a standard degree of wetness) of each category is determined. Values for the various kinds of items are summed and the results expressed as percentages of the weight of the total food in all the samples. This method is similar to the previous one (volumetric) and has similar advantages and disadvantages.

v. Points Method

This is a semi-quantitative volumetric method in which the various categories are defined beforehand, and subsequently the contents of the stomach or the intestine are examined on the basis of the categories. Each category is allotted a number of points on a scale, representing the proportion by volume of each category. Many small items in this method might be given the same number of points as a few large ones. The main objection to this method is that it is subjective in nature, but this criticism can be levied against all methods.

vi. Dominance Method

This is a two stage method. It involves determining the chief constituent of all the stomachs examined. The results are usually expressed as percentages of the number of stomachs examined.
vii. **Combination of Methods**

The results obtained from various combinations of any of the previous methods may be combined to give an index of feeding which may be more meaningful than any set of results taken separately.

3. **Interpretation**

The food or the diet of an organism is defined as those items that are ingested from the environment. Some of the items that are ingested are not digested, and have no nutritive value. Those items of food that are digested may not be digested to the same extent, and even those that are fully digested may not be of the same nutritive value. Thus, interpretation of any results obtained by the methods described, in terms other than of the food consumed, is unjustified without extensive nutritive experimentation, and this was not attempted because it would have extended the investigation much beyond the scope of this thesis.
B. The Programme

1. Sampling and collection

The various methods of obtaining fish have been mentioned and discussed in the previous section.

In the earlier part of the study the gill-net method was used to catch fish of all species. The main limitation of this method was found to be that fish had often been in the net for a considerable time, and had sometimes died before it was cleared; hence digestion was often in an advanced state, and regurgitation of food had often occurred. Another limitation is that gill-nets are selective in their design, but this was overcome to a certain extent by the use of graded fleets of nets. Despite the comparatively small size of B. paludinosus all sizes of this fish were caught in these nets because the serrated dorsal spine fouled the fine mesh of the nets.

In the latter part of the studies, a trawl-net and fish baskets were sometimes used. Trawling was the most convenient and preferable in many ways. The fish were obtained alive, and quickly, and this obviated some of the previous mentioned problems arising from the digestion or regurgitation of stomach contents, although the expected regurgitation and artificial forced feeding did occur possibly when the fish were compressed in the 'cod-end' of the trawl. Usually, large numbers of individuals of the three species were obtained from an easily-defined habitat, thus allowing selection of members of both sexes and fish of a good
size-range. This active capture method had many advantages over the passive method of gill-net capture, and it was unfortunate that in the earlier part of the study a perfected trawl had not been successfully developed.

In the swamps, where trawling and gill-netting were impracticable because of the density of vegetation, fish baskets were used to obtain samples.

One of the uncertainties throughout the sampling period was the sample size that was required to give meaningful results. It was, however, decided in the early stages, that monthly catches of about thirty individuals of each species (of both sexes and as wide a size range as possible) should be obtained, as this was the number of fish that could be conveniently examined.

As soon as possible after capture, species, total length, weight to the nearest gram, sex and maturity (see Tables 7 and 8), were determined and recorded for each fish. The stomach and intestine were then removed and preserved in 4% formaline solution in numbered bottles, for later examination in the laboratory. *B. paludinosus* specimens were preserved whole after inoculation of formaline solution into the body cavity, and the specimens were later dissected and examined.
### Table 7.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Barbus paludinosus</th>
<th>Clarias mossambicus</th>
<th>Tilapia shirana chilwae</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>External Features</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Internal Features</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>Ovaries larger than testes and of granular texture. Even in immature stages primordial ova may be seen under low power microscope</td>
<td>Ovaries shorter than testes and with a smooth surface</td>
<td></td>
</tr>
<tr>
<td>♂</td>
<td>Testes smaller than ovaries and non granular in texture.</td>
<td>Testes longer than ovaries with a serrated edge.</td>
<td></td>
</tr>
</tbody>
</table>

Differential characters for sex determination.
<table>
<thead>
<tr>
<th>Maturity</th>
<th>Sex</th>
<th>Barbus paludinosus</th>
<th>Clarias mossambicus</th>
<th>Tilapia shirana chilwae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immature</td>
<td>♂♀</td>
<td>Ovaries larger than testes; small, translucent, grey-pink in colour; of granular texture with ova invisible to the naked eye, but primordial ova clearly seen with L.P. microscope.</td>
<td>Testes smaller than ovaries, just visible as a thin white line. Non-granular texture and primordial sperm not apparent under low power microscope.</td>
<td>As immature state but larger</td>
</tr>
<tr>
<td>Inactive</td>
<td>♂♀</td>
<td>As immature state but larger</td>
<td>As immature state but longer and wider, more distinct, white-cream in colour.</td>
<td></td>
</tr>
<tr>
<td>Active</td>
<td>♂♀</td>
<td>Ovaries larger and small yellow ova clearly visible to the naked eye.</td>
<td>Testes thicker and longer but much smaller than ovaries, white-cream in colour, non-granular texture</td>
<td></td>
</tr>
<tr>
<td>Ripe</td>
<td>♂♀</td>
<td>Ovaries fill body cavity, full of large, yellow ova</td>
<td>Ovaries are large and full of large yellow ova, stretching about half the length of body cavity.</td>
<td>Testes larger than in active state but smaller than ovaries, white, non-granular; stretch neatly whole length of body cavity.</td>
</tr>
<tr>
<td>Ripe-Running</td>
<td>♂♀</td>
<td>Testes larger, white and non-granular, not filling body cavity.</td>
<td></td>
<td>As ripe stage but on stripping sperm ejected from vas deferens.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Not used for Barbus paludinosus as all were preserved in formalin before examination.</td>
<td>Embryos present in mouth.</td>
<td>As ripe stage but on stripping ova ejected from oviducts.</td>
</tr>
<tr>
<td>Spent</td>
<td>♂♀</td>
<td>Enlarged ovaries, but collapsed with few degenerating ova still present.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Enlarged testes but collapsed and grey in colour.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Criteria for the stages of maturity.
2. **Examination and analysis**

It was decided at the outset of the project, as already indicated, that a wholly quantitative approach would be unnecessarily complicated, and that the requirement of this study could be met without such a time-consuming analysis. The points method described here and used in this study is, essentially, the method first proposed by Swynnerton and Worthington (1940), adapted by Frost (1943) and again slightly modified and recommended by Hynes (1950). According to Wendell (1968), while other methods of analysis differ considerably in detail, in most studies the same comparative results are obtained whatever method is used.

Initially some thirty to forty individuals of each of the three species were examined to give an indication of the types of food ingested. With this background, and from the categories used in a number of other studies on fish feeding, the following food types were decided upon:

1. Higher plant material
2. Filamentous green algae
3. Non-filamentous green algae
4. Filamentous blue-green algae
5. Non-filamentous blue-green algae
6. Diatoms
7. Crustacea
8. Gastropods
9. Acquatic insects
10. Terrestrial insects
11. Rotifera
12. Fish eggs
13. Fish

14. Unrecognisable material (e.g. mucous secretions, organic matter and possibly bacteria).
Most fish were caught in the Kachulu Bay area of Lake Chilwa, but samples were also obtained from other areas of the lake in order to compare the results with those from Kachulu Bay and so indicate whether or not these were representative. For analytical purposes, Lake Chilwa was divided into four areas: Kachulu Bay, North Lake, South Lake and Swamp. (See Map).

The stomach and intestinal contents of *T. shirana chilwae* and *C. mossambicus* were examined. *B. paludinosus* has no discrete stomach, the digestive tract is slightly wider than the posterior end. Since this tract is relatively small, its contents were examined as a whole. By means of a pair of forceps and a seeker, the contents of a stomach or an intestine were teased and squeezed out into a petri dish. The contents were then separated and suspended with a little water, delivered as a jet from a wash bottle. Next the contents were examined by eye, and under a low-power dissection microscope. Then, with due care being taken to ensure that the contents were thoroughly mixed, two samples were taken with a pipette, and placed on separate microscope slides. These were then examined, ten fields each, under a high-power microscope at x150 magnification.

From these various observations the food types present were rated in proportion to their relative volumes on an eight point scale. With this method many small items might be given the same number of points as a few large ones and the sum of the points given to any one stomach or intestine was always eight; e.g. contents of the stomach of one fish comprised of:
fish   ½   points allotted = 4
aquatic insects  ⅔ points allotted = 2
unrecognisable material  ⅔ points allotted = 2
Sum = 8

Empty stomachs or intestines were allotted eight points in the unrecognisable material category but were excluded from calculations and only used to determine the proportion of empty fish caught.

All the data obtained from a single fish were subsequently transformed so that they could be punched onto computer cards from which the information could be retrieved as required, with the aid of a suitably programmed computer. (For arraying, coding and programs see Appendix 1-4).

During data analysis, computer cards for the different species were analysed separately. Stomach or intestinal contents were cross correlated with the following parameters:

1. Sex
2. Maturity
3. Length group
4. Presence or absence of vegetation
5. Time caught
6. Date of collection/water conductivity.
7. Area caught
8. Method of capture.
The computer output, for a selected species, gave:

1. the sum of points allotted to each food item
2. the number of fish
3. the number empty
4. the frequency of occurrence of each food item

for each group of a selected parameter. (see Appendix 5)

From these crude results the proportion of each food item was calculated as a percentage of the recognisable material and the percentage frequency of occurrence of each food was also calculated. These were then corrected to the nearest 1% and plotted as histograms.

What follows is a worked example for five fish at one grouping of a parameter to show the calculations.

<table>
<thead>
<tr>
<th>Item</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish 1</td>
<td>2</td>
<td>4</td>
<td></td>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish 2</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish 3</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish 4</td>
<td>6</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td>13</td>
<td>5</td>
<td>6</td>
<td>4</td>
<td></td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Sum of recognisable food items = 32 - 4 = 28

% proportion of food items

| 46.4 | 17.9 | 21.4 | 14.3 |

One fish empty = 20%

* Empty and therefore excluded.
The contents of the intestine as well as the stomach were examined for three reasons; first, because many of the initial samples of fish examined were found to have empty stomachs; second, in order to seek an indication of what in fact was being digested; third, to investigate the relationship between results obtained from examinations of intestines and examinations of stomachs.

In order to determine whether the feeding habits of the Lake Chilwa fish differed from those of other areas of southern Malawi, small samples of fish of the same species were obtained from two other localities - Lake Chiuta (to the north of Lake Chilwa) and the Elephant Marsh region of the Lower Shire river, which drains Lake Malawi and flows into the Zambezi river. (See Map).
Higher Plant Material

Green Algae, filamentous
Green Algae, non-filamentous
Blue-green Algae, filamentous
Blue-green Algae, non-filamentous

Diatoms

Crustacea

Cephalopoda

Aquatic Insects

Terrestrial Insects

Rotifera

Fish eggs

Fish remains
RESULTS

The histograms that follow show the relative proportions of the thirteen food items, as percentages of the total recognisable contents of the stomachs or intestines of the fish within the groupings of the various parameters. Superimposed on the histograms are the percentage frequencies of occurrence of each food item. Values for *B. paludinosus* were obtained from analysis of the contents of the whole digestive tract; those for *C. mossambicus* and *T. shirana chilwae* are for stomach content unless otherwise stated. The percentage of empty fish in each grouping is given after the number of fish examined. An overlay identifying the food items is provided.

Each month water samples were collected from selected areas of Lake Chilwa and analysed. The overall physico-chemistry is reflected by the electrical conductivity of the water. Each fish collection could be related to a particular conductivity. Initially the feeding patterns were plotted for 500 μmho/cm increments but no meaningful trends were apparent. The results were then recalculated to give feeding patterns in waters above and below 1500 μmho/cm.
Histogram 1
586 fish 6% empty
B. paludinosus
All conditions
A. *Barbus paludinosus*

Histogram 1. shows the feeding pattern for the species as a whole, under all conditions. A total of 586 digestive tracts were examined. The fish fed predominantly on zooplankton (56%); non-filamentous green algae (19%) and higher plant material (14%) were also important in the diet. Frequency plots reflected the same pattern.
Histogram 3
370 fish 7% empty
FEMALES

Histogram 2
185 fish 3% empty
MALES
Histograms 2 and 3 show the feeding patterns of 375 males and 185 males respectively. There were no major differences.
Histogram 12
78 fish 1% empty
RIPE (MALE)

Histogram 11
37 fish 5% empty
ACTIVE (MALE)

Histogram 10
12 fish 0% empty
INACTIVE (MALE)

Histogram 9
58 fish 5% empty
YOUNG (MALE)
Histograms 4-12 show the feeding patterns of each sex at different stages of sexual maturity. There were no major differences. The dominant food item for all stages of maturity was zooplankton, but young fish fed less on plant material. They also fed on rotifers, which mature fish did not. Young fish did not feed on aquatic insects, while adults did to some extent.
Histogram 15
85 fish 7% empty
8.0-11.9 cm

Histogram 14
458 fish 8% empty
4.0-7.9 cm

Histogram 13
44 fish 0% empty
0-3.9 cm
Histograms 13, 14 and 15 show the feeding pattern of fish in length groups: 0 - 3.9 cm (44 fish), 4.0 - 7.9 cm (458 fish) and 8.0 - 11.9 cm (85 fish). The patterns were very different. In the smallest length group the predominant food item was zooplankton (65%), followed by non-filamentous algae (15%), rotifers (6%) and fish eggs (5%). In the intermediate length group zooplankton was still the predominant food item (60%), followed by non-filamentous green algae (19%) and higher plant material (13%). In the largest fish zooplankton formed 33% of the contents, higher plant material 31%, non-filamentous green algae 17% and aquatic insects 10%.
Histogram 17
470 fish 7% empty
VEGETATION PRESENT

Histogram 16
118 fish 4% empty
VEGETATION ABSENT
Histograms 16 and 17 show the feeding patterns of 470 fish caught in areas where vegetation was present and 118 fish caught in areas where vegetation was absent. In areas of vegetation a broader spectrum of food items was consumed, with higher proportions of higher plant material and non-filamentous green algae but reduced zooplankton content. However the major food items were the same in both habitats.
Histogram 19
138 fish 10% empty
pm caught

Histogram 18
381 fish 5% empty
am caught
Histograms 18 and 19 show the feeding patterns of 381 fish caught before mid-day and 138 fish caught after mid-day. There were no major differences in the patterns but twice as many digestive tracts were empty in afternoon catches (10% as compared with 5%). This difference may not be very meaningful and is probably due to the methods of sampling employed. In particular when using gill-nets it was impossible to be precise about when fish were actually caught because this might have been at any time between setting and clearing the nets. More convincing evidence was obtained from fish caught during twenty-four hours of continuous sampling, using a trawl net, in an area of Kachulu Bay close to the reed fringe. The results of this programme showed that 70% (of 30 fish) were empty in hours of darkness while 10% (of 30 fish) were empty in hours of daylight.
Histogram 21
201 fish 2% empty
>1500 umhos/cm

Histogram 20
352 fish 8% empty
<1500 umhos/cm
**Histograms 20 and 21** show the feeding patterns of 352 fish caught in waters with conductivities greater than 1500 $\mu$mhos/cm and 201 fish caught in waters with a conductivity less than 1500 $\mu$mhos/cm. In the latter case there was a greater diversity of food items; more non-filamentous green algae (22% against 13%) and less zooplankton (48% against 69%) were consumed.
Histogram 27
11 fish 0% empty
LAKE CHIUTA

Histogram 26
48 fish 2% empty
LOWER SHIRE

Histogram 25
6 fish 0% empty
SWAMP

Histogram 24
60 fish 0% empty
SOUTH LAKE

Histogram 23
135 fish 7% empty
NORTH LAKE

Histogram 22
328 fish 9% empty
KACHULU BAY
Histograms 22-27 illustrate the feeding patterns of fish caught in four areas of Lake Chilwa, the Lower Shire and Lake Chiuta. Except for the swamp sample, of only six fish, the diets of fish in Lake Chilwa were similar. The feeding pattern of fish from the swamp showed a high proportion of non-filamentous green algae (52%) and a low proportion of zooplankton (20%). The pattern for Lower Shire fish was similar to that of Chilwa fish. Fish caught in Lake Chiuta had a high proportion of higher plant material (45%) and a relatively low proportion of zooplankton (34%).
Histogram 30
48 fish 2% empty
SEINE CAUGHT

Histogram 29
419 fish 6% empty
TRAWL CAUGHT

Histogram 28
121 fish 12% empty
GILL NET CAUGHT
Histograms 28-30 illustrate the feeding patterns of 121 fish caught with gill-nets, 419 caught with a trawl net and 48 caught with a beach seine. Gill netted fish showed a greater diversity of food items, with a reduced proportion of zooplankton (41%). Trawled fish had a higher proportion of zooplankton (59%). Seined fish showed least diversity of food items, with higher plant material (21%) and zooplankton (70%) formed the bulk of the diet.
Histogram 2
369 fish 13% empty
on intestines
ALL CONDITIONS
Clarias mossambicus

Histogram 1
474 fish 30% empty
on stomachs
ALL CONDITIONS
Clarias mossambicus
B. Clarias mossambicus

Histograms 1 and 2 illustrate the feeding patterns for the species as a whole, on examination of 474 stomachs and 369 intestines respectively. The patterns were similar. In each case the major food items were zooplankton, fish, higher plant material and aquatic insects. Of the recognisable fish present in the stomach the predominant fish prey was Barbus although some Haplochromis Tilapia and Clarias were also taken.
Histogram 4
204 fish (st) 26% empty
FEMALES

Histogram 3
227 fish (st) 57% empty
MALES
Histograms 3 and 4 show the feeding patterns (from stomach content analysis) of 227 males and 204 females respectively. There were no major differences.
Histogram 10
15 fish (st) 33% empty
SPENT (FEMALES)

Histogram 9
7 fish (st) 43% empty
RIPE RUNNING (FEMALES)

Histogram 8
28 fish (st) 43% empty
RIPE (FEMALES)

Histogram 7
11 fish (st) 18% empty
ACTIVE (FEMALES)

Histogram 6
43 fish (st) 23% empty
INACTIVE (FEMALES)

Histogram 5
105 fish (st) 22% empty
YOUNG (FEMALES)
Histogram 16
3 fish (st) 33% empty
SPENT (MALES)

Histogram 15
6 fish (st) 16% empty
RIPE RUNNING (MALES)

Histogram 14
25 fish (st) 32% empty
RIPE (MALES)

Histogram 13
46 fish (st) 23% empty
ACTIVE (MALES)

Histogram 12
65 fish (st) 52% empty
INACTIVE (MALES)

Histogram 11
28 fish (st) 22% empty
YOUNG (MALES)
Histograms 5-16 show the feeding patterns (from stomach content analysis) of fish at different stages of sexual maturity. There was considerable variation between the six stages of maturity in both sexes, which was probably due in part to inadequate sample sizes from certain stages (males: "ripe-running" and "spent"; females: "active", "ripe-running" and "spent"). The predominant food items for different stages of maturity were:

<table>
<thead>
<tr>
<th>Males</th>
<th>Stage</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton</td>
<td>Young</td>
<td>Zooplankton</td>
</tr>
<tr>
<td>Fish</td>
<td>Inactive</td>
<td>Zooplankton</td>
</tr>
<tr>
<td>Zooplankton</td>
<td>Active</td>
<td>Zooplankton</td>
</tr>
<tr>
<td>Zooplankton and</td>
<td>Ripe</td>
<td>Zooplankton</td>
</tr>
<tr>
<td>Higher Plant Material</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zooplankton</td>
<td>Ripe Running</td>
<td>Zooplankton</td>
</tr>
<tr>
<td>Fish</td>
<td>Spent</td>
<td>Fish</td>
</tr>
</tbody>
</table>
Histogram 20
8 fish (st) 75% empty
45.0-59.9 cm

Histogram 19
136 fish (st) 44% empty
70.0-74.9 cm

Histogram 18
222 fish (st) 22% empty
15.0-29.9 cm

Histogram 17
110 fish (st) 23% empty
0-14.9 cm
Histograms 17-20 illustrate the feeding patterns (on stomach content analysis) of four length groups of fish: 0-14.9 cm (110 fish), 15.0-29.9 cm (222 fish), 30.0-44.9 cm (136 fish) and 45.0-59.9 cm (8 fish). There were major differences in the feeding patterns of each length group. For fish less than 15.0 cm in length the predominant food item was zooplankton (69%) with aquatic insects (12%) and fish (11%), forming part of the diet. With increasing size the proportion of zooplankton decreased and that of fish increased to 35% and 88% in length groups 30.0-44.9 cm and 45.0-59.9 cm respectively in the largest fish gastopods had a proportion of 12.5%. (It should however be noted that only eight fish were present in this last group and six of these were empty).
Histogram 22
376 fish (st) 33% empty
VEGETATION PRESENT

Histogram 21
98 fish (st) 16% empty
VEGETATION ABSENT
Histograms 21 and 22 illustrate the feeding patterns of 98 fish caught in areas where vegetation was absent and 376 fish caught in areas where vegetation was present. In areas of vegetation, higher plant material, filamentous green algae, aquatic insects and fish remains were present in higher proportions. In both types of habitats the predominant food item was zooplankton, but its proportion was considerably higher in areas away from vegetation, (67% against 39%).
Histogram 24
111 fish (st) 34% empty pm CAUGHT

Histogram 25
320 fish (st) 29% empty pm CAUGHT

0 10 20 30 40 50 60 70 80 90

0 10 20 30 40 50

1 food items 13
Histograms 23 and 24 show the feeding patterns of 320 fish caught before midday and 111 fish caught after midday. They were similar. 34% of fish caught in the afternoon were empty as compared with 29% in morning catches. This small difference might have been due to the methods of sampling employed. In particular when using gill-nets it was impossible to be precise about the time fish were actually caught, because this might have been at any time between setting and cleaving the nets. Information obtained from fish caught during twenty-hours of continuous sampling, using a trawl net, in an area of Kachulu Bay close to the reed fringe showed that 38% (of 16 fish) were empty during hours of darkness, while 21% (of 24 fish) were empty during hours of daylight.
Histogram 26
145 fish (st) 21% empty
>1500 umho/cm

Histogram 25
260 fish (st) 32% empty
<500 umho/cm
Histograms 25 and 26 show the feeding patterns of 145 fish caught in waters with conductivities above 1500 \( \mu \text{mho/cm} \) and 260 fish caught in waters with conductivities below 1500 \( \mu \text{mho/cm} \). In the former case 17% more zooplankton, 14% more plant material, 7% more aquatic insects and 16% less fish were consumed.
Histogram 32
6 fish (st) 67% empty
LAKE CHIUTA

Histogram 31
28 fish (st) 14% empty
LOWER SHIRE

Histogram 30
17 fish (st) 24% empty
SWAMP

Histogram 29
44 fish (st) 25% empty
SOUTH LAKE

Histogram 28
92 fish (st) 19% empty
NORTH LAKE

Histogram 27
260 fish (st) 36% empty
KACHULU BAY
Histograms 27-32 illustrate the feeding patterns of fish caught in four areas of Lake Chilwa, the Lower Shire and Lake Chiuta. There were considerable variations in the proportions of food items in fish from different localities possibly due to small sample sizes from the swamp and Lake Chiuta. The major differences were:

- no fish remains in fish caught in the southern area of Lake Chilwa.
- high proportion of aquatic insects, reduced proportion of zooplankton and the presence of gastropods in fish from the Chilwa swamp.
- high proportion of plant material and reduced proportion of zooplankton in fish from Lower Shire.
- high proportion of plant material and fish remains, and the lack of zooplankton and aquatic insects in fish caught in Lake Chiuta.
Histogram 35
22 fish (st) 5% empty
SEINS CAUGHT

Histogram 34
258 fish (st) 20% empty
TRAWL CAUGHT

Histogram 33
196 fish (st) 44% empty
GILL-NET CAUGHT
Histograms 33, 34 and 35 illustrate the feeding patterns of 196 fish caught with gill-nets, 258 caught with a trawl net and 22 with a beach seine. Gill-net caught fish had the most diverse range of food items, with a high proportion of fish and aquatic insects and a low zooplankton proportion. Trawled fish had a very high proportion of zooplankton, seined fish had a very high proportion of higher plant material.
Histogram 2
267 fish 8% empty on intestines
*Tilapia shirana chilwae
ALL CONDITIONS

Histogram 1
360 fish 40% empty on stomachs
*Tilapia shirana chilwae
ALL CONDITIONS
C. Tilapia shirana chilwae

Histograms 1 and 2 illustrate the feeding patterns for the species as a whole. 360 stomachs were examined for histogram 1 and 267 intestines for histogram 2. Higher plant material was the major food item in both, with various types of algae forming a large proportion of the contents. The proportion of the major items present in the stomach were higher plant material - 28%, filamentous green algae - 16%, zooplankton - 14%, filamentous blue-green algae - 12%, diatoms - 10%, rotifers - 7% and non-filamentous green algae - 7%. In the intestines the proportion of higher plant material, diatoms and rotifers were greater, while no trace of fish remains was found.
Histograms 3 and 4 illustrate the feeding patterns of 164 males and 156 females on stomach content analysis. There were no major differences.
Histogram 10
20 fish (st) 70% empty
SPENT (MALES)

Histogram 9
11 fish (st) 18% empty
RIPE-RUNNING (MALES)

Histogram 8
30 fish (st) 43% empty
RIPE (MALES)

Histogram 7
31 fish (st) 36% empty
ACTIVE (MALES)

Histogram 6
30 fish (st) 43% empty
INACTIVE (MALES)

Histogram 5
43 fish (st) 44% empty
YOUNG (MALES)
Histogram 16
22 fish (st) 32% empty
SPENT (FEMALES)

Histogram 15
13 fish (st) 54% empty
RIPE-RUNNING (FEMALES)

Histogram 14
42 fish (st) 43% empty
RIPE (FEMALES)

Histogram 13
18 fish (st) 50% empty
ACTIVE (FEMALES)

Histogram 12
27 fish (st) 56% empty
INACTIVE (FEMALES)

Histogram 11
35 fish (st) 46% empty
YOUNG (FEMALES)
Histograms 5-16 illustrate the feeding patterns (from stomach content analysis) of fish at different stages of sexual maturity. In both sexes the feeding patterns were similar for different stages of maturity.
Histograms 17, 18 and 19 illustrate the feeding patterns (on stomach content analysis) for the length groups: 0-9.9 cm (70 fish), 10.0-19.9 cm (267 fish) and 20.0-29.9 cm (24 fish). The feeding patterns were fundamentally different. In the smallest size group of fish the predominant food item was zooplankton (46%) and there were no fish remains. In the intermediate size group of fish the predominant food item was higher plant material, 34%, rotifers formed 10% of contents and fish remains were present (6%). In the largest size group of fish higher plant material (51%) and diatoms (18%) were the major food items, rotifers were present (1%) and fish formed 10% of the contents.
Histogram 21
300 fish (st) 45% empty
VEGETATION PRESENT

Histogram 20
59 fish (st) 17% empty
VEGETATION ABSENT
Histograms 20 and 21 illustrate the feeding patterns (on stomach content analysis) of 59 fish caught in areas where vegetation was absent and 300 fish caught where vegetation was present. In areas of vegetation the proportions of all items except zooplankton was higher. Zooplankton formed 57% of contents (against 2%) in areas away from vegetation.
Histogram 23
46 fish (st) 48% empty
pm CAUGHT

Histogram 22
240 fish (st), 48% empty
am CAUGHT
Histograms 22 and 23 illustrate the feeding patterns on stomach content analysis of 240 fish caught before mid-day and 46 caught in the afternoon. There were no major differences, in both cases 48% of fish were empty. Information obtained from fish caught during 24 hours of continuous sampling, using a trawl net, in an area of Kachulu Bay close to the reed fringe showed that 66% (of 30 fish) were empty during the hours of darkness while 33% (of 30 fish) were empty during hours of daylight.
Histogram 25
40 fish (st) 30% empty
>1500 umho/cm

Histogram 24
262 fish (st) 47% empty
<1500 umho/cm
Histograms 24 and 25 illustrate the feeding patterns (on stomach content analysis) of 282 fish caught in waters with an electrical conductivity below 1500 μmho/cm and 40 fish caught in waters with an electrical conductivity above 1500 μmho/cm. The patterns were basically similar but the proportion of plant material was greater in waters of higher conductivity (43% against 33%). The proportions of rotifers and fish remains were higher in waters of lower conductivity.
Histogram 29
30 fish (st) 43% empty
LAKE CHIUTA

Histogram 28
21 fish (st) 52% empty
SOUTH LAKE

Histogram 27
40 fish (st) 13% empty
NORTH LAKE

Histogram 26
229 fish (st) 50% empty
KACHULU BAY
Histograms 26-29 illustrate the feeding patterns (on stomach content analysis) of fish caught in three areas of Lake Chilwa and from the only other place in which the subsepcies is found - Lake Chiuta. Only two specimens were obtained from the Chilwa swamp and have not been included. The proportions of the food items observed in the stomachs of fish from different areas varied considerably, but in general the same items were present. Notable differences were: the high proportion of rotifera in fish from the northern part of Lake Chilwa; the high proportion of non-filamentous green algae in fish from the southern part of the lake; the high proportion of plant material from Lake Chiuta; the lack of rotifera in fish from southern Lake Chilwa and Lake Chiuta.
Histogram 31
144 fish (st) 24% empty
TRAWL CAUGHT

Histogram 30
217 fish (st) 52% empty
GILL NET CAUGHT
Histograms 30 and 31 illustrate the feeding patterns of 217 fish caught by gill-nets and 144 fish caught by trawling. Higher proportions of plant material and filamentous algae were found in gill-netted fish, while higher proportions of zooplankton, rotifers and fish were found in trawled fish.
DISCUSSION AND CONCLUSIONS

Gause's principle, a major tenet of ecology, holds that different species may not occupy an identical niche in an ecosystem and that speciation tends to reduce intraspecific competition.

As has been described the Chilwa system undergoes major periodic fluctuations and with its shallowness, high salt concentrations, pHs, temperatures and turbidities the conditions are extreme and relatively few fish species have adapted to them. In the short term these conditions will also tend to limit the number of the food species. However with shorter life cycles and more efficient methods of dispersal of relatively small organisms the long term diversity of species may be considerable - different species predominating under different conditions. Thus in order to survive under these conditions the feeding patterns of fish species in Lake Chilwa must remain flexible and relatively unspecialised. This factor would counteract any tendency for speciation to occur.

Broadly speaking the findings of this investigation corroborate with Gause's principle, for when the results of all the individuals of each fish species are considered as a whole, the diets are different, although zooplankton forms an important part of each:
However within this generality individuals of each species may be described as opportunist feeders - consuming in varying proportion a wide variety of different food items, which are available and which they are capable of obtaining.

**Barbus paludinosus**

There is very little information available about this species and no detailed study has been carried out. The range of food items consumed was wider than Kirk (1967) or Kalk (1969 a & b) thought and the feeding pattern varied considerably, depending on a number of factors. Of the fish parameters - sex, maturity and length - greatest variation in feeding was found with length. Small fish, less than 4 cm in length, fed almost exclusively on zooplankton (65%) and non-filamentous algae (15%). Larger fish fed on a wider range of items, while in fish above 8 cm in length zooplankton formed 33%, higher plant material 31%, non-filamentous green algae 17% and aquatic insects 10% of the diet. (See B. paludinosus histograms 13-15).

The variation of diet with length would explain the slight differences found with different stages of sexual maturity - the category "young" fish being made up of small fish. No major
differences in feeding were found with sex.

Vegetation provides shelter and a substrate on which epiphytic algae and aquatic insects can live and this would account for their increased proportions, and that of higher plant material, in fish caught in areas of vegetation.

The differences in feeding patterns with water conductivity would be explained by the greater variety of organisms that were able to tolerate less extreme physico-chemical conditions, although open water areas generally had higher water conductivities than peripheral waters close to vegetation. The presence of vegetation rather than lower water conductivities could thus explain the differences in diet. It is interesting to note, in this respect, that the feeding patterns of fish in waters of conductivity in excess of 1500 \( \mu \text{mho/cm} \) and in areas where vegetation was absent, were almost identical; as were those of fish caught where the conductivity was less than 1500 \( \mu \text{mho/cm} \) and where vegetation was present. (See \textit{B. paludinosus} histograms 16, 17, 20 and 21). The much higher percentage of empty digestive tracts that was found during hours of darkness in comparison with that found during hours of daylight (70% against 10%) strongly indicated that the species fed predominately during the day.

The similar feeding patterns for fish caught in non-swamp areas of Lake Chilwa and the Lower Shire indicated a uniform diet in these areas although in Lake Chiuta and the Chilwa swamp the fish had a very different diet which possibly reflected the availability of foods and the adaptability of the fish. (see
B. paludinosus histograms 22-27).

The differences in feeding patterns with method of capture were probably because the different methods sampled different habitats - trawling tended to be adjacent to or away from vegetation; gill-nets were often set through or very close to vegetation; and seineing occurred on a few isolated beaches where vegetation had been cleared. (See B. paludinosus histograms 28-30).

Enzymatic investigations of the alimentary canal (Cookson & Bourn in prep.) have shown that there was similar amylase activity in the anterior and posterior intestine, with an optimum activity at pH 8. Protease activity with a pH optimum at pH 6 was greatest in the anterior intestine, which indicated the presence of a pepsin. There was also protease activity at pH 8-9 in the posterior intestine which indicated the presence of a trypsin. The anterior intestine thus appeared to have a similar function to the stomach of other species.

The overall findings conform with the hypothesis that in Lake Chilwa this species feeds predominately during the day by filtering water through which it moves and obtaining zooplankton, non-filamentous phytoplankton, plant detritus and aquatic insects. As the fish grows its ability to filter larger food items (e.g. aquatic insects and plant detritus) increases, presumably because of a larger gape.
**Clarisas mossambicus**

The overall pattern of feeding suggested that this species fed predominately on zooplankton, other fish (mainly *Barbus*), aquatic insects and plant material. Under Hulot's classification (1950) it was described as an omnivorous ichthyophage. However on breakdown of the results to show the diet under various conditions other patterns emerged.

Munro (1967) working on *C. gariepinus* - the southerly member of the *Clarisas* cline - has shown the importance of zooplankton in the diet increased with the size of the fish in Lake Moliwaine, Rhodesia. The importance of zooplankton in *C. gariepinus* has also been recorded by Groenewald (1964) and its occasional predominance in the diet has been noted by Schoonbee (1969). Munro (1967) suggested that the increased importance of zooplankton was due to increased mouth gape and also to more efficient filtering because of an increased number of gill-rackers in large fish. He found:

<table>
<thead>
<tr>
<th>Length</th>
<th>Zooplankton</th>
<th>Dipterous larvae and pupae</th>
<th>Fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>20-40 cm</td>
<td>0.4%</td>
<td>75.4%</td>
<td>2.8%</td>
</tr>
<tr>
<td>40-60 cm</td>
<td>20.9%</td>
<td>45.2%</td>
<td>1.9%</td>
</tr>
<tr>
<td>&gt; 60 cm</td>
<td>65.5%</td>
<td>14.0%</td>
<td>0.9%</td>
</tr>
</tbody>
</table>

The *C. mossambicus* of Lake Chilwa showed the opposite trend in feeding patterns with length, with the importance of zooplankton decreased in larger fish. (See *C. mossambicus* histograms 17-20).
In this investigation no fish were caught with a length greater than 60 cm, presumably because very few survived the drying of the lake in 1968. It was thus impossible to compare the feeding of Chilwa \textit{C. mossambicus} with Munro's largest group of fish. However the indication, from comparison of smaller fish, was that the diets of the two related species differed considerably in the two lakes.

No differences in the diet were found with sex of this species. The considerable variation in diet with maturity was to some extent explained by the diets of fish of different sizes, but some of the samples were too small for reliable interpretation. All that may be said is that they indicated the wide range of food items consumed in varying proportions (See \textit{C. mossambicus} histograms 5-16).

As with \textit{B. paludinosus} the differences in the diet of fish caught in areas with and without vegetation and in waters of high and low conductivity could be accounted for by the availability of various food items but could also be due to preferential feeding or to distribution differences of various sizes of fish. The proportion of fish in the diet was higher in areas of vegetation and in waters of lower conductivity which might reflect the observed increased abundance of fish prey in peripheral areas of the open waters, on the swamp margin, where as has also been noted before, the fishing activity is heaviest. (See \textit{C. mossambicus} histograms 21, 22, 25 and 26).
In view of the very high turbidity of Chilwa water, sight can be of little importance to *C. mossambicus* in detection of highly motile prey, especially other fish; presumably the barbels have an important sensory function. This was born out by the fact that the species appeared to feed throughout the twenty-four hour period. (62% of fish caught in hours of darkness and 79% of fish caught in hours of daylight had some contents in their stomachs.)

Feeding in non-swamp areas of Lake Chilwa was found to be more or less uniform, but fish from the swamp and other localities in southern Malawi showed marked differences - which illustrated the dietary adaptability of this species. (See *C. mossambicus* histograms 27-32).

The marked differences in feeding pattern with method of capture, also found in the other species, were probably because the different methods sampled different habitats - trawling tended to be adjacent or away from vegetation; gill-nets were often set through or close to vegetation; and seineing occurred on a few isolated beaches where vegetation had been cut back. (see *C. mossambicus* histograms 33-35). The percentage of empty stomachs found with the different methods show the marked disadvantages of using gill-nets for sampling this species. 44% of gill-netted fish as opposed to 20% of trawled fish were empty. This was probably due to regurgitation of stomach contents, or their digestion while the fish was in the net before clearing. Regurgitation would seem to be most likely, as many intestines were found to have envaginated into the stomach.
Analysis of intestinal contents provided useful information which generally confirmed the results obtained from stomach content analysis but intestinal analysis yielded results biased towards less digestible material, particularly insects and plant material. (see *C. mossambicus* histograms 1 and 2).

Groenewald (1961) described the anatomy of the alimentary canal of *C. gariepinus* as that of a typical carnivore. Enzymatic investigation of the alimentary canal of *C. mossambicus* (Cookson and Bourne in press) has shown protease activity optima at pH 4 and 6 in both the stomach and the intestine, but virtually no activity above pH 7. The activity was of greater magnitude in the stomach and indicated the presence of a pepsin. Amylase activity was confined to the intestine with an optimal pH at pH 10.

The overall findings conform with the hypothesis that this species in Lake Chilwa has a highly variable omnivorous diet, but that when relatively small, zooplankton are particularly important and as length increases so does the consumption of fish. 

*Tilapia shirana chilwae*

Kirk (1970) stated that *T. shirana chilwae* caught during 1966 and 1967 fed mainly on blue-green algae but that little digestion of them appeared to take place. However such large quantities were consumed that their extracellular nitrogenous secretions might have been of some nutritional value. He also suggested that the high level of organic matter (14%) and bacteria in Chilwa mud might have contributed to the diet. In this study the proportion of blue-green algae in the diet was found to be relatively small (12% + 1%). The discrepancy may be due to the
different environmental conditions that existed before and after the drying of the lake. The conductivity of the water in the open water of the lake was well in excess of 4000 \( \mu \text{mho/cm} \) for most of the period of Kirk's study (Morgan and Kalk 1970), which as described in an earlier section is particularly suitable for blue-green algae.

In common with a number of other species of *Tilapia* (*T. esculenta* and *T. variabilis* (Fish 1955); *T. mortimeri* (syn. *T. mossambica*) (Matthes 1965); *T. zilli*, *T. melanopleura* and *T. galilaeae* (Petr 1967b); *T. mossambica* and *T. melanopleura* (Munro 1967)), the overall feeding pattern of *T. shirana chilwae* showed a mainly herbiverous diet of higher plant material and algae, although zooplankton was also consumed. The ingestion of this item has also been reported by Munro (1967).

The presence of fish remains in the stomach and their total absence in the intestine was surprising. (See *T. shirana chilwae* histograms 1 and 2). Scales, bones, and eye lenses would tend to be resistant to digestion and some trace should have been detected in the intestinal contents, unless the presence of fish in the stomach was an artifact of the method of capture. In view of the much higher proportion of fish remains in trawled fish as compared with gill-netted fish this would seem likely (See *T. shirana chilwae* histograms 30 and 31).

A breakdown of the overall results showed that there were marked differences in the diet of fish of different sizes (See *T. shirana chilwae* histograms 17-19). Fish less than 10 cm. in
length fed predominantly on zooplankton which in larger fish was of little importance; with increasing size the proportion of plant material and diatoms increased. Le Roux (1956) has also noted the importance of zooplankton in the diet of young T. mossambica, T. melanopleura, T. sparmanii and T. andersoni.

No major differences in the diet of fish was found with sex or stage of sexual maturity. (See T. shirana chilwae histograms 14-16). The same was true for T. mortimeri (syn T. mossambica) in Lake Kariba (Matthes 1965).

The variation of diet with the presence or absence of vegetation and the variations with locality may reflect the availability of the various food items and or differential distributions of fish of different lengths. (See T. shirana chilwae histograms 20, 21, 26-29). There were however only minor differences in diet of fish caught in waters of conductivity greater or less than 1500 μmho/cm. (See T. shirana chilwae histograms 24 and 25).

Twice as many fish had empty stomachs when caught at night as compared with number caught in daylight (66% against 33%). Thus indicating that this species fed predominately during the day, as has also been reported for T. melanopleura (Munro 1967).

The considerable variation of diet of fish caught by different methods of capture was probably because the two methods sampled different habitats - trawling tended to be adjacent to or away from vegetation, while gill-nets were often set through or very close to vegetation. (See T. shirana chilwae histograms 30 and 31).
The high proportion (52%) of empty stomachs obtained from gill-net caught fish illustrate the considerable disadvantage of this method of sampling, digestion or regurgitation having occurred before the nets had been cleared. The high proportion of empty stomachs in gill-netted fish has also been reported by: Matthes (1965) working on *T. mortimeri* in Lake Kariba where 47% of adult fish were empty; and Munro (1967) where 58% of *T. mossambica* and 50% of *T. melanopleura* were empty.

Enzymatic investigations of the alimentary canal of *T. shirana chilwae* (Cookson and Bourn in press) have shown no protease activity in the stomach; pH optima were found at pH 4.5 and pH 10 in the anterior intestine, indicating the presence of a pepsin and a trypsin. Amylase activity was found in all tissues, with an optimum at pH 8 in the stomach, while in the intestine activity was maximal throughout the range of pH 7-11. These observations supported the view that this species was adapted to a herbivorous diet.

Analysis of intestinal contents gave results which generally confirmed those obtained from stomach content analysis, but biased the proportions of less digestible items - higher plant material, diatoms and rotifers. The lack of fish remains in intestinal contents has been discussed earlier. (See *T. shirana chilwae* histograms 1 and 2).

Vaas and Hofstede (1952), Fish (1955) and Kirk (1970) attempted to determine the degree of digestion of various algal constituents of the alimentary tract of *Tilapia* by culture
experiments and/or visual observations. They concluded that some algae were not destroyed by passage along the digestive tract, but were unable to determine whether or not the algae were of any nutritional value. With the method employed in this study, which involved storage of the stomach, intestine and their contents in formalin, assessment of the degree of enzymatic degradation was not possible, because formalin preservation itself tended to disrupt cellular organisation.

The overall findings conform with the hypothesis that T. shirana chilwae in Lake Chilwa feeds mainly during the hours of daylight and has a predominately, although not exclusively, herbiverous diet, feeding on higher plant material, filamentous green algae and zooplankton. In areas where vegetation is absent zooplankton forms a larger proportion of the diet, as it does in small fish, which because of their size are less well suited for consuming larger food items.

* * * * * * * *

The number of fish in some of the result groupings was undoubtedly inadequate for valid comparison - particularly in the swamp regions of Lake Chilwa and from Lake Chiuta. This was not for want of effort - problems of access and/or non-availability of fish made collection of suitable samples extremely difficult.

Only when comprehensive results on the relative abundance of various food items over the lake as a whole are available and the parameters that influence them are understood will it be possible
to definitely evaluate the capability of the three species to expand into the open water regions of Lake Chilwa, which at the moment appear to support a lower fish biomass than the peripheral waters close to vegetation. Studies on the aquatic macrophytes, the algae, the bacteria, the zooplankton, the aquatic insects and the fish are still in progress and the various parameters which influence their distribution and abundance have yet to be clarified. Present indications are that: greatest zooplankton biomasses occur in the waters adjacent to the swamps and their densities vary inversely with the water conductivity (Schulten personal communication); the biomass of aquatic insects decreases with distance from the shore (McLachlan, personal communication); epiphytic algae are dependent on substrate and presumably their biomass is higher where vegetation is present; and higher plant material must be more available in areas close to the swamp. It would thus appear that because of the availability of food items, fish biomasses are likely to be maintained at a higher level in the zone between swamp and open water, although, at this time it is not possible to determine when availability of food would become limiting.

This study was semi-quantitative in its approach and as such the relative proportions and importance of the food items in the diets can be compared but not in absolute terms. Although a measure of the degree of fullness of each stomach would have been useful in this respect, without extensive experimentation on the rates of consumption, quantitative values for the amounts of food
consumed could not have been determined. In order to estimate the potential fish populations that Lake Chilwa would be capable of sustaining the amounts of food consumed, their dietary value, and measures of the productivity at various levels are required. Until all these are known it will not be possible to estimate the optimum fish yield of Lake Chilwa.
ACKNOWLEDGEMENTS

I should like to thank the following people who helped in so many ways: my supervisor in Malawi Professor M. Kalk, Dr. A.J. McLauchlan, Mr. C. Howard-Williams, Mr. M.T. Purse, Mr. A. Cockson, Mr. A. Mpote and Mr. S.F. Nchema, all of the Lake Chilwa Co-ordinated Research Project; Dr. J. van Vleman of the Mathematics Department of the University of Malawi; Mr. C. Ratcliffe of the Fisheries Department of the Malawi Government; my supervisor in the Zoology Department of the University of Edinburgh Dr. R.A. Kille; Mr. W. Watson of the Edinburgh Regional Computing Centre; and finally Mrs. P. Williams for getting it together and typing it all.
REFERENCES


Petr. T. 1967(a). Fish population changes in the Volta Lake in Ghana, during the first sixteen months. Hydrobiologia. 30, 193-220.


Intestinal values given by fourteen columns

Stomach values given by fourteen columns

Method of capture
0 = Gill-net
1 = Trawl
2 = Seine

Time caught
0 = am
1 = pm

Vegetation
0 = Absent
1 = Present

Area caught
0 = North Lake
1 = South Lake
2 = Swamp
3 = Lower Shire
4 = Lake Chita
5 = Youth

Maturity
0 = Young
1 = Inactive
2 = Active
3 = Ripe
4 = Ripe-running
5 = Spent

Sex
0 = ?
1 = Male
2 = Female

Length given by three columns in mm.

Weight given by four columns in gm.

Species
0 = B. paludinosus
1 = C. mosambicus
2 = T. shirama chilwae

Collection number given by two columns

Specimen array of data for one fish on computer card.

APPENDIX 1.
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<th>Month</th>
<th>Location</th>
<th>Number of fish</th>
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<td></td>
<td>B.D.</td>
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<tr>
<td>Nov/Dec 69</td>
<td>Jan 70</td>
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<tr>
<td>0-</td>
<td>Jan 70</td>
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<td>33</td>
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<tr>
<td>0-</td>
<td>Jan 70</td>
<td>Chenjeriani Island South Lake</td>
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<tr>
<td>1-</td>
<td>Feb 70</td>
<td>Kachulu Bay</td>
<td>30</td>
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<tr>
<td>2-</td>
<td>Apr 70</td>
<td>Kachulu Bay</td>
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<td>6-</td>
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<td>7-</td>
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<td>7-</td>
<td>Dec 70</td>
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<td>Dec 70</td>
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<td>9-</td>
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<td>-0</td>
<td>Mar 71</td>
<td>Nchisi Island - North Lake</td>
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<td>Jun 71</td>
<td>Kachulu Bay - 24 hour sample</td>
<td>60</td>
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<td>-2</td>
<td>Jul 71</td>
<td>Lake Chiuta</td>
<td>11</td>
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<tr>
<td>-2</td>
<td>Jul 71</td>
<td>Lake Chilwa - Swamp</td>
<td>6</td>
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**Totals**: 623  507  373

**Grand Total**: 1,503

**APPENDIX** 2.
C FORTRAN PROGRAM FOR FISH FEEDING ANALYSIS

C DIMENSION IA(80), IC(14,72), IY(30), IX(50), IJU(30), K(30)

C

11 FORMAT (20A4)
12 FORMAT (4I3)
13 FORMAT (8011)
14 FORMAT (/5HOX = ,14, 6H Y = ,14 )
15 FORMAT (IX, 4I10)
16 FORMAT ( RHOSUMS = ,12X,2I10)
17 FORMAT ( // // 6X,10NSPECIES : , 20A4)

C ECHO TITLE OF SPECIES

READ (5,11) (IX(I), I=1,20)
WRITE (6,18) (IA(I), I=1,20)
READ (5,12) N, M

DO 51 I = 1, N
51 READ (5,12) IX(I), IY(I), IJU(I), K(I)

DO 52 I = 1, N
DO 52 J = 1, M
52 IC(I,J) = 0

READ (5,13) IA
IF (1A(50) .EQ. 9) GO TO 610
DO 53 I = 1, N
53 J = IA(IX(I))
IF (JE .LT. 0) GO TO 53
JE = IA(IY(I))
IF (JF .LT. 0) GO TO 53
L = K(I)*JE + JF
IF (L+1 .GT. M) GO TO 53
53 CONTINUE
C GO TO 200

DO 54 I = 1, N
WRITE (6,14) IX(I), IY(I)
JZ = IJU(I)
DO 54 JY = 1, JZ
JE = JY - 1
54 IT1 = 0
IT2 = 0
JW = K(I)
DO 55 JU = 1, JW
55 JF = JW - 1
L = K(I)*JE + JF
IT1 = IT1 + IC(I, L+1)
51 IO = JF*IC(I, L+1)
52 IT2 = IT2+10
55 WRITE (6,16) JF, JF, IC(I, L+1), IO
54 WRITE (6,17) IT1,IT2
55 STOP
56 END

APPENDIX 3.

CODE+GLA+LOADDATA+SYNTABS+ARRAYS = 2192+ 728+ 88+ 184+ 4832 = 8024 BYTES
C FORTRAN PROGRAM FOR FISH FEEDING ANALYSIS
C WITH LENGTH SORTING MODIFICATION

C GROUP 1 LENGTH IS 1 TO 149 MM
C GROUP 2 LENGTH IS 150 TO 299 MM
C GROUP 3 LENGTH IS 300 TO 449 MM
C GROUP 4 LENGTH IS 450 TO 599 MM
C GROUP 5 LENGTH IS 600 TO 749 MM

DIMENSION IA(80), IC(14,72), IY(30), IX(30), IU(30), K(30)

FORMAT(20A4)
FORMAT(413)
FORMAT(711,13,7011)
FORMAT(/5H0X = '14, 6H Y = ', 14)
FORMAT(4110)
FORMAT(8H0SUMS = ',12X,2110)
FORMAT( /// //, 6X,10HSPECIES : ', 20A4)

ECHO TITLE OF SPECIES
READ (5,11) (IA(I), I= 1,20)
WRITE (6,18) (IA(I), I= 1,20)
READ (5,12) N, M

DO 51 I = 1, N
READ (5,12) IX(I), IY(I), IU(I), K(I)

DO 52 I = 1, N
DO 52 J = 1, M
IC(I,J) = 0

200 READ(5,13) (IA(I),I=1,8),(IA(I),I=11,80)
IF (IA(80) .EQ. 9) GO TO 610
DO 53 I = 1, N
IA(9) = (IA(80)+149)/150
JE = IA(9)
IF (JE .LT. 0) GO TO 53
JF = IA(IY(I))
IF (JF .LT. 0) GO TO 53
L = K(I)*JE + JF
IF (L+1 .GT. M) GO TO 53
IC(I, L+1) = IC(I, L+1) + 1
CONTINUE

GO TO 200

DO 54 I = 1, N
WRITE (6,14) IX(I), IY(I)
JZ = IU(I)
DO 54 JY = 1, JZ
JE = JY - 1
IT1 = 0
IT2 = 0
JW = K(I)
DO 55 JY = 1, JW
IF (JY .LE. 0) GO TO 55
L = K(I)*JE + JF
IT1 = IT1 + IC(I, L+1)
IQ = JF*IC(I, L+1)
IT2 = IT2+10
WRITE (6,16) JE, JF, IC(I, L+1), IQ
STOP

APPENDIX 4.
Correlation between cols. 16 & 17 is method of capture against food item 1.

Code 0 = Gill-net.

Code 2 = Trawl.

Subtraction gives frequency of occurrence, i.e., 258 - 184 = 74.

Eight point scale values:

Number of fish with given scale value.

Product of scale value & number of fish.

Sum of products.

In column 30 or 45, this figure would denote the number of empty fish.

Number of fish.
Addendum to page 16.

The 1969 invertebrate benthic fauna included the pulmonates Lanistes ovum Troschel and the bilharzia vector Bulinus (Physopsis) globosus Morsell, Hirudines, and larvae of Anisoptera, Ephemeroptera and Chironomidae. Chironomus (Chironomus) transvalensis Keiffer, accounted for over 99% of the faunal biomass.

Addendum to the discussion and the conclusions.

It is not possible at this stage to determine whether or not the three species of fish in Lake Chilwa are utilising each food type to its full extent but it would appear that the broad Catholic tastes of the fish, as revealed in this study, are adapted to include all available food categories. This may well account for the rapid repopulation and the high fish yields obtained so soon after the dry period.

In view of this, their proven tolerance to a wide range of environmental conditions and the acceptability of the fish in the diet of the local human population, they might be considered suitable species for stocking the artificial fish ponds planned for construction in Southern Malawi.

The importance of the fish population dynamics work now being carried out must be stressed, as a knowledge of the distribution patterns, movements and numbers of fish in Lake Chilwa are essential to the efficient future management of the lake. The dangers of overfishing in periods immediately following the drying of the lake or very low water levels must also be understood, as the rate of expansion of recolonising fish populations may be seriously retarded by excessive fishing activity at a critical stage in population expansion.