LAKE TANGANYIKA FISHERY RESEARCH AND DEVELOPMENT PROJECT

TANZANIA

FISHERY BIOLOGY AND STOCK ASSESSMENT

UNITED NATIONS DEVELOPMENT PROGRAMME

FOOD AND AGRICULTURE ORGANIZATION
OF THE UNITED NATIONS
ROME, 1978
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FISHERY BIOLOGY AND STOCK ASSESSMENT

Report prepared for
the Government of Tanzania
by
the Food and Agriculture Organization of the United Nations
acting as executing agency for
the United Nations Development Programme

based on the work of
D.W. Chapman, H. Rufli, P. van Well and F. Roest

UNITED NATIONS DEVELOPMENT PROGRAMME

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

Rome, 1978
The 'Lake Tanganyika Fishery Research and Development Project' was started in 1973 to assist the Government of Tanzania in optimizing the exploitation of the fisheries of the lake. This report attempts a description and an assessment of these resources, suggests ways of increasing present production and recommends some national and international management measures.

The limnology of Lake Tanganyika is briefly described with indications of its most typical features. Circulation of water in the lake is thought to result from both wind-driven surface currents (with compensating surface and/or deep currents) and currents associated with internal waves. Plankton distribution is discussed and related to the observed physical and chemical processes.

Major types of fishing are identified, and although catch-effort data are as yet somewhat meagre, potential annual catches are estimated. Biological examination of the most common fish species has led to a greater understanding of their life history and general behaviour; growth and mortality rates have been estimated, and length/weight equations formulated. The distribution and abundance of these species is shown to be related to their physico-chemical environment. The results of the project's acoustical surveys are summarized and have given information both on schooling behaviour and biomass. Finally the potential yield has been estimated from the biomass, supplemented by extrapolations from other sources and regions.

It is concluded that the lake’s yield could be in excess of 300 000 tons but that until more detailed information becomes available, this must be considered only a preliminary estimate. Considerable expansion of the present fishery is therefore possible by exploitation of the offshore fish stocks, but over-investment based on exceptional catches in individual years must be avoided. Continuation of stock and catch monitoring at national and international level is recommended and suggestions are given for programmes of biological research and acoustical surveys.
The Food and Agriculture Organization is greatly indebted to all those who assisted in the implementation of the project by providing information, advice and facilities.
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1. INTRODUCTION

In 1970, the production of Tanzania's share (41%) of Lake Tanganyika was estimated at about 50 000 t a year, and the lake's sustainable yield potential at over 200 000 t per year. The discrepancy between the anticipated yield potential and the actual catch made a further development of the fisheries desirable, especially so as protein deficiency is very common in the countries bordering the lake. The fact that these figures represented guesses made systematic work all the more imperative.

The Government of Tanzania therefore requested the United Nations Development Programme to assist in the development and management of the fishery on the Tanzanian part of Lake Tanganyika, through a research and development programme on the fish stocks in the lake and training of personnel. The 'Lake Tanganyika Fishery Research and Development Project' (URT/71/012) was subsequently established (1973 to 1977), with the Food and Agriculture Organization of the United Nations as the designated executing agency. The long-range objective of the project was expansion of the fisheries of Lake Tanganyika to its fullest potential by exploring the possibility of industrial fishing, using bigger boats in the unexploited parts of the lake, and by improving the catch, preservation and marketing methods as well as the organization of the fishermen in the traditional sector. It was understood that with the resources and limited time available, the project could make only a first step toward the expansion of the fisheries.

The immediate objectives, as related to this Technical Report on 'Fishery Biology and Stock Assessment' were to:

- provide an assessment of the fish stocks and/or design a permanent monitoring system of the fish population so as to establish a rational system of resource development;

- conduct a programme of research on the abundance distribution, life histories and behaviour and other biological characteristics of the commercially important fishes, as well as further investigations on the physical, chemical and ecological characteristics of Lake Tanganyika;

- make recommendations on the introduction of fishery regulations.

The report is based on the work of D.W. Chapman, Fishery Biologist (March 1973 to September 1976); H. Rufli, Fishery Biologist/Associate Expert (April 1975 to January 1977); P. van Well, Biologist/UN Volunteer (November 1974 to June 1976); and F. Roest, Consultant. National staff who collaborated were Z. Njugumbi and J. Bayona, Fishery Biologists, Y.N.Y. Kapilimba and other staff members.

The project was based in Kigoma. Close research cooperation was established with the UNDP/FAO project in Bujumbura, Burundi 'Fishery Research on Lake Tanganyika' (BDI/73/020), in the form of mutual visits, discussions on the work programmes, sharing of data and conclusions, and quantitative echosurveys. In addition, the following research institutions participated in various subjects of research:
- Scripps Institution of Oceanography, University of California, San Diego, U.S.A. - H. Craig, Ms. Craig, R. Weiss, F. Dixon (geochemistry and hydrography);

- Massachusetts Institute of Technology, Cambridge, U.S.A. - J. Edmond, J. Stallard (nutrient chemistry);

- Freshwater Institute, Winnipeg, Canada - R. Hecky, E. Fee, Ms. Kling (phytoplankton and primary production);

- City of London Polytechnic, England - H. Burgis (zooplankton);

- University of Texas, Houston, U.S.A. - K. Thompson, B. Lyon (temperature tolerance and nutrition of Lates spp).

Active field work started shortly after the arrival of the Fishery Biologist in March 1973. In November, the first acoustical survey of the lake was completed in collaboration with the Burundi project. Deck sampling and analysis of data began with the chartering of the ringnetter MV FRANCE by FAO in July 1974, and was extended to the commercially operated boats of Uvuvu Kigoma Ltd. in 1975. The staff moved into the new laboratory provided by the Government in April 1975, although water supply and electricity was missing. A second acoustic survey was completed in May 1975. The project obtained a Simrad acoustic sounder in April 1976, but the subsequent acoustic survey in May 1976 was not successful because of technical difficulties. A complete survey with the new equipment was made in November 1976.
2. LIMNOLOGY

2.1 GENERAL DESCRIPTION OF LAKE TANGANYIKA

Lake Tanganyika is situated at an elevation of 773 m in the western Rift Valley of East Africa, between 30°23' and 8°50' S and 29°-31° E. It has a length of 673 km, and a maximum width of 48 km (Welcome, 1972). The four countries surrounding the lake – Tanzania, Burundi, Zaire and Zambia – occupy respectively 41%, 8%, 45% and 6% of its approximately 32,900 km² surface area.

Lake Tanganyika is the world's second deepest lake, with a maximum depth of 1,470 m; the mean depth is 570 m (Coulter, 1977), the volume 18,880 km³. Evaporation accounts for 95% of the annual water loss, the lake level being maintained mainly by rainfall on the mostly mountainous catchment area (249,000 km²). Inflowing rivers are relatively unimportant, and with the exception of the Ruzizi River, low in salt content (Coulter, 1963). The only outflow of Lake Tanganyika is the Lukuga River, communicating with the Congo River and originating near Kalemie, Zaire.

The following description of the limnology of Lake Tanganyika is based on observations near Kigoma, Tanzania, results of the Burundi Fishery Research Project, cooperative research with overseas institutions and on the existing literature. Tanzanian research emphasized long-term monitoring of limnological conditions four miles northwest of Kigoma as well as lakewide surveys associated with test fishing and acoustical estimates of fish abundances.

2.2 CLIMATE OF KIGOMA

Kigoma has one dry and one wet season each year. The rains usually begin around October-November and stop about April-May, but there are considerable yearly differences in both total amount of rain and the periods of rainfall.

The wind is strongest during the dry season. Generally, the wind blows harder in the afternoon (15.00 hours) than in the morning (09.00 hours), and the direction pattern generally remains the same throughout the year, on average easterly to south-easterly in the morning, westerly to southwesterly in the evening and shifting through southerly in the middle of the day. These changes in wind direction can be explained by differences in heating of the land and water surfaces: at night, the land cools more than the lake, so the air above the land will be denser than the air above the lake. Consequently, in the early morning hours, an offshore wind blows (east-south-east). During the day, the land heats rapidly and the air becomes less dense than the air over the lake. The wind then blows in an opposite direction (west-southwest). At midday, the southeasterly trade winds dominate in the dry season. Because the wind is strongest in the dry season between 12.00 and 15.00 hours and shifts then from east-southeast through south to west-southwest, the net movement of air is northward.
2.3 PHYSICAL PROCESSES AND PARAMETERS

2.3.1 Wind regime

Unlike in temperate regions, where the incident solar radiation is the major factor regulating the annual production of a water body, in Lake Tanganyika it is the wind regime that is responsible for the characteristic productivity pattern. Here, the annual hydrological cycle is divided into the two distinct periods.

From May to August/September, Lake Tanganyika is subject to constant, strong southerly to southeasterly winds (trade winds), blowing along the lake axis. In Zambian waters, this wind stress leads to upwelling of anoxic deep water in July-August (Coulter, 1963). Important quantities of nutrients are thus added to the epilimnion, resulting in phytoplankton blooms. The constant wind forces the cool surface water northward. Consequently, the thermocline sharpens and tilts down towards the north.

Upon the cessation of the trade winds in August/September, thermal stratification restores in Zambia, while stability decreases in the north (Burundi and Kigoma), with isotherms showing spectacular rises.

In the central part of the lake, between Kirando and the Kungwe Mountains, the wind regime is different. Here, the winds are notoriously strong and contain an easterly component, probably resulting from the channelling along the neighbouring Rukwa rift valley. Emerging in the low-lying country around Karema, this wind is diverted by the Kungwe Mountains across the lake toward Kalemie. This sector of the lake is often subject to stronger wind stress (Coulter, 1969). Upwelling might occur along the Tanzanian shore in this area.

2.3.2 Temperature

Except for the Zambian waters and possibly some inshore areas where upwelling occurs, Lake Tanganyika has a permanent thermal stratification. During the warm, wet season (October–April), the epilimnion reaches its maximum annual temperature of 27° C. Minimum temperatures of 25° C are recorded in the dry season. Thermocline depths are 25 to 70 m in the rainy season and 60 to 110 m in the dry season. Following the cessation of the strong south-southeast winds of the dry season, the thermocline rises and is not well defined in September–October. Heating of the epilimnion starts in October.

The hypolimnion is very stable in temperature, and varies between 23.5 and 23.7° C at 200 m depth.

2.3.3 Internal waves

Coulter (1969) described internal waves in the southern part of Lake Tanganyika, while Ferro (1975) has described them in the north. Coulter found a periodicity of 25 to 30 days and supposed that these waves originate from the first strong southeast winds in June/July. Ferro observed internal waves of at least three different frequencies of which the two longest were visible throughout most of the year. In limnological sampling off Kigoma, no evidence was found for internal waves, but sampling was frequently less than weekly. In November 1974, during test fishing in Tanzanian waters, a vertical movement of 75 m was observed of the 24.6° C isotherm over 14 days. Temperature profiles apparently do not always satisfactorily predict
the bottom of the oxygenated water layer. Internal waves can lead to considerable variations in oxygen and chemical composition in shallow waters. The internal waves may also play an important role in bringing deep fertile water to the surface along the margins of the Lake in a manner analogous to marine upwelling. This point, however, has not been satisfactorily confirmed.

2.3.4 Currents

The constant south-southeast winds create a northward flow of surface water. Coulter (1968, 1969) suggests that this northward flow would be deflected westwards by Coriolis force. The downward tilt of the isotherms towards the west should result in a deep current along the western (Zaire) shore. The return current along the Tanzanian shore might flow quite superficially. A clockwise epilimnion current around the lake is supported by the following observations: (a) the visible westward swing of the Lufubu River after it enters the lake (Coulter, 1969); (b) direct observations on current direction and velocity off Kigoma Bay - sonic tagging and observations with drogues indicated an average north-south current of 0.25 mi/h, which was significantly higher in the wet season than in the dry season; and (c) the deposition of sand on the north side of the harbour jetty of Bujumbura.

2.3.5 Dissolved oxygen

Surface oxygen values range from 7.5 to 9 mg/litre and indicate occasional supersaturation. The oxygen isolines show the same trends as the isotherms, although somewhat more irregular, especially when the thermal stratification is weak. Off Kigoma, at several occasions, 3 mg/litre oxygen values were found at depths of 100 m, far below the thermocline. In Burundi waters, Ferro (1975) found a close correlation between zero oxygen values and the 24.0 to 24.5°C isotherms (60 to 130 m depth).

2.3.6 Conductivity

Conductivity values in the epilimnion (down to 50 m) off Kigoma vary between 670 and 685 µmho, and are thus slightly higher than those of Ferro (1975) for Burundi, at 635 to 670 µmho (680 to 695 µmho at 200 m depth). In general, variations in conductivity at depth follow temperature variations.

2.4 CHEMICAL COMPOSITION

In Lake Tanganyika, the major ionic constituents are relatively uniformly distributed with depth. A slow circulation would be sufficient to prevent a major chemical stratification below 250 m and maintain a supply of nutrients to the biotic layer. The epilimnion is generally homogeneous and the concentrations of the major ions are higher in the hypolimnion. Most of the inflowing rivers are low in salt content except the Ruzizi River, the major inflow of Lake Tanganyika. Because of its lower temperatures and its silt load, water from this river sinks rapidly when reaching the lake. Table 1 illustrates the relative importance of the nutrient input of some rivers (Edmond, 1975).
Table 1
LAKE TANGANYIKA - NUTRIENT INPUT OF WATER
(concentrations in $10^{-3}$ mol/litre)

<table>
<thead>
<tr>
<th>Inflow</th>
<th>Na</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
<th>PO$_4$</th>
<th>SiO$_2$</th>
<th>Cl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruzizi River</td>
<td>2.57</td>
<td>1.09</td>
<td>1.51</td>
<td>0.170</td>
<td>5.42</td>
<td>10.2</td>
<td>14.3</td>
</tr>
<tr>
<td>Muzazi River</td>
<td>0.11</td>
<td>0.03</td>
<td>0.11</td>
<td>0.100</td>
<td>0.00</td>
<td>10.2</td>
<td>0.7</td>
</tr>
<tr>
<td>Muzazi Tributary</td>
<td>0.10</td>
<td>0.02</td>
<td>0.11</td>
<td>0.096</td>
<td>0.00</td>
<td>190.6</td>
<td>-</td>
</tr>
<tr>
<td>Mutumba River</td>
<td>0.17</td>
<td>0.04</td>
<td>0.11</td>
<td>0.116</td>
<td>0.23</td>
<td>197.6</td>
<td>-</td>
</tr>
<tr>
<td>Ruzibazi River</td>
<td>0.04</td>
<td>0.02</td>
<td>0.06</td>
<td>0.086</td>
<td>0.06</td>
<td>105.6</td>
<td>-</td>
</tr>
<tr>
<td>Kagongo River</td>
<td>0.12</td>
<td>0.02</td>
<td>0.16</td>
<td>0.110</td>
<td>0.06</td>
<td>247.6</td>
<td>0.2</td>
</tr>
<tr>
<td>Malagarasi River</td>
<td>-</td>
<td>0.04</td>
<td>0.21</td>
<td>-</td>
<td>0.00</td>
<td>108.3</td>
<td>14.0</td>
</tr>
<tr>
<td>Lubugwe River</td>
<td>0.48</td>
<td>0.04</td>
<td>0.65</td>
<td>-</td>
<td>1.76</td>
<td>220.0</td>
<td>0.6</td>
</tr>
<tr>
<td>Lufubu River</td>
<td>2.04</td>
<td>0.03</td>
<td>0.18</td>
<td>-</td>
<td>0.18</td>
<td>96.4</td>
<td>0.1</td>
</tr>
</tbody>
</table>

Aspects of the chemical composition of Lake Tanganyika water were studied by Kufferath (1952), Degens et al. (1971), Kilham and Hecky (1973), Edmond (1975), Hecky et al. (1977) and Coulter (1977), as well as by the project. These data generally agree.

2.5 PLANKTON PRODUCTIVITY

2.5.1 Annual production cycle

The transparency of the offshore lake is considered by Coulter (1963, 1969) and Ferro (1975) as a fairly reliable indicator of phytoplankton abundance. There is a yearly cycle with increasing transparencies of 10 to 17 m in December-April, a maximum of 22.5 m in late April-May and an annual minimum of 2.5 m in October. Even during rains, the transparency of the offshore water does not change appreciably. This cycle is approximately the same as for the abundance of the clupeids.

Three mechanisms have been proposed for the higher phytoplankton production in the second half of the year:

(a) the northward drift of enriched Zambian epilimnion water (Section 2.3.1);
(b) the rain runoff from the land. The first runoffs would be much richer in terrestrial organic matter than the later ones.
(c) the periodic lifting of the thermocline. Upon cessation of the trade winds, the thermal stability of the northern lake weakens and the thermocline becomes ill-defined and rises to the surface. The absence of a density barrier would facilitate the mixing of water layers (internal waves), so that nutrients can be added to the epilimnion.
The latter mechanism is considered by Ferro (1975) to be the most likely. Ferro and Coulter (1974) suggest that the lifting of the thermocline may cause shorebound advections of anoxic hypolimnion water. This would severely restrict biological activity in the northern inshore areas of the lake, and explain why the gillnet fishery in the north is much less productive than in other parts of the lake.

Little information is available on zooplankton production. Zooplankton is much more abundant during phytoplankton peaks than at other time (Coulter, 1963).

2.5.2 Results of cooperative research on production

The following summary outlines the significant results of the research undertaken by the Freshwater Institute of Winnipeg, Canada (Hecky et al., 1977), in collaboration with the UNDP/FAO projects of Kigoma and Bujumbura.

Until recently, the fish production of Lake Tanganyika was assumed to depend on the food chain zooplankton-phytoplankton. While zooplankton is indeed the main food source of the clupeids, phytoplankton is unlikely to be the sole basis of the foodchain. The low metabolic activity of the phytoplankton suggests that bacterial production must play an important role. The following five observations support this hypothesis:

(a) Respiration measurements reveal a high C\textsuperscript{14} uptake indicative of heterotrophic and chemosynthetic growth.

(b) The lake is permanently oligotrophic in appearance and supports a high fish population. Bacteria do not possess pigments capable of changing water transparency.

(c) During a great part of the year, the average protozoan biomass is greater than the phytoplankton biomass. Most protozoa feed on bacteria.

(d) The respiratory rates observed are excessive for phytoplankton and protozoa populations, and are independent of the standing crops of these organisms.

(e) Bacterial counts are high and indicative of eutrophic conditions.

2.5.3 Further conclusions

Based on their two lakewide cruises (March/April and September/October 1975), the Canadian research team has drawn two further conclusions:

(a) Three major water masses can be distinguished in Lake Tanganyika: (a) the northern area down to the Ubwari Peninsula; (b) the area from the Ubwari Peninsula to Kibwesa; (c) the area south of Kibwesa. These water masses differ in thermocline depth, surface chlorophyll values, chemical composition (sulphate) and concentrations of bacteria.

(b) In contrast to Secchi disk values, the transparency of the lake water as measured with a transmissometer does not change between May and September. The Secchi disk is overly sensitive to accumulations of floating algae near the surface and therefore overestimates changes in transparency and chlorophyll concentrations in the euphotic zone. Lake Tanganyika is highly transparent at all times, the average depth of the euphotic zone being 30 m.
Results of cooperative research with the Scripps Institution of Oceanography and the Massachusetts Institute of Technology are published in preliminary form (Craig, 1975), but cover only the first of their two expeditions (1973). Further reports on their work, including the 1975 expedition results, are not yet available. The geochemical and hydrographic studies of these institutes should lead to a better understanding of the circulations and chemistry of Lake Tanganyika.
3. THE FISHERY

3.1 MAJOR TYPES OF FISHING ON LAKE TANGANYIKA

Apart from minor fishing activities like gillnetting and beachseining for inshore cichlids and dagaa, all fishing on Lake Tanganyika is based on the attraction of fish to artificial light sources at night (Ben Yami, 1976). It is therefore most successful during moonless nights, and practically all fishing activities stop during full moon periods.

Six species, all endemic to Lake Tanganyika, make up most if not all of the pelagic ichthyomass: two sardines (family Clupeidae), Stolothrissa tanganicae Regan (dagaa) and Limnothrissa miodon Bouleneger (lumbo), and four predators (family Centropomidae), Luciobates stappersii Bouleneger (migebuka), Lates mariae Steindachner (sangala), Lates microlepis Bouleneger (nonzi) and Lates angustifrons (gomba).

Four major types of fishing exist, three at artisanal and one at industrial level:

(a) Artisanal fishery

- the canoe fishery (lusenga), using large dipnets (Collart 1954, 1956 and 1958), the traditional fishing method on Lake Tanganyika, well represented in many of the lake’s inshore areas.

- the catamaran fishery (kipe), using liftnets (Collart 1958, Haling 1974), well developed in Burundi and spreading to the adjacent areas in Zaire as well as to the Kigoma Region.

- the chiromila fishery, only developed in southern Tanzania and Zambia (Coulter and Znamensky 1971, Ben Yami 1976). The chiromila net is a surrounding net of semi-circular shape used traditionally on Lake Malawi.

(b) Industrial fishery

The industrial fishing unit consists of a ringnetter (purse seiner), an auxiliary barge and usually five lamp boats (Andrianos, 1976). This type of fishery was introduced by Greek fishermen, and is still mainly practised by expatriates, except in Tanzania. The ringnet (purse seine) is 250 to 400 m long and 50 to 110 m deep.

Recent additions, e.g. the fishing vessels TUMAINI (modified water taxis, Smart, 1976) and IRIDINA (metal semi-industrial catamarans, FAO 1977, Schreder 1977), fish with somewhat smaller ringnets and are quite successful, but are still in the experimental stage.

3.2 CATCH AND EFFORT DATA

The industrial fishing effort on Lake Tanganyika is very unevenly distributed, with high concentrations in Burundi (at present 16 ringnetters) and in Kalemie, Zaire (about 15, but rapidly increasing), while other areas are less heavily fished,
with at least 5 ringnetters in Uvira, Zaire (opposite Bujumbura), 4 in Kigoma and 2 in Mpopungu, Zambia. This fishery operates usually well offshore, and catches all six pelagic fish species. Catch and effort data of the Kigoma-based fleet are available from December 1975. From these data it appears that, with regular fishing (21/22 days per lunar month), the average ringnetter could bring in an annual catch of 280 t.

The catch and effort data of the artisanal fishery along the Tanzanian shoreline have been summarized by a project consultant (Bazigos, 1975a), and further reports by the Kigoma fishery staff summarize similar data since April 1975 (Sasidharan, 1975 and 1976).

In its operations, the artisanal fishery is mostly limited to the 5 km inshore area, and catches almost exclusively clupeids and young Lucioliates, marketed together as "dagaa". The traditional and artisanal fishery sector contributes well over 90% of the total fish production of the lake in Tanzania. There are at present about 11 000 fishermen operating along the coast from some 5 000 fishing canoes. Two-thirds of the total fishing power accounts for theusenga fishery. The fish production is estimated at 50 000 t per year. This fishery utilizes about 50% of the available fishing nights.
4. FISH BIOLOGY

The biological characteristics of the six pelagic fish species were obtained from samples of the ringnet catches in Kigoma, from publications, and from internal reports and personal communications from Burundi as well as from similar data from Zambia.

So far, much of the life history data are based on indirect evidence. All six pelagic fish species spend part of their life inshore. Hypotheses concerning their life cycles might be verified by regular sampling of the inshore artisanal catches or by regular test fishing with industrial gear in the inshore zones. Research vessels on Lake Tanganyika have not been equipped for test fishing, and the gaps in the present knowledge of the biology of the pelagic species are characteristic of this situation.

4.1 LATES SPP

The genus Lates is well represented in Lake Tanganyika with three endemic, large-sized predatory species: L. mariae, L. angustifrons and L. microlepis. The following summary of their biology is largely from data obtained in Zambia (Coulter, 1976) as well as from work at the Kigoma project (December 1973 to May 1976). Of each of the three species, in Kigoma, 10 to 20 individuals were examined from the weekly ringnet catches.

Juveniles of all three species, 30 to 180 mm fork length, live in shallow inshore weedbeds dominated by Ceratophyllum. Directly around Kigoma, these juveniles have been taken in several inshore biotopes (Thompson et al., 1977).

In the Kigoma area, Lates under 400 mm fork length are rare in the ringnet catches, indicating that they occupy other zones of the lake. An examination of monthly length-frequency distributions does not show clear recruitment patterns for either of the three species. Spawning appears to be continuous; maximum numbers of ripe females were found in August to November-December (Zambia). In Kigoma, there are differences in the timing of the spawning peak between the three species.

In Zambia, highest condition factors are found in September-November, in the period of highest clupeid abundance. There is generally little difference in condition factors of males and females, and mature and immature fish show similar variations throughout the year. Monthly condition factors were higher after some years of exploitation than before.

As a result of their long life cycles, Lates spp are much more vulnerable to the industrial fishery than the other pelagic fish species of Lake Tanganyika. Indeed, they have declined to low levels in the heavily fished areas of Zambia and Burundi. Lates mariae and L. angustifrons are more vulnerable than the pelagic L. microlepis because of their sedentary mode of life. Consequently, L. microlepis dominates in exploited populations.
4.1.1 *Lates mariae*

Bottom gillnetting in Zambia indicates that *Lates mariae*, after leaving the inshore weeds, move progressively deeper with age. From the difference in catch composition between ringnets and gillnets, it appears that only a part of the population migrates upwards at night to feed on clupeids.

Spawning takes place at depth (in Zambia below 100 m) and ripe-running fish do not participate in the nightly rise to the surface. Spawning fish congregate and first maturity (50%) is at 440 mm for males and 490 mm for females. Unclear recruitment indicates that spawning is probably continuous, but peaks in gonad condition show greater activity in August-October and possibly January (Zambia), and December-January and April-May (Kigoma). Recruitment to the offshore fishery of Kigoma is usually at 500 mm, sometimes at 300 mm.

After the first maturity (500 to 550 mm), the diet changes from mostly prawns and cichlid fish to almost exclusively clupeids. This implies a change in distribution. During periods of high clupeid abundance, a larger part of the benthic population appears to rise to the surface at night. There is no significant difference in the size of prey taken by *L. mariae* of 210 to 750 mm length; prey length is up to 35% of predator length. The selection of prey is governed more by availability than by preference. Condition factors are generally lower for immature fish and roughly constant after maturity.

Growth rates were determined from mean length progressions (Zambia) and scale rings (Kigoma). Maximum length observed is 720 mm and Bertalanffy k equals approximately 0.25 per year. From about 450 mm, growth seems to be more or less constant and of the order of 30 to 50 mm per year. Ring formation is not linked with temperature changes, but rather with cyclical physiological changes like food availability and spawning. The length (FL) - weight (W) relationship is: log W = 2.96 log FL - 1.857 (Kigoma, 1974-75), and log W = 3 log FL - 2.047 (Zambia).

4.1.2 *Lates angustifrons*

*Lates angustifrons* move deeper with size increase, although less clearly so than *L. mariae*. Immature fish seem to live in groups, adults are solitary, lurking predators, probably preferring rocky bottoms. Adults are eurybathic and their abundance near the surface at night is less subject to seasonal variations than in the other species. In the ringnet catches off Kigoma, juveniles smaller than 400 mm are rare; recruitment length is about 660 mm, sometimes 540 mm.

Spawning takes place at depth, ripe-running females do not rise to the surface to feed. Spawning is continuous: maximum numbers of ripe females were found in August-November/December (Zambia) and in June (Kigoma). First maturity (50%) is reached at 500 mm for males and 570 mm for females.

Fish appear to compose a larger part of the diet than in other *Lates* species. Thompson et al. (1977) indicate a possible change to a complete piscivorous diet at 80 mm. Not enough data are available to define a seasonal shift towards clupeid feeding. Prey is taken up to 33% of the predator length. Condition factors in Zambia increased steadily to maturity and decreased in older fish.

The maximum observed lengths in Zambia are 1 910 mm (male) and 2 050 mm (female). Asymptotic length for the population, is of the order of 1 000 mm. No further data on growth are available.
4.1.3 *Lates microlepis*

*Lates microlepis* is a surface water predator. Fluctuations in the catches indicate that this species ranges freely and tends to concentrate where prey is abundant. Recruitment length in the Kigoma fishery is usually 620 mm, sometimes 400 mm. *L. microlepis* does not enter the pelagic zone before reaching maturity.

Spawning is continuous; maximum numbers of ripe females are found in August-November/December (Zambia) and around April off Kigoma. Absence of ripe-running females in the catches probably indicates that they concentrate outside the fished zone. Fifty percent maturity is at 470 mm for males and 510 mm for females.

*L. microlepis* are frequently seen in large numbers, feeding on offshore clupeid shoals. Clupeids make up most of their food, but occasionally Lucioliates are taken up to 40% of the predator length. *L. microlepis* is the top predator of the pelagic zone. Condition factors increase steadily to maturity and decrease in old fish. Highest condition factors coincide with maximum clupeid abundance.

The maximum length observed is 1010 mm, asymptotic length for the population possibly 800 mm.

4.2 *LUCIOLATES STAPPERSII*

Adult Lucioliates are pelagic and appear to prefer the upper water layers. They show a strong seasonal abundance pattern with a peak in December-June. This pattern is similar all around the lake and therefore not explained by migration. Catch data from different fishing centres on the lake indicate a cyclicity in Lucioliates abundance of 6 to 8 years, alternating with a similar cycle of *Stolothrissa*, its main prey species. There is an overall strong negative correlation between the abundances of these two species, even in daily ringnet catches.

Juvenile Lucioliates are unevenly distributed over the lake and vary greatly in abundance in successive years. In Burundi, their average contribution to the dagaa catch is about 20%, against less than 10% in Kigoma and none in Zambia.

Poll (1953) mentions that spawning is continuous, with an annual peak in February-April. This is confirmed by observations from Burundi (December-March) and Kigoma (February-April). Peak spawning apparently means increased vulnerability to the offshore ringnet fishery. Spawning takes place in the pelagic areas and juveniles from 20 mm onwards appear in the catches. Peak abundance of juveniles in the catch is usually in August-September (Kigoma and Burundi), dropping to almost zero in October-November. Inshore scoopnet catches are highest in October-December. Lucioliates of 100 to 200 mm are relatively rare in the ringnet catches and they probably prefer inshore waters where suitable Stolothrissa prey are plentiful (see Section 5.3.2). A second recruitment to the offshore fishery occurs at 180-200 mm, usually in October-November.

Juveniles Lucioliates up to 130 mm feed on zooplankton, but start taking fish at 70 mm. From about 130 mm, they become entirely piscivorous and feed practically only on Stolothrissa. The rate of decomposition of fish in Lucioliates stomachs suggests that feeding takes place before darkness.

Fifty percent maturity lengths of 280 mm for males and 300 mm for females are mean values and vary throughout the year. Sizes of first maturity are smallest in February-June. Males make up about 44% of the adult population.
Mann et al. (1975) derived the following growth equation for Lucioliates in Burundi: 
\[ L_t = 400 (1 - e^{-0.3 \cdot t}) \]
whereas in Kigoma, the first year's growth was found to follow the equation: 
\[ L_t = 400 (1 - e^{-0.5 \cdot t}) \]. The fork length (FL) - weight (W) relationships found in Burundi and Zambia are respectively: 
\[ \log W = 3.09 \log FL - 5.31 \] and \[ \log W = 3.14 \log FL - 5.43 \], but do not differ significantly.

Total mortality rates from catch curves of Lucioliates were estimated by the project (Henderson, 1976), assuming that the right hand limb of the length frequency distribution was composed of several year classes of about equal strength and catchability. Z values of 0.5 (Kigoma) and 0.8 to 2.6 (Burundi) were found, and it is suggested that the difference is due to the much heavier fishing in Burundi. In view of the low fishing intensity in Tanzania, 0.5 would probably be close to the natural mortality rate. In 1974, the mean length in the ringnet catches was considerably higher in Kigoma than in Burundi. A comparison of the length frequencies from Kigoma and Burundi suggests that the major modes are similar. Levels of mixing of the adult populations from the two areas are therefore probably low, but recruitment to both areas may be from the same area or from areas where spawning and early life history are subject to similar conditions.

The uneven distribution of juvenile Lucioliates in Lake Tanganyika possibly indicates preferences in spawning areas or feeding grounds (like concentrations of juvenile clupeids). Test fishing with ringnets in the Tanzanian waters in October 1974 showed that juvenile Lucioliates (under 250 mm) were most abundant in the central part of the lake (Kibwesa-Kipili), and that most adults (over 300 mm) were concentrated between Mgambo and Kigoma. This suggests age-specific behaviour.

In spite of the heavy fishing in Burundi and Zambia, no permanent decline has been apparent in the catches per unit effort of Lucioliates. On the contrary, catches in 1976 and 1977 were the highest since ringnetting was introduced to Lake Tanganyika. The longevity of Lucioliates should make it much more vulnerable to intensive fishing than the clupeids, but fishing effort on Lake Tanganyika is very localized and there is some evidence (Section 6.1) that Lucioliates moves about the whole lake, so that fish removed can be replaced by recruitment from other (unfished) areas.

4.3 STOLOTHRISSA TANGANICAE

Stolothrissa tanganicae is by far the most important commercial fish species of the lake. It alternates in abundance offshore with Lucioliates, its main predator, and reaches an abundance peak every 6 to 7 years. Stolothrissa contribution to the ringnet catches in the Kigoma area is therefore variable (10 to 70%). The artisanal inshore fishery usually catches still higher percentages of Stolothrissa.

Apart from the longer-term cycle, there is also a very marked seasonal abundance pattern with minimum annual biomass in May-July and maxima in the second half of the year - September (Zambia), September-October (Kigoma), and November-December (Burundi). This pattern follows closely the hydrological cycle of Lake Tanganyika and can be fully explained by variations in recruitment strength (Roest, 1977). Stolothrissa movements in the lake are rapid, but it is probable that stock movements are localized and do not cover the whole lake area.

Spawning is continuous and the timing of the peak periods varies annually - January-April (Kigoma), March-July and November-February (Zambia), February-July and October-December (Burundi). Spawning seasons probably overlap in the three
areas. Fifty percent mature sizes vary throughout the year, and average 70 mm fork length for males and 75 mm for females (Ellis, 1971). Spawning areas have not yet been defined, but were generally supposed to be pelagic (Poll 1953, Matthen 1968, Coulter 1970). There is, however, considerable indirect evidence for inshore spawning (Roest, 1977): (a) during the main spawning period, offshore Stolothrissa biomass is minimal, and (b) inshore catches show at this time a distinct peak and consist of older Stolothrissa.

Inshore plankton is more abundant during the main spawning season, January to June (Coulter, 1970), guaranteeing survival of the developing fry. Youngest Stolothrissa are reported to feed on phytoplankton. It is not known at what length they change over the zooplankton. Some individuals of 3 to 7 mm total length examined had green intestines (phytoplankton), but samples were too few to be conclusive. From about 30 mm, juveniles become vulnerable to the artisanal inshore fishery, where highest catches are made in June-August. At about 50 mm, they start moving further offshore and recruit to the catamaran and ringnet fisheries at 55 mm. The peak catches of the offshore ringnet fishery occur in September-January, first in the south (Zambia), and later in Kigoma and Burundi. Stolothrissa biomass is then highest, coinciding with the annual offshore plankton peak.

Stolothrissa feed almost exclusively on zooplankton. Stomach analyses (Marlier 1957, Matthes 1968, Chene 1975) indicate that crustacean shrimps (Athyidae: Limmocaridina spp), Calanoids (Diaptomus simplex) and Cyclopoids (Mesocyclops, Tropocyclops) are the main food organisms. Further items taken were Chironomid nymphs, fish eggs and fry. Small quantities of green algae (Scenedesmus) and diatoms (Nitzschia) would be taken accidentally or may represent stomach contents of the zooplankters ingested. From examinations of stomachs taken throughout the night, it appears that feeding takes place in daylight and stops after dusk. Feeding in bright moonlight is possible, and supported by schooling patterns revealed by echo-sounding (see Section 6.2).

Growth is rapid and life cycles are short (up to 19 months). Generally, a high reproduction peak occurs when the population density is lowest and vice versa (Roest, 1977). This suggests a Ricker reproduction model. The annual exploitation rate determined from this model is 66%. Because of their rapid turnover rate, Stolothrissa are capable of adjusting their numbers rapidly under heavy exploitation.

Two growth equations have been proposed: 
\[ L_t = 89.0 \left(1 - e^{-0.222 \cdot t}\right), \]
suggested by the project, and based on a number of monthly sequences in length frequency distributions from Zambia, Kigoma and Burundi (van Well and Chapman, in press), and 
\[ L_t = 93.8 \left(1 - e^{-0.211 \cdot t}\right), \]
based on six years length frequency data from the Burundi fishery (Roest, 1977).

The length-weight relationship for Stolothrissa of 60 to 87 mm is, for Burundi: 
\[ \log W = 3.2072 \log PL - 5.4577. \]

The project found a total mortality rate of 5.2 for Stolothrissa in Kigoma, corresponding to 99.5% annual mortality. A comparable value of 5.48 per year was found for the Burundi area.

4.4 **LIMNOTHRISSA MIODON**

Limnothrissa miodon is unimportant in the ringnet catches off Kigoma, but may represent 25 to 50% of the catches in the shallower waters of Burundi and Zambia. Even the inshore scoopnet catch of Kigoma contains few Limnothrissa, probably because of the narrowness of the littoral.
No regular abundance patterns have so far been defined, although *Limnothrissa* seem to be more abundant throughout the lake in April-August. Abundance patterns of *Limnothrissa* may be largely determined by *Stolothrissa* abundance, with whom this species possibly competes for food in the pelagic area. A large part of the *Limnothrissa* stock inhabits the inshore areas. Absence of juveniles under 60 mm fork length in the Kigoma ringnet catches suggests that they probably live nearshore. Lengths in the offshore catches (Kigoma) range from 60 to 175 mm, averaging 116 mm over 19 months. At the approach of maturity, a part of the adult population appears to disperse in the pelagic waters (Coulter, 1970). The project (Henderson, 1976) suggests that the larger *Limnothrissa* may follow the massive offshore recruitment of *Stolothrissa*.

Spawning takes place along the shore, and unclear recruitment patterns indicate that it continues throughout most of the year. Timing of the annual spawning peak is probably variable as in *Stolothrissa*: December-February and August-September (Kigoma), March-July and September-January (Zambia) (Matthes 1968, Coulter 1970, Ellis 1971). Fifty percent maturity lengths vary throughout the year with the composition of the population, and average 70 to 80 mm fork length (Coulter 1970, Ellis 1971).

Coulter (1970) remarks that in the Zambian waters massive appearance of *Limnothrissa* fry coincides with the annual plankton maximum (July-September). According to Matthes (1968), shoals of juveniles tend to stay in the littoral zone during the day, and move into deeper water at night.

Food habits are much the same as for *Stolothrissa*, but more diversified (insect larvae), in relation to their inshore life (Matthes, 1968). Young fish are reported to feed on zooplankton (mostly small crustaceans and clupeid alevins), insects and insect larvae, adults mostly on Atyid shrimps, young *Stolothrissa* and other small fish, including their own young.

Two growth rates have been determined for the Kigoma area, characterized by the parameters $L = 175$ mm and $k = 0.056$ and $k = 0.0765$ per month. The highest $k$ was derived for the largest mode (over 120 mm), and is possibly higher because old fish almost exclusively feed on *Stolothrissa*. Most *Limnothrissa* seem to live more than one year, and the growth may be constant for the first nine months.

Mann et al. (1975) propose the following relation between weight ($W$) and fork length ($FL$): $\log W = 2.9811 \log FL - 4.007$. 
5. INTERACTION BETWEEN THE FISH SPECIES AND THEIR ENVIRONMENT

Mutual relations between the six pelagic fish species and the influence of their physical and chemical environment largely explain the distribution and abundance patterns. At the same time, these relations determine their most characteristic behaviour aspects.

5.1 THE PHYSICAL AND CHEMICAL FACTORS DETERMINING FISH DISTRIBUTION AND ABUNDANCE

The annual hydrological cycle of Lake Tanganyika with its periodic advections of nutrient rich hypolimnion water is detailed in Section 2.3.1. Although phytoplankton is no longer thought to be at the basis of the lake's foodchain (Hecky et al., 1977), these nutrients lead to increases in bacterial concentrations on which the protozoa, the main food source of the zooplankton, feed. Coulter (1970) and Ferro and Coulter (1974) suggest that occasional failure of a clupeid year class may be due to the anoxic conditions in the inshore waters and that the latter may also explain the relative poverty of the inshore fish community at the northern end of the lake. The rising of the thermocline following the cessation of the strong trade winds in September is considered the most likely event triggering the high plankton and subsequent clupeid production of the northern lake. Coulter (1969) suggests that upwelling along the Tanzanian shore might explain the high production there, and the concentration of fishing villages in the area between the Kungwe Mountains and Kirando.

Limnological observations during echosurveys revealed that the pelagic fish community, at least the clupeids and possibly also Luciolates, are limited in their vertical distribution to water containing at least 3 mg oxygen per litre.

There is some indication that Stolothrissa tends to move against the current. Epilimnetic water off Kigoma moves southward consistently, and direct measurements of school movement suggest more movement northward than southward. When the skipper of the ringnetter chartered by the project searched for fish concentrations, he was successful more often when he searched to the south. Also, when he left or lost concentrations, he most often found them by searching northward.

5.2 THE BIOTIC ENVIRONMENT

5.2.1 Plankton abundance and composition

Although little direct evidence is available, it is likely that the annual maximum offshore clupeid biomass (September-December) coincides with a similar maximum in its main food, the zooplankton.

From January to June, pelagic plankton is generally sparse (Coulter, 1970), but remains plentiful inshore. Clupeid biomass decreases in this period to its annual low in May-July. Limothrissa and probably also Stolothrissa spawn inshore, and planktonic food is likely to be abundantly present when required for the initial development of the clupeid fry.
Because of the strong wind action, the lake reaches its most unstable state in June-August (Coulter, 1970). Surface drifts away from the shore and upwelling cause offshore plankton increases. In this period, Stolothrissa massively recruit to the pelagic zone.

Correlations between zooplankton samples and acoustically determined fish abundance indicate a significant negative quantitative relation, especially with major food items like crustacean shrimps, Diaptomidae, small Cyclopidae, instars, fry and fish eggs. The mean size of the crustacean shrimps is significantly higher where Stolothrissa are present.

The lake also contains a large biomass of small coelenterata (jellyfish). No precise estimate of this biomass has been possible. Studies on relative abundance were made by the Burundi Project in their waters and it was found that from September 1974 to May 1975 they were never really absent. In December and January there seem to be somewhat higher concentrations although zero observations still exist. This coincides with high catches of clupeids; fishermen say they do not catch fish in the immediate vicinity of the jellyfish.

Supposedly, Stolothrissa move about the lake in large masses, searching for food, preferably dense zooplankton populations consisting of many large crustacean shrimps. Once such a population is found and cropped by the fish, the latter move on, permitting the cropped population to increase. Thus, Stolothrissa may optimize yield and production of prey organisms.

Daily vertical movements of Stolothrissa are probably food-related. The migration towards the surface at dawn can be explained by the higher concentrations of plankton at the surface at that time. The return to deeper water as light increases each morning probably results from predator avoidance, as well as from the downward movement of the zooplankton. The observed schooling in bright moonlight may also be food-related.

Differences in feeding habits would explain the different distribution of adult Limnothrissa and Stolothrissa. The wider range and regular availability of planktonic food inshore is more suitable for Limnothrissa's unspecialized feeding habits, whereas the food preferences of Stolothrissa would give it competitive advantages in the pelagic zone.

Because of its suggested unspecialized food habits, Limnothrissa was considered the best choice for introduction into Lake Kariba (Matthes 1968, Bell-Cross and Bell-Cross 1971). Both Limnothrissa and Stolothrissa fry were introduced into Lake Kivu, but only the former managed to survive and build up an important population.

5.2.2 Predation and species interaction

The project (Henderson, 1976) noted that the largest Limnothrissa appear in the Kigoma catches when there are relatively more small Stolothrissa present. This suggests an offshore movement of Limnothrissa over 100 mm, probably accompanying the recruitment of 50 mm long Stolothrissa to the offshore fishery. There is little doubt that Limnothrissa is a facultative predator of Stolothrissa and of its own young. In Zambian waters, where Limnothrissa sometimes exceeds Stolothrissa in abundance, this predation may be an important element in the stock dynamics of the clupeid populations (Henderson, 1976).

Other species preying on inshore clupeids are listed in Matthes (1968) and Poll (1953). Unpublished results obtained in Burundi indicate a strong positive correlation between the abundance of Luciolates of 100 to 200 mm and the inshore Stolothrissa.
before they recruit to the offshore fishery. This suggests a temporary inshore life of young Luciolytes. Between 100 and 200 mm fork length, Luciolytes are indeed relatively rare in the ringnet catches and annual length frequency graphs of all Luciolytes sizes are always strongly bimodal. Luciolytes are entirely piscivorous from 130 mm onwards, but start taking fish from 70 mm.

Adult Luciolytes are truly pelagic and feed almost exclusively on adult Stolothrissa. Both species show pronounced seasonal abundance patterns, Luciolytes with highest abundance in the first half of the year and Stolothrissa in September-December. There is an overall strong negative correlation between the abundances of the two species.

Apart from this seasonal abundance pattern, there is in both species a longer-term abundance cycle. Long series of catch data from Burundi indicate a cyclicity in Luciolytes abundance of 6 to 8 years, with successive peaks in 1956-57, 1962-63, 1966-69 and 1976-77. Stolothrissa abundance alternates with Luciolytes, with maxima in 1961, 1966-68 and 1973-74. Data from other areas where commercial ringnet fishing takes place show similar trends.

Because of the stability of Lake Tanganyika, it has generally been supposed that the timing of the main biological events like spawning, recruitment and maximum biomass development would be very rigid within the annual calendar. However, a comparison of the spawning periods in consecutive years of Stolothrissa in Zambian waters (Matthes 1968, Coulter 1970, Ellis 1971) as well as in Burundi (Marlier 1957, Mann et al. 1975, Enderlein 1976) shows that there is little unanimity between the different workers. In fact, there is often a 13 to 14 month interval between two successive spawning maxima, corresponding to the time necessary for two generations to reach sexual maturity (Roest 1977).

The timing of the biological cycles of Lymnothrissa and Luciolytes is probably strongly inspired by the biological cycle of their common prey species Stolothrissa. Lymnothrissa might, for example, reach its maximum biomass of individuals over 100 mm long at the moment of maximum abundance of Stolothrissa prey of the right size, and Luciolytes of 100 to 200 mm should find at their peak abundance very great numbers of inshore Stolothrissa (30 to 40 mm).

Much less is known, so far, about the influence of the Lates spp on the clupeid stocks. Coulter (1960, 1970) suggests that the fishing-up of the combined predators in Zambia and Burundi resulted in an increase of the clupeid populations, but at that time it was not yet known that Stolothrissa and Luciolytes alternate in abundance. While it may be true that the overexploitation of the Lates spp has resulted in higher clupeid abundance (Turner, 1977), Luciolytes, too, has considerably increased; 1976 and 1977 catches of this species, at least in Kigoma and Burundi, were the highest recorded since ringnet fishing started on Lake Tanganyika. Luciolytes therefore seems much less vulnerable to heavy exploitation than might have been expected on the basis of its longevity, but recruitment from other, unfished or underfished, areas would mask the real situation.

Lates mariae and L. angustifrons are benthic predators, and their abundance has probably never been very important in the northern part of the lake or in the Kigoma area, where stretches of oxygenated bottom are rare. Lates microlepis, however, is fully pelagic, and as such a more important predator of the clupeids. Like in Luciolytes, its greater agility makes it appear to resist much longer under heavy exploitation. The longevity and the abundance cycle of L. microlepis are not well known, and the latter does not appear to be directly linked with Stolothrissa abundance. Possibly, larger prey like Luciolytes are taken during low clupeid abundance. Coulter (1970) reports to have found Luciolytes in L. microlepis stomachs up to 40% of the predator length.
Generally, in ringnet catches there is a negative correlation between the abundance of Luciolates and Stolothrissa, and a positive correlation between Lates microlepis and Stolothrissa. Apparently, Luciolates is incapable of following the rapid vertical and lateral movements of Stolothrissa, while L. microlepis can. During periods of high clupeid abundance, Lates mariae abundance also correlates positively with Stolothrissa, as witnessed by Coulter (1970) in Zambia, and by test fishing throughout the Tanzanian waters of Lake Tanganyika in October 1974.

Henderson et al. (1972) discussed the fishing-up process and the implications of predator reduction and found that fluctuations in the clupeid (dagaa) catches were more closely related to predation than to harvest by humans, the kill by predators being probably 4 x the fishery harvest.

The dense schooling of Stolothrissa and possibly Limnothrissa during the day, and the formation of layers at night, are likely to be adaptive reactions to predation.
6. FURTHER ASPECTS OF FISH BEHAVIOUR: MOVEMENT, DISTRIBUTION AND SCHOOLING PATTERNS

Information on the schooling and distribution patterns of the pelagic fish species was obtained by lake-wide acoustical surveys (Chapman et al., in press). The following summary describes aspects of fish movements and distribution and the characteristics of schools and layers of clupeids.

6.1 FISH MOVEMENT AND DISTRIBUTION

Over short periods of time, drastic changes in ichthyomass distribution have been recorded. Repeated echosurveys in the same area show large differences in fish distribution. This was first observed by Johannesson (1975) during his lake-wide acoustical survey of November 1973. Two measurements of fish biomass in the northern end of Lake Tanganyika within two weeks yielded estimates of respectively 120 000 and 260 000 t. At the same time, in other areas of the lake similar differences were found during long north-south tracks through areas covered some days earlier. The project, working in a rectangular grid off Kigoma, found large differences in biomass, even over 24 hours (Chapman, 1975).

These observations correspond with the great differences in sequential nightly catches of Stolothrissa in the same location. Rapid clupeid movements are adaptive reactions to predation by Lucioliates. The latter follow clupeid movements less efficiently than Lates microlepis, and also Lucioliates catches in the same location vary less in successive nights.

Direct measurements of the movement of 78 fish schools (presumably Stolothrissa) were performed off Kigoma with a crude "sonar". The rates of displacement of these schools varied from 0 to 68 m/min (0 to 4 km/h). In 71 cases of discernible movement, 29% of the schools moved northward, 18% southward, 44% eastward and 9% westward. The mean movement rate in both north and south directions equalled about 11 m/min (0.6 km/h).

Night movements of fish layers were usually negligible, although some movement was measured (0.4 to 0.6 km/h) on three nights out of eight.

Test fishing in October 1974 showed that Stolothrissa were absent from the southern half of the lake (south of Karema). Echograms obtained by Johannesson (1975) clearly show that Stolothrissa were spread throughout the lake in the corresponding period in 1973.

In conclusion, it appears that the lateral movements of clupeids and possibly also Lucioliates may be quite extensive. An analysis of the dynamics of the Stolothrissa stocks in the north end of the lake, however, suggests that the movements are either localized or that the movements out of the area may be compensated by immigration from other areas. The differences in ichthyomass in this area over two weeks as measured by Johannesson have so far not been explained.

Collart (pers. comm.) participated in tagging several hundred Lucioliates near Bujumbura in 1959 and 1960, of which one was recovered at the other end of the lake near Mpongwe in Zambia. The rate of movement is not known, but this observation supports the hypothesis of extensive fish movements in Lake Tanganyika.
Arithmetic estimates of biomass from Johannesson's data are highly variable among 2-mile track samples. Night estimates were overdispersed and fitted the negative binomial distribution; day estimates were also overdispersed, but could not be easily fitted to the negative binomial as well. Bazigos (1975b) also fitted the negative binomial and discussed the statistical aspects of fish distribution. Log-normalized data from Johannesson (1975) indicate significant relationships between fish density and area, depth and time domains. There was a significant difference between biomass in the east and west parts of the lake, with the eastern half containing more fish. There was no significant difference between biomass in the north and south halves of the lake. Overall estimates of biomass by Johannesson were four times greater at night than in daytime. This difference is probably due to measurement errors caused by fish behaviour (see Section 7.1.1).

6.2 CHARACTERISTICS OF LAYERS AND SCHOOLS

Echosounding throughout the lake carried out by the project (Chapman, 1975) has revealed that Stolothrissa show varying vertical distribution patterns during the day and at night time. At night the fish concentrate in layers and move towards the surface in schools at daylight, then move deeper again at 08.00 hours, shallower again in late afternoon, and diffuse into layers at dusk.

Measurements on echograms and integrator rolls indicated that densities of night layers throughout the lake ranged from 0.04 to 6.08 kg/100 m³, and total weights from 0.6 to 223.6 t. Layer dimensions ranged from 0.2 to 24 n mi and averaged 2.2 n mi for 64 discrete layers. Of these, 58% measured more than 2 n mi, 27% exceeded 6 n mi and 9% exceeded 12 n mi. Mean layer thickness equalled 11 m.

Schools were divided into five categories according to their appearance on the echosounder:

Type 1: taller than wide, relatively low in density, average weight 238 kg.
Type 2: wide, short schools of high densities, average weight 335 kg.
Type 3: irregularly-shaped schools with drooping fingers below, low density, average weight 595 kg.
Type 4: very dense cone-shaped schools, average weight 1423 kg.
Type 5: extremely dense cone-shaped schools with one or two fingers from the lower corners.

These schools were assumed to be largely Stolothrissa in most areas of the lake, because Limnothrissa are not abundant offshore and there is no evidence that Luciokrantes is a schooling species.

Luciokrantes, however, does form layers at night. This conclusion is based on comparisons of echogram traces with ringnet catches.

School types 2 and 4 became most abundant in midday, with Stolothrissa probably not feeding in these configurations. Types 1 and 3 may be feeding configurations, and tend to lie closer to the surface than other school types. Type 1 schools also formed at the lake surface in bright moonlight.

In November 1973, the greatest depth at which fish was recorded ranged from 60 m in Burundi to 180 m in Zambia. In the second survey through Burundi waters, maximum fish depth had increased to 100-110 m. These changes were probably caused by movement of oxygen isopleths because of internal waves (Perro, 1975).
Coefficients of variation (CV) in lengths of fish blast-killed (dynamite) in discrete schools were significantly less than the CV in layers of fish (as measured in samples from ringnet catches). This suggests size-specific schooling.
7. EVALUATION OF THE FISHERY RESOURCES

7.1 BIOMASS ESTIMATES

7.1.1 Echosurveys

A number of quantitative acoustical surveys were conducted by the project, of which the first, in October and November 1973, was directed by FAO Consultant Johannesson (1975), and undertaken in close collaboration with the Burundi Fishery Research Project of Bujumbura. First, the acoustical equipment was calibrated by measuring the amount of echo trace of a known quantity of juvenile Lucioliates confined in a cage beneath the anchored survey vessel. Lucioliates were chosen because no method of capturing and successfully holding Stolothrissa could be developed in the time available to Johannesson, and no method of efficiently straining known volumes of water with fishing gear was available. The estimated lake-wide pelagic ichthyomass was 2.6 million tons (Chapman, 1974; Johannesson, 1975a) or about 1 200 kg/ha, a value much higher than expected. This survey was, however, conducted not only during the annual peak in Stolothrissa abundance, but also during the maximum in the 6-7 years abundance cycle of this species.

Only night estimates were used since day assessments lead to an underestimation of the biomass of 4 x, due to the effect of survey errors described by Bazigos (1975b, 1976) and the behaviour of the fish. The most probable explanation for the difference in day and night estimates may be that the fish lie quiescent in layers at night, but in daytime swim actively and often with a tilt, head up or head down. Tilt reduces target strength. Stolothrissa do not feed in darkness, thus fish in layers should present maximum dorsal aspects for echo return.

A second survey was completed in May 1975, at the time of lowest annual biomass. Dr. Mathisen of the University of Seattle conducted this survey, of which the primary objective was a feasibility study of a somewhat different technique than used by Johannesson. Mathisen's estimate of total pelagic ichthyomass was 467 000 t. His survey consisted of a single track down the lake centre, with samples every 4 to 6 mi. Given the contagious distribution of the pelagic fish, this transect probably included too few samples. Bazigos (1975b, 1976) discusses desirable sampling frameworks for future acoustical surveys on the lake.

A third lake-wide survey was conducted in May 1976, but technical difficulties arose and no estimate was obtained.

In November 1976, a successful survey using Mathisen's method was completed by the Kigoma project. The total biomass estimate at the time of a supposed biomass maximum was 680 000 t. However, 1976 was a year of low Stolothrissa abundance, but a peak year for Lucioliates, of which annual biomass maxima are reached in the first half of the year.

Mathisen's method relies on estimated target strengths for individual fish of a presumed mean size of 70 mm for the whole lake. This mean length should be valid for fish ranging from Stolothrissa of perhaps 50 mm to Lates of 100 cm, and is a statistic potentially in serious error. On the other hand, Mathisen's estimate of
mean target strength probably should, if applied to all fish, result in an underestimate of the ichthyomass. In November 1976, Lucioliates biomass was probably higher than Stolothrissa, judging from the ringnet catch data.

Table 2 summarizes the estimations of biomass per area obtained during the three successful echosurveys.

<table>
<thead>
<tr>
<th>Section</th>
<th>Area</th>
<th>Nov. 1973</th>
<th>May 1975</th>
<th>Nov. 1976 1/</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) <strong>Biomass in metric tons</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burundi-Cape Banza (3020' - 4030' S)</td>
<td>2 394</td>
<td>120 000</td>
<td>11 300</td>
<td>14 900</td>
</tr>
<tr>
<td>Tanzania-Kigoma (4030' - 5040' S)</td>
<td>4 836</td>
<td>360 000</td>
<td>45 100</td>
<td>134 000</td>
</tr>
<tr>
<td>Tanzania-Lagosa (5040' - 6030' S)</td>
<td>3 845</td>
<td>340 000</td>
<td>45 800</td>
<td>43 700 H</td>
</tr>
<tr>
<td>Tanzania-Kipili-Karema (6030' - 8000' S)</td>
<td>8 390</td>
<td>1 700 000</td>
<td>221 100</td>
<td>300 100 H</td>
</tr>
<tr>
<td>Zambia (8000' - 8045')</td>
<td>2 686</td>
<td>80 000</td>
<td>144 000</td>
<td>294 700 L</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>22 151</td>
<td>2 600 000</td>
<td>467 000</td>
<td>685 700 H</td>
</tr>
</tbody>
</table>

| (b) **Biomass in kg/ha** | | | | |
| Burundi-Cape Banza (3020' - 4030' S) | | 501 | 47 | 62 |
| Tanzania-Kigoma (4030' - 5040' S) | | 744 | 93 | 277 |
| Tanzania-Lagosa (5040' - 6030' S) | | 884 | 119 | 114 H |
| Tanzania-Kipili-Karema (6030' - 8000' S) | | 2 026 | 264 | 358 H |
| Zambia (8000' - 8045' S) | | 298 | 536 | 719 |
| **Total** | | 1 174 | 211 | 310 H |

1/ H - high estimate; L - low estimate.
2/ Second estimate.
Table 2 (b) indicates that the ichthyomass is very unevenly distributed over the lake. Highest biomass densities are consistently in the Kipili-Karema area or in Zambia (below 6°30' S).

7.1.2 Other assessments

Coulter (1977) supposed that the growth rates of Stolothrissa, Limnothrissa and juvenile Luciolates (dagaa) would be similar so that they can be treated as a single species stock. Gulland's (1970) yield model $C_{max} = X \cdot M \cdot B_0$ can then be used, in which $X$ is the proportion of the total annual production that can be taken (here estimated at 0.6 to 0.7), $M$ is the natural mortality rate (supposed to be close to the total mortality rate of 5.2 determined for Stolothrissa in Kigoma) and $B_0$ the virgin biomass to be determined. $C_{max}$ is the sustainable yield. Assuming that the catches in kg/ha observed in the intensively fished areas of Burundi and Zambia (southeast arm) are close to the sustainable yield (respectively 116 and 140 kg/ha), these values can be used. The following virgin biomasses were obtained:

Burundi 32 - 37 kg/ha, Zambia 38 - 45 kg/ha,

which, extrapolated on an area basis, lead to an estimated potential fish yield for the whole lake of 380 000 to 460 000 t per year, the pelagic ichthyomass being 104 000 to 147 000 t.

These estimates place Lake Tanganyika in the class of productive fish waters, but the relative yield is remarkably high, the total annual production being much higher than the average biomass.

7.2 FISH YIELD ESTIMATES

Mann and Ngomirakiza (1973) summarize the evaluations of the pelagic fishery resources of Lake Tanganyika. The first estimate resulted from the Belgian Hydrobiological Expedition (1946-47). Kufferath (1952), based on the chemistry of the lake, estimated that at least 10 kg/ha or 30 000 t could be harvested annually. Later estimates of Capart and Kufferath (1956) were 30 to 35 kg or 100 000 t per year. In 1961 (ASED), revised estimates of fish production were 70 to 100 kg/ha per year, which extrapolated for the whole lake represents 230 000 to 330 000 t.

Coulter (1977) used the morphoeidaphic index (MEI) - catch regression of Henderson and Welcome (1974) to estimate potential fish yield and found 39 kg/ha. This is a much too low value, suggesting that the trophic system of Lake Tanganyika represents a special case.

Turner and Herman (1977) estimated the potential average annual fish yield from catch and effort data for the Burundi sector of the lake at 90 kg/ha.

Until more is known about the integrity of the fish stocks, extrapolations of data from fished areas to calculate the potential yield of the whole lake should be made with care. Fishing could attract fish from other areas (Turner and Herman, 1977), and the present knowledge of the biomass distribution throughout the lake is very scanty since it is based on only three points in time.
In assessing the lake's fishery potential, considerable attention should be given to the regularly occurring natural fluctuations in fish biomass caused by the alternating abundance of the two most important species, Stolothrissa tanganiae (dagaa) and Luciolas stappersii (migebuka). Although future years of maximum abundance of both species can probably be predicted, it is still impossible to foresee what absolute levels of abundance the stocks will reach during their maximum. A thorough understanding of the predator-prey relationship and possibly of other sources of natural variation is necessary to predict exact values for the individual years to come. Present estimates are either minimum or mean values and do therefore not offer enough security for justifying detailed fishery development plans. At the moment, it would seem that rational fishery development should aim at the low values.

An improved beach seine was developed by the project during 1977 and successfully caught substantial amounts of small benthic cupleids in the Malagarazi delta. Further research is needed before any benthic potential yield for that area can be estimated.

Based on catch data and the quantitative echosurveys, at present, a prudent estimation of the lake's potential yield would be of the order of 100 kg/ha, or 330 000 t for the whole lake and some 135 000 t for the Tanzanian waters. It should be stressed, however, that this estimate is preliminary and likely to be changed when more detailed information is available.
8. RECOMMENDATIONS

8.1 MANAGEMENT

Although present yield estimates are only preliminary and do not offer enough security to justify detailed fishery development plans, it is clear that a considerable expansion of the present fishery in Tanzania is possible by utilizing the offshore fish stocks. Predator (Luciobates) and prey species (Stolothrissa) alternate in abundance, so that, as in the past, large variations in catch weight and composition can be expected in the future. Over-investment in fishery development based on exceptional catches in individual years should therefore be avoided, as well as over-concentration on the processing and marketing of a single temporarily abundant fish species.

Lates catches should be closely watched as experience in Zambia and Burundi, as well as biological data gained in Tanzania, suggest that these species are particularly vulnerable to increased fishing effort.

The crucial decisions which must eventually be made regarding optimal harvest levels can only be soundly reached through knowledge of stock levels at low as well as high levels of exploitation. It is, for this reason, essential that a minimal programme of stock monitoring and a sound programme of catch monitoring be developed and continued indefinitely. Assistance in the form of visits by biological consultants at least twice per year will be needed to assure such continuity of data.

8.2 INTERNATIONAL COOPERATION

Because of the huge size of Lake Tanganyika and the extensive movements of the two most important species, Stolothrissa and Luciobates, research and management of the stocks can only be fully successful if based on the cooperative efforts of the countries sharing the lake. Such cooperation is needed not only in exchange of data and research, but also eventually in agreements on harvest levels and other management responsibilities.

In November 1977, during the 3rd session of the Committee for Inland Fisheries of Africa (CIFA), an ad-hoc Subcommittee for the promotion of international cooperation between the countries surrounding Lake Tanganyika was created. The Subcommittee had its first meeting in Lusaka, Zambia, 27 to 31 March 1978 with representatives from all four riparian countries represented. The Subcommittee strongly supported the proposal for a regional research project with emphasis on development needs, recommended that the Subcommittee review the final version of the draft document before formal submission to the representative governments, requested a meeting of statisticians from each of the countries to compare sample methods, techniques and results, and considered other forms of inter-government cooperation on matters concerning the fisheries of Lake Tanganyika.

It is recommended that the Sub-committee be given full support by the riparian countries as an instrument for cooperation until such time as it becomes feasible to establish, by treaty, a formal mechanism of joint development and management of the fisheries of the lake.
8.3 RESEARCH

8.3.1 Biological research

The alternating abundance cycles of the two most important fish species, *Stolothrissa tanganicae* (dagaa) and *Luciolates stappersii* (migebuka), indicate that the predator-prey relationship plays an important role in determining the abundances of the species. Examination of further biological data on the other pelagic fish species shows that also *Lates microlepis*, *Limmotrichia miiodon* (over 100 mm), *Lates mariae* (over 500 mm), as well as possibly *Lates angustifrons* at some stage, almost entirely depend on *Stolothrissa* as food. *Stolothrissa*, therefore, is the key species, and it is very likely that the other species in their timing of spawning, recruitment, maximum abundance, etc., are greatly adapted to the timing of *Stolothrissa*’s life cycle. Timing of the main spawning and thus of all major events of *Stolothrissa*’s life cycle, varies from year to year, with often a 13 to 14 months’ interval between corresponding events (see Section 5.2.2). It is therefore likely that life cycles of the other species show similar variations in timing.

Further research should therefore be oriented towards the integration of biological data from all six pelagic fish species. Thus, the individual pieces of Lake Tanganyika’s ecological puzzle would be fitted together, and the timing of the main events in the life cycles of the predators would get the proper biological significance. This approach shows where quantitative relationships between predator and prey species should be looked for, and would indicate what combination of predatory or feeding intercations determines the abundance of the prey and predator species at any given moment. Once the relations between *Stolothrissa* and its predators are understood and quantified, it should be possible to improve the forecasting of future catches and their composition, and to design management programmes which would reduce variability in catches while maintaining an optimal balance between reproductive stock and yield to the fisheries.

8.3.2 Acoustical surveys

Acoustical surveys should be continued, in order to define fish distribution and biomass over time.

For the improvement of estimates of the potential fish yield of the individual countries surrounding Lake Tanganyika, it is necessary to combine the predator-prey analysis with a knowledge of the distribution of the pelagic ichthyomass over time. It is not known if there are regularly occurring distribution patterns due to fixed movement patterns of the pelagic fish. Echosurveys so far show that the ichthyomass is very unevenly distributed over the lake, but represents only three points in time. In May 1975 and November 1976, fish biomass in Zambia was 11 x higher than in Burundi, but in November 1973, there was more fish in Burundi than in Zambia. Within the Tanzanian territorial waters, there may be areas that are permanently richer in fish than other areas. Such information, too, will be of great importance for the rational development of the fishery.

Improvement of the accuracy of fish biomass estimates by acoustical methods depends heavily on reliable calibration of the acoustic gear. This is preferably done by test fishing with small meshed ringnets at night, or by the method of Johannesson (1975b), taking the fish species dominating at the time of the survey. Up to now, due to circumstances, *Luciolates* has been used for calibrating acoustic gear in a peak year of *Stolothrissa*, and the average size of *Stolothrissa* (70 mm) has been used in Mathiessen’s calibration in 1976, peak year of *Luciolates* abundance.
Further improvements would be a separate depth recorder for additional assistance in identifying false bottom echoes.

8.3.3 Study and surveys

Ageing of *Stolothrissa* and *Luciolates* should be attempted by study of daily growth increments in otoliths. To define possible spawning areas and movements of young fish in the post larval stages, larval surveys could be undertaken, coupled with current studies.
Appendix 1

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Appendix 2

LIST OF PROJECT FIELD DOCUMENTS RELEVANT TO THIS REPORT

The Fishery


Fishery Statistics


Fish Biology and Stock Assessment


Seasonal changes in zooplankton abundance and composition off Kigoma. H. Rufli. 1978.


Limnology


URT/71/012/20 Collective preliminary reports of scientists from overseas research institutions on their work on Lake Tanganyika. C.W. Coulter et al. 1975.
