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OF THE FISHERIES ON LAKE
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A PRELIMINARY REVIEW OF THE LTR SCIENTIFIC SAMPLING PROGRAMME

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PREFACE

The Research for the Management of the Fisheries on Lake Tanganyika project (LTR) became fully operational in January 1992. It is executed by the Food and Agriculture Organization of the United Nations (FAO) and funded by the Finnish International Development Agency (FINNIDA) and the Arab Gulf Program for the United Nations Development Organization (AGFUND).

LTR's objective is the determination of the biological basis for fish production on Lake Tanganyika, in order to permit the formulation of a coherent lake-wide fisheries management policy for the four riparian States (Burundi, Tanzania, D.R. of Congo and Zambia)

Particular attention is given to the reinforcement of the skills and physical facilities of the fisheries research units in all four beneficiary countries as well as to the build-up of effective coordination mechanisms to ensure full collaboration between the Governments concerned.

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Résumé

Lake Tanganyika has been in existence for at least ten million years and probably contains about one fifth of all the standing freshwater in the world. With a maximum depth of almost one and a half kilometres it is the second deepest lake on earth. About 7 to 10 million people live in the catchment area of the lake and depend on it in one way or another for their livelihood and well being.

The fishermen form an important link between the lake’s resources and the people’s need for protein. As the population grows their demands increase but the supply is not infinite. A conservative estimate suggests a yield up to 300,000 tonnes per year but this can only be sustained, for the good of all the people dependent on the lake, if the fish stocks are very carefully managed.

A management plan will have to rely on knowledge of the dynamics of the exploited fish species and the production system of the lake that sustains them. One approach to acquire this knowledge is to analyse data on long-term, historical fish landings and estimate optimal yields and exploitation rates. This is often referred to as the ‘top down’ approach. A study of the major inputs of light and nutrient ‘energy’ and trophic level organisation is termed a ‘bottom up’ approach. It is the latter approach that the current FINNIDA/FAO Lake Tanganyika Research Project (LTR) has largely adopted.

The scientific sampling programme (SSP) has been carried out for three years. The preliminary results confirm some previous work and add some new and important discoveries on the lake dynamics. Further information will be forthcoming when the data are fully analysed. The study is unique in that it has been carried out continuously over an extended period, and at three main locations spread over the lake. Many differences in the physical dynamics, species composition and strategies for survival have been found between the north and south. In comparison with previous studies the present investigation has identified many ways in which conditions in Lake Tanganyika are more like those in the oceans than in other lakes. In particular the nutrients are in the deep water and primary production is dependent on vertical mixing processes.

Primary production in the pelagic ecosystem is confined to the upper 100 m of the water column, the euphotic zone. Production depends on a supply of nutrients, in particular nitrogen and phosphorus, for algae and other primary producers to grow. The surface layer, referred to as the mixolimnion, is often short of these nutrients. They are mostly supplied from a reservoir in a deeper layer, the permanently stratified monimolimnion which is devoid of oxygen, by vertical mixing and diffusion. However when conditions of the lake are stable, especially during the wet season, the thermocline, in the mixolimnion, acts as a barrier for nutrient diffusion. The external force of the wind causes water movements at all depths. During the dry season, strong southerly winds blow and push water to the north.

Although previous studies have identified the primary producers this has not been done in the present study and estimates of production rates from radiocarbon experiments are still awaited. However some initial results indicated that

increases in nutrients led to increases in the level of chlorophyll *a*, a major photosynthetic pigment of the phytoplankton. Despite greater upwelling of nutrient rich water in the southern part of the lake, plant production was greater in the north. This is due to differences in the physical and chemical environments between the northern and southern ends of the lake: algae have greater access to nutrients in the euphotic zone (to 1% of usable light) in the north compared to the south.

The zooplankton community, one of the main secondary producers, is made up of protozoans, crustaceans, coelenterates and fish larvae. In comparison to the species rich, primary producers community it is remarkably simple in the number of species present. The distribution of these species varies from north to south. There are more copepod crustacea and freshwater jellyfish at the northern end but more decapod shrimps at the southern end. The community also exhibits marked seasonal variation that may be a response to primary production and to predation. The link between primary production and the production of zooplankton has still to be determined.

The pelagic fish community is also very simple with only six species, all of which are endemic to the lake. They are two clupeids and four centropomids. Only the clupeids and one centropomid, *Lates stappersii,* are important to the fisheries. Although the feeding of clupeids has not yet been analysed previous studies indicate that they feed on phytoplankton, zooplankton and fish larvae. *Lates stappersii* is an opportunistic feeder and preys mainly on the clupeids and on shrimps. Possible links between relative abundance of the exploited fish and their prey are at present being sought. Lake-wide information is still required on the abundance of the three main fish species and how they are distributed. Fish catches have highlighted important spatial and temporal differences between these species and have provided data on their life histories and vulnerability to exploitation, which can be used to manage them.

Common to many clupeids, both the Lake Tanganyika species, in particular *Stolothrissa tanganicae,* are fast growing and very short-lived; the generation time for most individuals is less than one year. Therefore, a stock studied in one year can differ in the next. The fish are prone to recruitment failure because reproductive output depends on only one or two cohorts. Small shoaling pelagic fish are considered by many fisheries biologists to be the most unreliable on which to make stock assessments. If fishing reduces the stock, the number of schools is reduced but the size of the schools remains the same. Therefore catches are poor indicators of the state of the stock. By contrast the centropomid is a relatively long-lived fish (5-7 years); therefore its life history strategy and the way it should be managed are different from those of the clupeids. Recruitment relies on several cohorts. However they are more vulnerable to over-exploitation than the clupeids. All three species are multiple spawners. At present there are no indications that any of the three species are being overexploited lake–wide. However there is local over-fishing, in particular of *L. stappersii,* in the south.

Our understanding of the dynamics of Lake Tanganyika has been improved by this project. This understanding will become clearer with further analysis. However the dynamics change very rapidly and it is only by thorough and constant monitoring that changes will be identified and an appropriate management policy implemented.

1. Introduction

This report is descriptive in nature. The data collected during the Scientific Sampling Programme (SSP) need analysis in depth, and further data are required from scientific cruises and experiments before quantitative statements can be made. The primary aim is to describe how the SSP carried out by LTR has furthered knowledge about the dynamics of the lake both temporally and spatially. This includes outlining the main physical processes, which affect nutrient availability in the pelagic, and thus primary production, and examining secondary and fish production and the potential yield of fish to the fisheries. Research has been focused on the pelagic zone of the lake because the pelagic resources generate food and livelihood for the people living around the lake. Various aspects of the pelagic ecosystem of Lake Tanganyika have been studied in the past (Coulter 1991), but simultaneous sampling in different parts of the lake over an extended period had not been achieved until the present LTR project became operational. The SSP was carried out from July 1993 to July 1996 although weather stations had been established earlier. Data available at the time of writing cover two and a half years of sampling, from July 1993 to December 1995.

The background and basic aims of the Lake Tanganyika Research project (LTR) were summarised in the original project document. The main points are as follows:

‘The general conclusions derived from ten earlier national-level fisheries development projects executed by FAO in particular sectors of Lake Tanganyika in Burundi, Tanzania, The Congo and Zambia, are that the nature of major fluctuations of the fish stocks needs to be better understood, and the rapid local changes in the abundance of the pelagic fish stocks could also be due to extensive fish movements over the entire lake. However these phenomena and their consequences cannot be appraised by national projects alone confined to their respective territorial waters: a subregional approach to fish resource evaluation and management is clearly required if the full potential of the lake is to be realized for the sustained harvest of fish to supply the animal protein requirements of the expanding human populations of the four riparian States. Moreover, being a special type of deep lake, Tanganyika’s limnology and hydrology, in terms of biological and eventual fish production, possesses features that can best be approached only on a lake-wide basis

‘Lake Tanganyika has valuable fisheries and pelagic fish stocks, although they are apparently not yet utilized to their full capacity. These pelagic fish stocks are subject to large seasonal and inter-annual fluctuations but the biological basis of fish production is incompletely known; the lake has a “poor” oligotrophic appearance and yet its assumed maximum fish production is high’.

A concentrated collaborative research programme is required to cover the whole lake on a subregional basis over at least a five–year period, so as to be able to collect and analyse the required data during a series of annual climatic cycles and during a significant part of the cycles of fish stock abundance which may be as long as seven years

‘Longer–term research and monitoring will also be required, thus it will be important during the project’s duration to build up the necessary skills and physical facilities within the fisheries and other related research institutes in all four riparian States'.

A major question to ask in the management of a large aquatic resource such as Lake Tanganyika is 'Is the effect of predation plus harvesting or the physical nature of the lake responsible for the major changes in abundance?' It should be remembered that as bottom-up effects are not under human control, particularly for a lake the size of Tanganyika, and ecosystems cannot be totally managed, the control must come from the top–down effects. A project such as LTR must try and understand both these types of effect. Ideally it should link understanding of the processes of physical, chemical and biological limnology with population biology, interactions of the component species of the fish community and the influence of humans (i.e. treat humans as part of the ecosystem) . Thus the aim of LTR has been to gain scientific understanding of the system and to harmonise catch-monitoring methods. Catch statistics are often unreliable. This may be caused by a number of factors including logistic difficulties, dishonesty, fish killed but not caught by the gear, illegal fishing and landed fish recorded incorrectly by species and number. The cost of carrying out an adequate census may be prohibitive. When the aims of LTR have been achieved, agreement can be reached for a comprehensive management plan for the whole lake for sustainable yield of products and the maintenance of biodiversity. The resource will then need to be monitored and the study plan revised if necessary.

A model of the holistic dynamics of an aquatic ecosystem has not yet been achieved. Various sub-systems have been modelled with some success. The latter include nutrient levels and phytoplankton, grazing of zooplankton on phytoplankton and feeding of fish on zooplankton. However putting these subsystems together in terms of temporal and spatial variation has so far proved to be unmanageable. The problem lies in the number of variables to be considered and the way small errors in their estimation compound into large errors in the simulated result. There has been lack of data for all the trophic levels and at all scales of time and place. In most ecosystems there are insufficient historic data to provide reliable indications of the natural range of variability. Many fish move from one trophic level to another, as they grow larger. Some move to other areas during ontogenetic development. In other words the system mitigates against a neat summation-of-parts approach.

2. The Lake

Lake Tanganyika lies in the Tanganyika Trough of the African Rift System between 3° 20' – 8° 48' 5 and 29° 03 – 31° 12 E. It is 673 km long and as such experiences a range of climatic regimes as illustrated by differences in rainfall (Fig. 1) . The lake has a maximum width of 48 km and a surface area of 32900 km^2 (Hanek *et al.* 1993) . The maximum depth is at least 1470 m while the mean depth is about 700 m. The volume is 18880 km^3. Due to the length of the lake covering over 50 of latitude the climate in the north differs from that in the south (*et al.* Kotilainen et al. 1995)

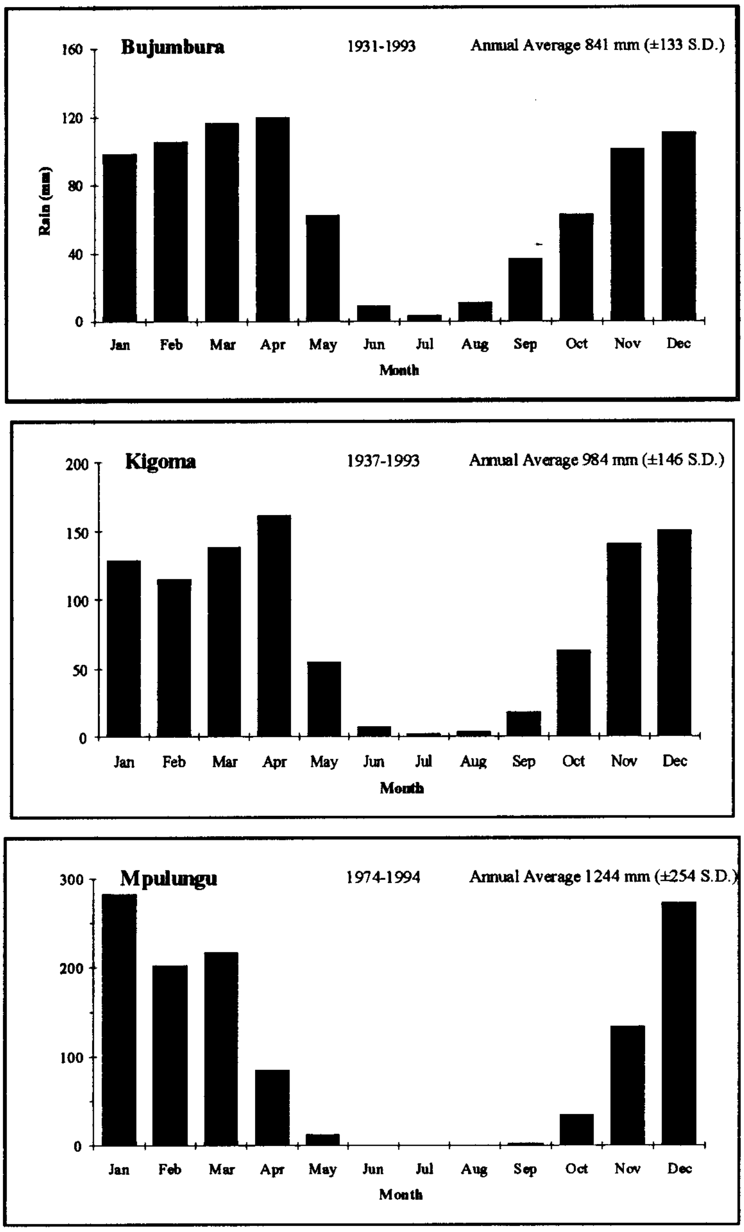


Figure 1. Mean monthly rainfall (mm) on the shores of Lake Tanganyika at Bujumbura, Kigoma and Mpulungu. Note that the y—axes are not drawn to the same scale. (supplied by Verburg).

3. General Methods

The principal approaches adopted by LTR to achieve the objectives have been data collection, processing and analysis at fixed stations and using *R/V Tanganyika Explorer* for lake-wide surveys. Sampling at fixed stations started in July 1993 but the first lake-wide cruise did not begin until April 1995. Three years of intensive sampling have been carried out in hydrodynamics, nutrients, zooplankton and fish biology. Detailed methods used within each component of the project have been given in eponymous reports and will not be repeated here. Some of the problems encountered with the methods will be discussed in the results.

The three main sampling stations were situated off Bujumbura, Kigoma and Mpulungu and will be referred to by these place names. The years have been divided into two and a half– solar, sampling years, that is July 1993 – June 1994 (Year 1), July 1994 - June 1995 (Year 2) and July - December 1995 (Year 3). The seasons have been defined as the 'wet season' from October to May and the 'dry' season from June to September.

4. Summary of Results

The basic data collected during SSP are stored in the LTR database. A list of the main variable values, by sampling date, and some summary statistics are also held at the LTR Headquarters, Bujumbura.

4.1 Hydrodynamics

Climate

There are two main seasons within a year in the Lake Tanganyika region. The wet season extends from September/October to May, characterised by weak winds, high humidity, considerable precipitation and frequent thunderstorms. The very different dry season (June to August/September) has moderate precipitation and strong, regular southerly winds. Also during this period a global wind convergence zone is located in the region. Changes in the seasons are regulated by the austral and boreal trade winds, which determine the dynamics of the Inter-Tropical Convergence Zone (ITCZ) and its active wet zone movement (Huttula *et al.* 1996)

LTR recorded the following: wind on the shore at Bujumbura, Kigoma and Mpulungu, wind, air temperature and water temperature at eleven depths (1 to 300 m) on the lake at buoy stations 40 km NW of Mpulungu and 14 km SW from Kigoma and water levels near the three field stations. Water currents were measured with simple drogues whose positions were determined using the Global Positioning System (GPS)

The main goal of hydrodynamic modelling within the LTR component was to estimate the role of various factors affecting water currents in Lake Tanganyika; also to understand spatial and temporal variation in horizontal and vertical flow and water temperature. The lake is surrounded by mountains which makes the wind system very complicated. Trials with a mesoscale meteorological model highlighted the significance of a coastal, diurnal, slope-lake breeze system; this intensified during the dry season, while southeasterly trade winds supplied the main input of energy to the middle of the lake. NOAA satellite images were used to obtain spatial information on water upwelling and validation of the upwelling model.

The shear stress on the lake is greatest in the south. During a typical week in July the stress per unit area on the lake at Mpulungu Buoy was three times the stress at Bujumbura harbour (Huttula *et al.* 1994) . Wind is the primary force moving lake water at all depths (Huttula *et al.* 1996) . Its kinetic energy is transferred to the water causing motion. Currents build up slowly. At Bujumbura where the winds are weakest the currents are the slowest. At Mpulungu (in the south where shear stress is greatest) the strongest winds generate the fastest currents. These currents generally flow in the same direction as the wind over the uppermost 40 m. However, the variability in wind speed and direction making prediction of the currents unreliable. The shape of the lake, the coastal effect and bottom depth all influences the currents.

Wind at Bujumbura

In March and April 1993 (wet season), weekly mean wind speeds were 2.5 $m.s^{-1}$ and the dominant wind direction (>50%) was between NW–NNE (Kotilainen *et al.* 1995) . In contrast in mid-June the weekly mean wind speed approached 4 m s^{-1} and blew mainly from SSE. Strong winds continued until late October but after the first rains the mean wind speeds of <2 m s^{-1} prevailed. The northerly winds did not return until January 1994 but they persisted for a further 4 months. Values measured for all these features varied more or less with the seasons. However, perhaps not unexpectedly, variation in the different factors was most noticeable during the shifts between seasons. In 1995 the wind speeds were significantly higher than in 1994 (Verburg *et al.* 1996)

Wind at Kigoma

Weekly mean wind speeds measured at the land-based recording station at the beginning of the dry season in 1993 was 4.5 m s^{-1} (Kotilainen *et al.* 1995) and the prevailing wind direction was E–NE. During the dry season in 1993 the wind blew across the lake from E or from W. Weekly mean wind speeds were reduced to 2.5 m s^{-1} towards the end of the dry season and at the start of the wet season until late November. During the wet season the weekly mean wind speed varied between 2.5 and 3.5 m s^{-1}. The wind speeds during the wet season were significantly higher in 1994-95 than in 1993-94 (Verburg *et al.* 1996)

On the lake surface, as measured by the buoy weather station, the easterly winds prevailed during March to May 1993. The weekly mean wind speed was 3-4 m s^{-1} (Kotilainen et *al.* 1995) . The wind speed decreased slightly towards May but the dominant direction was still the same. The magnitude of wind stress was considerably less than in the south (Mpulungu). In March and April 1994 the vertical stratification was clear and the thermocline was situated at a depth of 50 - 70 m. The temperature difference between the surface and 300 m was 4.5 °C maximum.

Wind at Mpulungu

At Mpulungu shore station during the dry season, starting in mid–April, the wind speed was very variable especially from July to early September (SD up to 1.2 m s^{-1} in July). The prevailing winds were from the SSE. In mid-September 1994 the wet season started and the wind speed gradually decreased to 3.1 m s^{-1} in September and 2.0 m s^{-1} in December. In general the wind speeds were higher at Mpulungu than at the other stations.

The recordings at the buoy station were similar in seasonal trends to the land weather station although values were higher (Verburg *et al.* 1996) . The water column was vertically stratified in March 1993 and the thermocline was at c. 50 m depth. The weekly mean water temperature was >27.0 °C at 1 m, >24.0 °C at 90 m and 23.4 °C at 300 m. In April, well before the start of the dry season, at depths between 30 and 50 m the water temperature decreased more than one degree indicating weakening of stratification due to increased forcing by the winds.

Increase in wind speed coincided with cooling of the air and of the surface waters. The surface water temperature decreased rapidly in June 1993. The strong winds during 1 - 10 June mixed the surface water down to 50 m depth. The vertical mixing continued and was most intense in July in the middle of the dry season. The difference in water temperature between 1 and 300 m was c. 1.0 °C. Stratification started in August and was established by the end of September.

<u>Water</u> <u>currents</u> <u>near</u> <u>Bujumbura</u>

Near Bujumbura wind driven currents 2 - 40 m depth were rarely **>** 10 cm s^{-1} (Kotilainen *et al.* 1995) and then only at 2 m depth. The currents followed the wind especially near the surface. Further south the currents, maximum speed >20 cm followed the coastline.

<u>Water</u> <u>currents</u> <u>near</u> <u>Kigoma</u>

In general the currents were stronger at Kigoma than at Bujumbura. Currents exceeding 25 cm s^{-1} were indicated from 3 of the 4 drogue lines deployed.

<u>Water</u> <u>currents</u> <u>near</u> <u>Mpulungu</u>

The maximum current speed of 40 cm s^{-1} was the highest measured at the 3 sampling areas.

<u>Tilting</u> <u>of</u> <u>the</u> <u>thermocline</u>

During a longitudinal cruise in May 1993 seven temperature profiles were measured with a CTD. Fairly strong SE winds prevailed (wind gusts between 6.5 to 8.5 m s^{-1}) . The spatial variation of surface temperature was within 1 °C. It was not possible to record the profiles deeper than 160 m, but the thermal structure of the surface layer was recorded. The depth of the thermocline was similar to earlier reported values. The tilt of the thermocline was c. 26 m over the measured region (320 km) . This variable depth of the thermocline was not significantly affected by internal waves since the waves have a very long period (30 days) as compared the survey duration of 4 days.

<u>Internal</u> <u>waves</u>

The great depth (mean c. 700 m) of the lake and the regular forcing by the winds during the dry season result in a long and persistent internal wave motion. The LTR project has detected internal waves for the first time with automatic devices. Internal temperature fluctuations were studied by spectral analysis (Huttula *et al.* 1996) . The analysis revealed a strong period (23.4 days) of fluctuations in the dry season at the Mpulungu Buoy at depths of 50, 150, 200 and 300 m. The same but weaker period was also found at depths of 70, 90 and 110 m. Near the surface the period was not found due to noise and shorter term fluctuations. The internal waves were spread throughout the water layers but the small density gradient in the upper layers and intensive vertical mixing allowed noisy fluctuations to penetrate downwards. The thermocline prevented their penetration and thus below the thermocline this outer (noisy) component decreased and internal waves were located more easily.

The period of internal waves differed between seasons, 23.4 days in the dry and 34.8 days in the wet season. The frequency of the waves supports the theory that they were Kelvin internal waves, the marginal type was considered less likely than ‘normal’ internal waves (Coulter 1991) . The shorter period in the dry season resulted from periodic forcing by the winds.

Numerical experiments

The first models were two dimensional vertical flow and temperature models (Huttula *et al.* 1996) . Later a three dimensional barotropic model was used.

2-DV model

The model was used to study such aspects as the boundary conditions for the upper layer and longitudinal tilting along the main axis of the lake.

The first experiments were made with steady wind over the lake. Heat fluxes on the air-water interface were ignored. In most cases mixing and upwelling in the lake were observed and were strongly dependent on the wind speed.

The second set of model runs was carried out with actual weather data collected from the Bujumbura meteorological station from 10 June to 14 July 1993. The short wave radiation fluxes calculated matched the observed ones quite well.

3-D model

The model predicts the following variables: the three components of velocity, the free surface water level height and the temperature field. The main driving forces are the time dependent, wind-induced shear stresses and surface heat flux. This modelling work is still in progress although some results are given by Huttula *et al.* (1996)

Upwelling at Mpulungu

A combination of water current and temperature data, numerical modelling and satellite images was used to study upwelling in the Mpulungu region (Huttula *et al.* 1996). NOAA11 daytime satellite images were used to detect the spatial evolution of upwelling. The satellite images together with flow modelling results suggested that the upwelling of metalimnion waters took place in the south part of the lake along the steep slopes of the basin. The upwelling waters were transported by the complicated wind driven flow system of the lake.

Water balance

Theeuws (1920) and more recently by Verburg (1996) calculated a lake water balance (mm y^{-1}) . The values are as follows:

	Theeuws (1920)	Verburg (1996)
Inflow	530	1000
Precipitation	900	1000
Evaporation	1350	1700
Outflow	80	310
Lake level change		-10

Precipitation contributed to 50% of the water entering the lake and c. 85% of the annual input of water was lost by evaporation (Verburg 1996)

4.2 Nutrients

The ‘limnology’ component of the LTR project was concerned with the physical processes in the lake and how these influenced factors such as light, nutrients and chlorophyll a. Chlorophyll *a* and primary production (*in situ* radiocarbon incubation) were only measured during Year 3. The results for primary production are not yet available. They are essential for quantifying trophic levels.

The seasonal cycle in limnological events was summarised by Plisnier *et al.* (1996) (Fig. 2) **.** This was based on observations from Year 1 of SSP and was reconfirmed in Year 2 (Plisnier 1996) and Year 3 (Langenberg 1996) **.** During the dry season starting in May-June, south east winds drove the surface water to the north. The volume of warm water accumulated in the north depended on the strength of the wind. Thermocline depth in the north could be used as an indicator of the volume of water moved. At the Bujumbura Station a well developed thermocline at 70-90 m was found in August and September. At the south end of the lake the winds cooled the surface water by convection and wind mixing and the thermocline rose in the water column. By August the thermocline was broken down at Mpulungu. Water returned to the south as deep currents and caused upwelling and further cooling. The SE winds ceased in September or October. In September 1993 the surface temperature started to increase and vertical stratification was re-established by November. Stratification continued during the whole wet season i.e. until April 1994. In mid–April the vertical stratification started to break down and the water column was apparently unstratified in July.

Just before the wet season in 1994 the water temperatures between 1 and 5 m started to increase rapidly and in late October the temperature reached 27.0 °C. There was a clear seasonality in the water temperature down to 150 m**.** The temperature variation between the seasons was highest in the surface to 50 m range. In deeper water 70-150 m seasonality was apparent but the variation in temperature was fairly small, between 0.1 and 0.3 °C (Huttula et al. 1996)

In Year 3 Langenberg (1996) noted a weakening and tilting of the thermocline in October and a cooling down of the epilimnic waters at Bujumbura. By November the thermocline was re-established and increased in depth accompanied by a warming of the epilimnion. By December the thermocline rose from c. 85 to 45 m and was well defined with a strong temperature gradient in the water column. At Mpulungu the thermocline was re-established in September and deepened towards December as the epilimnion warmed up. However no true epilimnion of uniform temperature was found from October to December 1995 and there was an almost linear decrease in temperature from the surface to c. 75 m depth.

Month	Processes		Observations
	SE winds start		
May-June	Drives surface water northwards		
	Tilting of the epilimnion		Deep thermocline in the north
	Upwelling in the south		Phytoplankton blooms in the south
	Currents and turbulence		Patchiness
September-October	SE winds stop		
	Metalimnion oscillates to get back to equilibrium level		Dampening of pH and conductivity isopleths
		Secondary upwelling in the north	Phytoplankton blooms in the north
		Surge	Chimbanfula waves in the south
		Internal waves reactivated	Pulses of production
January-February	Stratification increases		Turbidity layer develops near the thermocline

Figure 2. Limnological events in Lake Tanganyika during a May-February cycle. (Redrawn from Plisnier et al. 1996).

The tilting of the thermocline results in a density imbalance that acts as a store of potential energy. When the wind causing the tilting decreases, the water masses will move towards equilibrium and the thermocline will return to the horizontal plane. It is then generally accompanied by short term mixing and a decaying oscillation of the thermocline. The degree of wind shear stress on the lake surface and subsequent lake mixing has been indicated by the dimensionless Wedderburn number (W) (Coulter 1991; Langenberg 1996) . This number combines the influence (values) of the intensity of stratification, the ratio of epilimnion depth to overall lake length and wind speed. For derivation of W in the present study see Langenberg (1996) . High values of W indicate stability while from low numbers a strong shear stress, tilting of the thermocline with related mixing and possible upwelling at the windward end of the lake can be inferred. Wedderburn numbers calculated for all three years of SSP at Mpulungu (Fig. 3) were low, as expected, during the dry, windy season (June to September) and were high for the rest of the year. In Year 3 values of W were higher than in the previous years studied. This was combined with an overall warming of the water column.

Plisnier *et al.* (1996) determined the lower metalimnion boundary to be at 300 m depth. Hypolimnion water (<23.50 °C) was found at c. 300 m except during upwelling in the south. Plisnier (1996) inferred that upwelling was less in the dry season of Year 2 compared to Year 1 as the surface temperature was higher and the thermocline was shallower in the north.

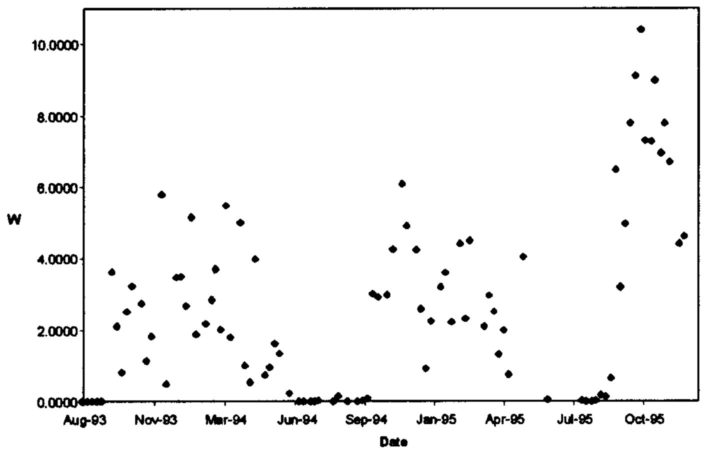


Figure 3. Wedderburn numbers calculated for Mpulungu August 1993 - December 1995. (Data provided by Langenberg).

The seasonal changes in the physical limnology of the lake affected its water chemistry and the nutrient regime. Internal waves were found throughout the year at all sampling stations. These were inferred from fluctuations of water temperature, pH, conductivity, turbidity, phosphorus, ammonia, nitrate and nitrite. Eleven waves in Year 1 were observed by Plisnier *et al.* (1996) corresponding to a period of c. 33 days duration each. The vertical distribution of nutrients was influenced by the meromictic condition of the lake. In general epilimnic concentrations of phosphate, nitrate, ammonia and silica were low compared to those in the hypolimnion, probably due to uptake by autotrophic organisms. See Plisnier *et al.* (1996), Plisnier (1996) and Langenberg (1996) for values. In Year 3 chlorophyll *a* was measured and a closer examination of this period (five months) of SSP provides information concerning the relationship between nutrients and primary production. However chlorophyll *a* concentrations or phytoplankton biomass are poor predictors of phytoplankton production (Hecky & Fee 1981) . Langenberg (1996) identified three distinct phases of nutrient fluctuations and consequent chlorophyll *a* production at Bujumbura. The first, from August to mid-September, was characterised by a deep, well developed thermocline, nutrient impoverished epilimnetic waters, low chlorophyll *a* concentrations and a clear vertical distribution of most of the variables measured that was related to water temperature. In the second phase, mid-September to November, the thermocline rapidly moved up and down, most of the variables measured were similar to those in the hypolimnion and chlorophyll *a* concentrations increased. From November to December, the third phase, there was a well defined thermocline again fluctuating in depth and high concentrations of chlorophyll *a* in the epilimnion (mean $\pm$ SD for November = 1.55 $\pm$ 0.98 $\mu g\ l^{-1}$) . The succession at Kigoma was similar to Bujumbura although the vertical distribution of the variables and the cycle of stratification were not so well pronounced. As at Bujumbura and Kigoma, three phases were identified at Mpulungu during Year 3 although these were different from the other two stations. During the first phase, from August to mid-September, the surface waters were cooled (there was extensive upwelling), there was no thermocline and in the upper 100 m the water was low in nutrients but there was a relatively high concentration of chlorophyll *a* (mean $\pm$ SD for August = 1.38 $\pm$ 0.60 $\mu g\ l^{-1}$). In the second phase, mid– September to November, the thermocline strengthened, the epilimnion warmed and the concentration of chlorophyll *a* decreased. The third phase, November to December, had a well established thermocline which fluctuated in depth and low concentrations of chlorophyll *a* (mean $\pm$ SD for December = 0.57 $\pm$ 0.49 $\mu g\ l^{-1}$).

The upwelling from October to November at Bujumbura and Kigoma increased the nutrients in the upper water layers and this was followed by an increase in chlorophyll *a* during November to December. There was no strong evidence for nutrient increases at Mpulungu although the vertical temperature structure suggested stronger upwelling there than at the other two stations. Langenberg (1996) suggested that this was due to different vertical distribution of temperature, dissolved oxygen and nutrients at each end of the lake. At the northern end the thermocline, oxycline and chemocline were found close together just above and below the euphotic zone. Any vertical movement of these boundaries in relation to each other could lead to a replenishment of nutrients into the euphotic zone stimulating biological production. At Mpulungu the oxycline and chemocline were much deeper and upwelling nutrient-rich waters (with reduced inorganic and dissolved organic compounds) had to pass through a ‘thick’ oxygenated layer before reaching the euphotic zone. The euphotic zone differed between stations and fluctuated with time (mean depth ± SD, Bujumbura = 41 ± 14, Kigoma = 49 ± 7 and Mpulungu = 46 ± 15 m).

During upwelling at Bujumbura, the concentrations of silicate, nitrogen and phosphate increased, N:P ratios were relatively high and chlorophyll *a* concentrations increased shortly after. This suggests that for most phytoplankton production, nitrogen and phosphorus were deficient. Results from nutrient enrichment studies undertaken during a cruise of *R/V Tanganyika Explorer* (Järvinen *et al.* 1996) showed that phytoplankton production was stimulated by combined additions of nitrogen and phosphorus rather than by separate additions.

4.3 Remote sensing

Huttula *et al.* (1996) have used satellite images to study upwelling at the southern end of the lake (see under hydrodynamics) . No further results have been made available to the author. A technical paper is under preparation (Mölsä---personal communication) connecting hydrodynamic modelling with lake surface temperature patterns.

4.4 Zooplankton

4.4.1 Crustacean mesozooplankton

The results of this study relate mainly to near-shore stations and to post-naupliar stages, as most of the earlier stages were not sieved by the 100 µm mesh. Samples were collected from 100 m to the surface. The results should be considered as preliminary since further statistical analysis is required.

Abundance

The yearly mean total number per volume of copepods was always highest in Bujumbura and second highest in Kigoma except in Year 3 when copepods were exceptionally abundant in Mpulungu (Kurki, 1996) The values were as follows:

Year 1 - Bujumbura=12385, Kigoma=9098 and Mpulungu=5617 m^{-3}
Year 2 – Bujumbura=13889, Kigoma=10045 and Mpulungu=7274 m^{-3}
Year 3 – Bujumbura=23173, Kigoma=9590 and Mpulungu=12206 m^{-3}.

The abundance values (and the dry weight biomass values given below) at Bujumbura and Mpulungu in Year 3 were almost double those in previous years but this year was only represented by six months of sampling.

The pelagic crustacean zooplankton was dominated by the calanoid copepod, *Tropodiaptomus simplex* (Diaptomidae) and cyclopoids. The proportions of each varied according to the region of the lake (Kurki & Vuorinen 1995; Kurki 1996) . In Year 1 calanoids and cyclopoids were similar in abundance (48 and 52% respectively) at Mpulungu. At Bujumbura and Kigoma cyclopoids were dominant as they were for all three stations during Years 2 and 3 (range 61 to 86%)

The yearly mean dry weight biomass per unit area of copepods for each station was:

Year 1 - Bujumbura=3478, Kigoma=2274 and Mpulungu=1479 mg m^{-2}
Year 2 - Bujumbura=3021, Kigoma=2107 and Mpulungu=1649 mg m^{-2}
Year 3 - Bujumbura=6516, Kigoma=1824 and Mpulungu=2274 mg m^{-2}
All years – Bujumbura=4176 ± 3615 (± 1 SD), Kigoma=2093 ± 1271 and Mpulungu=1751 ± 912 mg m^{-2}

Cyclopoids contributed to the total biomass of copepods by 76, 77 and 57% at Bujumbura, Kigoma and Mpulungu respectively.

Abundance estimates of mesozooplankton measured during the *R/V Tanganyika Explorer* cruises have not yet been synthesised.

Temporal changes

Although zooplankton fluctuated in abundance with a periodicity, which was repeated annually, the periodicity was not always distinct. This result is to be expected from the variability in estimates both spatially and temporally. At Bujumbura the numbers of *T. simplex* peaked annually in July/August. No distinct increases in abundance at this time were observed for cyclopoids in Year 1 but were for Years 2 and 3. At Kigoma the abundance of *T. simplex* reached a peak in August in Years 2 and 3 and in November, January and April/May of Years 1 and 2. Three periods of increased abundance in the year were noted for cyclopoids although these varied in degree and between years. In Years 1 and 2 these were in September, November and May and in Year 3 August and October/November. The overall changes in calanoids and cyclopoids abundance were positively correlated ($p<0.001$) . At Mpulungu the periodicity in copepod abundance was less distinct.

In general no significant differences were found in the mean numbers and dry weights between the wet and dry seasons. The effect of sample size and random variation between the samples has still to be determined.

Vertical movements

Vertical migrations of copepods were measured at all stations and for all species and development stages. At Bujumbura zooplankton were always concentrated between 20 and 40 m but they were found down to 140 m. At Mpulungu they occurred down to 220 m. *Tropodiaptomus simplex* concentrated between 80 and 100 m during the day and 20 to 60 m at night at Kigoma and Mpulungu. As a rule cyclopoids did not descend as deep as *T. simplex.*

Production

The results of experiments (at Kigoma) aimed at measuring the growth and development, and thus the production of zooplankton, have not been made available to field staff. A report is under preparation (Mölsä– personal communication)

4.4.2 Macrozooplankton

Counts were made of atyid shrimps, medusae of *Limnocnida tanganyicae* and fish larvae but only shrimps and medusae will be considered here. More extensive data will be available on this group when cruise survey samples have been analysed. Macrozooplankton caught by the vertical tow of a plankton net are probably not representative of the population.

In all years there were significantly ($p<0.001$) more shrimps in the Mpulungu samples than in those from the Bujumbura Station Fig. 4) . In Year 1 there was no difference ($p>0.05$) in abundance between Kigoma and Mpulungu but in Years 2 and 3 there were more at Mpulungu. In these last two years there were no differences between Bujumbura and Kigoma. There are strong indications that the density of shrimps is much greater in the south of the lake than in the north (Bosma personal communication)

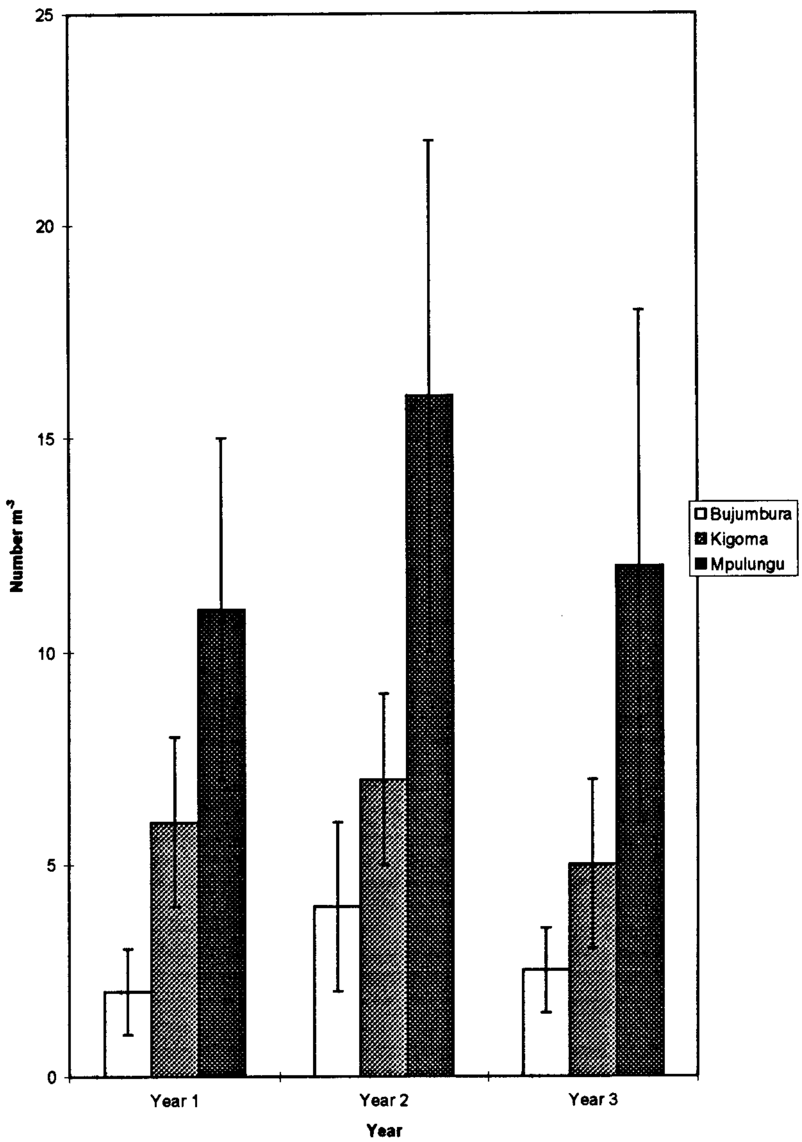


Figure 4. Yearly mean abundance (number m^{-3}) of shrimps at Bujumbura, Kigoma and Mpulungu Stations. Error bars are $\pm$ 2SE. (Data from Kurki 1996).

Medusae were caught throughout the year. Although the results were variable, the density of medusae at the Bujumbura Station was the highest throughout the study period (Fig. 5) Kurki (1996) suggests that there was a decrease in abundance from north to south of the lake.

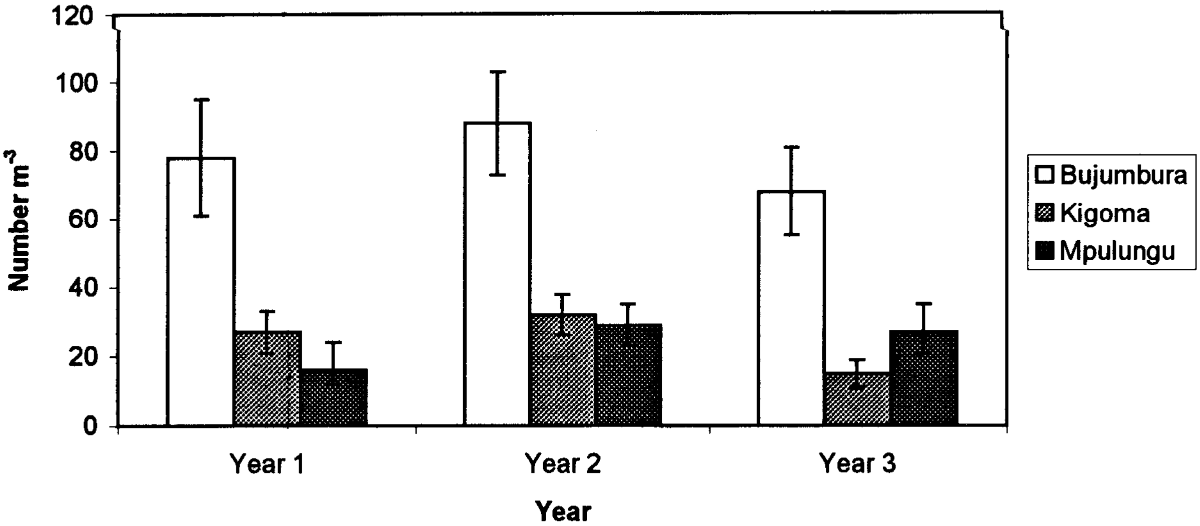


Figure 5. Yearly mean abundance (number m^{-3}) of medusae at Bujumbura, Kigoma and Mpulungu Stations. Error bars are ± 2SE. (Data from Kurki 1996)

4.5 Fish Biology

The study of fish biology has concentrated on the main commercial pelagic species, the clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon,* and the centropomid, *Lates stappersii.* Samples were collected from the artisanal and industrial fisheries. Sampling methods and analysis of the data are given by Mannini *et al.* (1996) . The results are presented by species. The sexes were not separated for estimates of growth and mortality.

Estimates of fish abundance from lake-wide acoustic and mid—water trawl surveys are not yet available. The biomass values are essential for stock assessment and understanding trophic relationships.

4.5.1 Stolothrissa tanganicae

Only the liftnet fishery exploited S. *tanganicae* in the northern end of the lake and juveniles made the highest contribution to the catch. At Kigoma the proportion of juveniles was highest in the catch from the purse seines although the mesh sizes of the two gears, purse seines and liftnets, were similar. The purse seines fished further from the shore in nursery areas that were identified during lake-wide cruises. At Mpulungu juveniles were caught mainly near the shore by beach seines. *Stolothrissa tanganicae* were negligible in the Mpulungu liftnet catches. From experiments Mannini *et al.* (1996) estimated L_c (the length at which 50% of the fish were caught by the liftnet) as 56 mm. In general this was thought to be a reasonable value for the whole lake except at Bujumbura where over 50% of the catch was <56 mm.

The growth of S. *tanganicae* was similar in all the areas studied. The asymptotic length and the rate it grew to this length (L_8 and K of the von Bertalanffy growth equation) ranged between 104 and 114 mm and 1.80 and 2.00 respectively. Longevity was estimated at 1.5 years although 99% of a cohort would die within one year with an annual total instantaneous rate (Z) calculated to lie between 4.0 and 5.0 yr^{-1}. The mean annual natural instantaneous total rate (M) was estimated at 2.3 yr^{-1}.

The mean length when 50% of the cohort were sexually mature (L_m) was similar for the areas sampled and between sexes, 78 mm for females and 77 mm for males. This was at a relative age of 0.72 yr. *Stolothrissa tanganicae* became mature when most of its somatic growth was complete, L_m/L8=0.73. From examination of the gonads, the gonadosomatic index confirmed that the fish were multiple spawners probably with a time interval of 3 to 4 months. There were insufficient fish captured to confirm this for Mpulungu. The ovary appeared to be fully developed in March/April, June/July and November/December (data of March 1994 to June 1995)

Recruitment to the fishery was almost continuous at Bujumbura. At Uvira and Kigoma there were two recruitment periods, February to April and June/July to October/November (August in 1995 at Kigoma) . The second period, in the dry season, was the most important.

4.5.2 _Limnothrissa_ _miodon_

Liftnets and beach seines exploited *L. miodon* in the north of the lake. The liftnets caught mainly juveniles and the beach seines mainly adults. At Kigoma only adult fish were caught, the largest by the purse seine which fished away from the shores. At Mpulungu large fish were also caught by purse seines. In that area beach seines and liftnets in which the codend was covered with mosquito netting were used. These nets harvested the inshore, immature fish. L_c values were 55 mm for Bujumbura, 76 mm for Kipili and 15 mm for Mpulungu.
The values of L_8 and K were similar for the above three areas, ranging from 180 to 182 mm and 1.01 and 1.06 respectively, and longevity was estimated at 2.50 yr. Annual Z estimated from catch curve analysis ranged from 5.4 to 6.6. yr^{-1}.

Mannini *et al.* (1996) suggested that these values were overestimates due to the emigration of adult fish from the fishing grounds. From data collected during lake-wide cruises, a value of Z = 3.1 ± 0.2 (±95% CL) yr^{-1} was derived which Mannini *et al.* (1996) considered to be more realistic when compared to Z values calculated for S. *tanganicae.* Annual M ranged from 1.2 to 1.8 yr^{-1}. Length at sexual maturity was L_m female = 101 and L_m male = 95 mm. As for S. *tanganicae* sexual maturity was reached at 0.72 years but it reached this maturity earlier in the development of its soma, L_m/L_8 = 0.54. The development of the gonads showed less distinct periodicity to *S. tanganicae.* The commercial catch samples were poorly representative of the population and the results were highly variable. At Kigoma there appeared to be two breeding periods, May-July and September-November. From *L. miodon* examined at Mpulungu, covering a shorter period (July 1993 to July 1994) than Kigoma, fish were found to be mature throughout most of the year. The highest frequency was found in May and June.

In the north *L. miodon* was mainly recruited during the dry season in 1994 but this was not repeated in 1995. At Mpulungu recruitment to the fishing gear was sustained throughout the year with increases at the beginning of the dry season (April/June) and in November/December.

4.5.3 _Lates stappersii_

Only open water gears exploited *L. stappersii* and no fish >100 mm were caught further north than the Rumonge sub-basin. At Kigoma the catch showed a classical bimodal length frequency distribution (Fig. 6) of juveniles and adults while

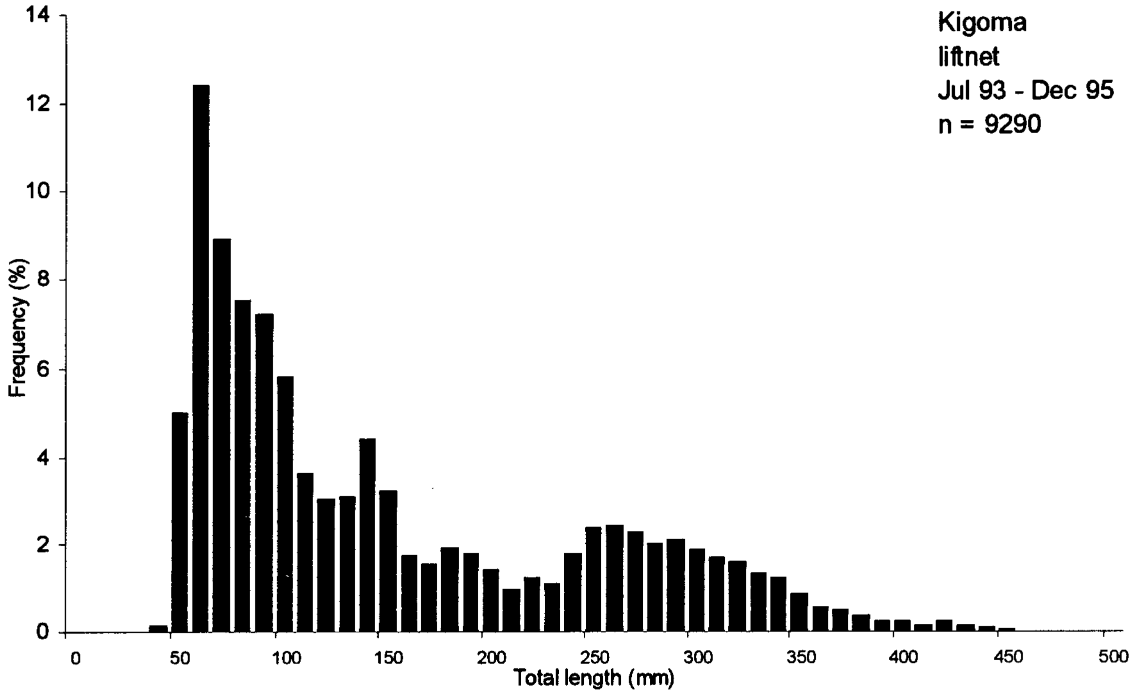


Figure 6. Length frequency distribution of *Lates stappersii* sampled from liftnets in the Kigoma area. (From Mannini *et al.* 1996)

the landings at Mpulungu were mainly composed of adult fish on which the industrial purse seine fishery concentrates. L_0 values were 103 mm for Kigoma, 250 mm for Kipili and 234 mm for Mpulungu.

The values for L_8 and K were similar for the above three areas, ranging from 510 to 551 mm and 0.36 and 0.44 respectively, and longevity was estimated at 7.00 yr. Mean annual Z values for the lake ranged from 1.7 to 1.9 yr^{-1} and annual M from 0.6 to 0.9 yr^{-1}. From data collected during lake—wide cruises, a value of $Z = 1.8 \pm 0.2$ (±95% CL) yr^{-1} was estimated. Mannini *et al.* (1996) found, although this was not statistically tested, a higher total instantaneous mortality rate at Mpulungu than at Kigoma. The exploitation rate CE = F/Z, where F is the instantaneous fishing mortality) was 0.6 yr^{-1} at Mpulungu and 0.4 yr^{-1} at Kigoma.

The length at which 50% were mature was only determined for fish from Kigoma and Mpulungu as no adult fish were caught at Bujumbura. $L_{m\ both\ sexes}$ = 278 mm for Kigoma and $L_{m\ female}$ = 237 and $L_{m\ male}$ = 255 mm for Mpulungu. Sexual maturity was reached at 1.70 years but like *L. miodon* it reached this maturity early in the development of its soma, $L_m/L_8 = 0.51$. Seasonal patterns of reproductive output were clear at Mpulungu but less distinct at Kigoma. At the former the reproductive season was from October to March.

In the north liftnets caught juvenile *L. stappersii* mainly during one period from April to August. This yearly single recruitment phase started in July and ended in November at Kigoma. Adults were caught in liftnets and purse seines at Kigoma during two main periods, February to April and August to October.

4.5.4 Feeding

Stomach content analysis on fish (all three species) collected during cruises of *R/V Tanganyika Explorer* has not been completed. Data are available for *L. stappersii* from samples collected at Kigoma and Mpulungu. Clupeid guts were not collected from commercial catches as rapid digestion made identification of stomach contents impossible. *Lates stappersii* at Mpulungu preyed almost entirely on clupeids and shrimps. The clupeids were mostly *L. miodon.* The shrimps, in particular *Palaemon moorei* and *Limnocaridina parvula,* were the commonest food items throughout the year. At Kigoma the diet was more heterogeneous and included copepods and S. *tanganicae* larvae. *Stolothrissa tanganicae* was the predominant prey and its frequency of occurrence was highest from July to January. Ontogenetic changes in feeding were observed in *L. stappersii* caught at Kigoma. Young stages fed on copepods and fish >100 mm on shrimps and S. *tanganicae.* Only *L. stappersii* >400 mm were almost entirely piscivorous. Some predators, mainly adults, were cannibalistic. These results indicated the opportunistic feeding behaviour of *L. stappersii.* Food availability was more important than size of the predator in prey selection.

4.5.5 Distribution

Stolothrissa tanganicae and *L. miodon* have adopted different life histories. Larvae and juveniles of the former are found in nursery areas offshore. As they grow there is some movement towards the coast (they are caught by the liftnet fishery) but they remain pelagic throughout their life. *Limnothrissa miodon* inhabits the inshore, shallow water during its first year of life moving into the pelagic during the second year. In this way the clupeid may escape predation by *L. stappersii* which are pelagic throughout their life. Large *L. miodon* are distributed and have the same feeding behaviour as adult *L. stappersii.* Nursery areas for *L. stappersii* have been initially identified during cruises in the Kigoma Basin. Further lake-wide cruises are required to locate nursery areas and to confirm the above distribution patterns.

4.5.6 Exploitation

The production/biomass ratio (P/B) was assumed by Allen (1971) to be equivalent to Z. *Stolothrissa tanganicae* therefore had the highest ratio, between 4 and 5 yr^{-1} and *L. stappersii* the lowest, c. 1.5 yr^{-1}, of the three species. Mannini *et al.* (1996) developed simple biomass models for a S. *tanganicae* cohort for the whole lake and *L. stappersii* cohorts at Kigoma and Mpulungu (Fig. 7). The S. *tanganicae* cohort reached maximum biomass at 5 months of age when the fish were fully recruited to the fishery.

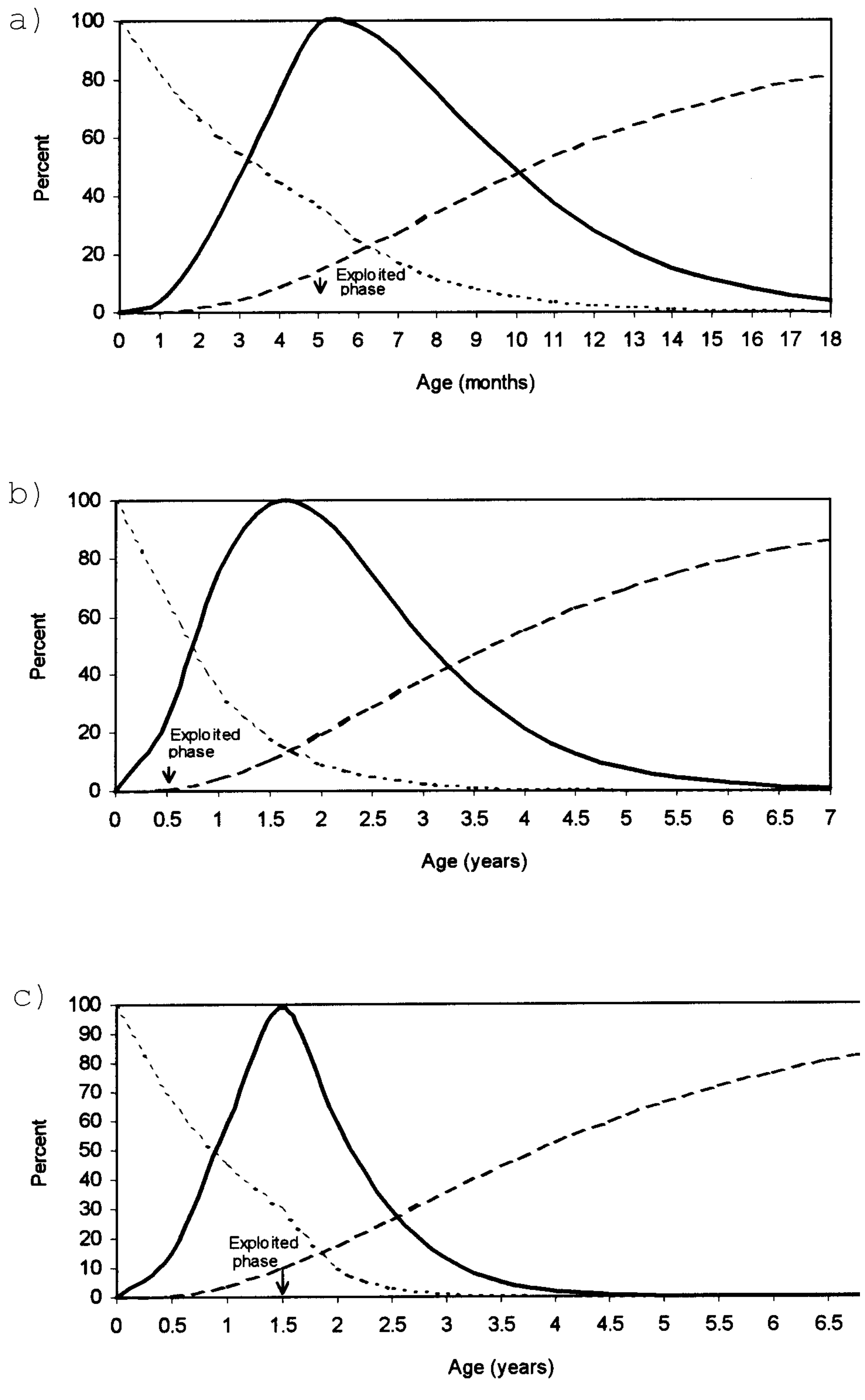
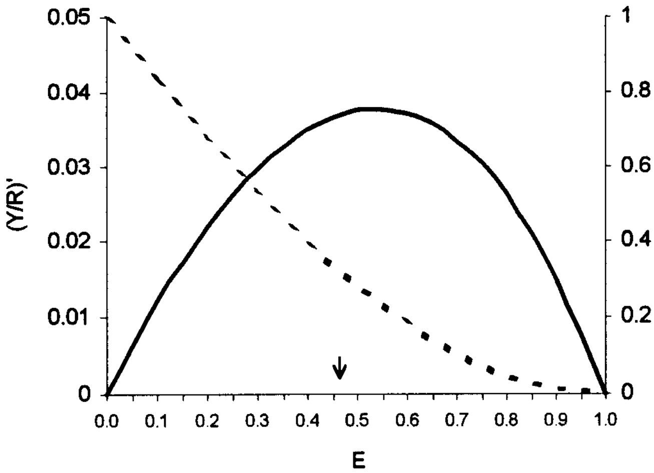


Figure 7. Relative numbers surviving (...), individual growth in weight (——) and cohort biomass (–) expressed as percentages of the maximum values against age for a) *Stolothrissa tanganicae* (whole lake), b) *Lates stappersii* (Kigoma) and c) *L. stappersii* (Mpulungu) . (From Mannini *et al.* 1996)

At Kigoma *L. stappersii* were lightly exploited from 6 months but at Mpulungu not until l.5 yr. The fish were then heavily exploited, noted in the sharp decline in cohort biomass. The short–lived clupeids are more vulnerable to recruitment failure than the longer lived *L. stappersii.*

Mannini *et al.* (1996) also produced relative yield per recruit curves (Beverton & Holt 1966; Pauly 1994) for the three main pelagic fish species although they expressed doubts about the validity of the curves for *L. miodon* due to the poor estimation of Z and thus F (fishing mortality) . Although S. *tanganicae* was fished below Lm it did not appear to be overexploited lake-wide (Fig. 8)) . The curves for *L. stappersii* were different for Kigoma and Mpulungu (Fig. 9) . At Kigoma the fish were not overexploited although an increase in fishing effort could be critical as L_c was low. At Mpulungu the fishing level was high in comparison and any further increase in effort should be avoided.

a)



b)

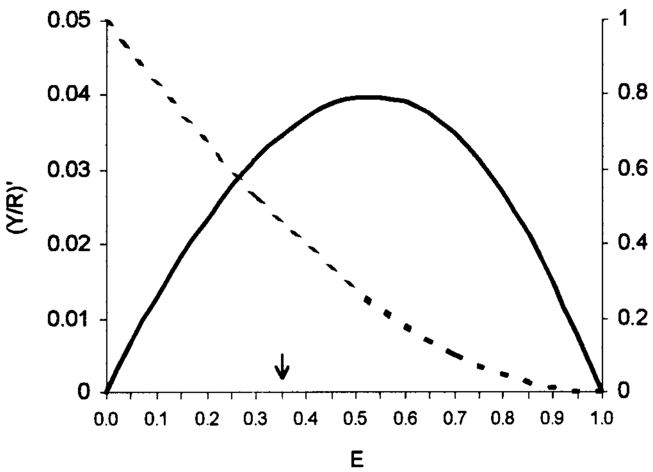
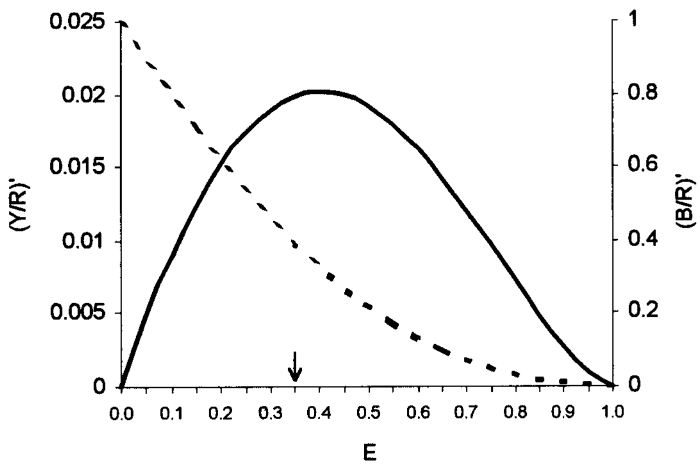


Figure 8. Relative yield per recruit (Y/R,—) and biomass per recruit (B/R, ···) expressed as a function of exploitation rate (E) for *Stolothrissa tanganicae* from a) Kigoma and b) Mpulungu. Arrow indicates estimated current E. (From Mannini *et al.* 1996).

a)



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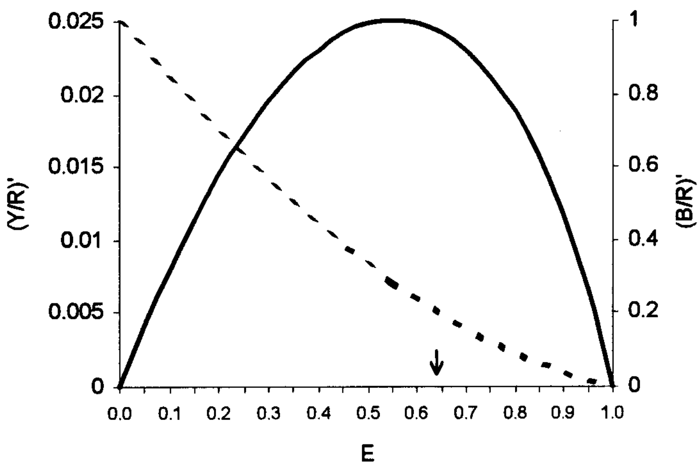

Figure 9. Relative yield per recruit (Y/R,—) and biomass per recruit (B/R,-) expressed as a function of exploitation rate (E) for *Lates stappersii* from a) Kigoma and b) Mpulungu. Arrow indicates estimated current E. (From Mannini *et al.* 1996).

4.6 Fish Genetics

The results of the fish genetics study have so far been inconclusive and no further information, to that given at the Fourth Joint Meeting of LTR (Hanek & Craig 1995) and repeated here, is available.

No clear picture about stock segregation of the pelagic fish species has been established. Genetic differences between *Lates mariae* collected from five localities were examined using Random Amplified Polymorphic DNA (RAPD-PCR). There was no evidence of total reproductive isolation as no conserved fragments specific to one population were found.

Life histories of *S. tanganicae, L. miodon* and *L. stappersii* appeared to be similar throughout the lake from the studies of fish biology (Mannini *et al.* 1996) and there were no apparent divisions into sub-populations.

4.7 Fisheries Statistics

The LTR project has assisted the four riparian countries in collecting fisheries statistics data.

The first lake-wide frame survey was made from an aircraft in 1992 (Hanek *et al.* 1993) . The numbers of landing sites and fishing boats were counted. The latter were divided into canoes, catamarans, trimarans and industrial units.

In 1995 a frame survey of fishing villages was carried out in all four riparian countries (Paffen 1996). Traditional fishing gears were gill nets along the north and south coasts, long lines on the west coast and hand lines on the east coast of the lake. The artisanal fisheries used lift nets on the north, east and west coasts and kapenta beach seines in the south. The industrial, purse seine fishery was based at Mpulungu.

In 1995 there were 786 landing sites, c. 45000 fishermen and c. 1600 active fishing boats. Data on landings, and therefore catch per unit of effort (CPUE) are still being processed. Unfortunately there are many missing data.

5) Summary and Conclusions

a) The main thrust of the Scientific Sampling Programme (SSP) of LTR has been the ecosystem approach and the principal studies have been on hydrodynamics, nutrients, zooplankton and fish biology. In addition LTR has been concerned with remote sensing, fish genetics and fisheries statistics.

b) The data collected have still to be quantified. The present report is descriptive. It covers the period July 1993 to December 1995 although SSP continued until July 1996.

c) There are two main seasons in the Lake Tanganyika region that influence lake dynamics and production: the wet season with weak winds and considerable precipitation and the dry season with strong normally southerly winds and some precipitation in the north. The influence of these external forces varies from north to south of the lake and the results of SSP illustrate the distinct differences in the freshwater ecosystem between the north and south.

d) The kinetic energy of wind is transferred to the lake water causing movements at all depths. In the dry season wind stress per unit area applied to the lake at Mpulungu can be three times that at Bujumbura. The wind drives the epilimnion water to the north and the thermocline deepens there. In the south the epilimnion cools, stratification breaks down and there is upwelling. Remote sensing has identified this upwelling. Wedderburn numbers were low during the dry season indicating high wind shear stress on the lake and thus extensive lake mixing. Numbers were high for the rest of the year from which stability could be inferred.

e) Internal waves, identified by spectral analysis, were of 23.5 days duration during the dry season and 34.8 days in the wet season. These waves were also identified from depth fluctuations in physical and chemical factors.

f) The vertical distribution of nutrients was influenced by the meromictic (long-stratified) condition of the lake. Concentrations of phosphate, nitrate, ammonia and silica in the mixolimnion were generally low compared to the monimolimnion. In a five month period three distinct phases were noted in the relationship between nutrient and chlorophyll *a* concentrations but these phases were different for Bujumbura and Kigoma in the north and Mpulungu in the south. The increase in concentrations of nutrients in the upper layers, and subsequent increase in chlorophyll *a,* resulting from upwelling was greater at the northern stations although upwelling was greater at Mpulungu. This may be due to the position of the thermocline, oxycline and chemocline in relation to the euphotic zone.

g) The pelagic crustacean zooplankton was dominated *by Tropodiaptomus simplex* and cyclopoid species. The yearly mean abundance and dry weight biomass of total copepods was always highest at Bujumbura compared to Kigoma and Mpulungu. Abundance fluctuated with an annual periodicity but the periodicity was not distinct. Diel vertical migrations of copepods were observed. Zooplankton tended to be in shallower water at Bujumbura.

h) The abundance of shrimps was always greater at Mpulungu than at Bujumbura and the abundance of medusae was always greater at Bujumbura than at Kigoma and Mpulungu.

i) *Stolothrissa tanganicae, Limnothrissa miodon* and *Lates stappersii* are exploited by different gears in the various areas of the lake mainly due to differences in fish distribution. *Stolothrissa tanganicae* and *L. stappersii* are pelagic throughout their life. Immature *L. miodon* are thought to live inshore while in their second year they are pelagic. No *L. stappersii* >100 mm were caught further north than the Rumonge sub-basin.

j) Growth and mortality have been calculated for the three main commercial species. Values were similar to those already published and there appeared to be no within-lake differences. No segregation of the pelagic fish species has been found from DNA analysis. Estimates are also provided for length at maturity. *Stolothrissa tanganicae* becomes mature when 73% of its somatic growth is complete compared to 54 % for *L. miodon* and 51 % *for L. stappersii.* All three fish species are multiple spawners with varying periodicity between species within years and within species between areas and years.

k) The diet of *L stappersii* was more varied at Kigoma than at Mpulungu where at the latter it consisted mainly of clupeids and shrimps. At Kigoma *S. tanganicae* was the main clupeid eaten.

l) Preliminary biomass and relative yield per recruit models were developed mainly for *S. tanganicae* and *L. stappersii.* A *S. tanganicae* cohort (whole lake) reached maximum biomass at 5 months of age when the fish was fully recruited to the fishery. Although they were captured below length of maturity (in particular at Bujumbura) they did not appear to be overexploited lake-wide. At Kigoma *L. stappersii* were lightly exploited from 6 months. There was no indication of over-exploitation although an increase in effort could have significant impact due to the length of recruitment to the fishing gear. At Mpulungu intensive fishing started at 1.5 years and was noted in a sharp decline in the cohort biomass. Any further increase in fishing effort should be avoided.

m) The collection of fisheries statistics is ongoing around the lake in the four riparian countries and has been assisted by LTR. Results from frame surveys are available but catch statistics are still being processed although there are many missing data.

n) A bottom-up approach to ecosystem dynamics and lake production requires simultaneous estimates, on a seasonal basis, of rates of production and biomass for all major trophic groups and limnological factors (physical and chemical) . In-depth, short term studies can identify the rapid variation in and possible links between hydrodynamics, nutrients, primary production, zooplankton production and short-lived fish production; long-term studies are required to measure production of long-lived fish and also to measure the influence of climate (e.g. on the Mpulungu *L. stappersii* fishery) . Wedderburn numbers can be used to determine mixing between the epilimnion and hypolimnion and the potential upwelling of nutrients. At present there are no available estimates for primary, secondary or tertiary biomass and production. Some measurements have been made and require analysis (e.g. primary production, zooplankton development rates, zooplankton abundance from lake-wide cruise surveys, fish biomass from lake-wide acoustic surveys and clupeid gut contents) but so far the number of lake-wide cruises has been limited and there are not enough data for input into an ecosystem model.

o) Top down effects require comprehensive data sets gathered over an extended period. The available data sets need careful examination and analysis and future collection of fisheries statistics needs adequate planning and supervision so that it can be cost-effective and provide the information required.

Acknowledgements

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APPENDIX

1. Practical significance of the results obtained so far

1.1 Introduction

The main aim of the LTR project is to investigate the trophic basis for fish production and use this information to develop a management strategy for the whole lake. Data have been collected on the physical, chemical and biological features of the pelagic system of Lake Tanganyika. Some of these data have been partially analysed and relationships between some of the components identified. Work is still in progress on the prediction of yields using historic data and virtual population analysis (VPA) and on socio-economic aspects of the fisheries.

To understand an ecosystem, the investigator has first to observe and describe, and second, discern patterns in the functioning of the system. The next step is to try and understand the processes determining these patterns and the ‘cause—effect’ relationships. In ecology the patterns observed are usually complex because they result from the interactions of many factors. In this connection the investigator has to take care over the interpretation of significant correlations between factors. Patterns are observed over a range of scales, both temporal and spatial. It is important for example to account for these scales in sampling. Moreover if, as in the huge and deep Lake Tanganyika, water residence time is some 500 years, 105 generations of phytoplankters compared to 250 generations of a top predator (such as *Lates stappersii)* could develop. Such patterns, processes and scales are eloquently discussed in Giller *et al.,* (1994)

For the first time on Lake Tanganyika, the Lake Tanganyika Research project, LTR, has collected basic data at three fixed stations simultaneously. Lake-wide sampling has also been undertaken from *R/V Tanganyika Explorer.* Samples and the data derived from them thus describe changes at weekly, fortnightly and monthly intervals over a three—year time span. Of particular interest are the hydrodynamic processes that drive the biological production. Historically studies of tropical lakes have tried to link seasonal changes in climate with nutrient dynamics, algal biomass, zooplankton biomass and or fish biomass.

1.2. Empirical relationships

The study so far has shown the considerable variation between the different areas of the lake. The following results indicate correlations between variables over a short time period. In only some cases can reasons for the relationships be inferred.

There are extensive and significant spatial differences in lake dynamics and fish production of Lake Tanganyika as described in the full report. Mpulungu, at the south end, experiences far greater seasonal effects than Bujumbura, in the north. The seasonal effect of the climate on the lake dynamics is more apparent here than in other .parts of the lake. The spatial differences in climate also affect the behaviour of fishermen and their catch. For example strong winds in the south deter fishing, which is reflected in the landings. Thus in the short term, strong winds may result in a reduction in the catch but in the long term they may cause greater lake mixing and increased lake productivity, which is passed up the food chain, resulting in increased yields.

Wind speeds at Mpulungu showed a marked seasonal pattern (Fig. la) which negatively affected the water temperature (0 to 100 m) (Table la and Fig. 2a) . The Wedderburn number (Fig. 3a), which is derived from wind speeds and is an indicator of stress on the lake surface and therefore lake mixing (the higher the number the greater the stability), was thus positively correlated with water temperature. Secchi depth (Fig. 4a) was also correlated with water temperature. The monthly yields of clupeids (Fig. 5a) were negatively correlated with water temperature and the landings of *L. stappersii* (Fig. 6a) . The latter were negatively correlated with wind speeds and positively correlated with water temperature, Wedderburn number and secchi depth. The results probably reflect the habits of fishermen rather than indicating any trophic relationships. The relationship between climate and fish yields must be derived from the study of historic data (see Section 3 below)

Although not so marked as at Mpulungu, the mean water temperature of the top 100 m (Fig. 7a) and secchi depth (Fig. 8a) at Bujumbura also displayed a seasonal pattern. These variables were positively correlated (Table 2a) . Catches of juvenile *L. stappersii* (Fig. 9a), despite being few in number were negatively correlated with secchi depth. This relationship probably resulted from net avoidance. Catches of *L. miodon* (Fig. 10a) were negatively correlated with water temperature but the reasons for this are unknown. Of the three main exploited species of fish, *S. tanganicae* formed the major part of the catch at Bujumbura. The monthly landings of these fish (Fig. 11a) were positively correlated with the abundance of copepods (Fig. 12a), on which the fish fed.

At Kigoma wind speed and water temperature showed seasonal cycles (Figs 13a & 14a) and the two variable were negatively correlated (Table 3a) . Catches of *S. tanganicae* (Fig. 15a) were negatively correlated with water temperature and the landings of *L. stappersii* but positively correlated, as at Bujumbura, with the abundance of copepods (Fig. 16a)

The heterogeneous nature of the lake, the available budget and equipment and the technical abilities of the national institutions have all been considered in designing a future monitoring programme for the lake. This is as follows:

1.3 A monitoring programme for Lake Tanganyika

LTR has been collecting data for the last three years mainly in hydrodynamics, limnology and zooplankton and fish biology. The following is a proposal for a long-term monitoring programme which will be simple and inexpensive to run but will provide the necessary indicators of lake productivity. These indicators will then be used in establishing procedures for managing the pelagic fish stocks of the lake. Nationals attached to the appropriate research institutes should run the programme at each station in Burundi, Tanzania, Zambia and The Congo. The Congo station has not been established. The Lake Tanganyika Fisheries Commission, after it is created, should oversee the monitoring programme. This commission should ensure that dialogue takes place between the various researchers and statistical departments around the lake.

An initial time period for monitoring should be established. Due to the variability in the dynamics of the lake and in order to detect inter-annual changes a minimum of ten years should be planned.

Labour costs should be met by the national institutions. Operating and maintenance costs will have to be supplied by external funding. The overall cost of maintaining each station (computers, office supplies, vehicles, boats, etc.) is not included in the following estimates. Boat crew time is not included in manpower estimates.

Hydrodynamics

Wind speed and direction determine the extent of lake mixing and the upwelling of nutrients and thus lake productivity. Water temperature indicates the extent of stratification and the stability of the system. Automatic stations have been established at Bujumbura (weather station at the port), Kigoma (land wind station and lake (buoy) meteorological station) and Mpulungu (land wind station and lake (buoy) meteorological station) . These stations require one person each to visit each site (every 5 months for the Mpulungu buoy and 2 (months for the Kigoma buoy), collect the data that have been stored, carry out any necessary maintenance, enter the data and make preliminary analyses using suitable software.

Costs: (Total – 3 stations)
Operation of the automatic equipment: US$ 300 per year
Maintenance including spare parts: US$ 5000 per year
Time per station: 5 person days per month
Note - This programme should be integrated with the GEF project who will carry some of the costs.

Limnology

Only physical limnology measurements will be made to determine upwelling and indicate the extent of nutrient input into the epilimnion. The variables to include are water temperature, dissolved oxygen, pH, conductivity and turbidity.

Primary production can be indirectly estimated by measuring chlorophyll a and secchi depth and the depth of the photic zone from solar radiation measurements using light sensors. Two persons required per station.

Measurements to be made twice a month. Costs depend on boats being in good condition.

Costs: (Total – 3 stations)
Operation: US$ 7000 per year
Maintenance including spare parts: US$ 5000 per year
Time per station: 20 person days per month

Zooplankton

There is good evidence that zooplankton abundance can be correlated with fish abundance, the latter indirectly measured by local catch per unit effort. There is much spatial and temporal variability in zooplankton measurements but trends are very likely to appear if the monitoring is carried out over an extended period of years.

Zooplankton should be collected (at the same time as the limnological sampling) and counted twice per month. Three vertical hauls with a standard 100µm mesh net and three hauls with torpedo gear should be made. Two people are required per station for collecting, identifying, counting and data entry.

Costs: (Total – 3 stations)
Operation: US$ 300 per year*
Maintenance including spare parts: US$ 400 per year
Time per station: 20 person days per month
*The boat running costs are included under limnology

Fish biology

Important information concerning the local abundance (catch per unit of effort, CPUE) and biology of exploited pelagic fish has been collected from landings at Bujumbura, Kigoma and Mpulungu. These collections should be continued. Sampling is made from liftnets at Bujumbura, Kigoma and Mpulungu, purse seines at Kigoma and Mpulungu and beach seines at Mpulungu. For liftnets, samples are purchased weekly during the fishing season from 4 fishing units, the proportions of each species in the catches are determined and length distributions of each species measured. The data are extrapolated to the total landings on the beach sampled. Three persons per station are required to collect the data on the beach and to process in the laboratory and one to enter the data into a database. For purse seines, data are collected once per month from deck sampling on the single purse seine operating out of Kigoma and from two vessels chosen from the total number of purse seiners based at Mpulungu. In addition 14 purse seiners should be inspected at the landing sites once per month in particular to establish the proportion of clupeids (kapenta) in the catches. Two persons are required at Kigoma and Mpulungu stations to collect and record purse seine statistics. Beach seine samples should be collected weekly during the fishing season and treated as for liftnets. Attention should be paid to the species composition of the whole catch (littoral and pelagic) . Three persons are required at Mpulungu.

Costs: (Total – 3 stations)
Operation: US$ 2000 per year
Maintenance: US$ 500 per year
Time:
Bujumbura - 12 person days per month
Kigoma - 24 person days per month
Mpulungu - 36 person days per month

Note

Although not part of the lake ecosystem monitoring programme, the continuation and improvement of the national fisheries statistical systems should be supported by LTR and coordinated by the Lake Tanganyika Commission. Costs (coordination – meetings and travel and running frame surveys every three years)

TOTAL ESTIMATE: US$ 20500 per year

1.4 The practical implications

The results from SSP indicate that climate, in particular winds, may possibly be used as a predictor for fish productivity.

The external factors on the lake are spatially very heterogeneous but the internal dynamics resulting from these factors affect the whole lake and its productivity. Therefore changes, physical, chemical or biological, taking place in one area of the lake will affect all other areas to a greater or lesser extent.

The information gathered so far indicates the biological dependence on nutrient availability, which in turn is controlled by outside forces. The empirical relationships described between indices of food supply indicate the general bottom-up control of production. The relationships between copepods and *S. tanganyicae* and between shrimps and *L. stappersii* require further investigation from which a working hypothesis could be developed and applied to lake management. However until the results of the surveys are fully available, for example on fish distribution, nurseries, zooplankton-fish concentrations, etc., it is not possible to formulate management proposals for the lake. Indeed it is difficult to suggest how SSP is extrapolated into the 'management phase' of LTR.

In a management scheme for the lake it is important to consider the clupeid and *L. stappersii* fisheries separately due to the uneven distribution and abundance of the fish and to the different methods employed in harvesting them around the lake.

2. Priorities for future analysis

The primary objective of the Lake Tanganyika study is to develop the methods for the rational and sustainable harvest of fish resources from both ecological and socio-economical perspectives. Further the project should assist in unifying national systems of fisheries data collection and analysis and the implementation of international fisheries management policy. The intention of the present work was to identify and obtain the type and quantity of data required for assessing, monitoring and managing the component stocks in the small scale, multi—species, multi—gear fisheries. A system for the rapid exchange of information between riparian countries, sharing the same resource, needs be implemented. The project aims to evaluate the impact of human harvest on the fisheries resources and to address how their sustainable use may be reconciled with economic and social development. State-of-the-art ecological modelling must be used alongside evaluation of socio—economic impacts.

Future aims:

- To quantify the size, distribution and seasonality of the pelagic fish resources.
- To quantify the trophic base supporting the fishery.
- To estimate the potential sustainable yield from the fishery.
- Define an appropriate strategy for harvesting the fishery resource.

The data from Lake Tanganyika should be used for trophic modelling using ECOPATH (Christensen & Pauly, 1993) and ECOSIM (Walters, University of British Columbia) . Linear equations are used to describe trophic fluxes in mass-balance in the ECOPATH model. The equilibrium assessments of ecosystems can be re—

expressed as differential equations which define trophic interactions as dynamic relationships varying with biomasses and harvest regimes (ICLARM, 1995) . Thus the effects of changes in fishing pressures can be simulated. The ECOPATH model requires estimates for each trophic component on biomass, production/biomass ratios and consumption/biomass ratios. Other inputs can be derived. A scientist from one of the riparian countries could undertake this study at the Fisheries Centre, University of British Columbia, as part of a doctoral degree. Mr Chitamwebwa, TAFIRI, would make an ideal candidate. The Fisheries Centre, the University of Kuopio and ICLARM could undertake the supervision.

Further empirical relationships should be investigated, particularly the relationships between wind speed, nutrient dynamics, primary production, secondary production and fish yields. A study of the long-term cyclical availability of nutrients and their relationship to fish abundance is in progress (Plisnier personal communication) . Theoretically climate could be used as a predictor for fish productivity (as well as for agricultural crops) but this is not practically feasible in the near future. There is a lack of accurate, long-term series of data on a lake-wide basis. The collection of these data should be the target to be pursued by the forthcoming international body proposed for the fisheries management of the lake. The historic data on fish catches and fishing effort should be used in fisheries based models.

3. Reports and data not yet available

A major problem encountered by the project was the delay in lake-wide cruises due to the late commission of R/V Tanganyika Explorer. Data were collected for most of the scientific sampling programme (SSP) at fixed stations with all the inherent problems that involved.

All the raw data collected during SSP should be analysed or reanalysed using sound, quantitative, statistical techniques and the interactions between components identified. The data must be first resorted and outliers, of which there are a considerable number, should be identified and removed.

Analysis and modelling of the hydrodynamics data are not completed. The most important aspect of this work is the application of the modelling to predict spatial and temporal lake productivity. Remote sensing information is so far not available to the project. Predictions of lake surface temperature from satellite imagery and connections between surface temperature and hydrodynamic modelling are required. The main use of remote sensing data would be to provide spatial information on chlorophyll a concentrations but this has not been proved to be feasible in other studies.

Information on superficial temperature patterns are less important. The future acquisition of such data would cost too much to be afforded by local institutions.

Results from radiocarbon experiments for measuring primary production are not available. Primary producers have not been identified during this project although a proposal was written for a consultant. Estimates of phytoplankton biomass are required. Measurements of chlorophyll *a* were started too late in the SSP.

Zooplankton samples, collected during lake-wide surveys, have not been analysed for abundance estimates. The results of studies on zooplankton growth and development from which estimates of zooplankton production could be derived are not available. Estimates of macrozooplankton abundance, in particular shrimps and jellyfish, obtained from lake-wide cruises are not complete. Zooplankton and macrozooplankton abundance analysis can be completed in two to three months by national staff but this requires supervision by LTR staff. Those involved must concentrate mainly on this work.

Fish distribution data and fish abundance (biomass) estimates made by lake-wide acoustic surveys are not available. Fish biomass estimates are essential for stock assessment. Stomach contents of clupeids and *L. stappersii,* caught during lake-wide surveys, are not fully analysed.

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Table 1a. Levels of significance for correlation coefficients, Pearson's and Spearman's (the latter in brackets) between variables for the Mpulungu Station.
NS = non significant, * = p<0.05, **= p<0.01 and ***= p<0.001. +ve = positive correlation and -ve = negative correlation

	wind speed	water temp. 0-100 m	Wedderburn number	secchi depth	clupeids cpue
wind speed					
water temp. 0-100 m	* -ve (*** -ve)				
Wedderburn number	** -ve (*** -ve)	** +ve (*** +ve)			
secchi depth	NS	* +ve	NS		
clupeids cpue	NS	(* -ve)	NS	NS	
Lates stappersii cpue	(** -ve)	(*** +ve)	(** +ve)	** +ve (* +ve)	(** -ve)

Table 2a. Levels of significance for correlation coefficients, Pearson's and Spearman's (the latter in brackets) between variables for the Bujumbura Station.
NS = non significant, * = p<0.05, **= p<0.01 and ***= p<0.001. +ve = positive correlation and -ve = negative correlation

	water temp. 0-100 m	secchi depth	abundance of copepods	*Stolothrissa tanganicae* cpue	*Limnothrissa miodon* cpue
water temp. 0-100 m					
secchi depth	(** +ve)				
abundance of copepods	NS	NS			
Stolothrissa tanganicae cpue	NS	NS	** +ve (* +ve)		
Limnothrissa miodon cpue	* -ve	NS	NS	NS	
Lates stappersii cpue	NS	(** -ve)	NS	NS	NS

Table 3a. Levels of significance for correlation coefficients, Pearson's and Spearman's (the latter in brackets) between variables for the Kigoma Station.
NS = non significant, * = p<0.05, **= p<0.01 and ***= p<0.001. +ve = positive correlation and -ve = negative correlation

	wind speed	water temp. 0-100 m	abundance of copepods	*Stolothrissa tanganicae* cpue
wind speed				
water temp. 0-100 m	* -ve			
abundance of copepods	NS	NS		
Stolothrissa tanganicae cpue	NS	(** -ve)	* +ve (** +ve)	
Lates stappersii cpue	NS	NS	NS	(* -ve)

Fig.1a. Wind speeds (m s^{-1}) at Mpulungu Buoy on sampling days.

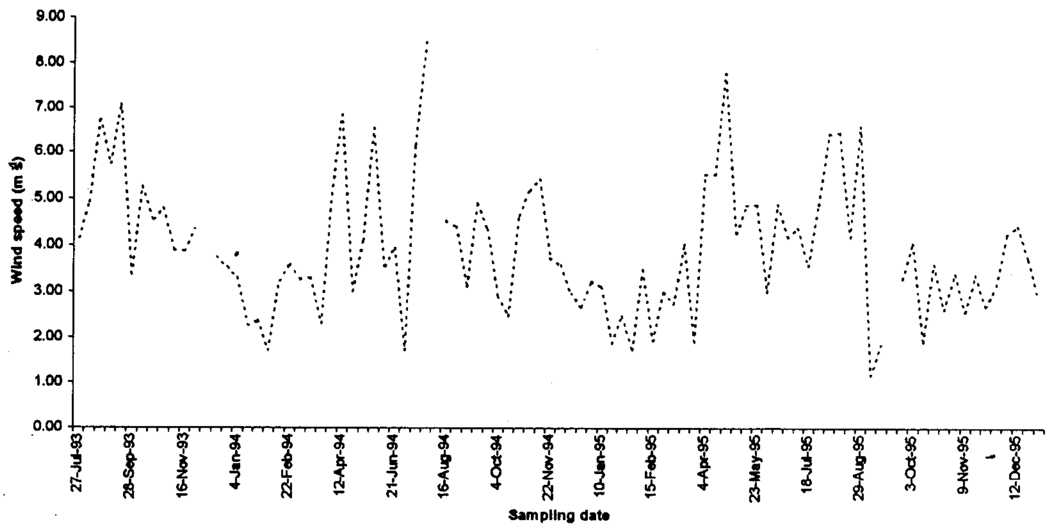

Fig. 2a. Mean (± 95% CL) water temperature from 0 to 100 m depth on sampling days at Mpulungu.

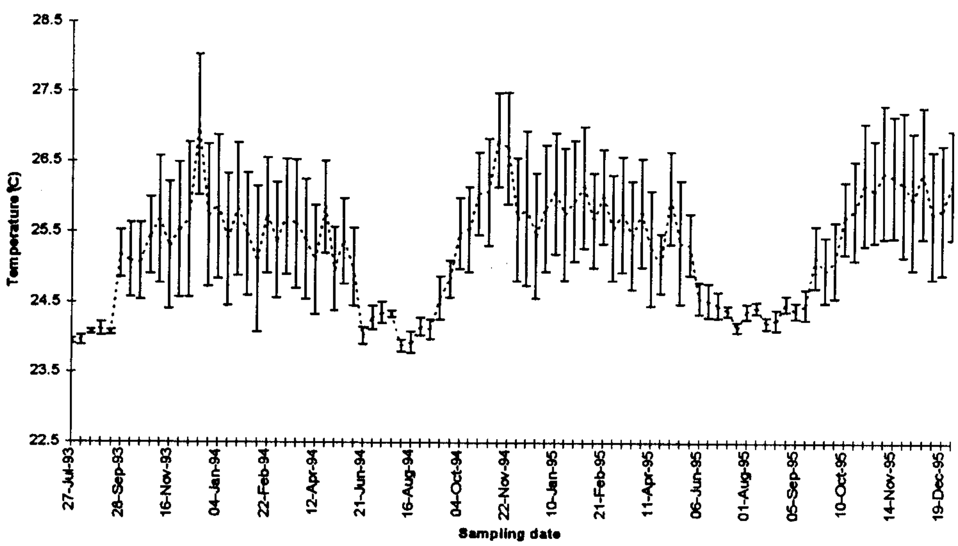

Fig. 3a. Wedderburn numbers calculated at Mpulungu on sampling days.

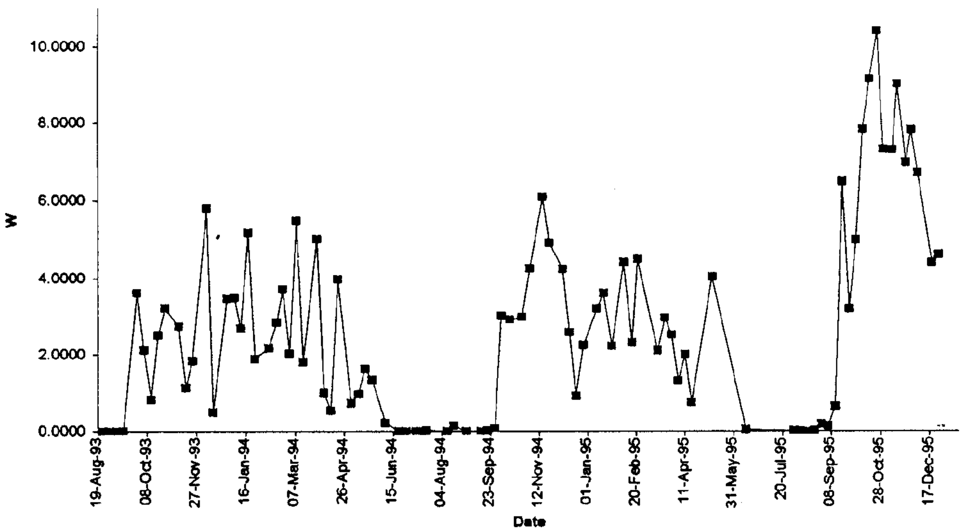

Fig. 4a. Secchi depth (m) at Mpulungu on sampling days.

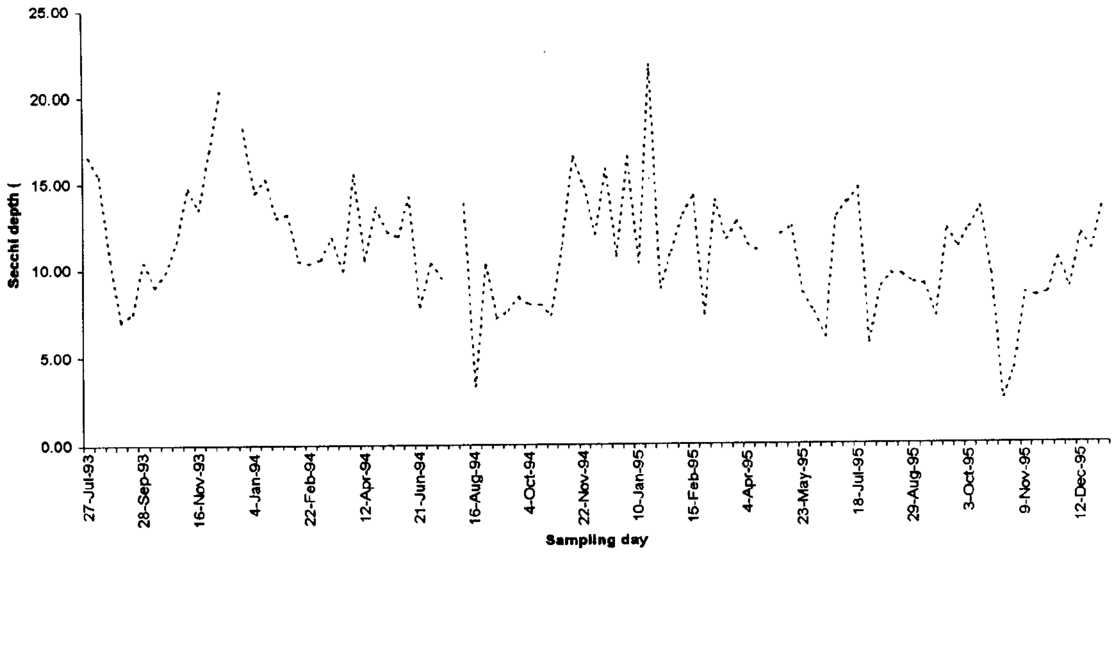

Fig. 5a. Catch per unit effort (kg/night) of clupeids landed monthly at Mpulungu.

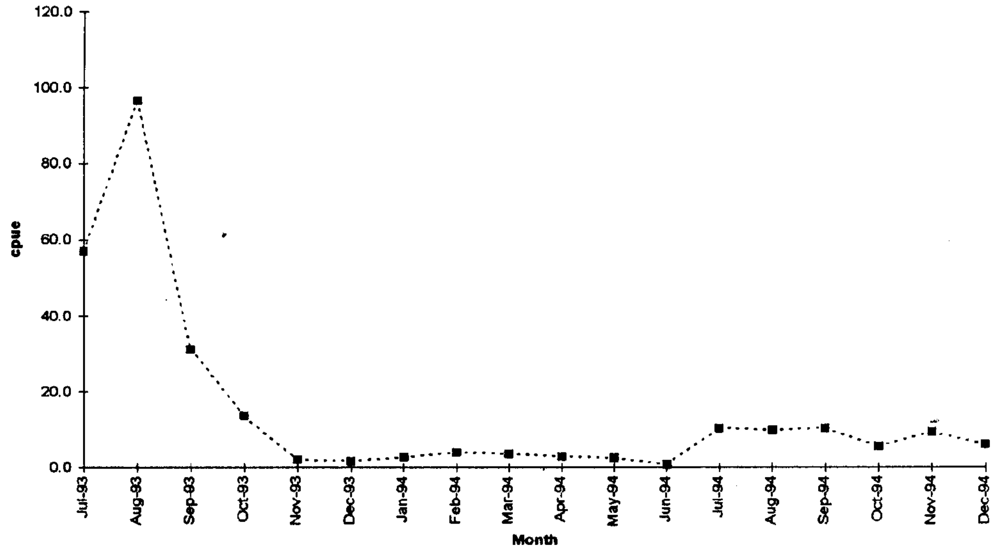

Fig. 6a. Catch per unit effort (kg/night) of *Lates stappersii* landed monthly at Mpulungu.

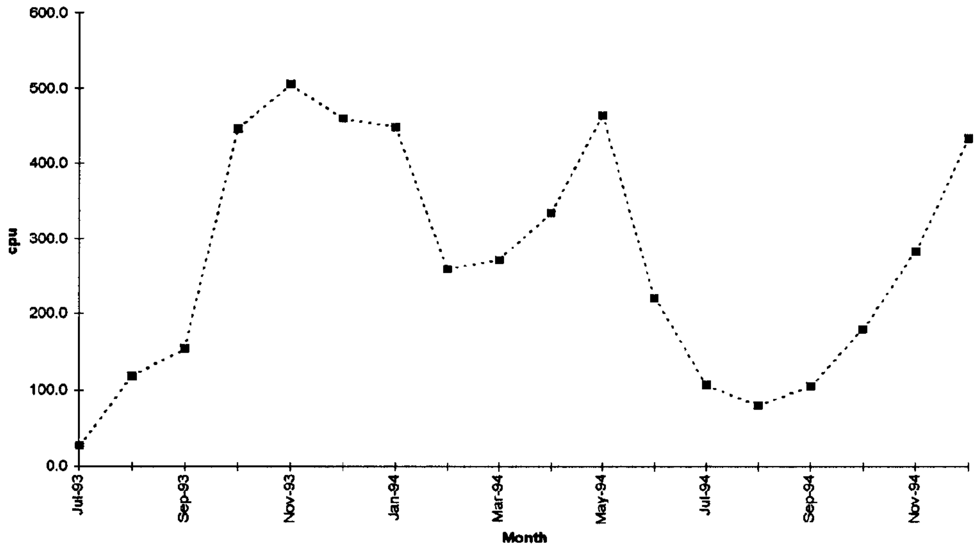

Fig. 7a. Mean (± 95% CL) water temperature from 0 to 100 m depth on sampling days at Bujumbura.

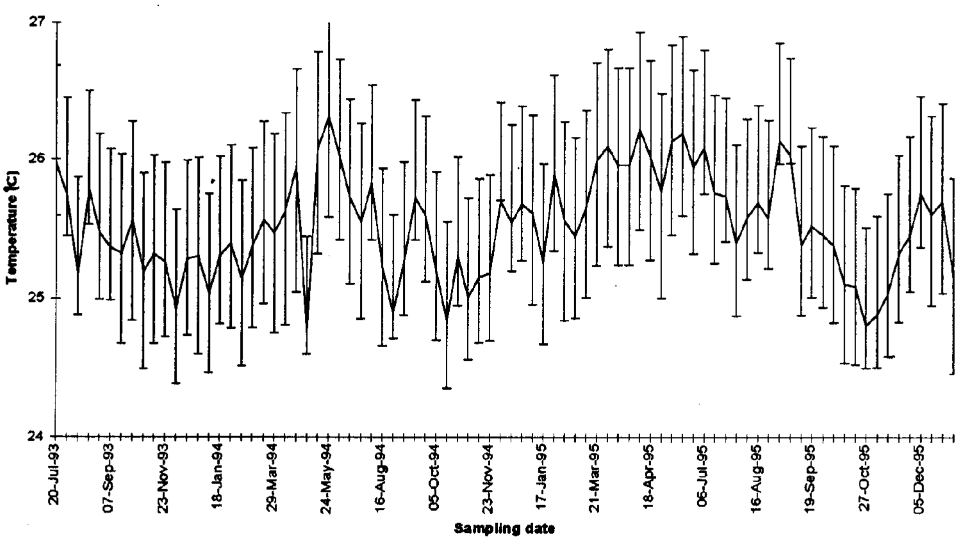

Fig. 8a. Secchi depth (m) at Bujumbura on sampling days.

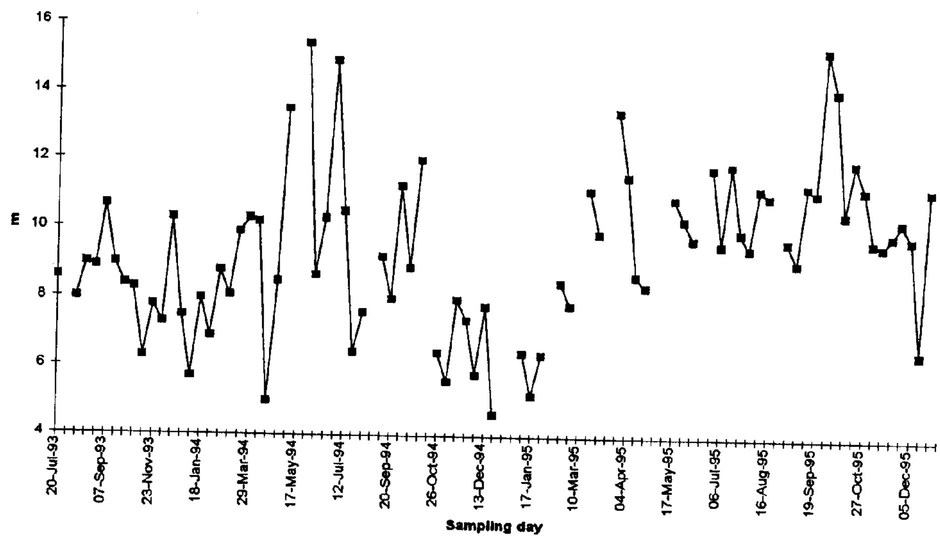

Fig. 9a. Catch per unit effort (kg/night) of *Lates stappersii* landed monthly at Bujumbura.

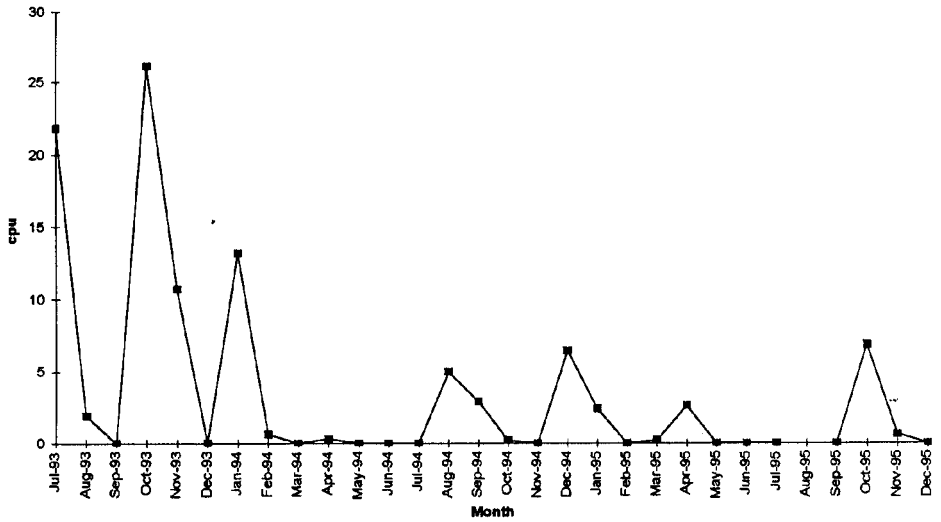

Fig. 10a. Catch per unit effort (kg/night) of *Limnothrissa miodon* landed monthly at Bujumbura.

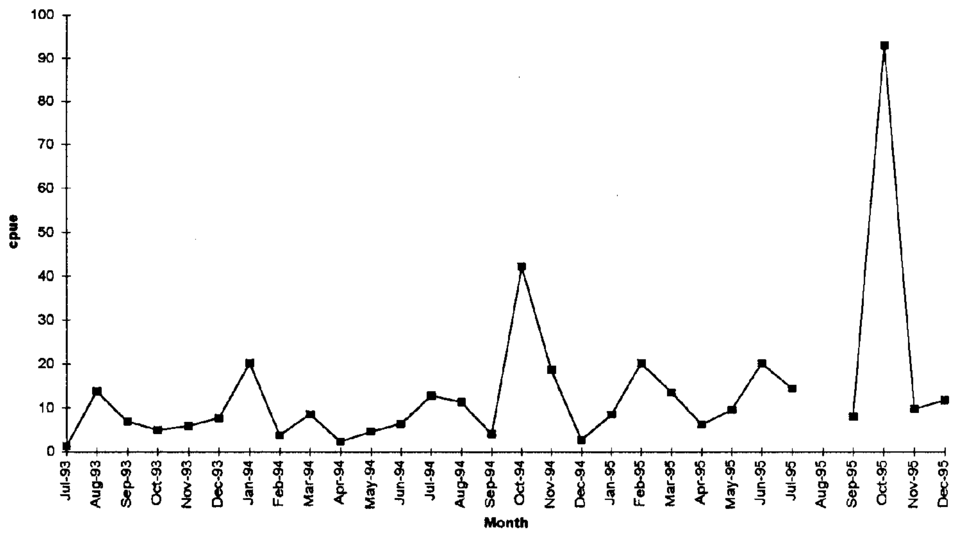

Fig. 11a. Catch per unit effort (kg/night) of *Stolothrissa tanganicae* landed monthly at Bujumbura.

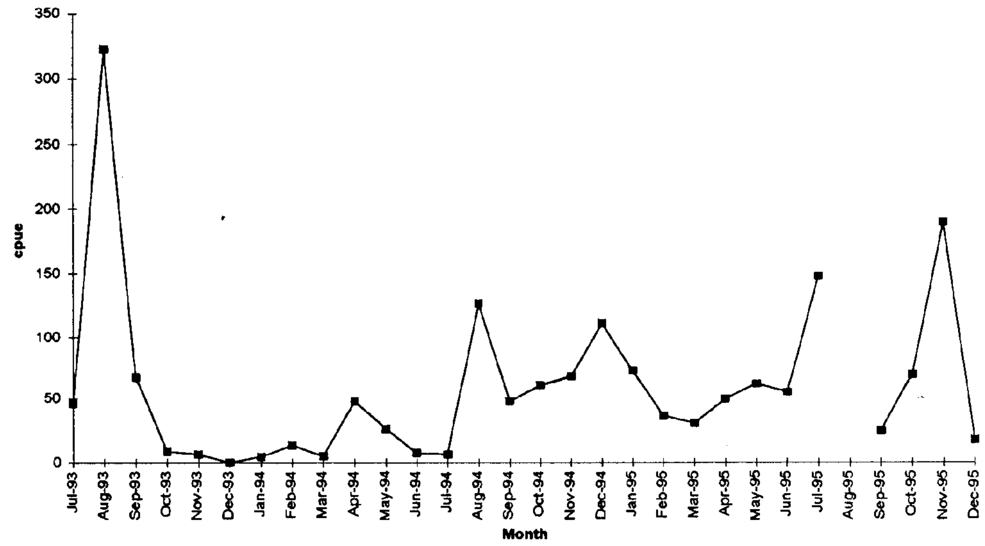

Fig. 12a. Total number m^{-3} of copepods caught on sampling days at Bujumbura.

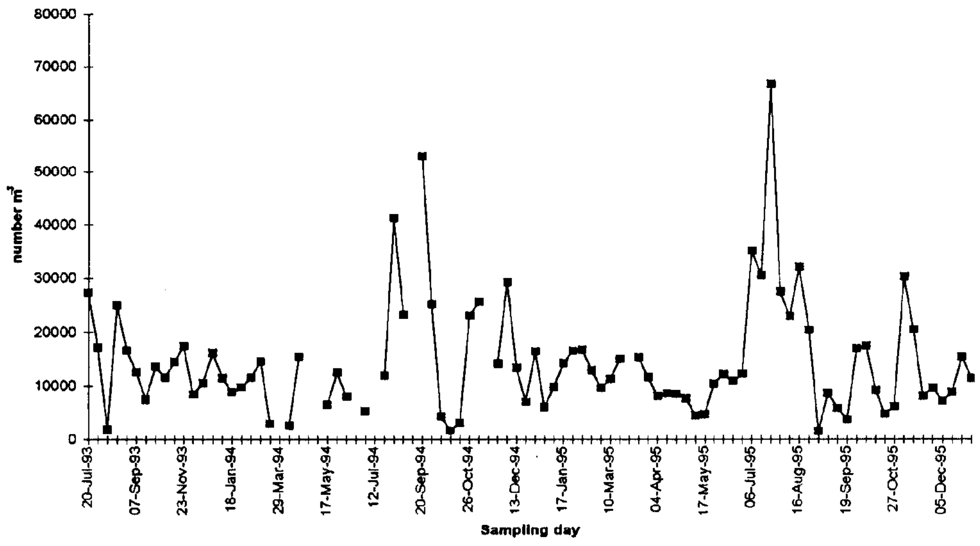

Fig.13a. Wind speeds (m s^{-1}) at Kigoma Buoy on sampling days.

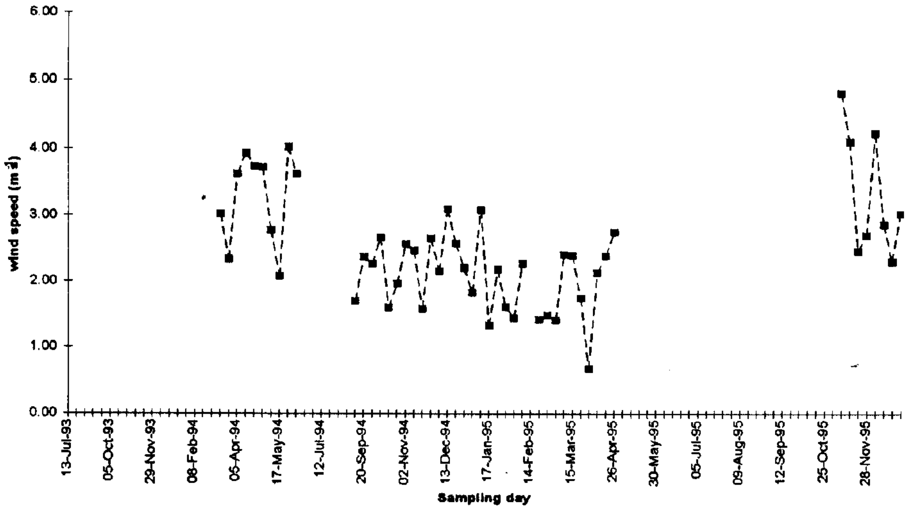

Fig. 14a. Mean (± 95% CL) water temperature from 0 to 100 m depth on sampling days at Kigoma.

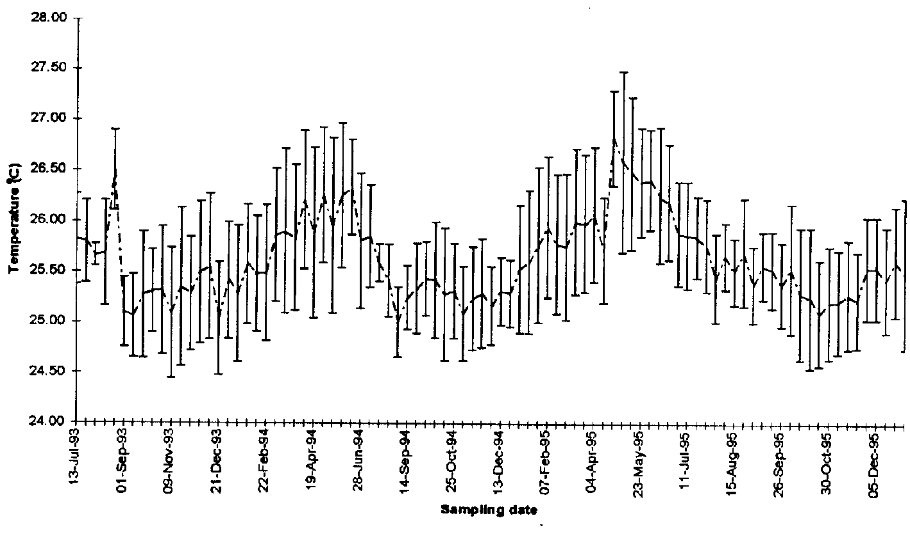

Fig. 15a. Catch per unit effort (kg/night) of *Stolothrissa tanganicae (—) and* Lates stappersii (- - -) landed monthly at Kigoma.

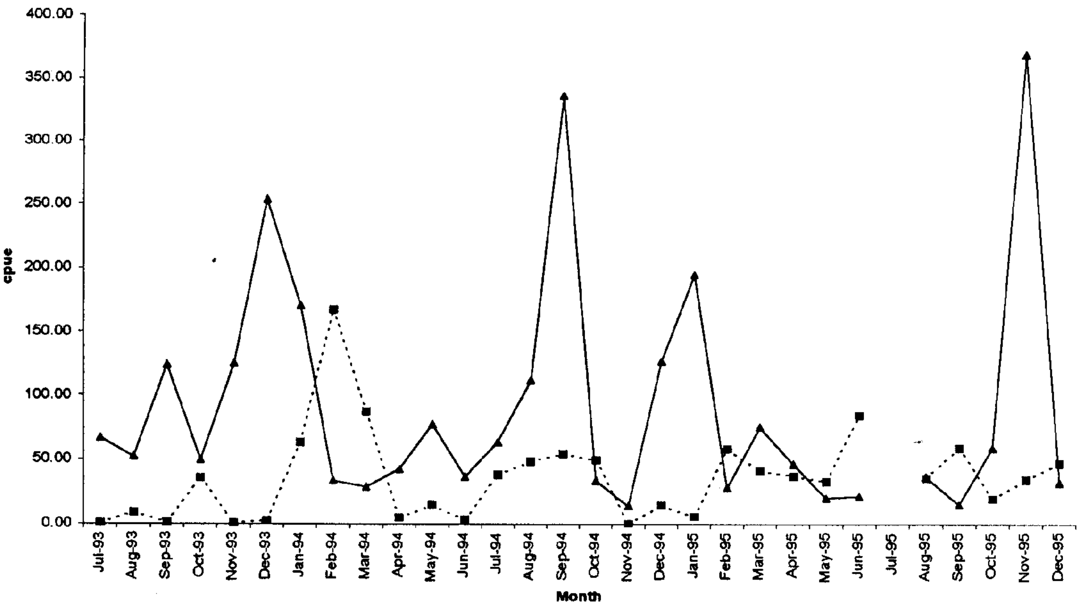

Fig. 16a. Total number m^{-3} of copepods caught on sampling days at Kigoma.