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LAKE TANGANYIKA RESEARCH:
SUMMARY OF THE SCIENTIFIC PROGRAMME 1992-98

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FINNISH INTERNATIONAL DEVELOPMENT AGENCY

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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, Democratic Republic of Congo, Tanzania, 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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The LTR Project Coordinator, Dr. George Hanek, deserves a special vote of thanks for his backstopping efforts, which kept the whole Programme on track.

CHAPTER 1

GENERAL INTRODUCTION

By:
Mölsä, H., J.E. Reynolds & O.V. Lindqvist

1.1 LTR SCIENTIFIC SUMMARY

This report has been compiled as an overall summary of work undertaken through the Scientific Programme of the Lake Tanganyika Research (LTR) Project. LTR became operational in 1992. The Food and Agriculture Organization (FAO) of the United Nations serves as the project's executing agency, and the University of Kuopio, Finland, as its Scientific Coordination Unit. Funding is provided mainly through the Department for International Development Cooperation, Ministry for Foreign Affairs of Finland (Finnida)[1]

The report is organised into nine chapters and a References Cited section. Following this Introduction (Chapter 1), Chapters 2 through 8 summarise investigations and findings within each of the major components of the Scientific Programme, and Chapter 9 reviews the major implications of component outcomes for Lake Tanganyika fishery management.

Sections 1.1 and 1.2 below set the context for the following chapters by providing a brief overview of the lake, its ecosystem and fisheries, and outlining LTR Scientific Programme objectives, implementation procedures, and the reporting and application of research outcomes.

1.2 LAKE TANGANYIKA OVERVIEW[2]

Understanding the immensely complex patterns and processes underlying Lake Tanganyika's fisheries clearly requires a broad, ecosystem-wide perspective. Yet the lake's vast size and remoteness can pose considerable logistical difficulties for the conduct of comprehensive, basin-scale physical and biological investigations or any other fisheries-related studies. Modern political boundaries dividing the lake between the different national sectors of Burundi, the Democratic Republic of Congo (DRC), Tanzania, and Zambia add a further dimension of complication to the organisational picture. Episodes of civil strife have also made for extremely difficult operating conditions over recent decades. Difficulties notwithstanding, a great deal of information has accumulated over the years on the geology, limnology, species composition, and other aspects of the lake and its fisheries. Pioneering studies date back to the late 19th and early 20th centuries, and extensive work of varying degrees of scale and ambition and covering a wide range of disciplines has since been carried out through numerous special projects and expeditions.[3]

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[1] The Finnish Department for International Development Cooperation is the successor agency to Finnida (Finnish International Development Agency), which was the original principal funding agency for the LTR project. LTR is officially chartered as project GCP/RAF/271/FIN, 'Research for the Management of the Fisheries of Lake Tanganyika.' Subsidiary funding has come from the Arab Gulf Program for the United Nations Development Organization (AGFUND).

[2] This section draws on earlier LTR Technical Documents, including Mikkola & Lindqvist (1989), Hanek (1995); Hanek *et al.* (1996); Craig (1997) and Reynolds (1998).

[3] All of these efforts have resulted in a very extensive literature. See Coulter (1991a) for an overview of major research projects and expeditions that have investigated various aspects of the lake and its ecosystem from the turn of the century to the present, and for a comprehensive bibliography.

Considerable initiatives have been taken from the early 1960s in fisheries research, technical assistance, and institution building within the Lake Tanganyika basin, under the new national development agenda of the post-independence era. However, these have mostly been organised as piecemeal, country-specific projects. Though of potential benefit to particular national sectors and resource user interest groups, from a regional point of view they have tended with few exceptions to operate in separate and uncoordinated ways. Recognition of the need to bolster regional integration of fisheries management efforts on the lake led to the preparation of a draft project document and its tabling at the First Session of the CIFA Sub-Committee for Lake Tanganyika in 1978. This initiative was followed up through a series of draft revisions and eventually resulted in the establishment of LTR (Hanek 1994).

1.1.1 General features

Basic geo-physical and biological characteristics of Lake Tanganyika (maps, Figs. 1.1 and 1.2) have been described in a variety of earlier reports and studies, and need only be briefly recapitulated here. With an area of 32,600 km^2, a maximum depth of 1,470m, and a volume of 18,880km^3, it qualifies simultaneously as: a) the largest of Africa's Great Rift Valley lakes, the second largest of all African lakes, and the fifth largest of the world's lakes; b) the deepest of all African lakes and the second deepest lake in the world and c) by cubic size, the greatest single reservoir of fresh water on the continent and the second greatest in the world. Entrenched within the Western Rift Valley between the countries of Burundi, the Democratic Republic of Congo (DRC), Tanzania, and Zambia, the lake's surface lies at an altitude of 773m and stretches in a generally north to south orientation between the narrow confines of the steep eastern and western escarpments of the Rift from 03°20'30"S to 08°48'30"S latitude. The lake averages almost 50 km in width and runs to a total length of 673 km. Mean depth is 570m. Maximum depths are found in the 'deeps' of the major northern and southern basins (1,310m and 1,470m respectively), which may in turn be divided into the several sub-basins listed in Table 1.1. As noted by Coulter and Spigel (1991:49), 'Despite high water temperatures (23.25 - 27.25°C), thermal stratification is well marked and varies seasonally above an apparently permanent anoxic hypolimnion. The lake can be classified as meromictic.' Table 1.2 summarises additional data on the allocation of surface area and shoreline frontage between each of the lacustrine states.

1.1.2 Ecosystem and fisheries

There are two main seasons within the Lake Tanganyika region year. The wet season extends from October/November to May, and is characterised by weak winds, high humidity, considerable precipitation and frequent thunderstorms. The dry season from around June to September/October has moderate precipitation as well as strong and regular southerly winds. The seasonal changes of weather and winds result from 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). These major climatic patterns and particularly the winds regulate the seasonal thermal regime of the lake (Coulter 1963; Coulter and Spiegel 1991), evaporation (Coulter and Spiegel 1991), water flows (Well and Chapman 1976), and the vertical mixing and transport of water masses (Degens *et al*. 1971; Tietze 1982). Hydrophysical phenomena are primary regulators of the spatial and temporal patterns of biological productivity, and were therefore accorded major attention under the LTR Scientific Programme (Huttula 1997).

Table 1.1 Lake Tanganyika: Geomorphological features*

Major Basin	Latitude Range	Sub-basin	Length	Width	Max. Depth
North-Tanganyika Trough	03°20' – 05°40' S	Bujumbura	70 km	25 km	350 m
		Rumonge (Karonda area)	80 km	35 km	1150 m
		Kigoma	170 km	80 km	1310 m
South-Tanganyika Trough	06°50'S – 09°S	Kalemie	130 km	40 km	800 m
		Moba	70 km	50 km	600 m
		East-Marangu (Kipili area)	120 km	30 km	1470 m
		Mpulungu	100 km	25 km	800 m

*Adapted from Mannini (1998), after Tiercelin and Mondeguer (1991).

Table 1.2 Lake Tanganyika: Division of national waters and shorelines

Country	Latitude Range	Lake Area (km^2)	Lake Area (%)	Shoreline (km)	Shoreline (%)
Burundi	03°20'30"S - 04°26'40"S	2,600 km^2	8%	159km	9%
DRC	03°21'00"S - 08°13'40"S	14,800 km^2	45%	795km	43%
Tanzania	04°26'00"S - 08°36'00"S	13,500 km^2	41%	669km	36%
Zambia	08°13'40"S – 08°48'30"S (West shore)	2,000 km^2	6%	215km	13%
Lakewide totals	03°20'30"S - 08°48'30"S	32,900 km^2	100%	1,850km	100%

1.1.2 Ecosystem and fisheries

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Lake Tanganyika is known for its productive fishery, which is based primarily on the exploitation of six endemic species. These include the two schooling clupeid 'sardines' (known variously as 'ndagala' (Burundi and DRC), 'dagaa' (Tanzania), or 'kapenta' (Zambia) along different sections of shoreline), *Limnothrissa miodon* and *Stolothrissa tanganicae*, together with four predators, all centropomids of the genus *Lates* -- viz.: *L. stappersii*, *L. angustifrons*, *L.*

mariae, and *L. microlepis*. Of the *Lates* species, the latter three are incidental to the catch: the lake's commercial fishery is essentially based on three pelagic species -- the two clupeids (ca. 65% by weight) and *L. stappersii* (ca. 30% by weight). Annual harvest levels in recent years have been estimated to vary in the range of 165,000 - 200,000 tonnes -- volumes that translate into annual earnings on the order of tens of millions of US dollars. The harvest is shared between the littoral States roughly in the order, if not exact proportion, of each state's share of the total lake area. Thus fishers in the DRC (45% of lake area) land about 50% of the annual pelagic catch, whilst those in Tanzania (41% of lake area) land about 31%, in Burundi (8% of lake area) about 21%, and in Zambia (6% of lake area) about 7%.

Though subject to marked fluctuation, Tanganyika catch yields have been claimed to be higher per unit area than for most great lakes of the world (Coulter 1981, 1991; Hecky *et al.* 1981; Lindqvist & Mikkola 1989; Hecky 1991; Roest 1992). The fisheries yield in lakes usually ranges between 0.02 and 0.2% of primary production (e.g. Morgan *et al.* 1980), while marine coastal seas often show an order of magnitude higher values (Nixon 1988). For Lake Tanganyika, a preliminary estimate of 0.45 %, resembling those in marine systems, has been given in the literature (Hecky *et al.* 1981; Hecky 1984, 1991).

Different hypotheses have been proposed to explain the high productivity of the pelagic fishery in Tanganyika (Hecky *et al.* 1981). One suggests that the flux of dissolved organic matter (DOM) from the anoxic hypolimnion complements phytoplankton primary production (Hecky *et al.* 1981), though this has not been supported by later analyses of available data (Hecky 1991). Another line of explanation emphasises the marine character of the lake's food web (Hecky 1991). As in many productive marine systems, the primary grazer is a calanoid copepod, and the dominant primary planktivores as well as the piscivores belong to predominantly marine fish families. The phytoplankton and bacterial biomasses are low but the growth rates are high. Organic carbon is not accumulated in plankton but is channelled into fish biomass and harvested as fish yield. The long geological history of the lake, combined with the special ecological conditions of these deep, continuously warm tropical waters, may have resulted in the evolution of a trophic structure consisting of highly efficient species (Hecky 1984).

Understanding of the lake's trophic structure and thus of its fishery potential has been hampered by the lack of comprehensive spatial-temporal data. Moreover, the role of human-induced perturbations in the modern era, though not sufficiently appreciated in earlier studies, must also be taken fully into account in assessing ecosystem structure and fish production efficiency. Recent changes in the pelagic fish community, marked by domination of the fast growing and productive *L. stappersii* at the expense of the other three *Lates* species, are notable outcomes of selective fishing pressure in the mechanised large-scale fishery (Coulter 1991).

Total lake-wide catches seem to be increasing over the long-term (Hanek 1994; Coenen 1995), but signs of decreasing catches per unit effort in some localities, especially the Burundi sector in the north and the Mpulungu (Zambia) area in the south, have aroused concerns about possible over-fishing (Roest 1992; Coenen & Nikomeze 1994; Coenen *et al.* 1998). On the other hand, there is still considerable local pressure to increase fishing effort in order to acquire more fish protein for human consumption. Concentrations of fishing activity have recently moved from the north to the middle and southern parts of the lake, giving increased urgency to the need for regional strategic planning and mutual collaboration between the lacustrine states. But the planning process will not be able to move forward unless essential fishery potential questions are effectively addressed. Are present harvest levels in the lake sustainable? Are these levels capable of further development? Or, have they already broached the limits of sustainability?

1.3 LTR SCIENTIFIC PROGRAMME

1.3.1 Objectives

Principal LTR objectives are to expand scientific understanding of fish production dynamics in the lake and to use this improved knowledge base in helping to build towards a common, regional approach to the management of its fisheries resources (Lindqvist & Mikkola 1989; FAO 1992; Roest & Salo 1997). The project design calls for all aspects of the research programme to be conducted in full collaboration with the national fisheries authorities and institutes of the respective lacustrine states, and to this end strong in-service training and other institution-building components are incorporated. Headquarters were established at the beginning of the project on the compound of the Département des Eaux, Pêches et Pisciculture in Bujumbura (Burundi), and the national research institutes at Uvira (DRC), Kigoma (Tanzania), and Mpulungu (Zambia) have from the outset provided facilities and counterpart staff for the operation of LTR sub-stations around the lake.

The fundamental goal of LTR's Scientific Programme was originally described by Lindqvist & Mikkola (1989) as the development of an understanding of the mechanisms underlying limnological, hydrological and hydrographical processes which, through various biological interactions, influence and determine patterns of fish production. Such an understanding would provide a basis for formulating a regional approach to fisheries management. This point was reiterated in the mid-term LTR project review (Roest & Salo 1997) observation that '...a proper understanding of the limnological and hydrological mechanisms present in the lake is essential in order to develop a coherent management plan and procedures. There are obvious gaps in understanding the lake dynamics behind highly fluctuating fish yields.'

As formalised through the LTR Project Document (FAO 1992), the Scientific Programme was expected to yield basic reference points for the formulation of a regional fisheries management plan through the combined results of investigations under eight components,[4] namely:

1) Hydrodynamic modelling;
2) Remote sensing;
3) Limnology and primary production;
4) Zooplankton biology;
5) Fish genetics;[5]
6) Fish biology;
7) Fish abundance and distribution (fisheries statistics); and
8) Assessment of trophic structure and energy flows

[4] For further details on project structure, see Lindqvist & Mikkola (1989), Hanek (1995), Hanek *et al.* (1996), Craig (1997), and Sarvala *et al.* (1999).
[5] Summary results under the fish genetics component have been combined with those of fish biology in Chapter 6 of this document.

Specific aims to be realised through the components of the Scientific Programme, first proposed by Lindqvist & Mikkola (1989) and later modified by the Scientific Co-ordination Committee, comprised the following.

1) modelling lake hydrodynamics through studies of standard meteorology, major upwellings/ downwellings and currents affecting the water circulation, stratification and nutrient/ energy flows that influence biological production;
2) assessing the basis of pelagic fish production through study of pelagic food webs, including their dynamics and vertical migrations, production and composition, and the mechanisms and efficiency of energy pathways to fish;
3) investigations of the ecology and life cycles of the six commercially important fish species, predator-prey relationships, population structure, possible discreteness, and biology and distribution of larval and post-larval stages; and
4) determinations of stock size and biomass distribution and their correlation with limnological and other events, with complementary work to collect precise catch per unit effort (CPUE) and related fish biology data.

1.3.2 Implementation

Core activities of the LTR Scientific Programme were undertaken through an extensive three-year exercise known as the Scientific Sampling Programme (SSP).[6] This represented a unique approach to the study the physical and biological processes in the lacustrine ecosystem, in that a standardised methodology was deployed on a regionally integrated and synchronised basis. Field and laboratory studies on lake hydrophysics, fish stocks and fishery as well as limnology and fish biology were conducted jointly by a team of scientists drawn from international and local counterpart institutions. A new field research station incorporated into LTR Project Headquarters was established on the premises of the Département des Eaux, Pêche et Pisciculture, in Bujumbura. In addition, existing field stations were upgraded and equipped at three other sites around the lakeshore, including: the Tanzania Fisheries Research Institute (TAFIRI) station at Kigoma, Tanzania; the Department of Fisheries station at Mpulungu, in Zambia, and the Centre de Recherche en Hydrobiologie station at Uvira, in the Democratic Republic of Congo. The SSP also entailed regular on-site training of national counterparts. Ecosystem assessment of the lake was complemented with other Scientific Programme work that entailed monitoring methods utilising automatic recorders, remote sensing technology, and integrated lake-wide surveys with the project research vessel, the *R/V Tanganyika Explorer*.

A total of 17 lake-wide cruises were executed in support of hydrodynamic, limnological, fish biological, and hydroacoustic studies. *R/V Tanganyika Explorer* was specially equipped by the project with modern sampling and navigational devices in order to serve as a research platform. Sampling schemes employed on the cruises were designed to accommodate multidisciplinary aims in order to combine physical and ecological observations and facilitate analysis of the interactions between trophic levels. Hydrodynamic modelling was completed partly under an Inter-Agency Agreement between LTR and the Lake Tanganyika Biodiversity Project (UNDP/OPS) projects (Huttula 1997).

[6] See Craig (1997) for preliminary summary.

1.3.3 Outcomes

Although this document provides the first overall summary review of Scientific Programme outcomes, a variety of reports have already been produced on component activities. Primary data and preliminary analyses have been extensively documented as part of the LTR publication series, which now numbers more than 90 titles.[7] Findings have also been reported at two symposia convened in Kuopio, Finland (Mölsä 1991, 1995) and in other international scientific fora (e.g., Huttula *et al*. 1996; Podsetchine *et. al*. 1997; Podsetchine *et al.* 1998; Hanek *et al.* 1997). Proceedings of the International Lake Tanganyika Symposium in Kuopio (11-15.09.1995) will appear as a specific issue in *Hydrobiologia* and in a forthcoming book (Lindqvist *et al.* 1999).

Evaluation of LTR results during the latter half of 1996 led to recommendations for the continuation of activities over the course of a further four year period (FAO/FINNIDA 1996; Hanek and Craig 1996). At the same time it was recognised that socio-economic and legal-institutional issues needed to be addressed more directly in order to complete the foundation work for a regional framework management plan. As final wrap-up, analysis, and reporting activities for Scientific Programme activities continued, therefore, the LTR team embarked on a complementary programme of legal-institutional studies (Cacaud 1996; 1999; Maembe 1996) and socio-economic (SEC) investigations that involved a lakewide survey of landing sites, fishers, and trader/processors. Particular efforts were made to collect information on fishery problems and prospects from the viewpoint of local stakeholders (Reynolds 1997, 1999a, 1999b; Reynolds and Paffen 1997a, 1997b; Reynolds and Hanek 1997).

With the finalisation of Scientific Programme work and complementary socio-economic and legal-institutional studies largely complete by mid-1998, the LTR team began the task of synthesising project outcomes to build towards a Framework Fisheries Management Plan (FFMP) for the Tanganyika region.[8] In late 1998, the donor agency of Finland (Department for International Development Cooperation), the University of Kuopio and FAO jointly prepared a work programme for an LTR Project extension phase for 1999-2001. Key activities earmarked for this phase, to be undertaken in collaboration with the interregional FISHCODE Programme,[9] are the organisation and operation under national execution of an extended Lake Tanganyika Monitoring Programme (Mannini 1999), the elaboration of the proposed FFMP, and facilitation of FFMP implementation through the preparation of a programme of accompanying measures (Reynolds 1999).

[7] See the LTR publications list appended to this document.
[8] For the initial draft management planning exercise, see Reynolds (1998).
[9] GCP/INT/648/NOR – FAO/Norway Programme of Assistance to Developing Countries for the Implementation of the Code of Conduct for Responsible Fisheries.

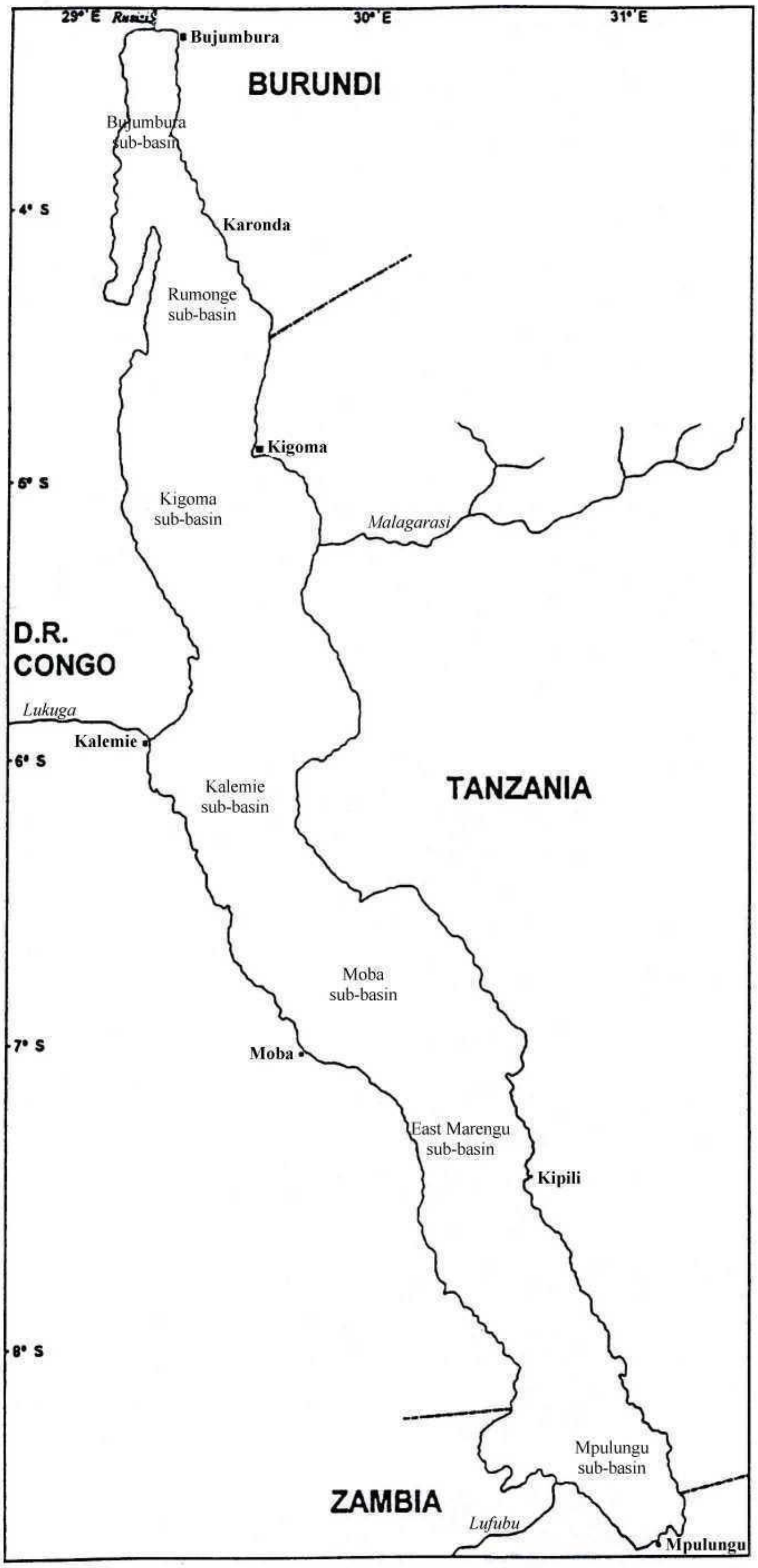

Figure 1.1 Lake Tanganyika

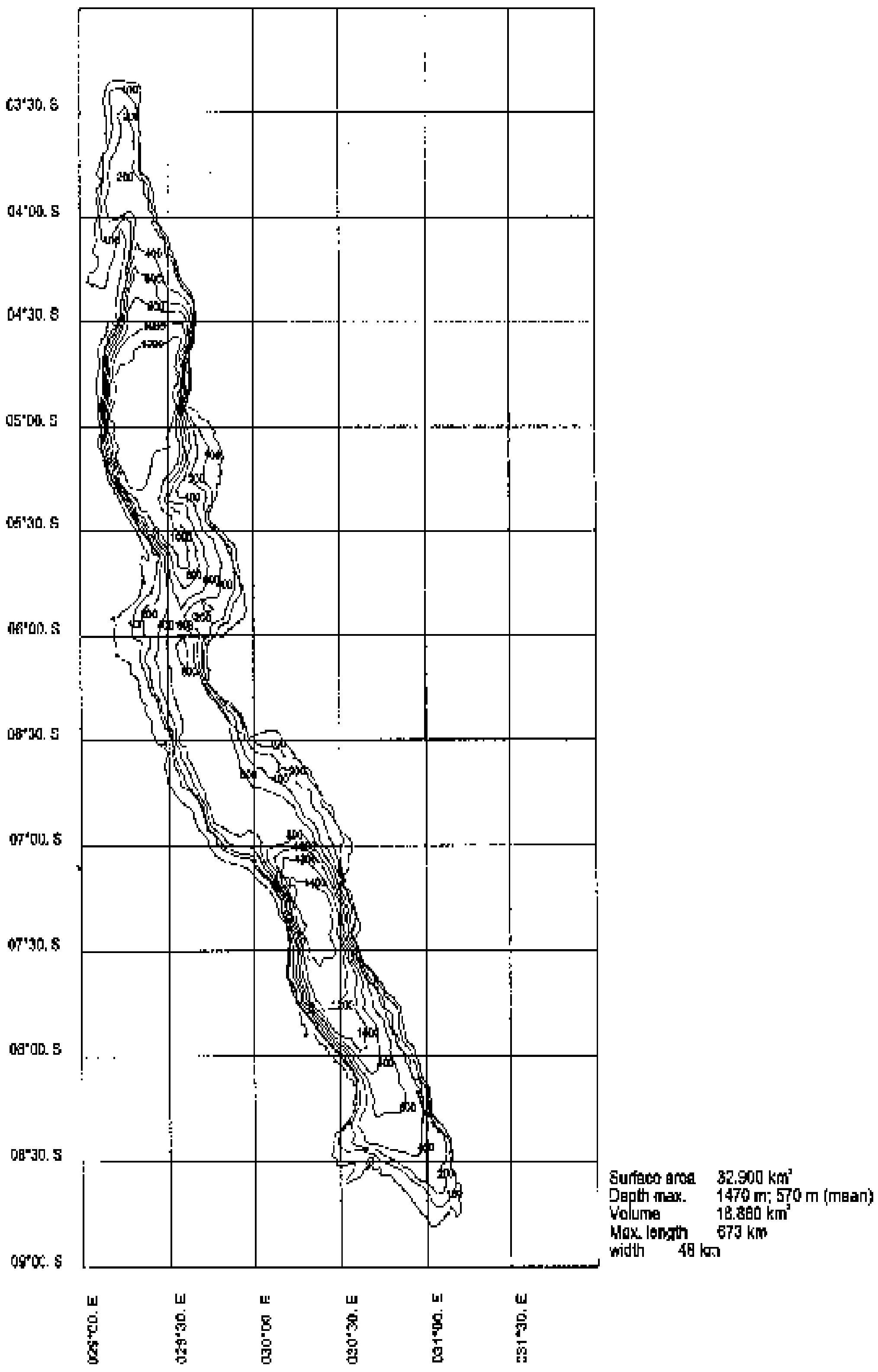

Figure 1.2 **Characteristics of Lake Tanganyika.**

CHAPTER 2

HYDRODYNAMICS AND HYDRODYNAMIC MODELLING

By:
Huttula, T., Peltonen, A. Podsetchine, V. & P, Kotilainen, B. Kakogozo, L. Makasa, S. Muhoza and J-M. Tumba

Abstract

LTR hydrophysical studies focused on wind-driven water circulation and current patterns, upwelling of nutrient-rich hypolimnetic waters, and the general role of hydrodynamics in regulating nutrient and energy distribution for biological production. These studies commenced in March 1993 as the first Scientific Programme activity of LTR. The data were used in planning the limnological studies and the development of numerical modelling. A total of eight lake wide surveys were conducted, the most extensive of which were organised jointly with the LTBP in 1996-97. Three different types of models were applied, including a two dimensional model in vertical plane to simulate thermocline tilting along the main axis of the lake and, for lake-wide horizontal modelling, two high-resolution flow and sediment transport models to study the horizontal transport and upwelling areas.

Two atmospheric models were also used to provide a realistic wind distribution for the flow models. The first model was used to predict winds along ten transects across the lake. Later a HIgh Resolution Limited Area Model (HIRLAM) was used to calculate typical winds for each month during the project duration. The models show that for the Kigoma Region during the dry season, mountain slopes contributed about 50% and the trades 25% of the diurnal variation of winds. The remaining 25% of wind variation was due to the lake effect. The SE tradewind enhances the lake breeze considerably at daytime and adds to downslope winds at night time.

Results revealed a high spatial variation of flow pattern applying to both seasons. The horizontal structure of the flow pattern is dominated by large scale gyres. The location and rotation direction of the gyres is determined by regional bathymetry and wind forcing. The largest wet season gyres covered parts of the lake from the eastern to the western shore. Having a typical velocity of 10 cm s^{-1} and mean lake width, one rotation of such gyre takes place in 20 days. Areas of very high horizontal current speed (more than 30 cm s^{-1}) were also found near the shallow shores. Several areas of upwelling and downwelling were also identified. The number of these areas was higher during dry season and upwelling velocities were about twice those of the wet season for given locations. The typical range for dry season upwelling velocity was about 3-25 m d^{-1}. The traditional theory of upwelling occurring only along the main axis and only during the dry season was thus greatly expanded.

2.1 INTRODUCTION

Lake Tanganyika is known to be very dynamic in its physical and biological nature. Friction at the deep bottoms has a secondary role in hydrodynamics on a lake-wide scale. Also, the high temperature of the waters makes the viscosity of the waters low as compared to waters in temperate regions. Regular diurnal and seasonal wind forcing provides very stable momentum input to the lake. The high and steep mountains and elongated shape of the lake affect the high spatial variation of wind forcing. Lake waters are thermally stratified although the temperature range is narrow; the difference between the epilimnetic and hypolimnetic waters is 4-5°C. Still, density differences are clear and thermal stratification is observed throughout the year. Upwelling of hypolimnetic waters substantially affects biological production. Intensive field measurements with several numerical model applications were used to study the spatial and temporal variation of transport patterns.

Tanganyika hydrodynamics were studied through exercises organised directly under the LTR project as well as in collaboration with the Lake Tanganyika Biodiversity Project (LTBP).[1]

Major focal points of the hydrodynamic studies included the following.

1) wind driven water circulation;
2) major upwelling phenomena in the southern lake basin and their role in vertical transport of hypolimnetic waters;
3) secondary upwellings and spreading of these waters along eastern and western coasts of the lake;
4) periodic oscillations in the lake; and
5) horizontal dispersion and transport of suspended sediments in the lake, especially near the main river inlets

2.2. MATERIALS AND METHODS

Earlier studies by Coulter and Spiegel (1991), Hecky & Bugenyi (19921) and Hecky *et al.* (1981) on upwelling and related biological production in Lake Tanganyika have been complemented under the LTR programme through intensive field measurements and modelling, as reported in Huttula *et al.* (1993, 1994), Huttula & Podsetchine (1994), Kotilainen *et al.* (1995a, b, 1998), Podsetchine & Huttula (1995, 1996, 1998), Podsetchine *et al.* (1998, 1999a, b), Verburg (1997) and Verburg *et al.* (1997, 1998a, b), and, most comprehensively of all, in Huttula (1997).

In March 1993 LTR equipped three stations around the lake (Bujumbura in Burundi, Kigoma in Tanzania, and Mpulungu in Zambia), and two other offshore buoy stations (Kigoma and Mpulungu), with automatic meteorological and hydrodynamical data recording instruments (Huttula *et al.* 1993, Kotilainen *et al.* 1995a). These stations register wind speed, wind gust, wind direction, air temperature, air pressure, relative humidity, rainfall, solar radiation and water level.

A Conductivity-Temperature-Dissolved oxygen profiler (CTD), a vessel based Acoustic Doppler Current Profiler (ADCP), and two buoy based ADCP's as well as a meteorological station on board *R/V Tanganyika Explorer* were used for extensive data collection on the lake. Flow cylinders were used as drifters for measuring current speed and direction weekly in the vicinity of the field stations. Altogether eight lake wide hydrodynamical expeditions were conducted in 1992-1997, three of them under the IAA arrangement with the LTBP.

The installed recorders collected data continuously all around the lake, in some cases for more than four years without interruptions. This provides a strong basis for hydrodynamic conclusions and model validation. Three different model types were applied. First, a two dimensional model in vertical plane was used to simulate the thermocline tilting along the main axis of the lake (Huttula & Podsetchine 1994). Later on, a lake-wide horizontal model with two high resolution flow and sediment transport models were used to study the horizontal transport and upwelling areas (Podsetchine & Huttula, 1995, 1996, 1998; Podsetchine *et al.*, 1998a, 1998b).

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[1] Such collaboration was made possible through an Interagency Agreement (IAA) between FAO and UNDP/OPS.

Characteristics of the LTR and LTBP models are described in Table 2.1. The further development of the circulation model was a logical extension of the earlier modelling work done directly under LTR auspices. This circulation model was developed for pelagic areas, although near-shore currents were also described. It was designed to simulate wind-driven circulation and upwelling phenomena in Lake Tanganyika.

Table 2.1. Main characteristics of numerical models applied to Lake Tanganyika during the years 1996 - 1997.

Characteristic	LTBP models	LTR model
Primary emphasis	Wind-driven circulation; Sediment transport	Wind-driven circulation; Upwelling
Spatial resolution	1 – 2 km	3 - 5 km
Wind forcing	3D mesoscale meteorological model	quasi 3D wind model
Visualisations	IDL graphics	simple

As part of the modelling work, two regional sediment transport models were introduced. Two atmospheric models were also used to provide correct wind distribution for the flow models. The first model was used to predict winds along ten transects across the lake (Savijärvi 1995, 1997). The High Resolution Limited Area Model (HIRLAM; Järvenoja *et al.*, 1997) was subsequently used to calculate winds for typical weeks of each month during the LTR years.

2.3 RESULTS

2.3.1 Water level

The lake water level was highest in April-May and lowest in November. The fall in the lake level during the dry season was 0.89 m (between daily means), and the mean lake level was 773.85 m. In 1996 the lake level reached the lowest level since 1959 (Verburg *et al.* 1998a, 1997), and stood at less than 1 m above its lowest recorded level. Verburg *et al.* (1998a) concluded that if the declining trend of the past years persists, the lake may be facing a new closed period in the near future, for the first time since 1874 (Camus 1965).

2.3.2 Thermal regime

The observed solar radiation was higher in the south than in the northern part of the lake. In the south there was no difference between the dry season (June-August) and the wet season (September-May), but in the north solar radiation was higher during the dry season (Verburg 1997, 1998a). On the average, air temperature was highest in the Mpulungu region and lowest at Bujumbura. During the dry season the average air temperature was higher at the Kigoma buoy than in the Mpulungu region. Seasonal variation in the south was high compared to the Kigoma and Bujumbura regions. At all stations the monthly mean wind speed was highest in the dry season, and the monthly mean wind gust was highest in the wet season. Wind direction distribution was very similar in the south and north. The proportion of the south-east winds increased at all stations during the dry season. Winds from the land were more frequent at all stations during the dry season, except at the Kigoma buoy.

In the mean monthly water temperature profiles during years 1996-97 vertical stratification was observed during whole year off Kigoma whereas off Mpulungu the profiles from June to August show a very weak vertical stratification. The surface waters in the south heated very rapidly after the dry season.

The upwelling of water below thermocline can be described with water mass, which has the temperature of 24.5-25.0^{o} C. During the wet season thermocline lies at the depth of 70-80 m. At the buoy off Mpulungu this thermocline water mass reached the surface and remained there for about three months in 1993. In 1994 it was impossible to record it after May 12 due to instrument malfunction. In 1995 the upwelling period in south was less than two months, but in 1996 it occurred at the same time as in 1993 and could be seen during two months. No upwelling has been observed off Kigoma. It is likely that the upwelling of sub-thermocline waters to epilimnion is of frequent occurrence, but that wind forcing is too weak to bring waters below thermocline to the surface. Outside Kigoma, waters with a temperature from 25.5-26.0^{o} C lie between 30-60 m in the upper part of thermocline during the wet season. This water was observed for the first time on the lake surface in the middle of September 1994. Obviously it had risen there already in July. It was twice noted again during November-December 1994 and once more in August 1995. In 1996 this phenomenon was observed for the longest duration, from early July to the middle of September. It is interesting to note that water with same temperature as off Kigoma in the upper part of thermocline was observed on the surface off Mpulungu during the second half of September 1996.

During four expeditions with *R/V Tanganyika Explorer* in 1996-98 the thermal regime in the lake showed great variation. Temperature transects were calculated from the CTD results using SURFER-software. The transects were selected along the main south-north axis of the lake and along the main transversal axis. In November 1996 thermocline depth decreased from 60 m in the south to 45 m in the north. The warm southern waters reached to the region of Kipili about 160 km from the south end of the lake. In April the thermocline was also at the depth of 60 m but no significant tilting along the main axis of the lake was observed. In April 1997 along the main transversal axis a slight SE tilt was found in the middle of the lake near Kungwe. At the end of the dry season in August 1997, a clear tilt was found along the main axis of the lake. The thermocline was at the depth of 25 m in the south and at the depth of 75 m in the north. Also at this time the waters from the south end to the region of Kipili were very different from the waters further north, with lifted and expanded thermocline waters. This was also the reason why there were no clear transversal tilt of thermocline in the south basin or any other location. In March 1998 no significant tilting was observed.

2.3.3 Water circulation

The water currents were measured for the first time on the lake during the expedition in May 1993 (Huttula *et al.* 1994), covering five areas. Fairly strong lake currents (maximum speed of 19 cm s^{-1}) were found near the eastern shore near Kungwe and also in the south at the lake buoy station. The direction and even the magnitude of the flow near Kungwe in May 1993 corresponds very well with the recent results from the dry season in 1997. The same applies to Utinta and the results near the lake buoy stations. The main results of the current measurements show the diurnal variation of surface currents. It has been proven that in certain areas the lake-land breeze system highly dominates the short scale current pattern. There are long term variations in the current field which are forced by seasonal winds and regional thermal as well as slope winds and the currents can vary greatly in space and time. The flow results together with temperature and echo intensity observations provided good information about transportation of the river waters. The episodic advection can be seen both in West and East directions. The observed magnitude of currents and their high variation results in an effective mixing in a fairly limited area near the river mouths. Therefore, no hypolimnetic effects by cool river waters could be seen in front of the rivers (Kotilainen *et al.* 1995, Vandelannoote *et al.* 1999) as been claimed since the 1930s.

2.3.4 Modelling

The diurnal variation and also values of air temperatures and wind speeds during the dry season are highest in Mpulungu, at the south end of the lake (Kotilainen *et al.* 1995a, b; Huttula *et al*. 1994). During the rainy season, wind forcing was fairly similar in the three observed regions. Occasionally, however, notable differences occur. In December 1993, for example, wind forcing was stronger in the Bujumbura region than in the south. Again, in late March 1994, it was strongest in the Kigoma region.

The offshore winds in Kigoma result from a lake-land breeze system, mountain slopes, and south-easterly trade winds. This has been observed also in earlier studies (Kotilainen *et al.*, 1995a). Savijärvi (1995, 1997) concluded from an atmospheric model application study in Kigoma region, that the mountain slopes contributed about 50%, and trades 25% of the diurnal variation of winds. The rest 25% of the wind variation was due to the lake effect. The SE tradewind enhances the lake breeze considerably at daytime and adds to downslope winds at night time.

Numerical experiments with high resolution three-dimensional flow and sediment transport models were focused at the main river mouths, Malagarasi (Tanzania) and Lufubu (Zambia). The dynamic calculations were made for two one-week periods, respectively in April and August 1997. They were representing typical wet season and dry season weeks.

Flow simulation results revealed a very dynamic flow structure that was proven by ADCP and flow drifter measurements around the lake. Calculated current directions correlate satisfactorily with the observed ones. The flow models underestimate the flow velocity due to the high numerical diffusion properties of the implicit integration time scheme used in the models.

Simulations showed that the winds over the region and lake bathymetry are the main factors determining the flow structure. Influence of river flows is limited to a very small area in the vicinity of river mouths due to the hydraulic friction. In Malagarasi region alongshore N-NW currents prevail. The currents there, as in other locations along the shallow coasts, follow the diurnal variation of the winds. Nevertheless, the duration of southward flow is short and its magnitude smaller than the main flow towards N-NW. The sediment transport models revealed that the areas of re-suspension due to wave forcing are limited to the areas adjacent to river mouths. The river water plumes follow the regional flow patterns.

Results in the lake revealed a high spatial variation of flow pattern due to the variations in the wind field (Figs. 2.1-2.2). The relationship between wind and flow pattern in the lake is demonstrated with modelling results in Figures 2.1-2.7. The horizontal structure of the flow pattern is dominated by large scale gyres (Figs. 2.3-2.4), whose location and rotational direction are determined by regional bathymetry and wind forcing. The largest gyres in the wet season covered sections of the lake stretching from the eastern to the western shore. Having a typical velocity of 10 cm s s^{-1} and mean lake width, one rotation of such a gyre takes place in 20 days. This is to be taken as the low value for the rotation time since in several locations two or even more gyres were observed and areas of very high horizontal current speed (more than 30 cm s s^{-1}) were found near the shallow shores. Several areas of upwelling and downwelling were also identified (Fig. 2.5-2.7). The number of these areas was higher during dry season and also the upwelling velocities were about twice of the velocities in same location during wet season. The typical range for dry season upwelling velocity was about 3 - 25 m d s^{-1}. The traditional theory of upwelling occurring only along the main axis and only during the dry season was thus greatly expanded through new findings.

Distribution of pelagic fish and macrozooplankton according to Mannini (1998) seem to be related to the water current patterns. We studied this by using in the flow model passively floating objects like larvae, medusae, or zooplankton, and visualised the results by TANGPATH-visualisation software. An example of particle trajectories simulations from the southern part of the lake from mid 1997 is presented in Fig. 2.8. The results show good accordance with distribution of *Lates stappersii* larvae in June 1995 (Fig. 2.9). Winds in August 1997 and in early June 1995 were fairly similar. Also the upwelling areas on 28 Aug. 1997, as presented in Fig. 2.7, correspond in the north quite well with the peak occurrence of *L. stappersii.*

2.4. CONCLUSIONS

On the basis of intensive hydrodynamic measurements and numerical modelling the following observations and conclusions can be drawn (Huttula, 1997):

1) Upwelling was observed both in 1996 and 1997 in the south, though it was less intensive than in 1993. In Kigoma the thermal stratification was not broken at all.

2) The water temperature revealed tilting of thermocline along the main axis of the lake, in accordance with Coulter (1963, 1968). Heating of deep waters and the deepening of certain isolines due to climatic changes was claimed by Plisnier (1997).

3) Transversal tilting of thermocline in the Kalemie strait during dry and wet seasons was observed in connection with the uninodal internal seiching.

4) Internal wave motion with a periodicity of 23.4 d during the dry season and of 34.8 d during the wet season was found with automatic devices for the first time.

5) High and variable current speeds were measured at surface waters down to 20-40 m whereas the water flows below this level were more steady but showed clear seasonal variations.

6) Acoustic Doppler Current Profilers (ADCPs) were used in validating the barotopic flow models. The High Resolution Limited Area Model (HIRLAM) was applied to provide adequate wind forcing data for such an elongated lake surrounded by high mountains .

7) Distribution of silted materials in the dry season is mostly limited to the river mouths and narrow littoral zones. During the rainy season, the turbid waters distributed over a wider range showing longitudinal, elongated shapes due to wind-induced flows.

8) Wind-driven currents initiate and maintain upwelling events in Lake Tanganyika. These events have a primary occurrence in the southern end, as remarked by Coulter & Spigel (1991), but also occur secondarily at several locations along the eastern and western coast.

9) In future studies it should be possible to combine the 3D-thermal current model of Lake Tanganyika with an oxygen model. Once verified, the combined model should allow more precise assessment of nutrient or organic particle distributions.

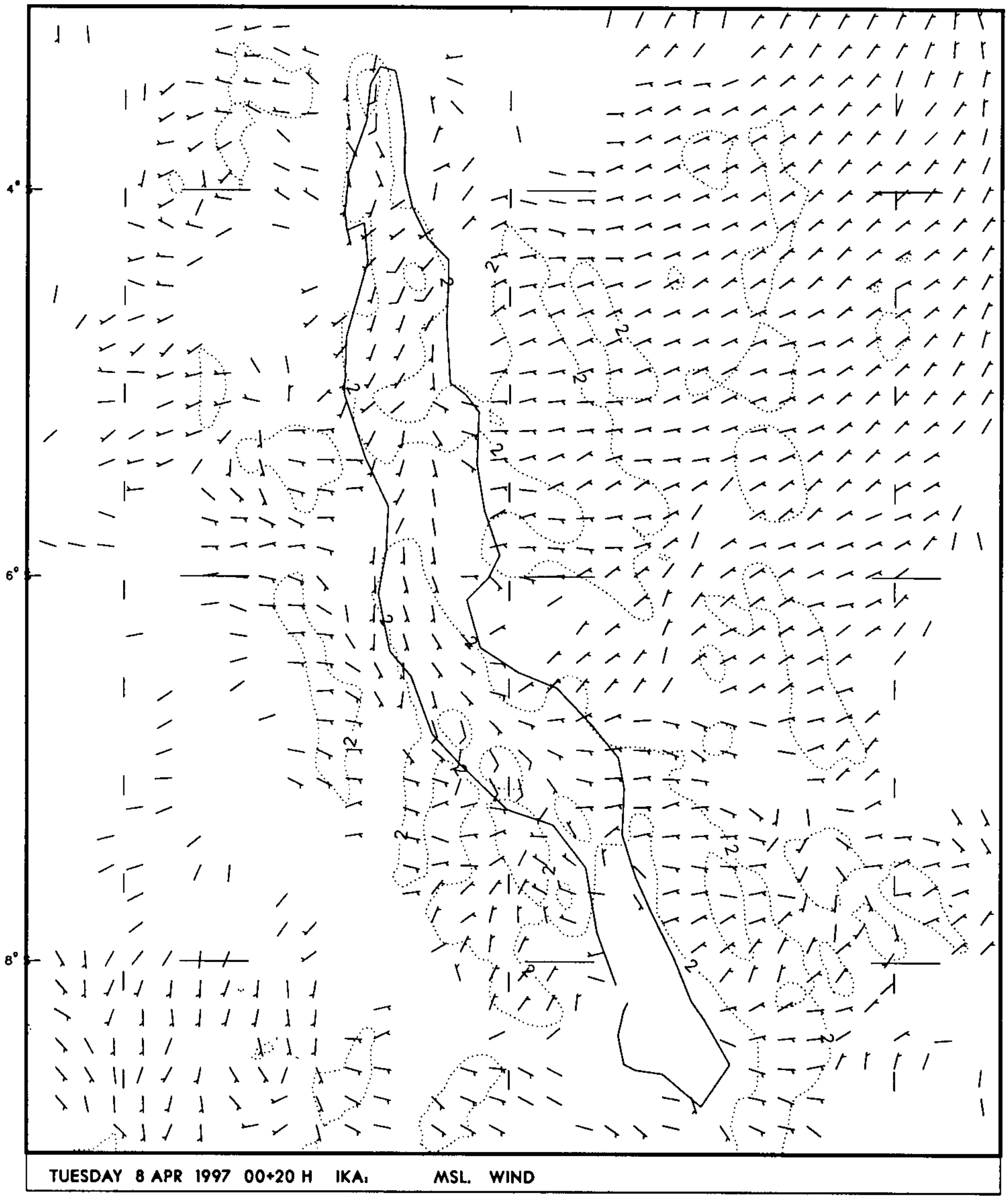

Fig. 2.1 Surface wind velocity and direction calculated by HIRLAM-model at 22 hours (LT) on 8 Apr 1997. The wind speed is low. The northward wind is observed in the middle part of the lake. Wind speed is highest near Kungwe mountains.

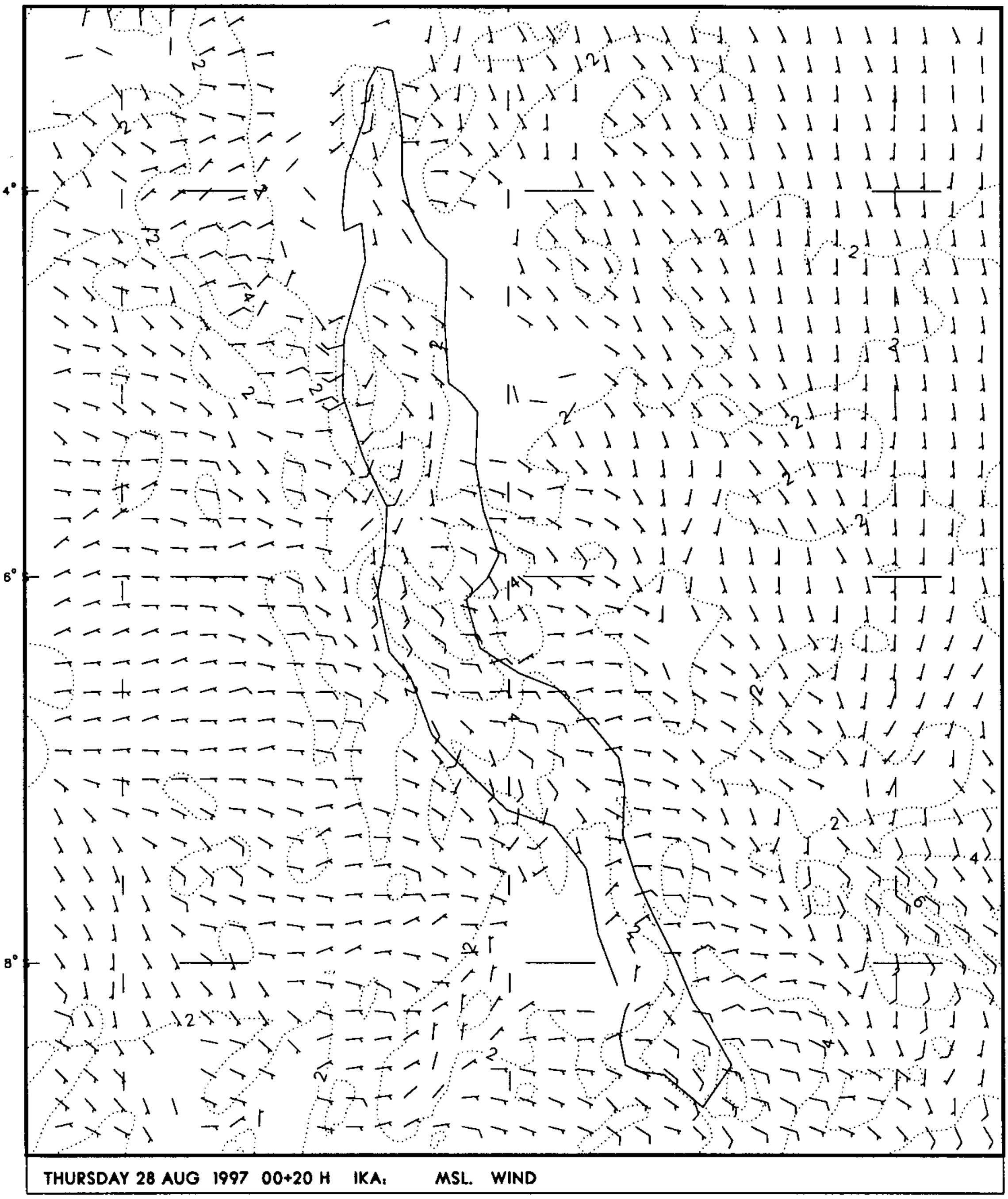

Fig. 2.2 Surface wind velocity and direction calculated by HIRLAM-model at 22 hours (LT) on 28 Aug 1997. The lake breeze is clearly seen along the east coast. The northward wind is observed in the middle part of the lake. Wind speed is highest near Kungwe mountains.

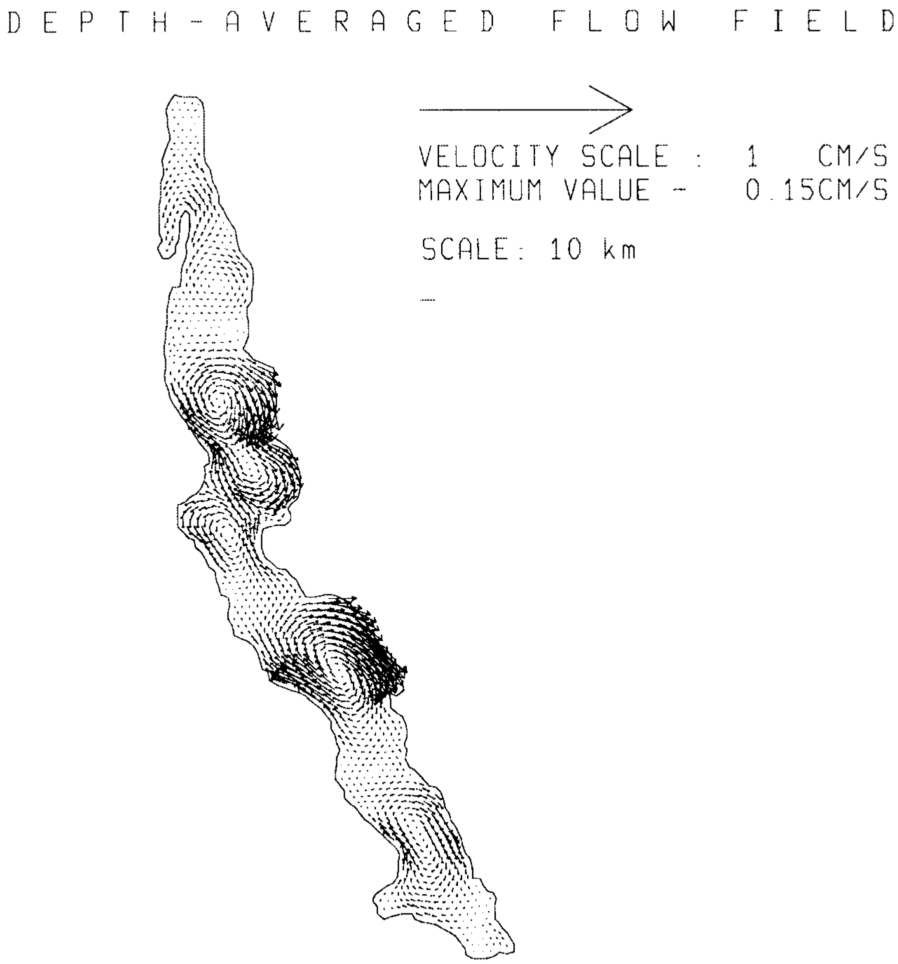

Fig. 2.3 Depth-averaged flow velocity calculated by 3D model at 22 hours (LT) on 8 Apr 1997. Several large scale gyres are seen. The magnitude of this depth integrated velociy is at maximum in shallowest regions.

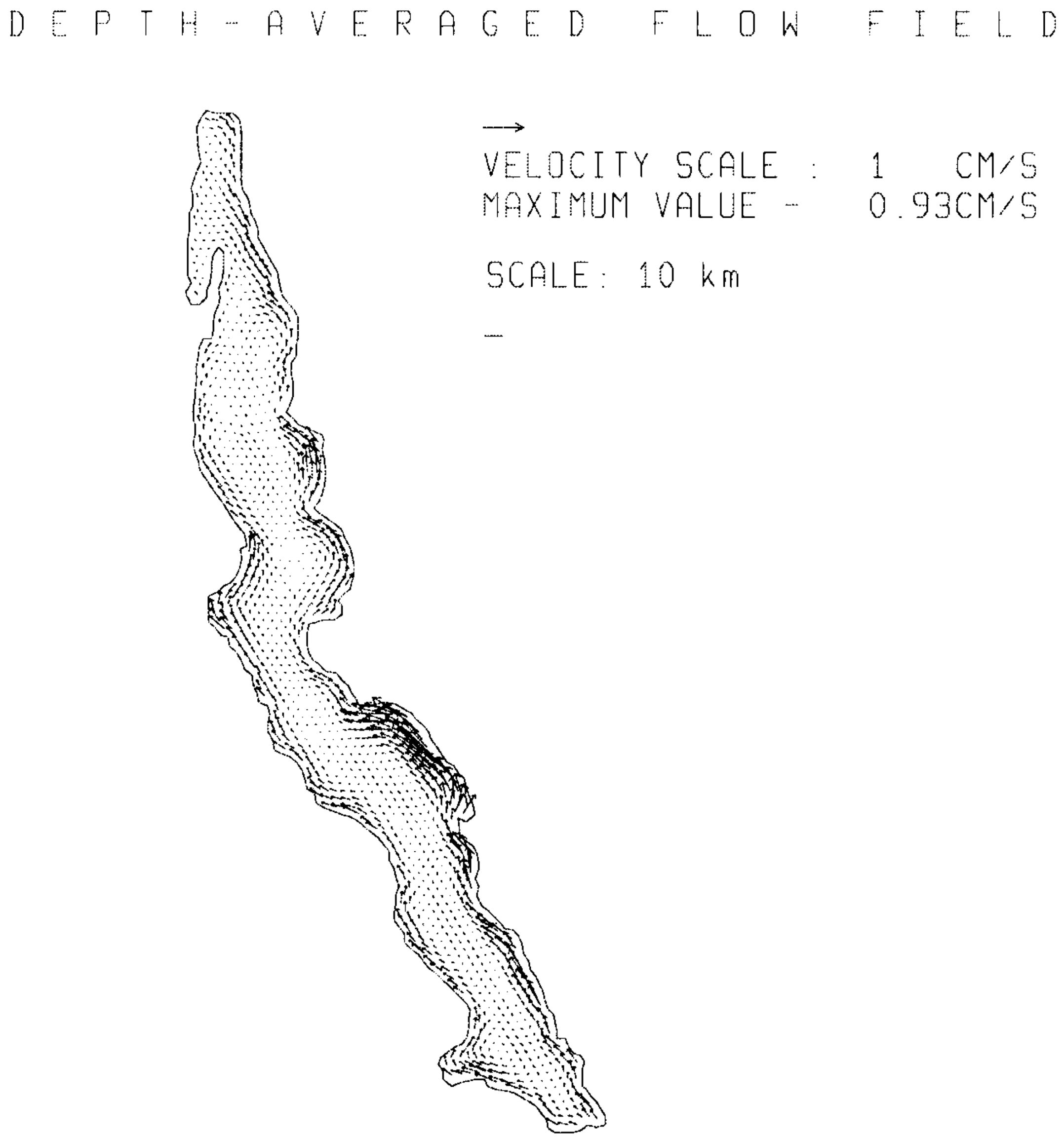

Fig. 2.4 Depth-averaged flow velocity calculated by 3D model at 22 hours (LT) on 28 Aug 1997. The number of large scale gyres is less than in Fig. 2.3. The magnitude of this depth integrated velociy is at maximum in shallowest regions.

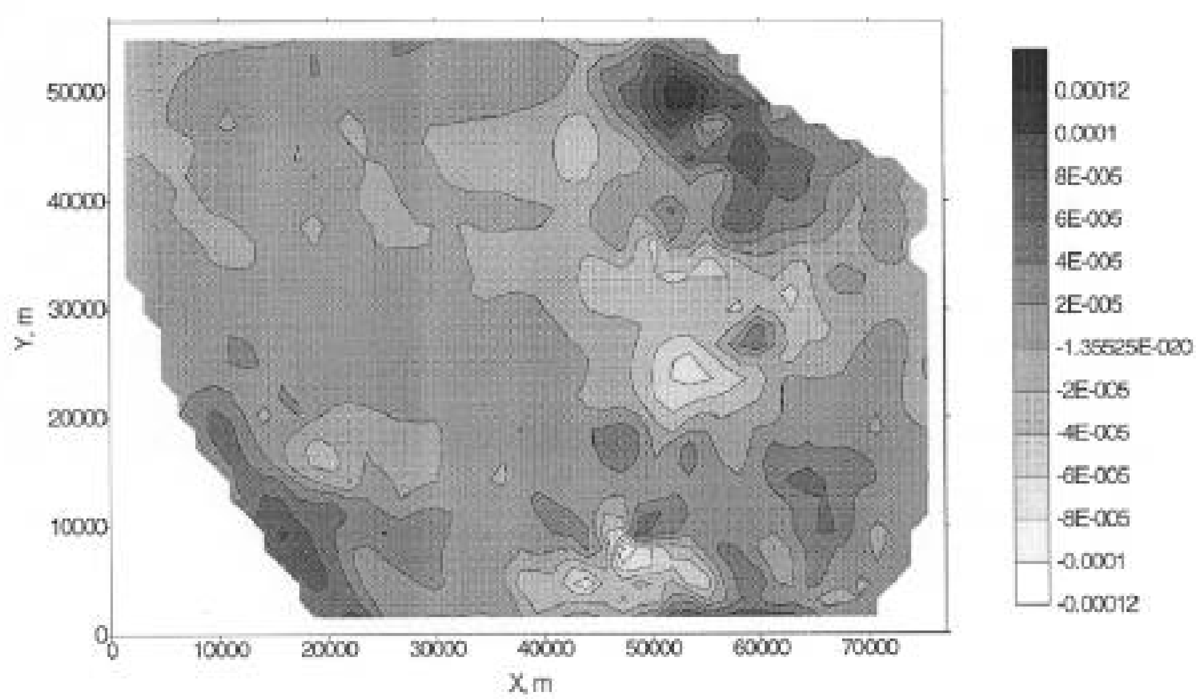

Fig. 2.5 Calculated vertical velocity (ms^{-1}) in Malagarasi region (high resolution flow model) at 22 hours (LT) on 8 Apr 1997. The high patchiness of the vertical flow structure is seen.

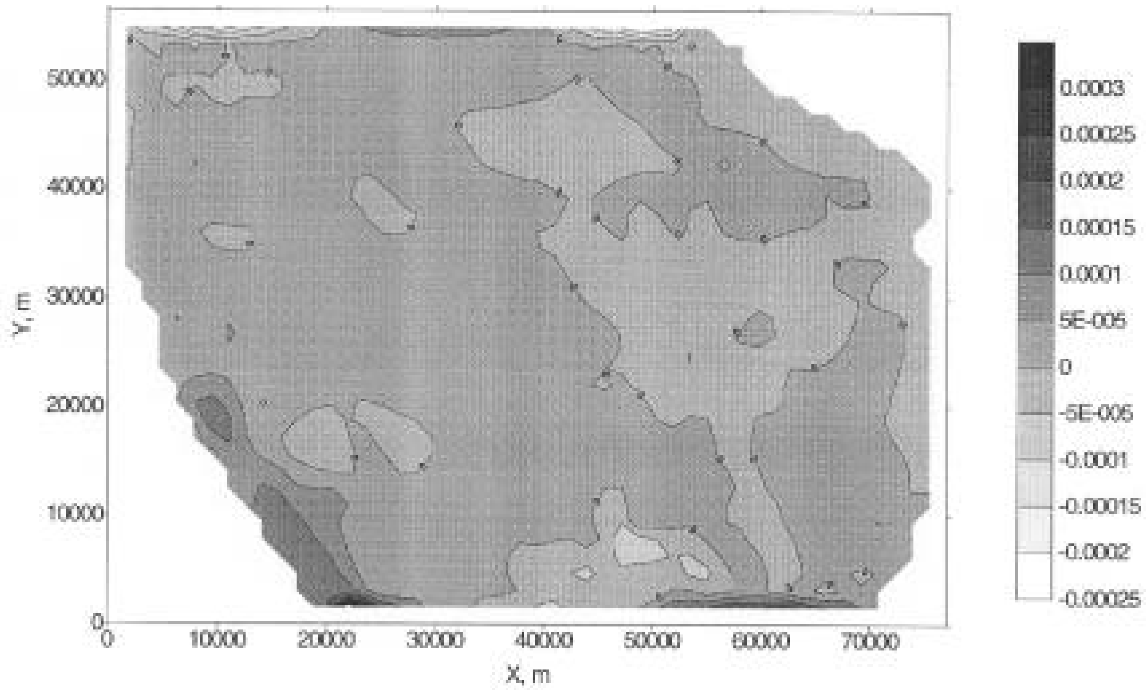

Fig. 2.6 Calculated vertical velocity (ms^{-1}) in Malagarasi region (high resolution flow model) at 22 hours (LT) on 28 Aug 1997. The degreee of patchiness in the vertical flow structure is less than is the case in Fig. 2.5. However, for the highest value areas along the western coast, values are about twice those seen in Fig. 2.5.

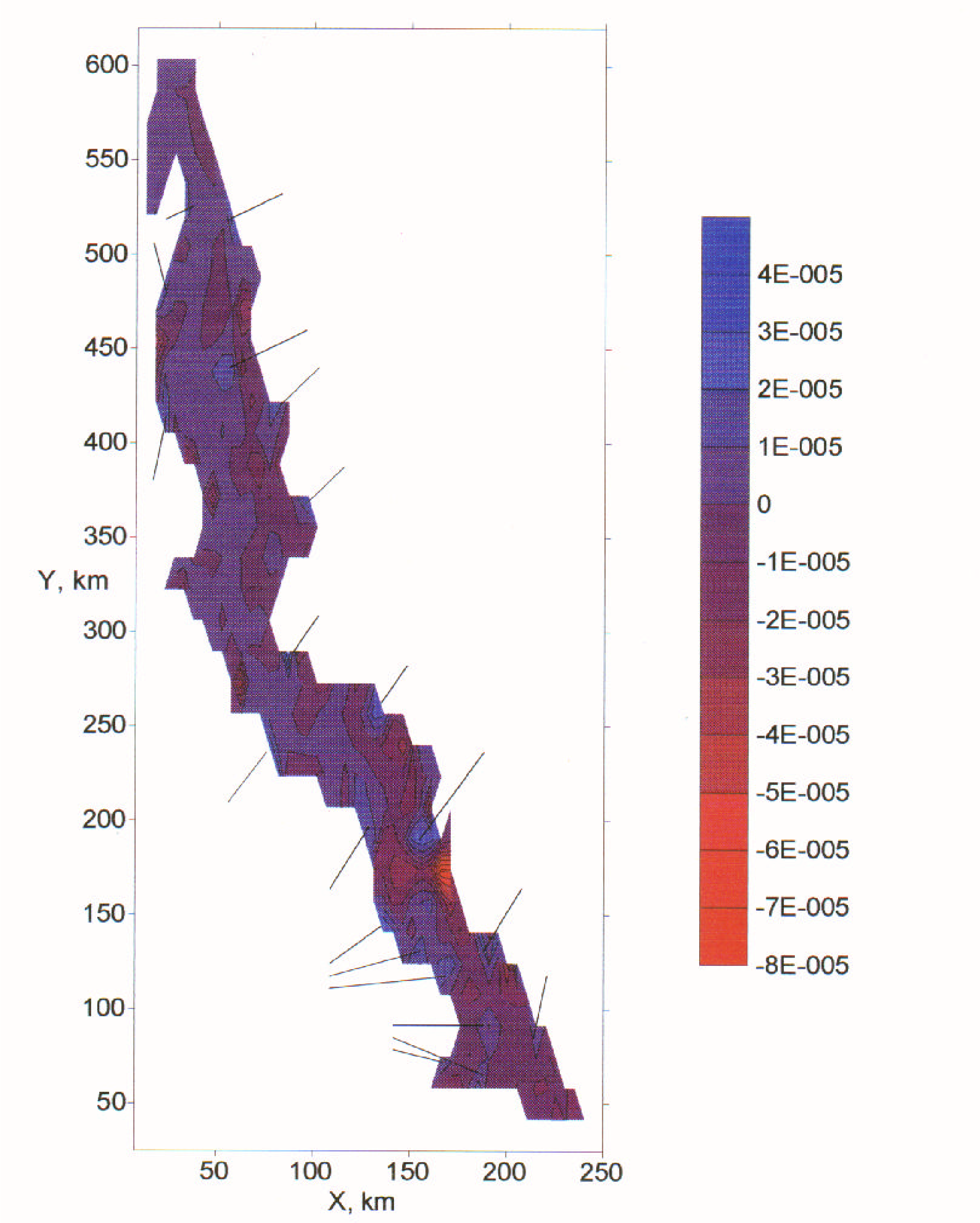

Fig. 2.7 Calculated vertical velocity (ms^{-1}) in lake-wide flow model at 22 hours (LT) on 28 Aug 1997. The core of each upwelling area is denoted with lines from the shore. Areas of upwelling and downwelling are closely connected. Even in the south basin upwelling occurs only in the middle part.

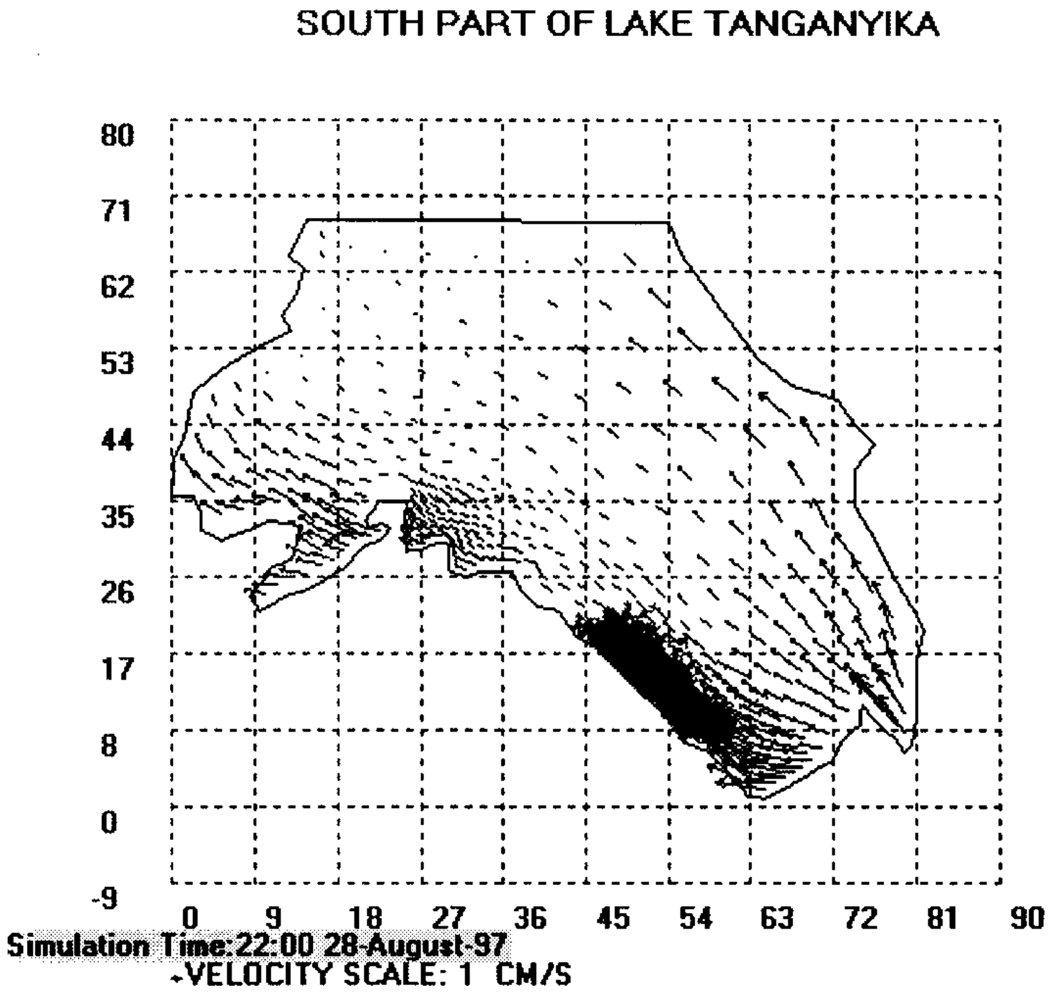

Fig. 2.8 Calculated transport of zooplankton in southern part of the lake during 22-28 Aug 1997. The origin of the community has been at a point near the coast (x=60 and y=8). The community has been transported with the flow around 20 km towards the north.

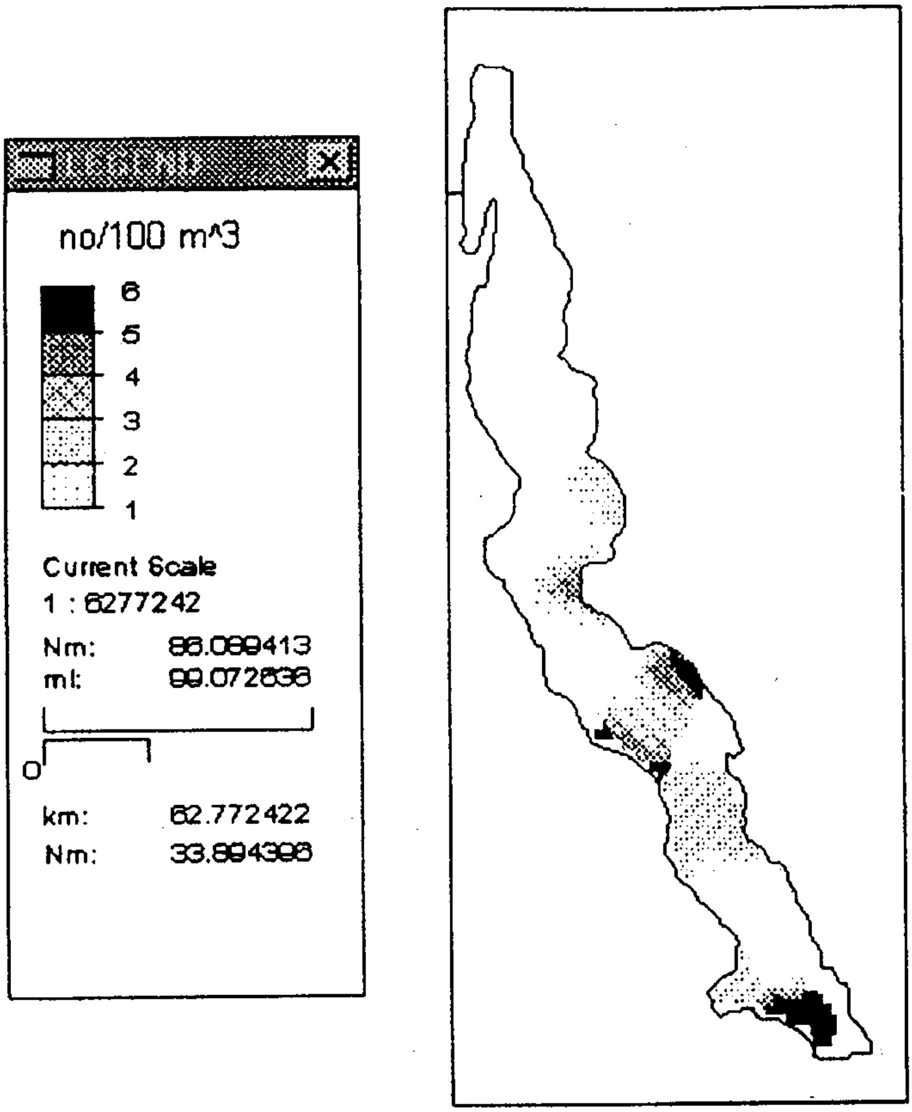

Fig. 2.9 Distribution of *L. stappersii* larvae within 0 – 100 m water column in June 1995 (Mannini 1998).

CHAPTER 3

REMOTE SENSING

By:
Tuomainen, V. J. Parkkinen, H. Mölsä & O.V.Lindqvist

Abstract

Satellite borne remote sensing technology using NOAA AVHRR imagery was applied to monitor the spatial and temporal variations of the surface water temperature of Lake Tanganyika. Studies on chlorophyll *a* and related vegatation indices (NDVI) were not suitable to monitor the primary production patterns as the maximal chlorophyll *a* concentration was usually found in comparatively deep water (around 30 m) and *in vivo* fluorescence of chlorophyll *a* at the surface often approached zero values during the day due to strong solar irradiance. Therefore only the remote sensing results of surface temperature were used to complement data for hydrodynamic modelling. Ground truth data was obtained from 1-m subsurface thermal sensors on meteo buoy off Mpulungu to develop own parameters for temperature data. The linear correlation coefficient between the measured and estimated temperatures for NOAA-11 satellite data was R^2 = 0.9425 (n= 14), and for NOAA-14 satellite data R^2 = 0.8897 (n= 28), respectively.

3.1. INTRODUCTION

Remote sensing technology was used at the LTR project in order to compile data of the spatial and temporal variations of surface water conditions of the Lake Tanganyika. The physical and limnological characteristics of the lake are claimed to show similarities with marine conditions (Hecky, 1991; Hecky *et al.*, 1991; Plisnier *et al.*, 1996; Huttula, 1997). This has led, particularly in the case of hydrodynamic studies, to the usage of modern devices developed for oceanic conditions. Given also the sheer size of the lake, isolated by high steep mountains, with poor logistic infrastructure (Coulter & Spigel, 1991), the application of satellite-borne monitoring was regarded as reasonable and was thus chosen to complement conventional field surveys at fixed stations. Remote sensing, validated by ground-truth data, has aroused growing interest in studies on eutrophication, thermal regimes, and sediment transport both in lacustrine (Malm *et al.*, 1994; Nakayama, 1994; Zilioli *et al.*, 1994,) and marine (Babin *et al.*, 1996) environments, including tropical environments (Nakayama, 1994; Wooster *et al.*, 1994). Simpson (1987, 1994) and Fiedler (1984) give examples of how remotely-sensed data and analysis methods have been used as tools in various applications, including fisheries management (by assessing the survival of fish eggs and larvae), assisting commercial fishermen in harvesting fish, and monitoring the onset of major interannual events (e.g. ENSO and associated warming events). Recently this technology has taken advantage of the reduced prices of satellite images and the developed image processing abilities.

In Lake Tanganyika, we aimed at combining the remote sensing results particularly with the hydrodynamic modelling to monitor the hydrophysical and limnological events of the lake environment. As stated by Parkkinen *et al.* (1994), remote sensing was proven useful in observing the possible upwellings that bring the cool and nutrient rich waters to the euphotic layers.

The initial task of the LTR remote sensing subcomponent was to determine the feasibility of different satellite sensors and their channels (see Parkkinen *et al.*, 1994). Initially studied parameters were the vegetation index (NDVI) and the lake surface temperature. During the study, it became obvious that the chlorophyll contents in the water layers nearest to the surface were too low for a reliable monitoring. The routines to analyse satellite images were developed at the University of Kuopio, entirely at no cost to the project itself and, accordingly, a number of sample images of Lake Tanganyika were processed for preliminary investigation. The NOAA AVHRR image analyses of surface temperature were specifically conducted on 1993-94 data. Problems of atmospheric and geometric correction were considered. Model parameters for channel calibration, e.g. in temperature determination dependant on object surface. One aim of this study was to determine these parameters for Lake Tanganyika by using NOAA-satellite imagery.

3.2 MATERIALS AND METHODS

From four alternatives (NOAA, ERS, Landsat, and SPOT) the NOAA platform with AVHRR radiometer was chosen due to its frequent passes over the lake (two times a day), operation of two functional satellites at the orbi (providing four images a day), and sufficient wavelength coverage (0.58-12.5 µm). The NOAA platform further offered spatial resolution of 1.1 km x 1.1 km which, though coarser than Landsat or SPOT (range 20 m through 120 m square), is adequate enough for the large, open area of Lake Tanganyika. For NOAA satellites, there are also "quick-look" images easily available for rapid scanning of cloudiness.[1]

All images for 1993-94 were purchased from the Eurimage either directly or via the National Land Survey of Finland. Images for 1994-95 came from EROS data center, RSA, La Reunion or Nairobi.

Determination of an index for **chlorophyll *a*** is not possible because of channel restrictions in NOAA satellites. Therefore the index was replaced with the ‘normalized difference vegetation index’ (NDVI) that uses the chlorophyll *a* absorption peak of Channel 1 (Los, 1993). Tuomainen *et al.* (1997) used the reflectance values instead of raw image data to enhance the equation. In this method the calibration tables from NOAA are used (Los, 1993) to determine the real pixel reflectances, which have been normalized to standard (90º) illumination angle.

As a short-cut for atmospheric correction, the darkest point of each image could be used as the offset value pixel, but because of the risk that the lowest value can be also an error, artefact or otherwise corrupted, this approach was not used. Using the preliminary atmospheric correction gives only relative values of the NDVI. In the project, real atmospheric corrections were based on own meteorological data. A number of NDVI-images were produced, but due to the low NDVI-values and too weak correspondence with ground truth, we concluded to use only surface temperature images in this study.

[1] For references on remote sensing technology and the characteristics of various satellite alternatives, see Tuomainen *et al.*, (1997); Colwell (1983); Jensen (1986); Lillesand & Kiefer (1987); Mather (1987) and Meaden & Kapetsky (1991). More information is also available at the following web sites: a) http://www.*nott.ac.uk/remote/satfaq.html;* and c) *http://ww.vtt.fi/aut/rs/virtual/.*

Currently, **lake surface temperature** is the most important attribute computed from the satellite images. Temperature can be determined directly from the thermal channels (4 and 5) of the AVHRR imager. The channel sensitivity is in the range of 10.3 µm and 11.5-12.5 µm for channels 4 and 5, respectively. For computing the actual temperature, we used the method based on the functional dependence between surface temperature and surface radiance, described in Tuomainen *et al.* (1997). Atmospheric effect can be reduced using the split window method (Anding & Kauth, 1970), in which the channels T_4 and T_5 are used to estimate surface temperature (T_S).

$$T_s = k_0 + k_1 T_4 + k_2 (T_4 - T_5) \qquad (1)$$

Tuomainen *et al.* (1997) have discussed in more detail the sources of geometric distortions that include the instrument error, panoramic distortion, Earth rotation and platform instability (Mather, 1987). As the instrument errors are caused exclusively by the instrument itself, panoramic distortion is introduced with the geometry of the imaging affecting more with increasing viewing angle. The third distortion is caused by the rotation of the Earth, which skews the image, and the fourth is caused by the instrument-carrying satellite.

Ground truth data on chlorophyll *a* and surface temperature were obtained from the project SSP at field stations and particularly from the thermal sensor of the meteo buoy located off Mpulungu station in the southern part of the lake (Huttula, 1997).

A UNIX-workstation (Silicon Graphics Crimson) and MATLAB and GMT-SYSTEM v. 2.1.4 (Wessel & Smith, 1991) software were used for processing and transferring the images from geographic coordinates to map projection (Mercator). In addition to the workstation, a PC (with Linux operating system) was used with a recent version of the mapping software, GMT-SYSTEM v. 3.0. These facilities were made available by the University of Kuopio at no cost to the LTR Project itself.

3.3. RESULTS

3.3.1 Satellite data and processing scheme

The study was done mainly on the basis of satellite images from the dry season of 1993 and 1994. The selection of the images was based first on the availability of the ground truth temperature values that were obtained from the buoy off Mpulungu, in the southern part of Lake Tanganyika and secondly, according to cloudiness in the region. After studying the quick-look images, fourteen datafiles delivered in SHARP-2A-format from 1993 to 1994 met those conditions.

Later in 1995 another buoy was set outside Kigoma, the middle part of lake, and further acquisition of satellite image data became necessary. As there were no data available at Eurimage, EROS online data service was utilised via the Internet, which lead to the purchase of 28 additional image data. These files were delivered in a Level-1 B format (see, Kidwell, 1995).

Necessary information on cloudiness conditions over Lake Tanganyika was taken via the Internet from Meteosat satellite, which provides this information every 30 minutes for 42% globe area, including Africa. During cloudy or very cloudy conditions, no satellite imagery data can be used in the visible or infrared region of the electromagnetic spectrum. Clear sky with ideal conditions to obtain satellite imagery first appears around April and becomes more common during June through September. Moderate cloudiness occurs during other seasons, allowing only partly image acquisition for the lake. In 1991 and 1993 clear sky conditions were observed only in late May and June (the last month analysed). For the first half of 1991 conditions were too cloudy.

3.3.2 Vegetation index

Vegetation indices were determined with the equation (3) of Los (1993). Maximal chlorophyll *a* concentration was generally found in quite deep water (around 30 m) and at the surface the *in vivo* fluorescence of chlorophyll *a* often approached zero values during the day (Salonen & Sarvala, 1994; Sarvala & Salonen, 1995; Järvinen *et al.*, 1996, 1999; Salonen *et al.*, 1999). Therefore, the results remained demonstrative only and no further use of satellite borne NDVI was reasonable.

3.3.3 Surface temperature

Data from satellite thermal channels were used to determine the surface temperature with the equation (1) above (Anding & Kauth, 1970). Ground truth data of temperature was taken from the sensor 1-m below the surface at Mpulungu buoy. The linear correlation coefficient between the measured and estimated temperatures for NOAA-11 satellite data was $R^2 = 0.94$ (n = 14), and for NOAA-14 satellite data $R^2 = 0.89$ (n = 28), respectively (Table 3.1.). An example of average surface temperature data is given in Figure 3.1.

Table 3.1. Temperature algorithms estimated in this study and according to literature.

Source	a_0	a_1	a_2	Standard Error (K)	R^2
Tuomainen *et al.* (1997)					
NOAA-11	5.3379	2.3348	-1.5155	0.3016	0.94
NOAA-14	3.3780	2.9946	-2.1719	0.3056	0.89
McMillan & Crosby, 1984	-0.5820	3.7020	-2.7020	0.8039	
McClain *et. Al.*, 1985	4.7400	3.6540	-2.6680	1.1382	
Yokoyama & Tanaba, 1991	0.5300	3.3310	-2.3310	0.6311	
Wooster *et. Al.*, 1994	6.9800	3.1961	-2.2130	1.9013	

3.3.4 Upwelling

The satellite images were used to describe the upwelling of deep waters. Parkkinen *et al.*, (1994) observed the only upwelling at the southern end of the lake apparent in the vegetation index on 29 June 1991, with some secondary upwellings along the eastern and western coasts. This may indicate that the vegetation index is not suitable for describing upwelling that takes place rarely or whose surface effects disappear quickly. The limnological and hydrodynamic data indicate, however, that these upwellings actually are very common and the vertical mixing happens down to 20 through 40 m due to local winds. Such mixing may occur within hours or a few days (Huttula & Podsetchine 1994; Peltonen 1997). In the south, the major upwelling is likely to take place more often and last up to several weeks during the dominating winds. Remote sensing data on these circumstances were combined in the hydrodynamic studies and water circulation modelling (Huttula 1997; Podstechine 1997).

3.3.5 Thermal changes

Daytime satellite measurements with NOAA-11 and NOAA-14 gave good overall picture of horizontal thermal regimes. Cooling effects of the Malagarasi river during May through September were seen, and south-north movements of cooler water mass were followed up during successive days in July 1995 (Tuomainen *et al.*, 1997).

3.4. CONCLUSIONS

The seasonal window (i.e., clear sky) for satellite imagery over Lake Tanganyika is generally from May through September, although occasionally cloudless days may be met at other times also. This is fortunate because the end of dry season is the time when the upwellings are most likely to occur.

The temperature results obtained through satellite images have been verified with ground measurements of the 1-m sensor attached to the lake meteo buoy outside of Mpulungu, providing significant positive correlations and development of own parameters within Lake Tanganyika data. This was noted regardless the fact that actual temperature at the depth of one meter is not always the same as the temperature of the uppermost surface layers of the water column. Wooster *et al.* (1994a) have paid much attention to the so-called ‘skin effect,’ i.e. a thin film on top of the water with a temperature that slightly differs from the deeper layers, and have therefore treated their results on Lake Malawi with caution. The top layer of 5-10 mm is caused by varying local wind, evaporation and temperature diffusion. Our results, however, indicate a highly significant correlation between the observed and measured temperatures, and therefore suggest the phenomenon to be less significant. Effective mixing of top layers of water mass with vertical speeds of 5-10 m/d cause a homogenous water layer to descend usually down to 20-40 m off Mpulungu (Huttula, 1997).

Determination of chlorophyll *a* is more problematic than determination of temperature. NDVI describes the reflective colour of the object (object looks green, when red light is absorbed). The values of vegetation indices are relative and need to be verified with field measurements done off the field stations and during the surveys. High Secchi disc values in Lake Tanganyika (5-12 m, even 22 m, see Plisnier *et al.*, 1995) may add doubts concerning the possibility of detecting chlorophyll *a* from the NOAA AVHRR images. Further, the clear inactivation of photoactive pigments due to photoinhibition was observed to take place within a few hours before noon (see Salonen *et al.*, 1999), and may be another source of error for this particular method. Babin *et al.* (1996) also noted a few aspects that make detecting the sun-induced chlorophyll *a* fluorescence difficult with remote sensing technology. Chlorophyll *a* fluorescence, with an emission maximum around 685 nm, is strongly absorbed by the water itself; therefore the fluorescence signal emerging from sea surface originates from the very upper layer and represents only a minute fraction of the whole water column chlorophyll *a* content. Secondly, near surface phytoplankton actually experience the most acute physiological stress due to excessive irradiance (see Salonen *et al.*, 1999, for Tanganyika) and possibly nutrient limitation, weakening the quantitative assessment of fluorescence.

Nakayama (1994) claimed, however, that the AVHRR Channel 1 was proven useful in water quality monitoring including algae blooms in temperate Lake Biwa (Japan) with an accuracy comparable to LANDSAT. Wooster *et al.* (1994 a) showed the triple window algorithms of McClain *et al.* (1985) to provide most accurate estimation of tropical lake surface temperature when studied in Lake Malawi conditions. A real-time PC-based receiving station was recommended by Wooster *et al.* (1994b) for directing scientists in immediate field activities.

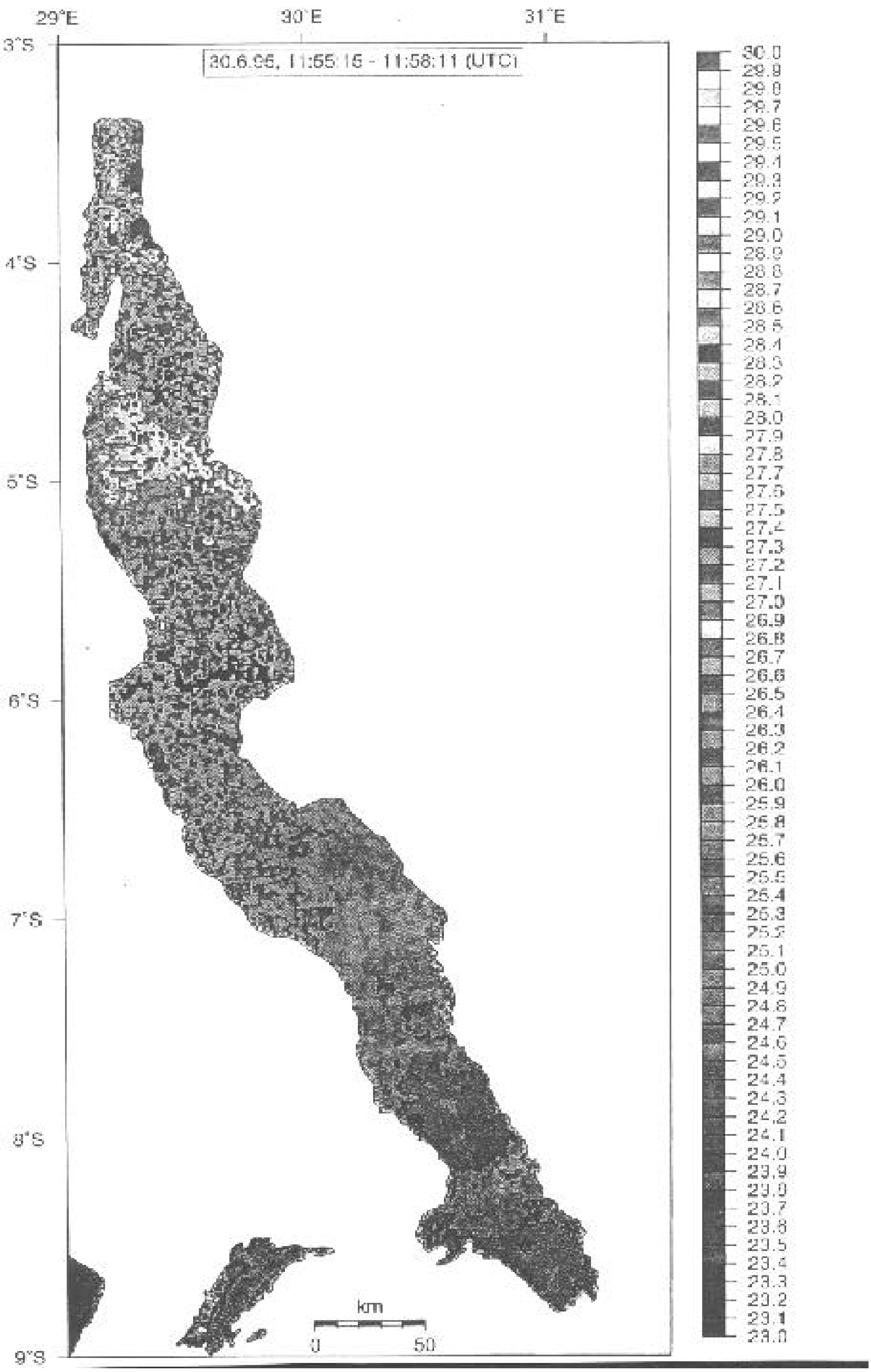

Fig 3.1 NOAA-14 AVHRR: SST (°C)

CHAPTER 4

LIMNOLOGY AND PHYTOPLANKTON PRIMARY PRODUCTION

By:
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Abstract

Basic limnological studies have dealt with the distribution and availability of macro-nutrients, patterns of primary production and the seasonal changes in the physical limnology affecting the water chemistry and nutrient regime of Lake Tanganyika. The access of nutrient rich waters to the productive euphotic layer is the primary factor affecting the phytoplankton production. The level and occurrence of primary production is mainly determined by the partial mixing within the epilimnion and the relation between mixing depth and euphotic depth, i.e., by the vertical distribution of temperature relative to ambient irradiance.

Phytoplankton of Lake Tanganyika was mostly distributed in a thick water layer, generally down to 60 m. Cyanobacteria contributed significantly to the phytoplankton biomass. During all seasons, bacteria-sized picocyanobacteria were very abundant. Including heterotrophic bacterioplankton, organisms <1 micrometer in diameter were thus probably an important food source for planktonic consumers. Near the surface phytoplankton was probably under a multiple stress of nutrient limitation and high solar UV-light radiation. Combined with the hydrodynamic properties of Lake Tanganyika, these features make phytoplankton primary production highly dynamic and hence difficult to assess. Compared to earlier estimates, the measured phytoplankton primary production was 47-128% higher, i.e. 426-662 g C m^{-2} a^{-1}. The concentration of dissolved organic carbon was confirmed to be low, 2-3 g C m^{-3}. Thus, although bacteria are evidently an important component of the plankton, with a production of ca. 20 % of that of phytoplankton, the epilimnetic food chains of Lake Tanganyika are probably mostly based on phytoplankton primary production.

4.1. INTRODUCTION

LTR limnological studies concern physical processes in Lake Tanganyika and their influence on such factors as light, nutrients and chlorophyll *a*. A 'typical' annual limological cycle studied by the LTR team includes the dry season, starting in May-June and featuring south-east winds driving the surface water towards north. This causes accumulation of warm water and a deepening of the thermocline in the north (down to 70-90m in Bujumbura). At the south end of the lake the winds cool the surface water by convection and wind mixing, first deepening the thermocline and finally breaking it by August. After the SE winds cease in September or October, the vertical stratification is re-established by November (Plisnier *et al*, 1996; Plisnier, 1996; Langenberg, 1996; Peltonen *et. al.*, 1997).

Apart from the regular limnological sampling programme (SSP) at three permanent locations (Plisnier *et al.*, 1996; Craig, 1997), the daily and seasonal patterns of primary production, phytoplankton *in vivo* fluorescence of chlorophyll *a* and biomass were assessed during lake-wide surveys. Special attention was given to the role of dissolved organic carbon (DOC) and bacterioplankton in the production process.

In large lakes phytoplankton primary production is generally the main source of carbon and energy for food webs. Thus the effects of the changes in primary production or even in its partition between different phytoplankton species are transmitted along the food chains and ultimately affect fish production. Earlier the phytoplankton primary production on Lake Tanganyika had been studied only during short time periods, resulting in the conclusion that the level of primary production was exceptionally low compared with the secondary production and fish yield (Hecky & Kling 1981; Burgis 1984; Hecky 1984). One of the main aims in the current research was therefore to improve the temporal coverage by distributing the determinations at three geographical regions over a whole annual cycle. Besides the determination of primary production, the general distribution of phytoplankton was also studied in order to reveal the general conditions for zooplankton feeding.

4.2. MATERIALS AND METHODS

Total solar **irradiance** was recorded along with other weather variables at automatic weather stations, including two land-based stations at Bujumbura and Kigoma Airport, and two buoy-based stations off of Mpulungu and Kigoma (Kotilainen *et al.*, 1995). A LI-COR instrument was used to record the depth attenuation of photosynthetically active radiation. Vertical profiles of *in situ* irradiance were measured during the cruises and during the third year of regular monitoring at the three field stations (Sarvala *et al.*, 1999). Phytoplankton ***in vivo*** **fluorescence** of chlorophyll *a* at different depths (down to 100 m) in 1995-96 and horizontal positions was measured with a field fluorometer off Kigoma and Bujumbura in 1994 (Salonen & Sarvala, 1994; Sarvala & Salonen, 1995) and onboard *R/V Tanganyika Explorer* in 1995, 1996, 1998 (Järvinen *et al.*, 1996, Salonen *et al.*, 1999). Fluorescence readings were calibrated against extracted chlorophyll *a*, which was then determined spectrophotometrically (Salonen & Sarvala, 1995) or using a fluorescence spectrophotometer (Järvinen *et al.*, 1996; Salonen *et al.*, 1999). Phytoplankton was counted using a settling chamber technique. Picoplankton was counted using the autofluorescence of chlorophyll *a* or phycoerythrin which is characteristic to cyanobacteria. Vertical series of extracted chlorophyll *a* determinations were also made on weekly samples from the permanent field stations off Bujumbura, Kigoma and Mpulungu, starting from August 1995. A **biomass** estimate for phytoplankton was obtained from the average chlorophyll (0-40 m depth) by assuming a carbon:chlorophyll ratio of 35 (Sarvala *et al.,* 1982).

Phytoplankton **primary production** was assessed with the whole-water modification of the radiocarbon method (Schindler *et al.*, 1972) *in situ* in 1994 off Kigoma, and in August 1995 - June 1996 at the three main sampling stations off Bujumbura, Kigoma and Mpulungu. Dissolved inorganic carbon (**DIC**) in water was determined in Finland with a carbon analyser according to Salonen (1981). During two lake-wide cruises (April-May 1995 and October-November 1995), primary production was also measured in an on-board incubator at different light intensities to obtain representative photosynthesis-irradiance (P-I) curves (Järvinen *et al.* 1996; Salonen *et al.* 1999; Sarvala *et al.* 1999).

Simulated *in situ* primary production was calculated separately for the dry and wet seasons using respective data on light extinction, transparency, chlorophyll measurements and production-irradiance curves (Sarvala *et al.,* 1999).

Bacterioplankton production was assessed with the leucine incorporation method of Kirchman (1995) during two cruises in 1995 (Järvinen *et al.* 1996). **Total respiration** of plankton was measured as oxygen consumption off Kigoma in April 1994 (Salonen & Sarvala 1994). Dissolved organic carbon (**DOC**) was determined from two vertical series from 0 to 80 m depth in 1995 at the southern and northern ends of the lake (Järvinen *et al.* 1996).

4.3. RESULTS

The tilting thermocline results in a density imbalance that acts as a store of potential energy. During the decreasing wind the water masses will move towards equilibrium. The degree of wind shear stress on the lake surface (measured as the Wedderburn number W) in Mpulungu was low as expected during the dry, windy seasons indicating thermocline tilting, mixing and possible upwelling.

The seasonal changes in the physical limnology of the lake affected its water chemistry and the nutrient regime. Weekly sampling at the main stations indicated the presence of tilting thermocline that results in a density imbalance acting also as a store of potential energy. Internal waves of of 23 days during the dry and 35 days during the wet season were observed. 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 very low compared to those in the hypolimnion, probably due to uptake by autotrophic organisms (Plisnier *et al.*, 1996; Plisnier, 1996; Langenberg, 1996). The lower metalimnion boundary was at is maximum in the southern end of the lake, where it approached the depth of 300 m during the dry season (Plisnier *et al.*, 1996).

According to Langenberg (1996) the chlorophyll *a* concentrations were lowest from August to mid-September, increasing after this, and highest in November- December both in Bujumbura and Kigoma. In Mpulungu the upwelling period from August to mid-September showed a cool water pulse, low in nutrients but high in chlorophyll *a*, whereas the other two periods were less productive in terms of chlorophyll *a* concentrations.

The access of nutrient rich deep waters to the productive euphotic layers does not as such directly lead into increased primary production. The different vertical distribution of temperature, dissolved oxygen and nutrients (particularly the position of thermocline, oxycline and chemocline, and the relation between mixing depth and euphotic depth) may lead to the replenishment of nutrients into the euphotic zone stimulating biological production. (Langenberg, 1996).

The average diurnal pattern of total solar **irradiance** was very similar at the northern and southern ends of the lake, although slightly lower values were recorded before noon in Bujumbura. This may be due to the shading effect of the mountainous terrain or to more frequent clouds in the north end of the lake. In Bujumbura, the average total irradiance in January-October 1995 was 230 Wm^{-2}; off Mpulungu the average for May-November 1995 was 256 Wm^{-2}. The 1993 annual average of total irradiance at Kigoma Airport, some kilometres east of the lake shore, was 206 Wm^{-2}, but higher values would be expected on the lake, because clouds tend to be more common over the land in this area. The irradiance levels experienced in different parts of the lake seem to be quite homogeneous (Sarvala *et al.* 1999).

Fluorescence and chlorophyll profiles showed values approaching 1 mg m^{-3} down to 50-60 m depth, in sunny weather a surface depression around noon, and often a maximum in fairly deep water at 30-40 m (Fig. 4.1; Sarvala & Salonen 1995; Järvinen *et al.* 1996; Salonen *et al.* 1999). In connection with local bluegreen blooms, much higher values (tens of mg m^{-3}) were observed immediately below water surface (Figs. 4.2 - 4.3). Likewise, primary production had its maximum usually at the depth of 10-20 m, and measurable production down to 40-50 m. The depth of the euphotic layer, depth to which 1% of the surface irradiance could penetrate, was also normally between 40 and 50 m throughout the lake in different seasons (Langenberg, 1996). The photic zone was usually deepest off Kigoma, which was the only permanent sampling station representing the conditions in the open central parts of Tanganyika.

During the first cruise in April-May 1995 the average fluorescence in surface water (excluding the midday depression) indicated a mean chlorophyll *a* concentration of 1.4 mg m^{-3} for the whole lake (Salonen *et al.*, 1999). For the uppermost 40 m the fluorescence-derived overall mean value was 0.96 mg m^{-3} (n = 53) and the corresponding mean for extracted chlorophyll *a* was 1.0 mg m^{-3} (n = 27). The average chlorophyll in the uppermost 40 m (calculated from fluorescence) was 2.2 mg m^{-3} in October-November 1995 (n = 76) and 2.8 mg m^{-3} in November 1996 (n = 27). Seasonal average values obtained from the first five months of weekly chlorophyll samples from off Bujumbura, Kigoma and Mpulungu were 0.6-1.6 mg extracted chlorophyll *a* m^{-3} (Langenberg, 1996).

Picocyanobacteria proved to be an important component of phytoplankton in Tanganyika (Salonen *et al.*, 1999) while eucaryotic picoplankton was always rare. Picocyanobacteria seem to be most abundant at the depth of 30-40 m.

Incubator measurements of primary production at different irradiance levels resulted in relatively flat photosynthesis-irradiance curves (Fig. 4.4), showing that the Tanganyika phytoplankton was capable of efficient photosynthesis even at the low irradiance levels obtaining in deep water at 30-40 m depth. No signs of photoinhibition were observed up to the highest experimental irradiance level of 512 mmol photon m^{-2} s^{-1}.

In the **incubator experiments** in October-November 1995 the chlorophyll-specific productivity *vs.* irradiance curves were practically identical from 1 to 30 m depth, allowing the use of common photosynthetic parameters for these depths.

The similar light responses suggest that phytoplankton in the uppermost 30 m had an identical history of light exposure, probably due to only partial mixing within the epilimnion. Indeed, vertical temperature profiles often showed secondary discontinuities at various depths above the major thermocline at 50-70 m (Salonen & Sarvala 1994; Huttula *et al.* 1994). At least down to a depth of 5 m, occasionally even down to 9-10 m the photoinhibition was likely for several hours per day, adding further complexity to the measurement of primary production.

DIC determinations resulted consistently at a very high concentration of ca. 72 mgC l^{-1}. This renders the radiocarbon method exceptionally insensitive in Lake Tanganyika compared to most other lakes. Average primary production assimilation numbers varied from 2.1 mgC (mg $chl)^{-1}$ h^{-1} during the April-May 1995 whole-lake cruise to 3.2 mgC (mg chl) $^{-1}$ h^{-1} during the

October-November cruise in 1995. The assimilation number obtained from *in situ* incubations in December 1994 off Kigoma (3.0 mgC (mg chl)$^{-1}$ h^{-1}) was similar to the latter value.

In April-May 1995, multiplication of the average assimilation number by the average surface chlorophyll value resulted in an estimate for the overall lake-wide primary production rate of approximately 2.0-2.1 mgC m^{-3} h^{-1}. Applying these values to a water layer of 40 m, the depth-integrated daily primary production would have been 0.80-0.86 gC m^{-2} d^{-1}. In October-November 1995, the corresponding production rate would have been 7.0 mgC m^{-3} h^{-1}, resulting in a daily productivity of 2.8 gC m^{-2} d^{-1}. Averaging these estimates would yield an annual production of 662 gC m^{-2} a^{-1} (Sarvala *et al.*, 1999).

The average simulated *in situ* production was 1.06 gC m^{-2} d-1 for the dry season and 2.49 gC m^{-2} d^{-1} for the wet season. Assuming a 6-month duration for both seasons, these values resulted in an annual production estimate of 647 gC m^{-2} a^{-1} for the whole lake (Sarvala *et al.* 1999).

A completely independent estimate for primary production was obtained from the seasonal *in situ* radiocarbon measurements done since August 1995 at the three permanent sampling localities in different parts of the lake (Fig. 4.5). The highest values were found off Bujumbura and the lowest off Mpulungu (the mean values (± 95 % CL) for the whole measurement period were 2.44±0.71 gC m^{-2} d^{-1} (number of measuring dates = 14), 0.52±0.09 (n = 8) and 0.54±0.38 (n = 7) for Bujumbura, Kigoma and Mpulungu, respectively). An overall average for the whole lake would be 1.2 gC m^{-2} d^{-1} or 426 gC m^{-2} a^{-1}; variability of the *in situ* measurements suggests that the 95 % confidence belt of this estimate might be about ±35 %.

The N:P ratios of seston indicated rather balanced N and P supply in the upper epilimnion of Lake Tanganyika plankton. But both particulate C:P and C:N ratios indicated moderate nutrient deficiency (Järvinen *et al.* 1999). In enrichment bioassays, a combined addition of P and N always increased primary production but a slight increase was also found after the addition of phosphate-P, while the additions of ammonium-N had no effect. The strong stimulation of primary production after the combined addition of P and N and the short turnover time of P (Salonen *et al.* 1999) support the conclusion of a restricted but balanced nutrient supply.

4.3.1 Bacterioplankton production

In April-May 1995 (Järvinen *et al.* 1996) the bacterial biomass production was in average 2.8 mgC m^{-3} d^{-1}, or slightly more than 20 % of the average phytoplankton primary production measured during the same cruise (13.6 mgC m^{-3} d^{-1}). In Oct-Nov 1995, the highest values usually occurred in the upper water layers, although at one site the maximum values were recorded below the thermocline (Fig. 4.6). Bacterial production correlated positively with the chlorophyll level of the same samples (r^2 = 0.76, n = 23;). During this cruise, bacterioplankton production amounted on an average to 21% of phytoplankton production estimated from chlorophyll and the average assimilation number.

4.3.2 DOC determinations and total community respiration

The mean concentration of DOC varied between 2.2 and 2.9 mgC l^{-1}, and was highest close to the surface (Järvinen *et al.*, 1996). Based on oxygen consumption by the whole plankton community in the uppermost 30 m, the community respiration would be 1.6-2.5 gC m^{-2} d^{-1} in a 0-50 m water column, representing the fully oxic epilimnion. This daily carbon consumption rate is less than 2% of the DOC storage, but it is almost in balance with the phytoplankton primary production estimated for the season, suggesting efficient carbon cycling within the epilimnion.

4.4 CONCLUSIONS

Phytoplankton primary production was found to be highly dynamic. Estimates based on three independent methods were higher than earlier reported. Due to the high density of picocyanobacteria and bacteria, food chains based on micrometer-sized organisms probably play an important role in Lake Tanganyika. However, because the concentration of DOC was low and bacterial production was only about one fifth of phytoplankton primary production, the latter seems to be the main driving force of planktonic food chains in Lake Tanganyika.

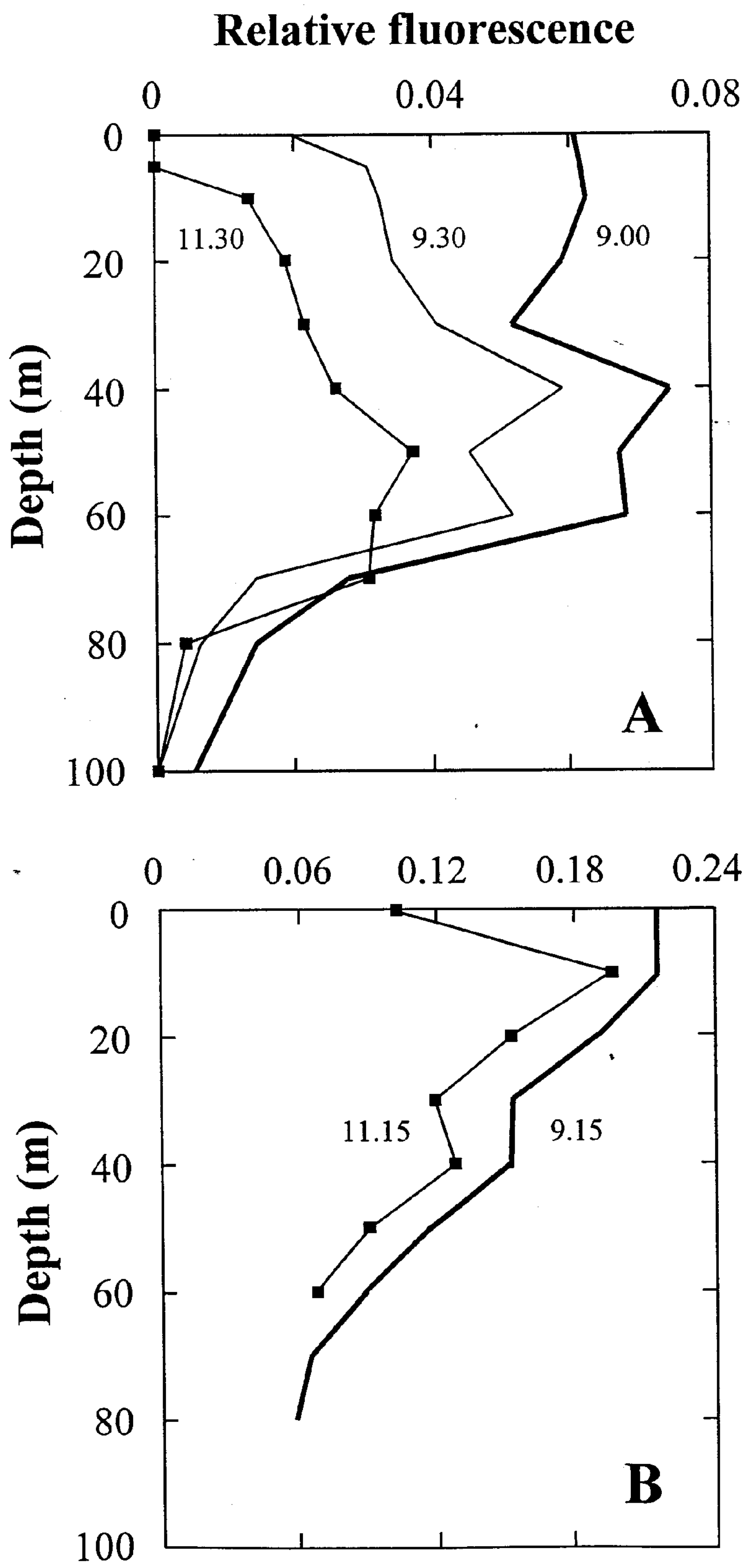

Fig. 4.1 Vertical distribution of blue excited *in vivo* fluorescence of chlorophyll *a* in Lake Tanganyika at different times of a day off Kigoma. A. 14 April 1994; B. 2 Dec. 1994 (Salonen *et al.* 1999).

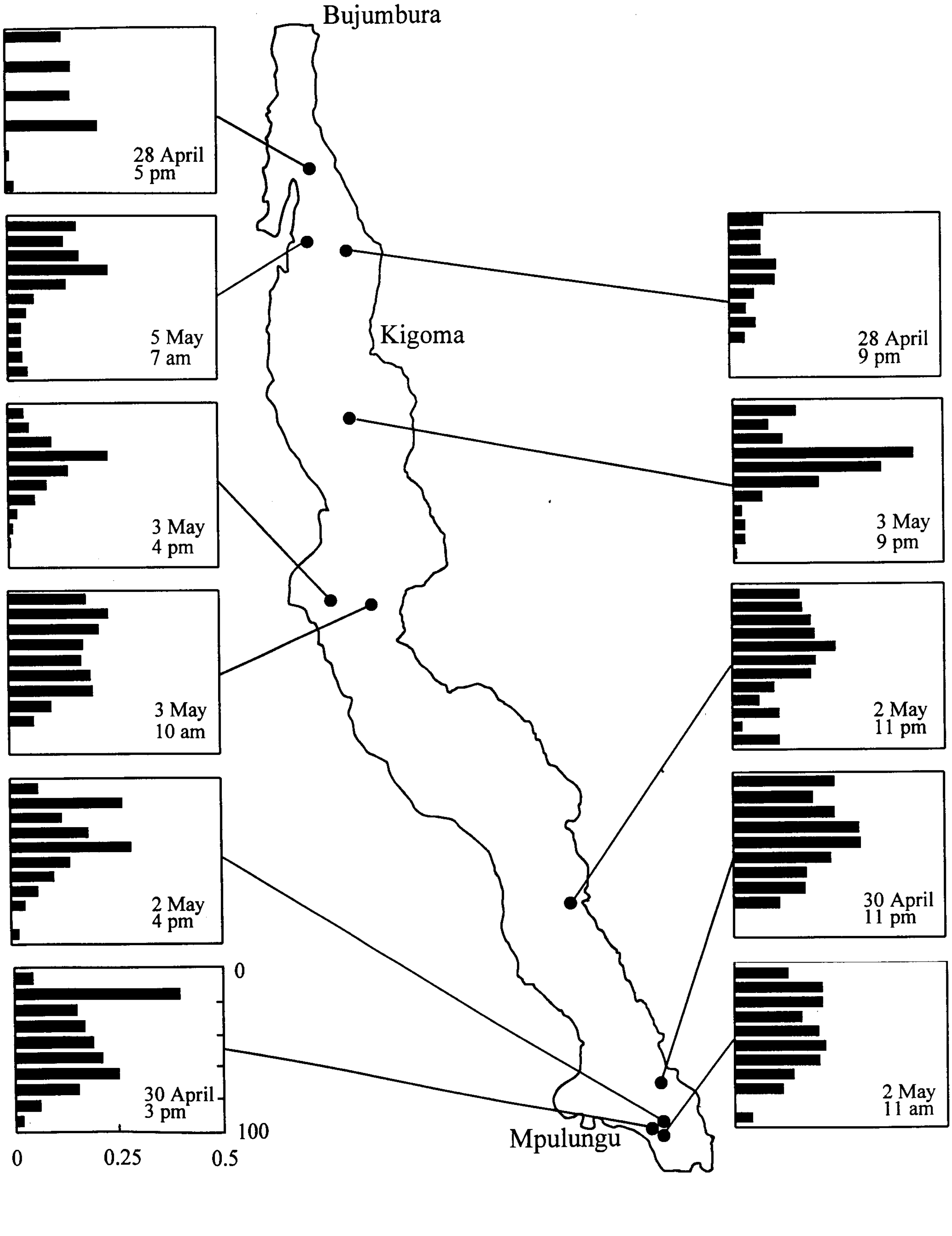

Fig. 4.2 Vertical (0-100 m) distribution of *in vivo* fluorescence (scale 0-0.5 relative units) of chlorophyll *a* in different parts of Lake Tanganyika in April-May 1995 (Salonen *et al.* 1999).

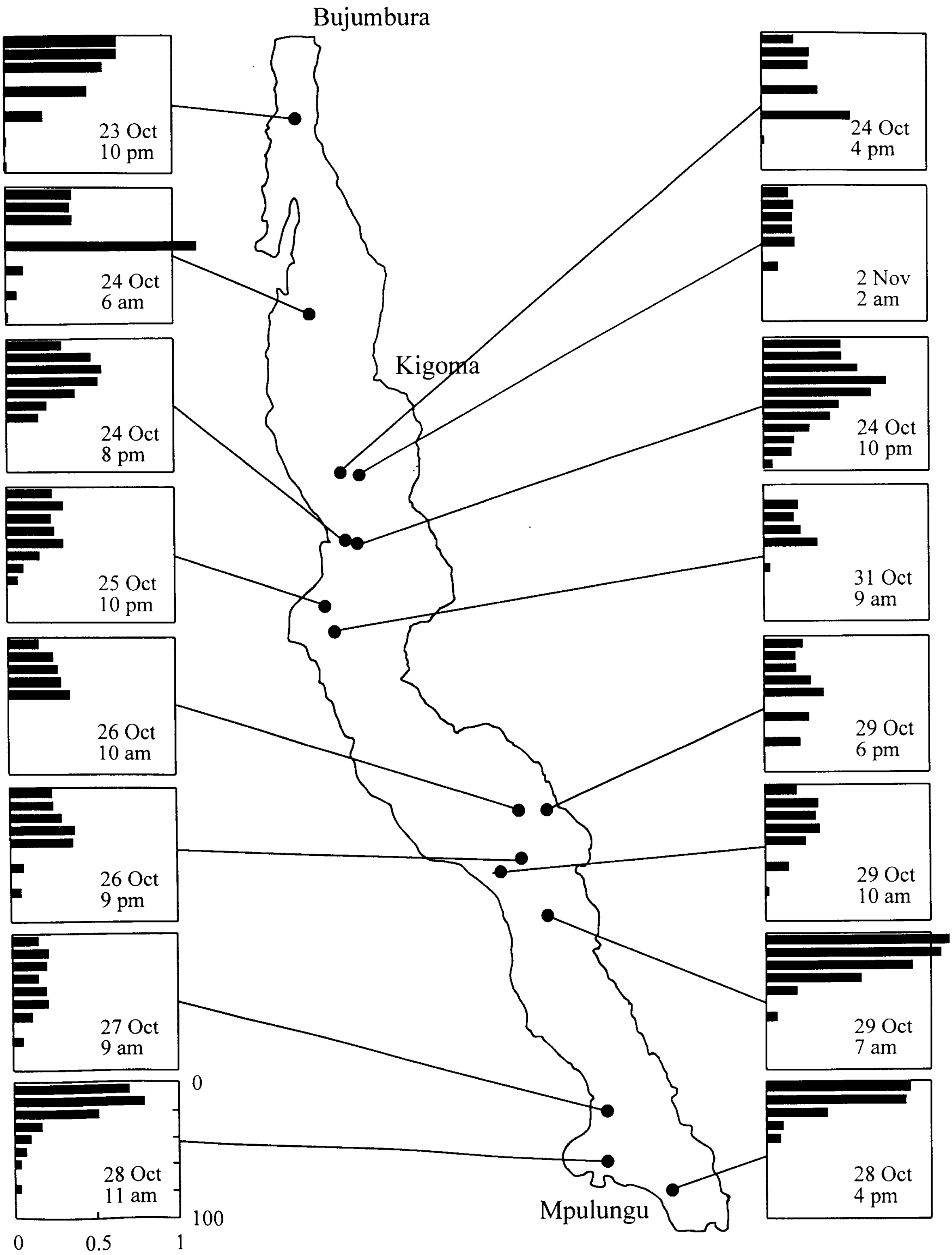

Fig. 4.3 Vertical (0-100 m) distribution of *in vivo* fluorescence (scale 0-0.5 relative units) of chlorophyll *a* in different parts of Lake Tanganyika in October 1995 (Salonen *et al.* 1999).

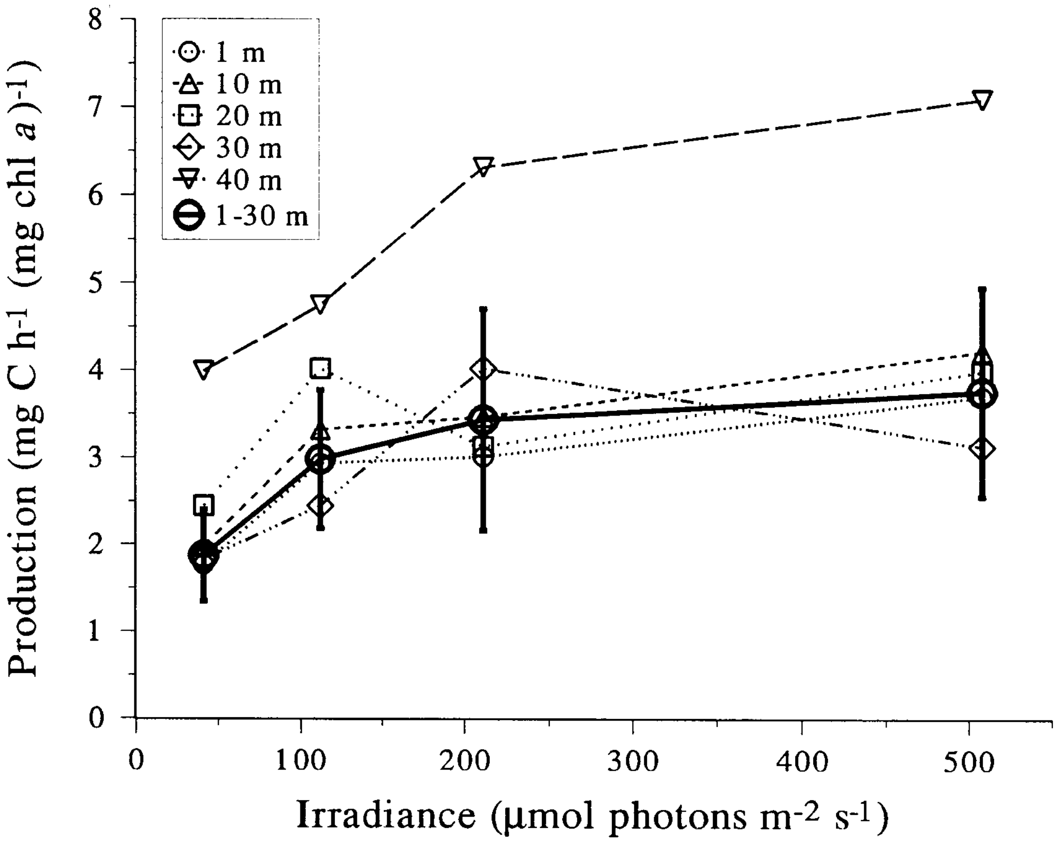

Fig. 4.4 Photosynthesis-irradiance curves for Lake Tanganyika phytoplankton from different depths, obtained from incubator experiments in October 1995. Combined curve for the depths 0-30 m given with standard deviations (vertical bars) (Sarvala *et al.* 1999).

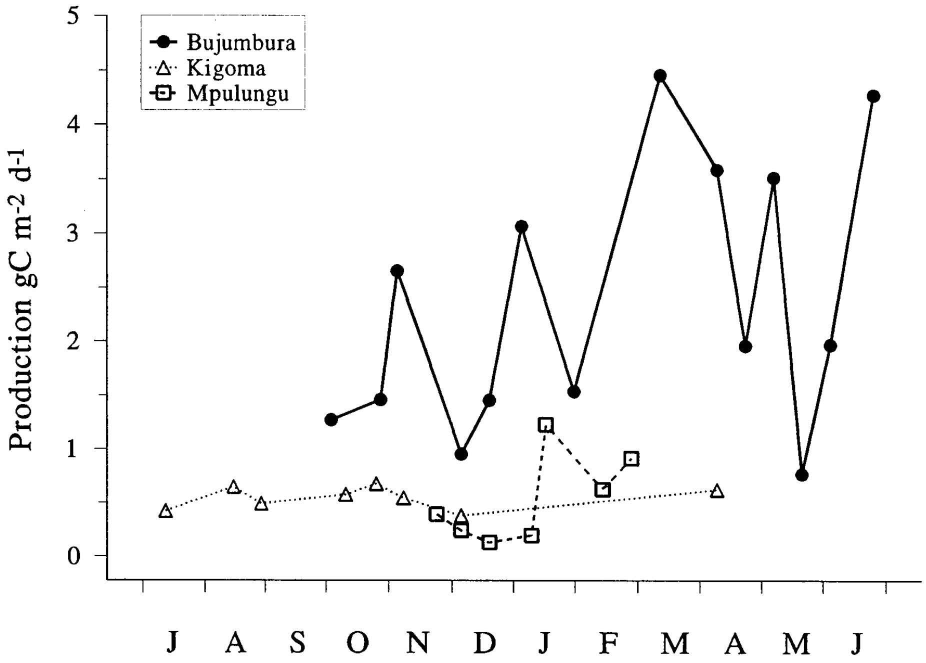

Fig. 4.5 In situ primary production in Lake Tanganyika at the three permanent field sampling stations in 1995-96. Original results of 4-hour incubations at different depths were converted into daily values using the hourly distribution of irradiance and integrated for the whole euphotic water column (Sarvala *et al.* 1999).

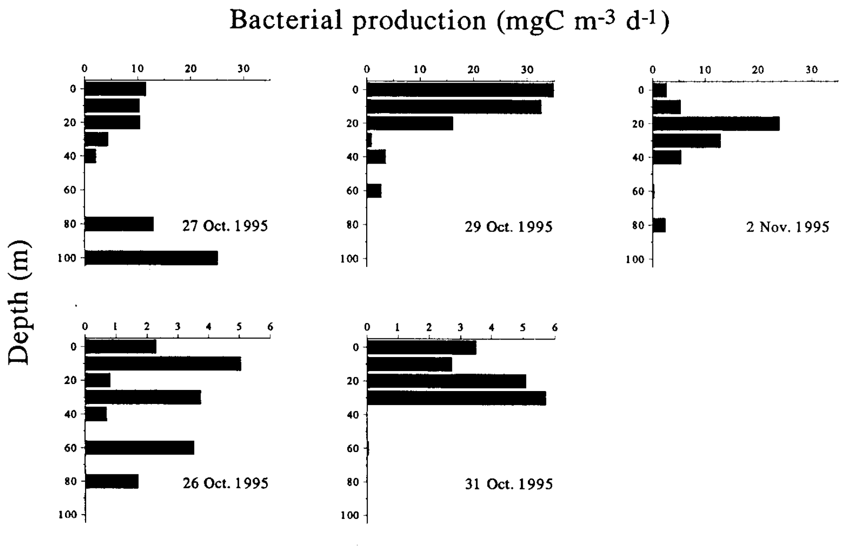

Fig. 4.6 Vertical profiles of bacterial producton (mgCm^{-3}d^{-1}, calculated from leucine incorporation (note different scales) in different parts of Lake Tanganyika in October-November 1995 (Sarvala *et al.* 1999).

CHAPTER 5

ZOOPLANKTON BIOLOGY

By:
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Abstract

Zooplankton studies demonstrate that the characteristics of the pelagic ecosystem in Lake Tanganyika are best understood in terms of physical limnology rather than those of traditional limnology. Upwelling and mixing create, together with the tilting thermocline, a more turbulent environment in the south than in the major parts of the lake where the hydrophysical conditions are more stratified. In the south the zooplankton were utilising a vertical space extending down to the depth of around 220 m, while in the north the respective depths were only half of that. Although there were clear differences in zooplankton between the seasonally sampled stations, the lake-wide cruise data showed that there was no consistent north-south gradient in the mesozooplankton community composition or biomass. The macrozooplankton communities did not show any consistent areal patterns either. The peak abundances of medusae were found randomly either in the north or in the south, and during many cruises the densities were rather evenly distributed in studied areas. Similarly the shrimp abundances were equally high both in the north and south, though fairly often their densities were highest in the south. The very patchy occurrence of shrimps made conclusions about their areal patterns uncertain. In spite of their modest role in the planktonic biomass and production, the atyid shrimps were very important in the diet of pelagic fish. Areal differences were clearly seen in fish diet and selective predation studies.

5.1 INTRODUCTION

The approach in the zooplankton studies was based on the classic idea that the pelagic community and also the fish diet would be dominated by one calanoid copepod, and this idea determined the field sampling design and the choice of sampling device. Another starting point was to look for seasonal changes in zooplankton such as demonstrated previously in Lake Malawi by Twombly (1983), and therefore a weekly sampling was planned at three field stations. A third approach concentrated on the behavioural adaptations of zooplankton facing highly selective predation, and was the basis for vertical migration studies. For practical reasons, sampling sites were selected within reasonable distance of the field stations and therefore they were established fairly nearshore to areas where fishing operations apparently also take place. Precedents were lacking as a thorough study on areal zooplankton differences had never been carried out prior to this exercise. The study was complemented in offshore areas during the lake-wide surveys with zooplankton samples integrated with other limnological, hydrophysical and fish biology sampling (Fig 5.1).

5.2. MATERIALS AND METHODS

Zooplankton abundance and composition for the one calanoid species (*Tropodiaptomus simplex)* and the cyclopoids as a group (divided into developmental stages) was monitored weekly or fortnightly at the three field stations. Three replicate hauls from 100 m to surface were taken with a 100-µm plankton net. *Limnocnida tanganicae* medusae, decapod shrimps, and fish eggs or larvae were also counted (Kurki *et al.* 1999b). Nets with mesh sizes of 50 and 100 µm were compared (Vuorinen & Kurki 1994; Kurki *et al.* 1999b) and vertical migration studies were made with a Limnos-sampler down to 140 m off Bujumbura and Kigoma and to 220 m off Mpulungu (Vuorinen *et al.* 1999). Individual carbon contents of the main crustacean zooplankton species were determined according to Salonen (1979) from preserved samples. Zooplankton production was calculated with the instantaneous growth rate method (Downing & Rigler 1984; Kimmerer 1987). Development times for *T.simplex* and *Mesocyclops aequatorialis* were derived from the literature on same or related species in the tropical lakes (Hart 1994; Irvine & Waya 1995) or from the LTR own rearings in Kigoma (Hyvönen 1997). For food selectivity studies, simultaneous zooplankton and fish stomach samples were collected during the surveys (Lensu 1998; Mannini 1998, 1999).

5.3. RESULTS

5.3.1 Zooplankton communities

According to weekly samples from the three main stations, the northernmost end of the lake was characterised by higher numbers of Cyclopoida, while in the southern end calanoids and cyclopoids were more or less equally abundant (Kurki *et al.* 1999a). Over two years, cyclopoids comprised 73%, 83%, and 63% of the total number of post-naupliar copepods in Bujumbura, Kigoma, and Mpulungu respectively. In biomass terms, the areal differences diminished because the small cyclopoids, which were dominant in the north, had a minor role in the south. The difference between calanoids and cyclopoids as clupeid food is important: a calanoid nauplius is comparable with a small cyclopoid adult in biomass. In Lake Tanganyika calanoids probably are more vulnerable to predation than cyclopoids owing to their larger size. High numbers of zooplankton in the northernmost part of the lake (Kurki *et al.* 1999a) supported the finding of Hecky & Kling (1981), that the water mass in the northern end is characterised by different biological properties from water in the main basins. Plankton abundances also showed higher variability in the north (Kurki *et al.* 1999a).

Data from the three permanent stations suggested that medusae predominated the macrozooplankton in the northernmost part of Lake Tanganyika, while the southern pelagic ecosystem was distinguished by predominance of shrimps. The role of atyid shrimps in the pelagic zooplankton community was notable, shedding new light on the zooplankton studies traditionally biased towards Calanoida. The shrimp abundances in the weekly samples 1993-1995 off Bujumbura were 2.8, in Kigoma 6.0, and Mpulungu 11.9 individuals m^{-3}, while the abundance of medusae in Bujumbura were 79, in Kigoma 25 and Mpulungu 25 individuals m^{-3}. From these figures approximate average standing biomass estimates off Bujumbura, Kigoma and Mpulungu were respectively 237, 75, and 75 mg C m^{-2} for *Limnocnida* and 8, 18 and 36 mg C m^{-2} for the shrimps. These values suggest a whole-lake mean biomass of 129 mg C m^{-2} for *Limnocnida* and

21 mg C m^{-2} for the shrimps. Especially the latter value may be an underestimate, because of possible net avoidance. A considerable part of the shrimp population may also have stayed deeper than 100 m at the time of routine sampling (Kurki *et al.* 1999b). Indeed, data from five lake-wide cruises (Bosma *et al.* 1998), collected with oblique hauls of a Gulf V sampler better suited for catching shrimps, resulted in a biomass estimate of 88 mg C m^{-2} (Fig 5.6-5.7).

Zooplankton data from lake-wide cruises indicated a more even distribution in zooplankton community in different parts of the lake than the studies on three permanent stations (Kurki 1998). There was no difference among the basins in the mean numbers of post-naupliar cyclopoids, naupliar cyclopoids and calanoids or in ovigerous cyclopoids when all the data were pooled and tested. However the mean numbers of post-naupliar calanoids and ovigerous calanoids differed among the basins (ANOVA p=0.001 for both groups), increasing towards the South Basin (Kurki 1998).

5.3.2 Zooplankton production

The zooplankton biomass and production estimates calculated from the vertical migration data and from the weekly sampling series were expected to be somewhat different, because of the different sampling sites, mesh sizes and water column depths sampled. Comparative tests with 50-µm and 100-µm net hauls and different samplers were made. The 100 µm mesh retained all copepodids and adults and most of the nauplii of *T. simplex*, but most of the small cyclopoid nauplii passed through. In contrast, the 100-µm net seemed more effective than a 50-µm net in capturing the adult copepods.

Off Bujumbura and Kigoma, the volume-specific biomass estimates for *T. simplex* obtained from the vertical migration studies were higher than those from the weekly time series. Off Mpulungu, both calanoid and cyclopoid biomasses in the weekly series were higher than in the vertical migration series, probably reflecting higher zooplankton abundances in the shallower part of the southern end. For cyclopoids, the large biomass difference between the data sets off Kigoma was especially due to the different retention of the cyclopoid nauplii by the 50- and 100-µm meshes. In area-specific biomass estimates the differences between the data sets became even more pronounced, because notable numbers of zooplankton were found deeper than 100 m (Fig 5.2 - 5.4)

Production calculations showed the importance of copepod nauplii in the crustacean zooplankton production. In the vertical migration data for Bujumbura, Kigoma and Mpulungu, the contribution of nauplii to the total calanoid production was respectively 65, 27 and 14%, and to the cyclopoid production respectively 55, 75 and 43 %. Because of the sampling bias, in the weekly sampling data the contribution of nauplii to the total calanoid and cyclopoid production was clearly smaller (12-31% and 17-21%, respectively).

For both calanoids and cyclopoids, the total biomass and production above one square metre were always highest off Bujumbura, while the order of Kigoma and Mpulungu varied between the data sets.

The production of herbivorous copepods off Bujumbura, Kigoma and Mpulungu was respectively 35.3, 27.3 and 6.5 gC m^{-2} a^{-1}, whilst the production of predatory cyclopoids was respectively 4.1, 0.3 and 2.1 gC m^{-2} a^{-1}. The resulting averages for the whole lake were 23.0 gC m^{-2} a^{-1} for the herbivorous copepods and 2.2 gC m^{-2} a^{-1} predatory copepods. From these figures, the annual P/B ratios for the herbivorous and predatory copepods were 28.5 and 11.1 a^{-1}.

5.3.3 Predation on zooplankton

Fish stomach analyses and simultaneous zooplankton sampling showed the shrimps were highly selected as prey by clupeids in all areas, though they were more common in the plankton towards the southern arm of the lake (Lensu 1998). There were more shrimps in the stomach contents of the centropomid *Lates stappersii* both in percentage and frequency in Mpulungu area in the south than in Kigoma area or in the north, where the *L. stappersii* diet contained a larger proportion of copepods (Kurki *et al.* 1999b; Fig 5.6-5.7).

Clear correlation was shown between the occurrence of *L. stappersii* and shrimps as well as between *S. tanganicae* and copepods (Mannini 1998). According to the 1995 survey samples, *L. stappersii* fed on heterogeneous targets (*S. tanganicae* clupeid larvae, and meso-zooplankton) in the northern half of the lake, whereas they preyed almost exclusively shrimp in the south. The same was noted earlier also in stomach content analyses of the commercial catch samples in 1994-95. The preference for shrimp prey was more pronounced in June than in November (Mannini 1998). The areal differences in shrimp abundances along the north-south axis of the lake were, however, less consistent in the data set from five lake-wide cruises (Bosma *et al.* 1998) using the Gulf V sampler. There is thus room for speculation on areal differences. In spite of their modest role in plankton biomass and production, atyid and palaemonid shrimps (*Limnocaridina parvula, Macrobrachium moorei)* were very important food for the fishes (Mannini *et al.* 1999; Sarvala *et al.* 1999).

5.4. CONCLUSIONS

The macrozooplankton results from permanent sampling stations indicated the northernmost Bujumbura sub-basin and the Mpulungu sub-basin in the southern arm to be different from the main basins (North, Kalemie shoal, and South). Such differences seem understandable, because the permanent sample site off Bujumbura is locally subject to apparent inflow from the Rusizi River and anthropogenic influences from the town, and the area nearest Mpulungu is known to be more liable to the wind-driven mixing than the rest of lake. This upwelling near Mpulungu has led zooplankton to extend its vertical range two times deeper than in the north, where more stratified conditions prevail. Vertical mixing of water masses due to local winds may create turbulent conditions, possibly inducing food web differences also in the central part of the lake. This was, however, not shown with the present data.

Differences in the plankton community are reflected also in the fish biology. The common relevance of atyid and palaemonid shrimps (*L. parvula, M. moorei*) within the lake pelagic ecosystem seems, in the production point of view, to be higher than previously thought (Mannini *et al.* 1999; Sarvala *et al.* 1999). The role of medusae in the pelagic food web still remains obscure even after the present study as no sampling was specifically designed to catch them.

Based on catch studies (Mannini *et al.* 1996), the northern end of the lake was dominated by young *L. stappersii* and clupeids whereas no adult *Lates* fish occurred in catches. Recently, *S. tanganicae* has contracted its distribution range more clearly to the northern half of the lake (Mannini 1998). The catches in the southern end of the lake consisted mainly of adult *L. stappersii* and various stages of the clupeids. The present structure of pelagic fish communities, that show enormous seasonal and spatial variations (Szczucka 1998; Mannini 1998), is the result of varying fishing pressure (Coenen *et al.* 1998), inter-specific relationships of predation and competition (Mannini 1998; Reynolds 1998), and, to some extent also, of food chain differences that may affect the recruitment and feeding ecology of fish. Our results indicate the importance of copepod densities to clupeid occurrence, and those of atyid and palaeomonid shrimps in affecting the presence of *Lates stappersii.* The primary food chain differences probably arise basically from different patterns of mixing due to seasonal winds and orientation of the lake relative to wind. The effect of seasonal mixing was clearly seen also in vertical distribution and migration (Fig 5.3; Vuorinen *et al.* 1999), as the planktonic community of the southern end occupied the water column to a depth of around 220 m. This is about twice as much as the vertical space utilised by zooplankton in the north. Deep mixing may speculatively have two-fold effects on zooplankton production. First, the physical forces may enhance the predator-prey encounter rates between fish and zooplankton as previously suggested for tropical lakes (Nixon, 1988) and for coastal sea areas (Nixon, 1988, Haury *et al.,* 1990, MacKenzie & Legget 1991, Archer, 1995, Landry *et al.*, 1995). Secondly, deep mixing may also decrease production if the food of zooplankton is widely distributed and the animals are forced to feed in such diluted environment. Lasker (1981) and Peter & Bradford (1987), for example, showed high wind speed events and dissipated patches of food aggregates to be associated with high mortality amongst first-feeding larvae of anchovies.

The present abundance data had a good temporal coverage with short-interval samples of crustacean zooplankton for two successive years. However, abundance estimates from the weekly sampling suffer from at least two sources of bias. First, as shown by Vuorinen *et al.* (1999), some of the crustaceans were found below the routine 0-100 m net hauls in the morning when these samples were taken. Second, considerable numbers of cyclopoid nauplii and small copepodids could escape through the 100-µm mesh of the vertical hauls. These biases could be largely circumvented in the production calculations by utilizing data from the vertical migration study, which used tube sampler and a 50-µm mesh net and in which sampling was extended as deep as copepods were found.

The present estimates for zooplankton biomass and production (Kurki *et al.* 1999a; Sarvala *et al.* 1999) were only half of those given earlier for Lake Tanganyika by Burgis (1984), but very similar to those reported from Lake Malawi (Irvine & Waya, 1999). Our most recent biomass calculations (Sarvala *et al.* 1999) were based on own carbon determinations. Production was calculated by developmental stage using literature-derived but locally checked development times. The resulting P/B ratios (24-26 a^{-1}) in Sarvala *et al.* (1999) did not differ much from those obtained for copepods in Malawi (31 a^{-1}) by Irvine & Waya (1999) or from those (23-29 a^{-1}) used by Burgis (1984) and Kurki *et al.* (1999a:).

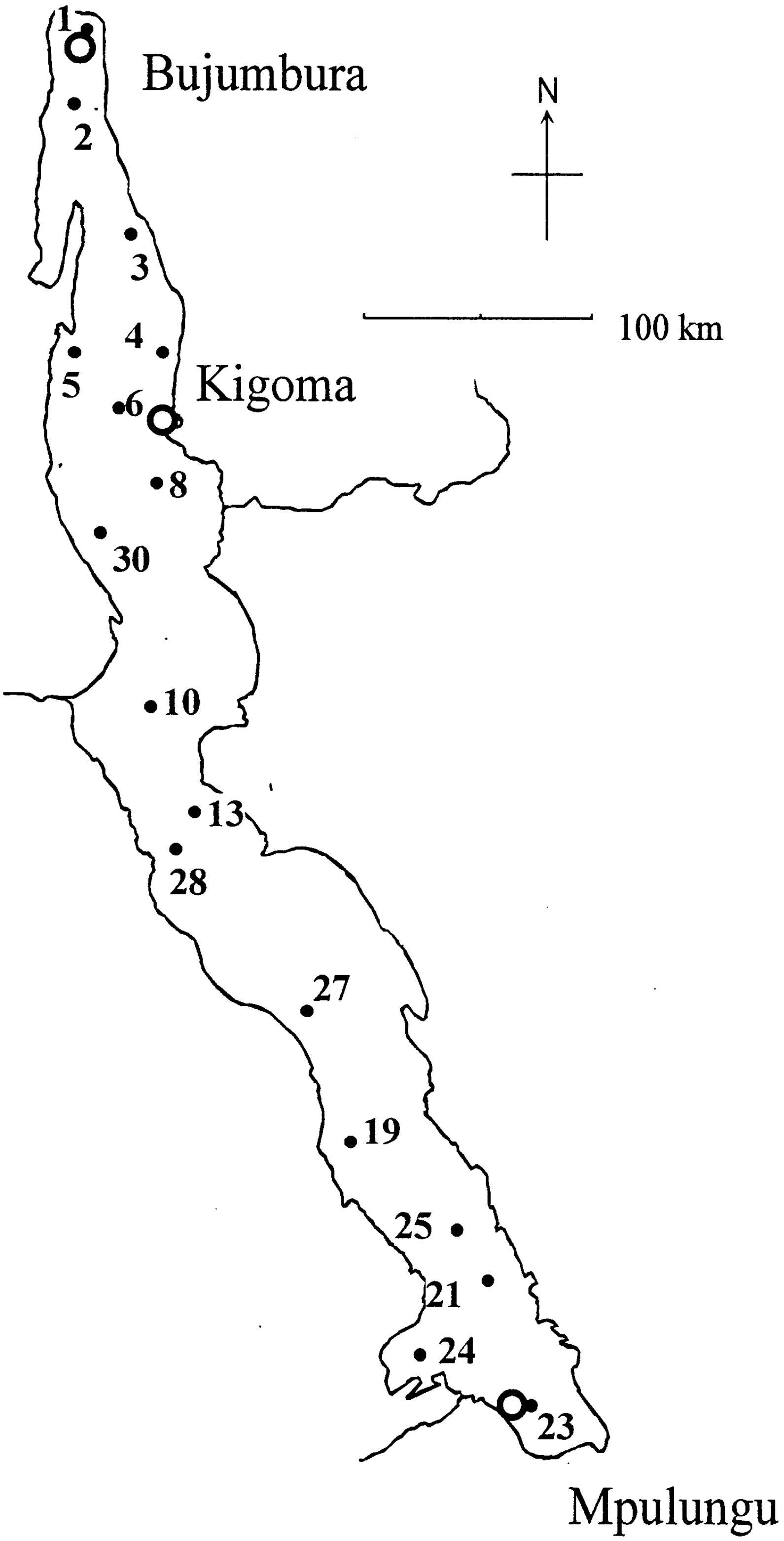


Fig. 5.1 Sampling stations for zooplankton (circles) and fish stomachs (black dots) used in Lake Tanganyika research in 1993-1995.

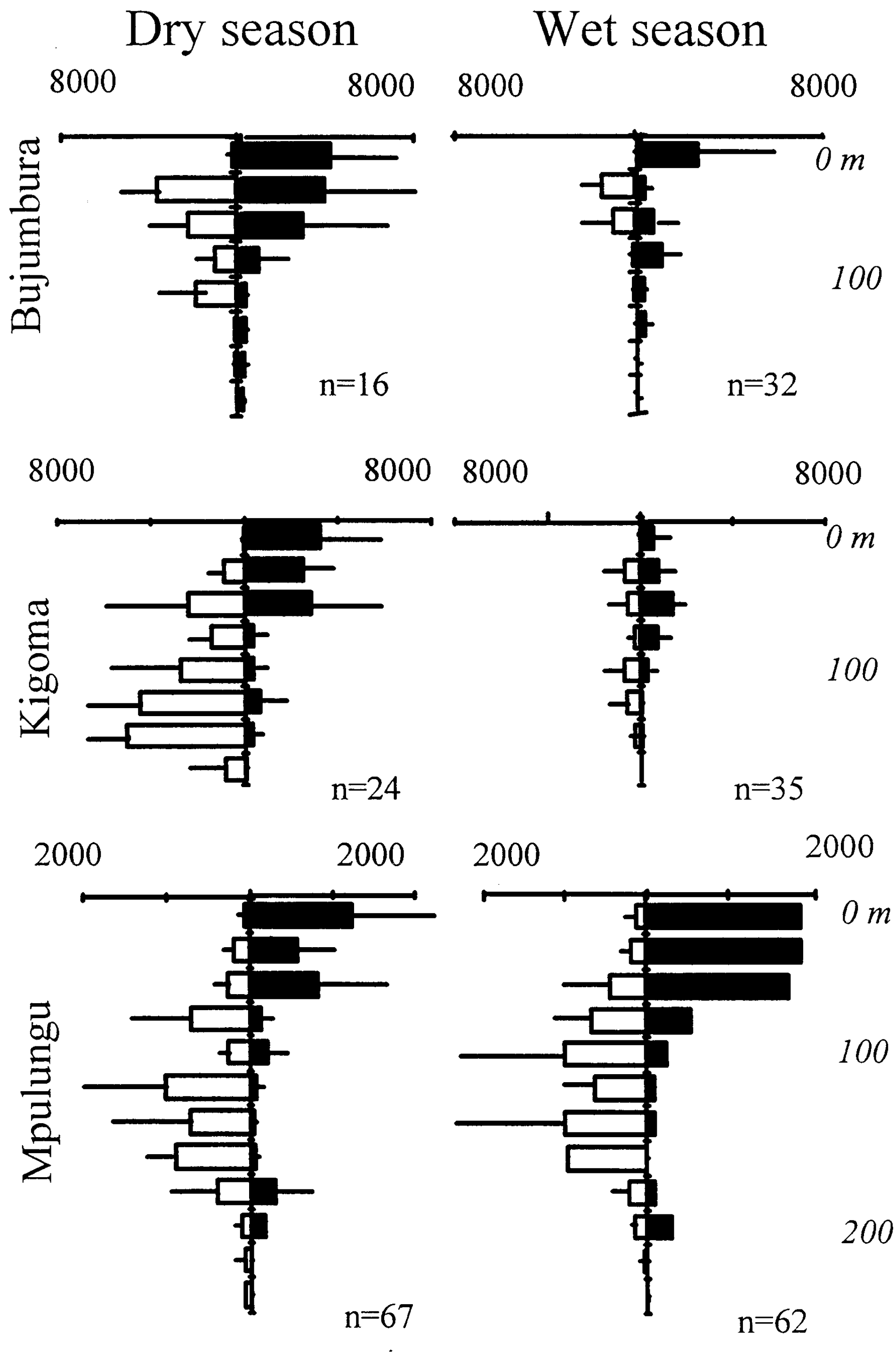


Fig. 5.2 Day (open bars) and night (black bars) vertical distribution (ind.m^{-3}) of *Tropodiaptomus simplex* adult and copepodid stages during dry and wet seasons in Lake Tanganyika, 1993- 1995. Error bars = standard deviation. n = number of samples.

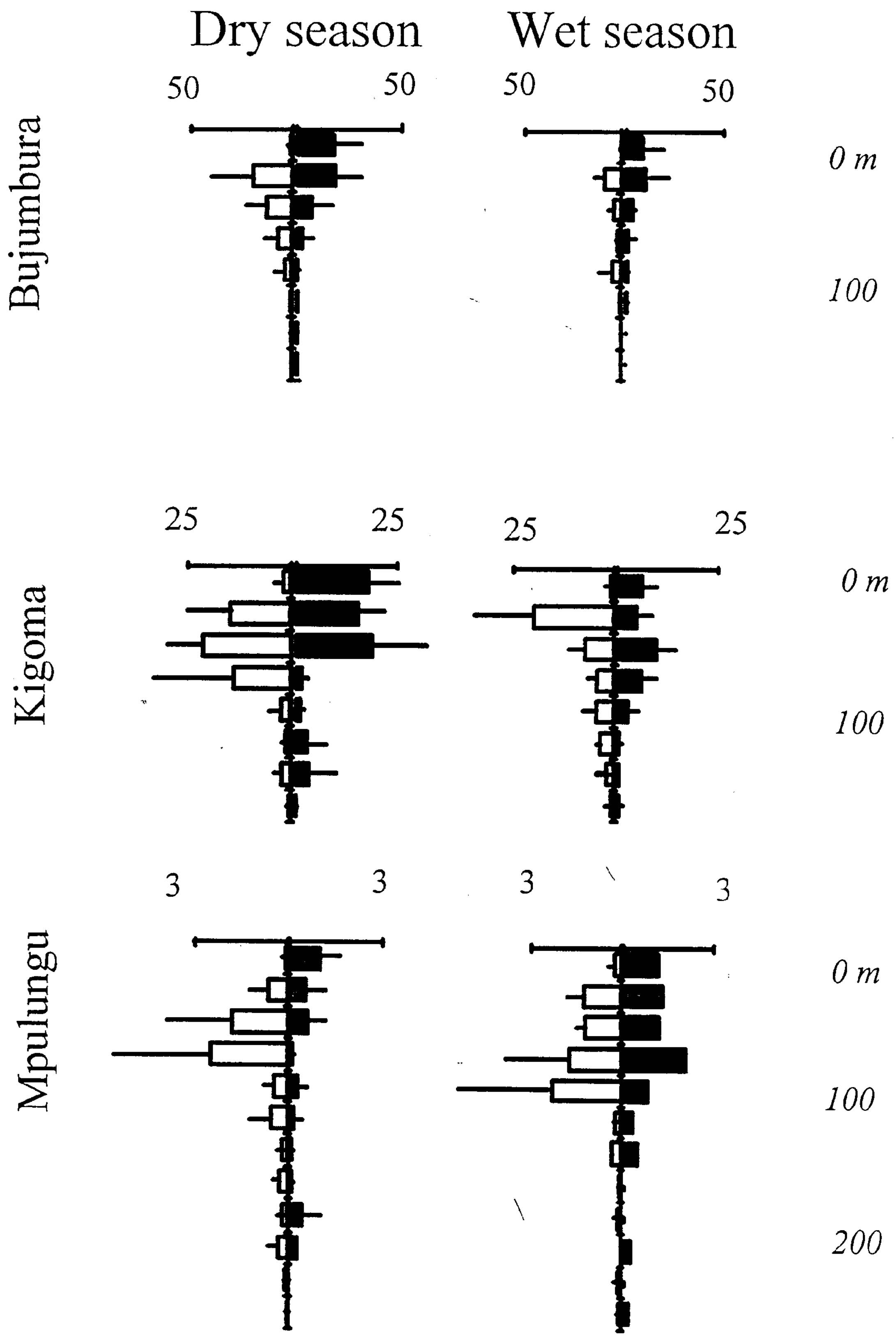


Fig. 5.3 Day (open bars) and night (black bars) vertical distribution (10^3 ind.m^{-3}) of *Cyclopoida* adult and copepodid stages during dry and wet seasons in Lake Tanganyika, 1993- 1995. Error bars = standard deviation.

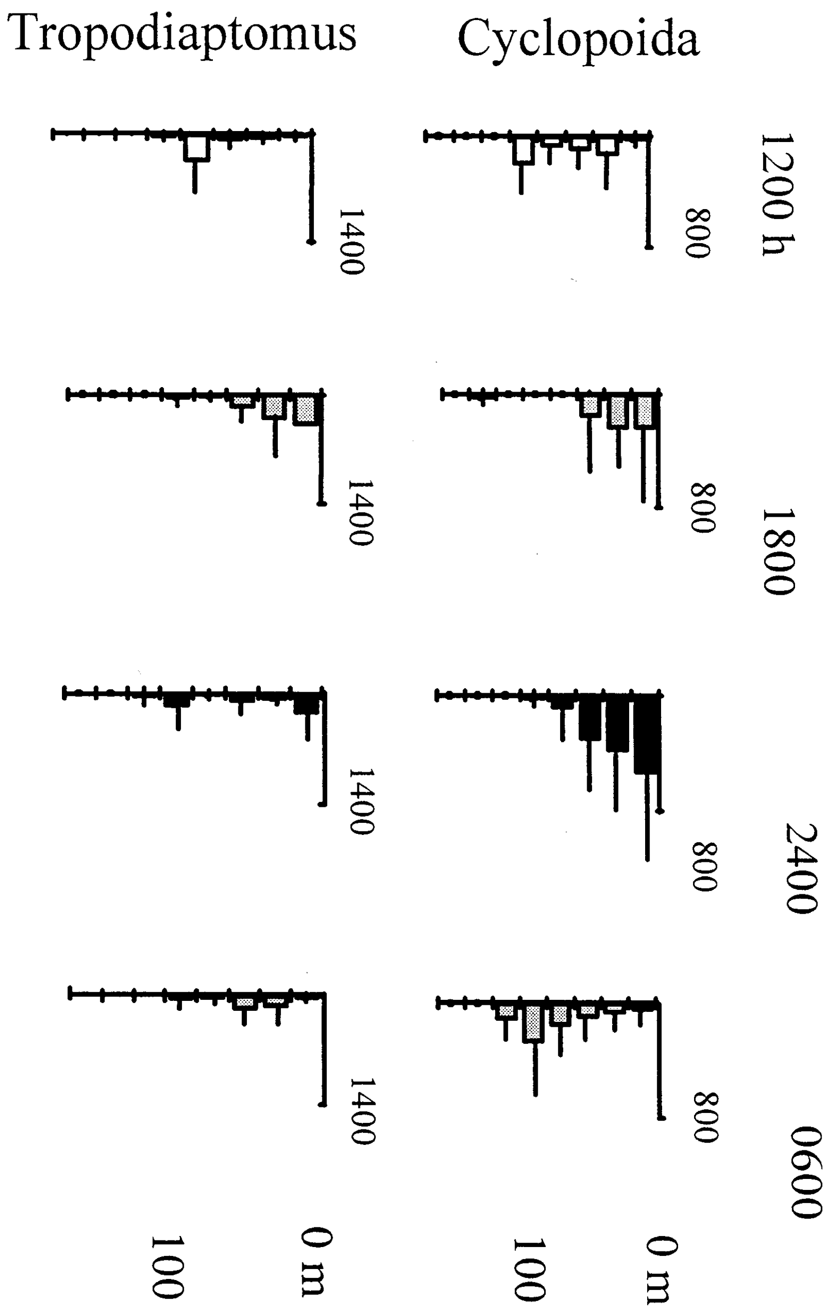


Fig. 5.4 Mean vertical distribution of ovigerous *Copepoda* females at different times of day in the wet season off Bujumbura, Lake Tanganyika, 1993- 1995. Error bars = standard deviation.

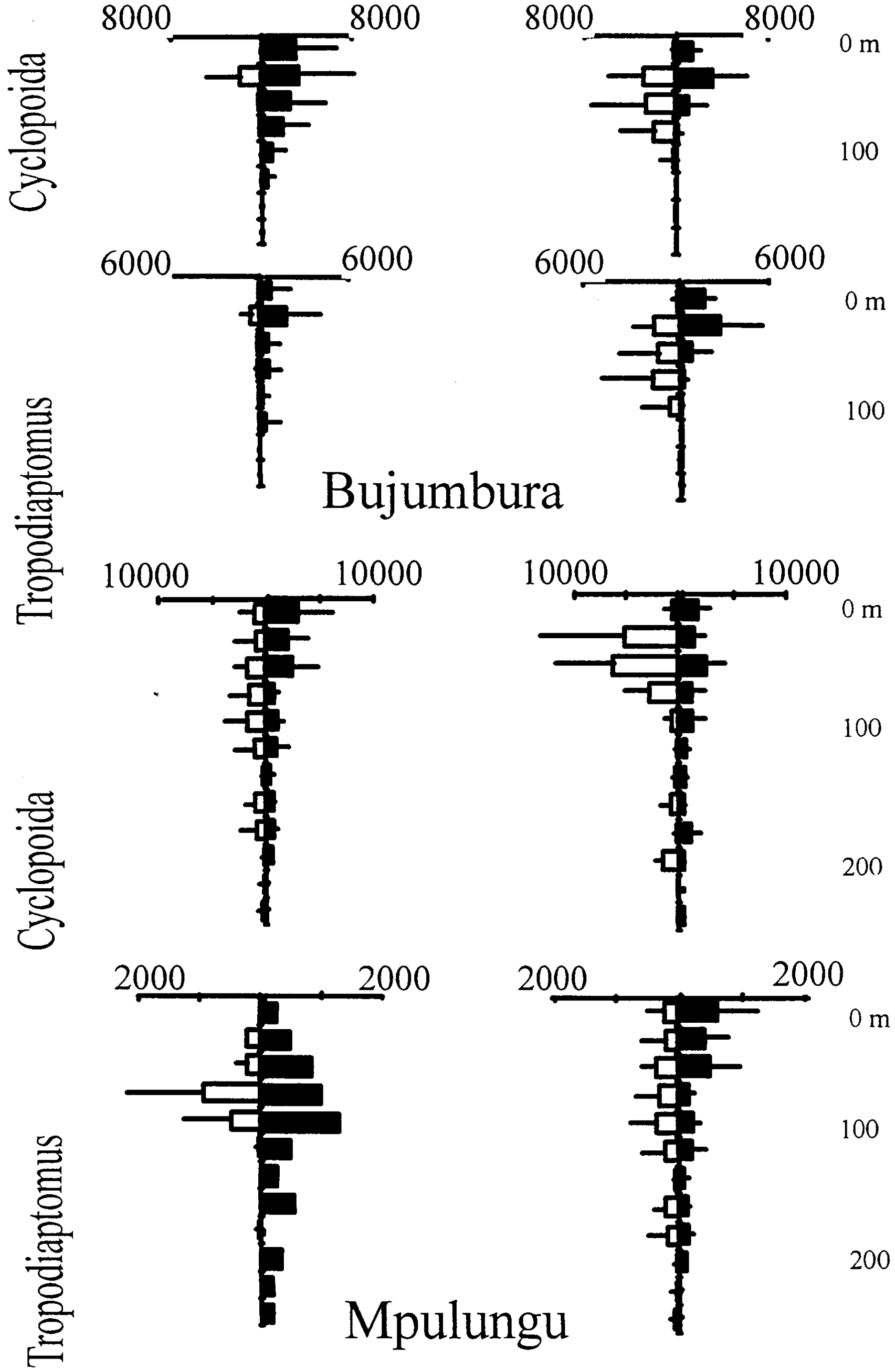


Fig. 5.5 Day (open bars) and night (black bars) vertical distribution of *Copepoda* nauplii (ind.m^{-3}) in dry and wet seasons in Lake Tanganyika, 1993- 1995. Error bars = standard deviation.

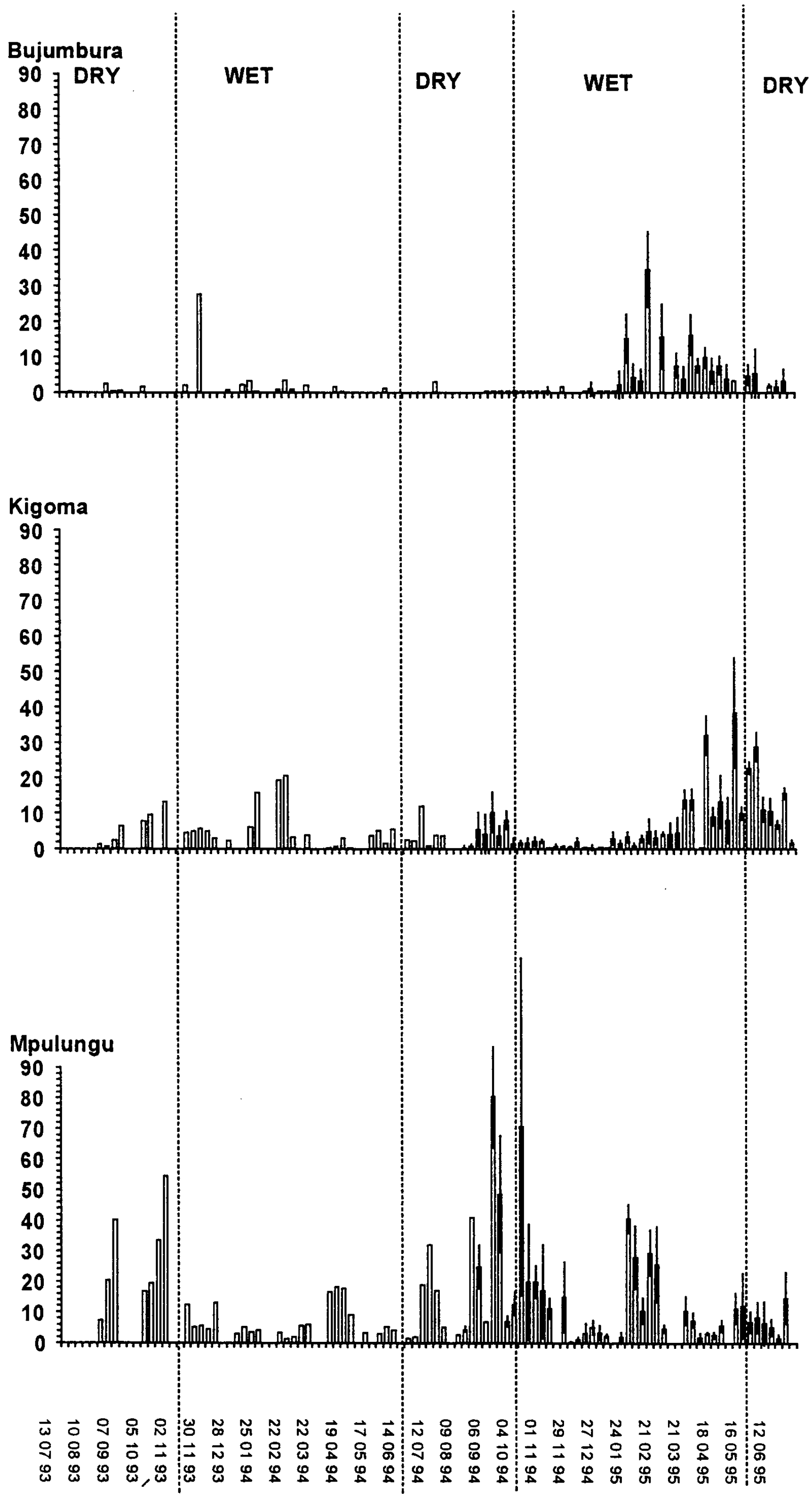


Fig. 5.6 Abundance of *Limnocnida tanganyicae* in Lake Tanganyika in 1993 – 1995 (vertical lines denote standard deviations). Gaps in time series indicate no sampling.

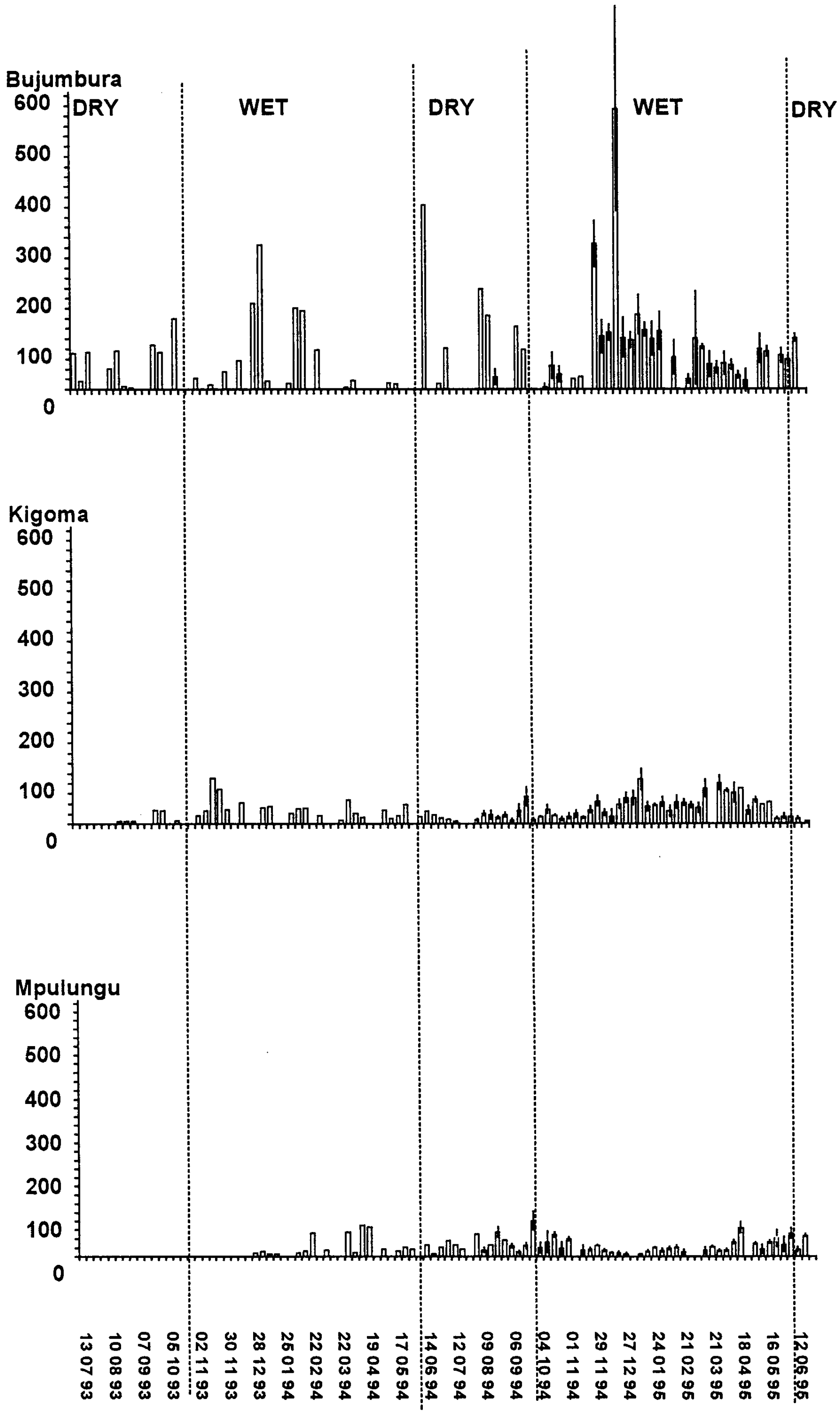
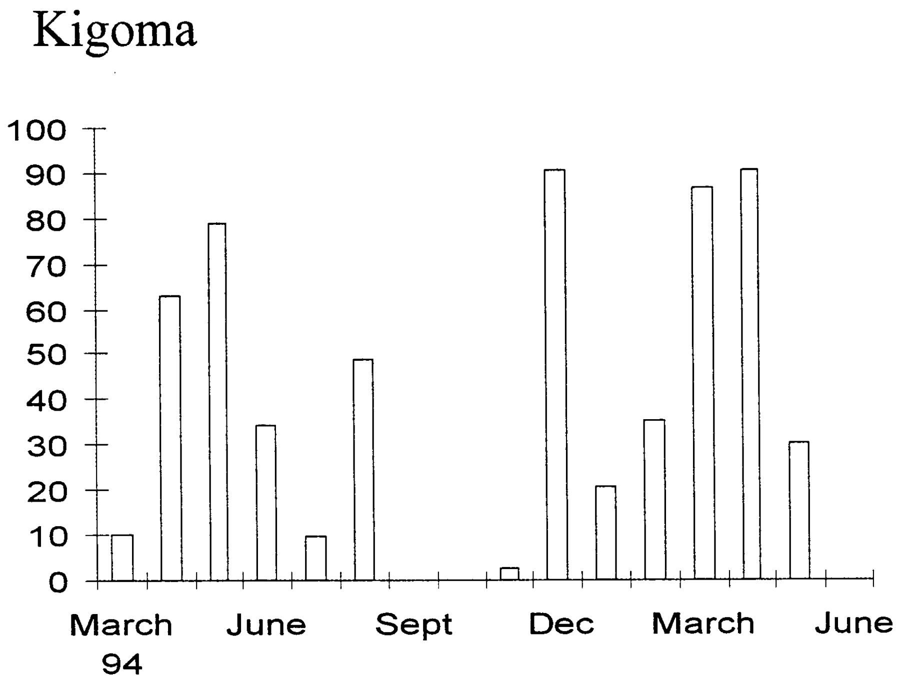


Fig. 5.7 Abundance of pelagic shrimps in Lake Tanganyika in 1993 – 1995 (vertical lines denote standard deviations). Gaps in time series indicate no sampling.



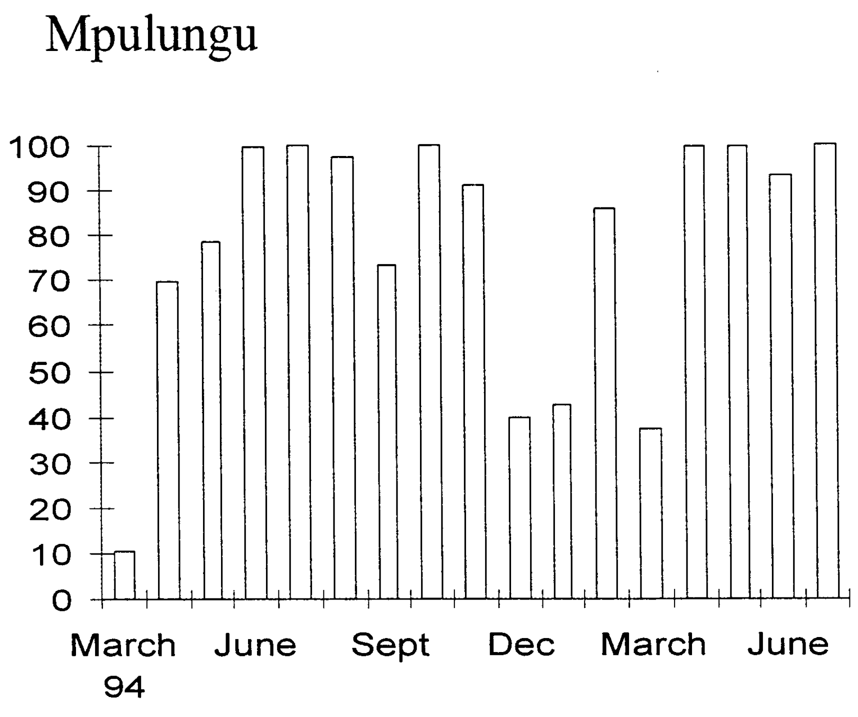


Fig. 5.8 Percentages of shrimps in the stomach contents of *Lates stappersii* in Kigoma and Mpulungu, in monthly samples 1994 – 1995.

CHAPTER 6

FISH BIOLOGY

By:
Mannini, P., J. Sarvala, E. Aro, I. Katonda, B. Kissaka, C. Mambona, G. Milindi, L. Kuusipalo, P. Paffen & P. Verburg

Abstract

The studies in fish biology combine results on basic population parameters of dominant pelagic species, catch assessments and stock size and distribution as conducted in catch studies, fish biology analyses, and acoustic surveys. The three target species, *S. tanganicae, L. stappersii,* and *L. miodon*, in the order of importance, contributed from 63% to 89% of the total catch weight.

The catch frequency and CPUE distribution showed *S. tanganicae* stock is very unevenly distributed in the lake; being mostly found from the Kalemie latitude northwards. A clear horizontal migration occurs with post-larval juveniles concentrating offshore and thereafter the young stages recruiting first to the industrial fishery and then to lift-net fishery closer inshore. *S. tanganicae* fishery is supported mostly by a single major cohort which is recruited during the dry season and makes the exploitable stock during the successive wet season. The availability of *S. tanganicae* resources in the local fishing grounds is very irregular due to high mobility of the schools. These migrations, both horizontal and vertical, are primarily determined by predation avoidance towards *L. stappersii* and by prey preference on copepod mesozooplankton.

Limnothrissa miodon is more evenly distributed in the lake than *S. tanganicae.* The juvenile stock comprising the post larval stage occurs in shallow waters where the fish are subject to the unselective beach seine fishery in certain areas. Large *L. miodon* occur almost exclusively offshore outside the range of artisanal fishery.

Lates stappersii stocks apparently consist of several annual cohorts and therefore sudden changes in stock size and composition are less likely than those in clupeids. Juvenile and adult *L. stappersii* stocks co-occur within the same geographical areas but the juveniles are more mobile in their distribution. Fish biology data or analyses of population genetic discreteness provide no indications of the existence of *L. stappersii* sub-populations in the lake. Fish apparently move and mix among sub-basins, leading to significant exchange of individuals among different parts of the lake. *Lates stappersii* stocks can, however, from a managerial point of view, be divided into northern and southern sub components.

The whole-lake averages for the P/B ratios obtained from experimental trawl results were 4.5, 2.7 and 1.6 a^{-1} for *Stolothrissa*, *Limnothrissa* and *Lates*, respectively. In Burundi the catch in 1995 amounted to 111.5 kg ha^{-1} yr^{-1}, in Zambia to 53, in Tanzania to 40 and in Zaire to 63 kg ha^{-1} yr^{-1}. In 1995, the realised catch of planktivorous fish for the whole lake was 23-38%, and in the most heavily fished Burundi waters about 43-52%, of the estimated planktivorous fish production.

6.1. INTRODUCTION

The studies in fish biology combined results on basic population parameters of dominant pelagic species, catch assessments and stock size and distribution that were conducted in catch assessment studies (Plisnier 1995; Coenen *et al.* 1998) and fish biology analyses (Mannini *et al.* 1996; Mannini 1998) as well as stock size assessments through acoustic surveys (Szczucka, 1998). The aims of these studies were to study the species composition by areas and seasons, to describe the reproduction and growth patterns of dominant species, and also to investigate the competitive and predatory relationships in the pelagic food web. Fish sampling was integrated with zooplankton and limnology studies particularly on the surveys. Quantitative stock size assessments were made with experimental midwater trawling and acoustic devices with wider areal and seasonal coverage than in any earlier investigation (Johannesson 1974; Chapman 1974, 1976; Roest 1977). Specific effort was given to the recruitment of main target species in environment and fishery although the studies on fish larvae biology were not made very comprehensively except those using the Gulf V high speed plankton net (Bosma *et al.* 1998; for the short-term survey in 1998, see Markkanen & Karjalainen, unpubl.).

Parameters of fish growth, mortality and length distribution were studied both in commercial catch samples and independently from commercial harvest methods in fish obtained through experimental trawling to estimate the standing stock and potential for production. Studies in fish biology were conducted to provide practical advice on potential fish production, its seasonal and areal distribution, and to link fish production with the physical and biological characteristics that regulate these spatial and temporal variations. Production and stock studies were made to evaluate the production efficiency and to compare the yield with the production rather than to provide a single figure as the total allowable catch (TAC) for lake-wide managerial use.

6.2 MATERIAL AND METHODS

Population analyses of pelagic fish (the clupeids *Stolothrissa tanganicae* Regan, *Limnothrissa miodon* (Boulenger) and the predatory *Lates stappersii* (Boulenger)) were based on weekly catch samples from commercial catch at three main stations and six substations around the lake (Aro & Mannini 1995; Mannini *et al.* 1996). The catch sampling covered all methods used in the traditional, artisanal and industrial fisheries (lift nets, beach seine and purse seine). Most fishing is done at night as virtually all of these methods rely on light attraction. Length, weight, sex and reproductive status were recorded for the sampled fish. Length-frequency analyses (LFA) were applied to derive growth and mortality rates from these data (Aro & Mannini 1995). To check the growth information thus obtained, age determinations of the clupeids were also made by counting daily increment rings in the otoliths (Pakkasmaa & Sarvala 1995; H. Ahonen, unpublished). Length-specific growth rates were derived from the von Bertalanffy growth curves and converted to weight-specific rates using biomass-length-regressions, and finally these were combined to average size distributions at each sampling locality to yield daily and annual production rates and production to biomass ratios.

Information on pelagic fish species composition and size distribution of three dominant species *S. tanganicae*, *L. miodon*, and *L. stappersii*, was collected during five integrated acoustic and pelagic trawling surveys conducted lake-wide in 1996-98 (Mannini 1998). This work was complementary to earlier investigations on commercial catches (Mannini *et al.* 1986). Fish and macrozooplankton data collection was carried out as described in Mannini & Aro (1995) and Kurki (1996) using a French-type pelagic trawl net and a high speed Gulf-net V sampler. Sampling areas were chosen from seven sub-basins. Sexual maturity stages were defined according to Aro (1993) and stomach contents of centropomid predator *L. stappersii* were analysed (see, Mannini, 1999). Gulf-net samples for crustacean zooplankton were analysed as described in Bosma *et al.*, (1998).

6.2.1 Genetic discreteness

To determine genetic discreteness amongst the clupeid and *Lates* spp. populations >1000 fish were collected all over the lake and analysed in 1993. A maximum of 30 individuals of each species were taken at one site. The genetic analyses applied the random amplified polymorphic DNA (RAPD) -PCR technology as described by Kuusipalo (1994, 1999).

6.3 RESULTS

6.3.1 Overall catch

The three target species contributed from 63% to 89% of the total uncorrected catch weight. In all but the June 1995 survey, *S. tanganicae* was the main contributor to the catch (up to 85% in November- December 1997), followed by *L. stappersii* and *L. miodon* in importance. The other *Lates* species (*L. mariae*, *L. angustifrons,* and *L. microlepis*) contributed from 3% to 30% of the catch weight, led by *L. mariae*. In all surveys the highest catches of clupeids were always made during daylight hours, e.g. the highest catches of *S. tanganicae* during day trawling were up to 1181 kg hr-1 (February 1998) compared with highest night catch of 54 kg hr-1 (April 1996). The possible bias in biomass estimations due these exceptionally high yields as well as those of zero catches were taken into account in biomass estimations (see Mannini 1998).

6.3.2 *Stolothrissa tanganicae* stock

The catch frequency and CPUE distribution showed that the *S. tanganicae* stock was very unevenly distributed in the lake. During most of the survey months the stock was found in the northern half of the lake running from the Kalemie area northwards. The relative biomass distribution and commercial catch composition as well as the acoustic work findings indicate that *S. tanganicae* is at very low density in the southern half of the lake (Mannini 1998; Szczucka 1998).

The adult and juvenile *S. tanganicae* do not show separate distributions along the longitudinal axis of the lake; both adult spawners and recruits co-occur within the same areas. The inshore-offshore distribution of juveniles and adults is, however, different and follows a clear pattern. Post-larval juveniles concentrate offshore in the open areas of the lake. Thereafter young *S. tanganicae* move towards shallow water from the length of 30-40 mm (at about the age of 2-3 months). They are recruited first to the industrial fishery and then to the lift-net fishery. Fishing grounds of the former are normally more distant from the coast than those of the artisanal fishery. The deep water sampling indicated larval stage distribution of *S. tanganicae* is rather even and homogenous (Mannini 1998). Markkanen & Karjalainen (unpubl.) in 1998 similarly found no differences of *S. tanganicae* larvae abundances between deep areas. Densities were lowest in turbid waters of the Malagarasi delta. Earlier Tshibangu and Kinoshita (1995) found that *S. tanganicae* larvae occur mostly offshore.

The reproductive process of *S. tanganicae* was shown to be continuous throughout the year as some mature fish are always present. The spawning stock biomass reached the maximum only in some periods around the first months of the year followed by extremely reduced density in the consecutive months.

To conclude, *S. tanganicae* fishery is supported mostly by a single major cohort which is recruited during the dry season and makes the exploitable stock during the successive wet season. The temporal pattern of the principal recruitment pulse to the fishery is similar around the lake (Mannini *et al.* 1996) and the catch statistics indicate the maximal commercial catch is obtained from September to December (Coenen *et al.*, 1998). The availability of *S. tanganicae* resources in the local fishing grounds is very irregular due to high mobility of the schools. These migrations, both horizontal and vertical, are determined primarily by predation avoidance towards *L. stappersii* (Mannini *et al.* 1999) and by prey preference on copepod mesozooplankton.

6.3.3 *Limnothrissa miodon* stock

Limnothrissa miodon is more evenly distributed in the lake than *S. tanganicae*. The contribution of *L. miodon* to the lift-net and purse seine pelagic catches is clearly smaller than that of *S. tanganicae* and *L. stappersii*. However, it dominated in the catch of the unselective beach seine fishery operated with cloth tissue-covered gear in shallow, coastal areas over sandy bottoms (Pearce, 1995; Mannini *et al.*, 1996). The juvenile stock comprising the post larval stage occurs in shallow waters from where the young fish move offshore. Large *L. miodon* (>125 mm) occur almost exclusively offshore outside the range of the artisanal fishery. These fish are believed to compete for food with *L. stappersii*, preying upon pelagic shrimp and young *S. tanganicae* (Ndugumbi *et al.* 1976). Cannibalism is probably sporadic.

Between the 1995-96 and 1997-98 surveys there was a marked difference in CPUE frequency distribution. *L. miodon* catchability changes, as shown by the increased frequency of zero and small catches. This might indicate reduced abundance of *L. miodon* compared to two years earlier, but also the result may be due to different fishing efficiency during the later survey (Mannini 1998).

6.3.4 *Lates stappersii* stock

Lates stappersii is a long-lived species with a maximum age of 5-7 years, and several annual cohorts contribute to the population structure. It is unlikely that sudden changes in stock size and composition can take place over a short time period. The survey data and low frequency of zero catches in 1995-96 show *L. stappersii* is homogeneously distributed in all areas of the lake. The relative biomass pattern, outlined by the CPUE distribution, was uneven over the lake basin. *L. stappersii* reaches its maximum occurrence in the deep central body of the lake, from Kigoma to East Marungu, characterised by steep shores and reduced shelf. The second survey period in 1997-98 indicated *L. stappersii* had become less common and more dispersed. Also, early young fish dominated the size composition of the 1997 catch.

Juvenile and adult *L. stappersii* stocks co-occur within the same geographical area but the highly mobile juveniles can live in either inshore or offshore whereas the adults are truly pelagic. Apparently there are spawning grounds in the southern part of the lake in the Moba and East Marungu sub-basins. Secondly, the northern *L. stappersii* stock has its spawning and nursery grounds in the Kigoma sub-basin. Adult fish can spread north as far as Rumonge, but juveniles are found even at the northern extremity of the lake.

Fish biology data of Mannini *et al.* (1996) have indicated that *L. stappersii* sub populations do not occur in Tanganyika. *L. stappersii* is highly mobile moving throughout the lake (Roest 1992). It may be reasonably assumed that fish move and mix among sub-basins. The 'northern' stock, located in the Kigoma and Kalemie sub-basins, is exploited almost exclusively by the artisanal lift-net fishery, whereas the 'southern' component, located in the Moba and East Marungu sub-basins, is mostly targeted by the industrial purse seine fishery.

6.3.5 Population discreteness

The migration clupeids and *L. stappersii* was not systematically followed at the LTR Project but the possible occurrence of genetically isolated sub-populations was studied through population genetics by Kuusipalo (1994, 1999) and later in collaboration with other studies on Lake Tanganyika (Hauser *et al.*, 1998). No remarkable genetic differentiation could be shown amongst the clupeids or *Lates* spp. (Kuusipalo, 1994), or in *Lates angustifrons* (Kuusipalo, 1999) by RAPD-DNA PCR amplification methods. Similarly, Hauser *et al.*, (1998) found only morphological associations in *Limnothrissa miodon* schools but the individuals were shown to be unrelated when studied for their mtDNA haplotype diversity. In allozyme analysis, genetic differentiation was found among individual schools but there were no clear geographical boundaries among the populations. The lack of genetic population structure suggested a significant exchange of individuals among different parts of Lake Tanganyika. Mannini *et al.* (1996) claimed the same for fish biology data obtained from catch samples. Mannini (1998) later considered that *Lates stappersii* stocks could be divided into northern and southern components, but only from a managerial point of view.

The rather random distribution of the pelagic stocks and lack of distinguished sub-populations bears an important implication for establishment of lake-wide fisheries management in that a holistic and regional management strategy appears more reasonable than one using local measures with different approaches in each country. Roughly speaking, however, the northern half of the lake can be regarded as being dominated by a clupeid-based fishery, and the southern areas by a *L. stappersii*-based fishery. Respective northern and southern managerial requirements should accordingly be recognised (Mannini 1998).

6.3.6 Growth and production

Growth rates derived from length frequency analyses (LFA) did not vary much between localities, and both clupeid species had similar growth rates. Extrapolation of the LFA growth curves to small fish (length < 40-50 mm) normally not present in the catches is arguable, and to reduce the potential bias, the von Bertalanffy growth curves were here forced to go through zero length at zero age. At least for *Limnothrissa* off Bujumbura, the LFA results were reasonably consistent with those from the counting of daily otolith increments (Fig. 6.1), but here the lift net catches included high numbers of small fish down to the length of 25 mm. Also off Mpulungu, where even smaller *Limnothrissa* (down to 15 mm length) caught with the beach seines were included in the LFA estimates, the latter were probably reliable even for the small size groups. For *Stolothrissa*, the length classes < 30 mm were poorly represented in catch samples, making the LFA growth estimates more uncertain. The mass-length regressions of all three species had exponents close to 3.0 (Mannini *et al.* 1996).

In fish populations exhibiting exponential biomass growth, the instantaneous mortality rate equals P/B ratio (Allen, 1971); indeed, the mortality coefficients calculated from the LFA analysis were close to, although usually slightly higher than the annual P/B rates obtained from the size distributions. The whole lake averages for the latter P/B ratios obtained from combined experimental trawl results, 4.5, 2.7 and 1.6 a^{-1} for *Stolothrissa*, *Limnothrissa* and *Lates*, respectively, were considered the most reliable and used for production calculations (Sarvala *et al.* 1999).

Hydroacoustic fish biomass estimates for the whole lake were 91 193, 175 681 and 304 463 tonnes in June 1995, November-December 1997 and February 1998, respectively (Szczucka, 1998). The observed wide range may reflect seasonal differences, because the catches per haul in experimental trawling were consistent between cruises performed in the same season, i.e. between June 1995 and April 1996, and between November-December 1995 and November-December 1997, respectively (data from Mannini 1998). The ratio between the acoustic biomass estimate and the mean catch-per-unit-effort in experimental trawling was very similar on all cruises. The overall mean for the hydroacoustic estimates was 190 446 tonnes (58 kg ha^{-1}) or 0.58 g C m^{-2}. According to the five lake-wide trawling surveys (142 hauls, 4592 kg), the contributions of *Stolothrissa tanganicae*, *Limnothrissa miodon*, *Lates stappersii*, other *Lates* spp. and all other species were 56.7, 12.0, 10.7, 12.7 and 7.9% of total fish biomass, respectively (Mannini, 1998). Using these proportions and the derived P/B ratios, the production of the pelagic clupeids (*Stolothrissa* and *Limnothrissa*) was 1.4- 1.7 g C m^{-2} a^{-1} and that of the *Lates* and other mostly piscivorous species 0.3 g C m^{-2} a^{-1}.

6.4. CONCLUSIONS

Our fish production estimates can be compared to the realised catch and will be discussed in Chapter 8 in more detail. According to the catch statistics by gear types and aerial frame surveys on respective fishing effort at the LTR project, the total catch was 167 000 metric tonnes (or 51 kg ha^{-1}) in 1992 (Hanek 1994, Coenen, 1995) and three years later 196 600 metric tonnes (Coenen *et al.*, 1998). In Burundi the catch in 1992 amounted to 94.5 kg ha^{-1} yr^{-1}, in Zambia to 69, in Tanzania to 60 and in Zaire to 34 kg ha-1 yr-1 (Hanek, 1994), and in 1995 to 111.5, 53, 40 and 63 kg ha^{-1} yr^{-1}, respectively. In 1995, the realised catch of the planktivorous fish was in the whole lake 23-38%, and in the most heavily fished Burundi waters about 43-52 % of the estimated planktivorous fish production.

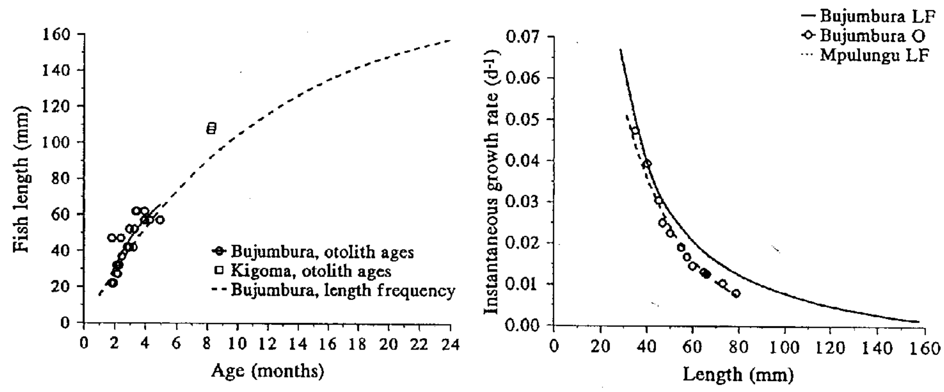


Fig. 6.1.1 (a) Length growth of *Limnothrissa miodon* off Bujumbura as estimated from the length frequency analyses (Mannini et al., 1996) and from daily otolith increments (Pakkasmaa & Sarvala, 1995). Two otolith-based length-at-age values for larger fish from Kigoma are shown for comparison. (b) Instantaneous length growth rates of *Limnothrissa miodon* off Bujumbura and Mpulungu as estimated from the length frequency analyses (LF; Mannini et al., 1996) and on the basis of daily otolith increments (O; Pakkasmaa & Sarvala, 1995).

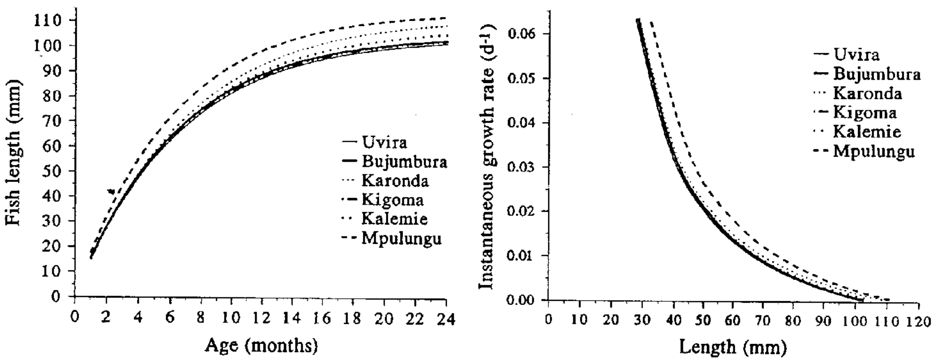


Fig. 6.1.2. Length growth (left) and instantaneous growth rate relative to length (right) of *Stolothrissa tanganicae* at the main sampling stations. Based on the length frequency analyses by Mannini et al. (1996).

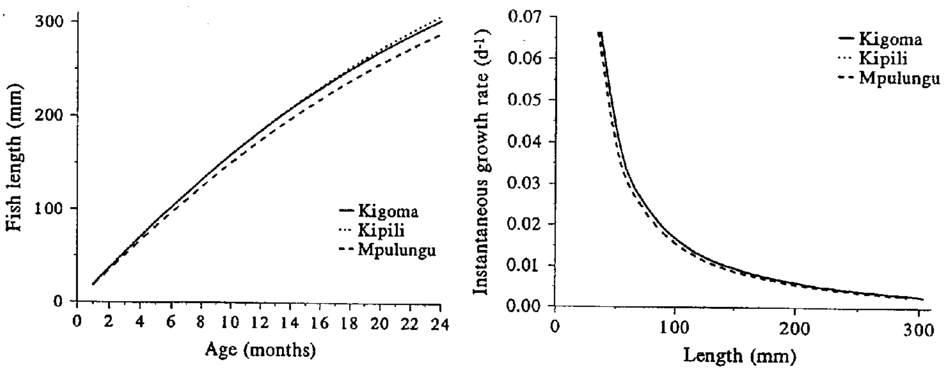


Fig. 6.1.3. Length growth (left) and instantaneous growth rate relative to length (right) of *Lates stappersi* at three sampling stations. Based on the length frequency analyses by Mannini et al. (1996).

CHAPTER 7

FISH ABUNDANCE AND THEIR SPATIAL DISTRIBUTIONS[1]

By:
Szczucka, J.

Abstract

Stock assessment was performed through hydroacoustic recordings of pelagic fish abundance combined with experimental trawl samples during LTR research cruises. The species of interest, *Stolothrissa tanganicae, Limnothrissa miodon,* and *Lates stappersii,* occurred in mixed aggregations and their acoustical parameters were almost the same. As such, only their combined total abundance could be estimated. Temporal variations in fish abundance and their spatial distributions in present data were enormous, suggesting, *inter alia*, large-scale movement in search of food and seasonal variations of the environmental conditions. The very low levels of fish biomass can also be a result of a temporary overfishing, especially in the industrial fishing areas of Burundi and Zambia.

7.1 INTRODUCTION

A total of five fisheries-acoustic surveys were conducted under the LTR Project over the years 1995-1998. They focussed on the pelagic fish stock and aimed at estimating total biomass and distribution patterns. Each cruise was planned to cover the whole area of the lake, but this was not always possible due to equipment problems. Complementary fishing operations (midwater trawls), zooplankton sampling, and CTD measurements were carried out in the course of the survey exercises.

7.2 MATERIAL AND METHODS

Stock assessment was performed through hydroacoustic recordings of fish abundance combined with experimental trawl samples during the research cruises. Collection of fish catch statistics was done in collaboration with the local fisheries administration of each country (Coenen, 1995). Unfortunately, the data from cruises 5 and 7 were useless for the estimate of absolute fish abundance, because of a very high noise level recorded. In consequence, the analysis concerned only the cruises 2, 17, and 19, respectively carried out in 1995, 1997, and 1998. Details are provided in Table 7.1.

[1] This chapter comprises a summary drawn from Szczucka (1998).

Table 7.1 Summary of the survey and operational information

Cruise No.	Dates	Distance Covered (kms)	No. acoustic transects	No. trawls	No. CTD stations	No. zoovertical stations	No. GULFs
2	15.06. - 30.06.95	978	?	32	32	23	25
5	16.11.- 04.12.95	1092	41	41	29	34	26
7	02.04.- 12.04.96	?	18	21	21	7	14
17	22.11.- 09.12.97	1185	54	26	23	29	15
19	05.02.- 20.02.98	1228	41	22	26	0	18

7.3 RESULTS

Acoustic measurements can indicate total biomass but could not discriminate between species if their acoustic properties are similar. The fish species of interest, *Stolothrissa tanganicae, Limnothrissa miodon,* and *Lates stappersii,* occurred in mixed aggregations and their acoustical parameters were almost the same. It was thus appropriate to consider them only in a combined way, as a broad behavioral category comprised of mixed species. As such, only the total abundance of the mixture could be estimated on the assumption that one unit weight of all the species reflected the same proportion of acoustic energy.

Table 7.2 presents the average values of fish length *<L>*, fish weight *<W>*, target strength *<TS>*, back scattering cross-section *<bs>*, back scattering cross-section per unit weight *<1 kg>=<bs>/<W>*, and target strength per unit weight *<TS1 kg>* obtained from *TS(L)* regression formula applied to the fish sample caught during three analysed cruises.

Table 7.2 Mean fisheries and acoustical parameters

Cruise No.	<L> [mm]	<W> [g]	<TS> [dB]	<bs> [m2]	<bs>/<W> [m2/kg]	<TS1 kg> [dB]
2	42.88	2.21	-62.61	5.48 10-7	2.48 10-4	-36.06
17	58.07	1.45	-56.30	2.34 10-6	1.62 10-3	-27.90
19	71.42	2.54	-56.42	2.28 10-6	8.98 10-4	-30.47

It was desired to examine the extent to which diurnal differences could influence a total fish estimate. A comparison of ‘day’ and ‘night’ records of the mean *TS* values and integram values from the surveys 17/97 and 19/98 indicated that the night values were a few dB higher than the day ones. It could be concluded that acoustic measurements performed at night only could result in a bias in the final fish abundance estimate.

In order to estimate the total fish abundance in Lake Tanganyika, the whole its area was divided along the latitudes into 5 regions, as follows:

1) 320’ - 430’ Burundi/Cap Banza
2) 430’ - 540’ near Kigoma
3) 540’ - 630’ near Lagosa

4) 630’ - 800’ Kipili/Karema
5) 800’ - 845’ Zambia

In each region the mean value of fish biomass (in tonnes) and its standard error were evaluated, as shown in Table 7.3.

Table 7.3 Mean fish biomass (in tonnes) calculated for 5 sub-regions in surveys 2, 17 and 19

Region	Area (nm^2)	Survey 02/95	Survey 17/97	Survey 19/98
1	1161.70	40137 13068	8774 6519	22269 14120
2	2350.85	42761 26276	57605 53249	49787 40012
3	1774.30	7211 5452	27154 16480	64753 35494
4	3385.43	1085 218	53614 20426	104835 23720
5	1382.35	.. no data	28543 5663	62819 32232

Finally, on the basis of the regional means and areas, the total abundance and the 95% confidence limits were calculated. These are indicated in Table 7.4.

Table 7.4 Total fish biomass estimated in surveys 2, 17 and 19

Survey	Total biomass (tonnes)	Confidence limit
02/95	91 193	45 014
17/97	175 681	102 337
19/98	304 463	145 577

It is evident that each of the cruises gave a different distribution of fish biomass. The results of the 02/95 survey could be biased because of the insufficient number of samples, but it is obvious that the majority of fish concentrated in the northern part of the lake, especially in the layer 60 - 80 m. In December 1997 (cruise 17/97), fish mass moved toward the south with the maximum in Cape Banza area, Kabimba - Lagosa line, below Cape Kibwesa and the western part of Zambian waters. The depth distribution seemed to be quite uniform. In February 1998 (cruise 19/98) the majority of fish mass concentrated in the middle part of the lake, around Cape Kabogo, and in the southern part, around the Kirando and Kala areas. There was definitely a small amount of fish in the north.

Another division of the whole lake area was made for estimation of fish abundance in waters of the four riparian countries: Burundi, Tanzania, Congo and Zambia. The results are shown in Table 7.5.

Table 7.5 Mean fish biomass (in tonnes) calculated for the four Lake Tanganyika countries in surveys 2, 17 and 19

COUNTRY	Approx. area (km^2)	Survey 02/95	Survey 17/97	Survey 19/98
BURUNDI	580.85	23562	1533	10509
TANZANIA	4241.01	44897	82201	157493
CONGO	4496.78	24482	72130	120121
ZAMBIA	735.99	.. no data	14116	15522

No acoustic data were available for the southern part of the lake from the cruise of 02/95.

It is known from the previous acoustic surveys performed on Lake Tanganyika in the 1970's (Johannesson 1974; Chapman 1974, 1976; Mathisen & Rufli 1980) that a rough estimate of the total abundance of pelagic fish in Lake Tanganyika was in a range of 0.4 to 2.8 million tonnes. Our estimates were lower. The extreme estimate by Johannesson (1974) was 4 to 10 times higher than all the others and was an artifact of the sampling strategy.

7.4 CONCLUSIONS

It must be emphasised that the temporal variations in fish abundance and their spatial distributions in present data were enormous. Johannesson (1974) noted more than a twofold difference in the biomass measured at the interval of a few weeks in Burundian waters. Chapman (1976) found completely different fish distributions in Kigoma waters during two consecutive nights. Such changes should be interpreted in terms of large-scale movement among the plankton of Lake Tanganyika (all dominant fish species are migratory) and seasonal variations of the environmental conditions. The very low levels of fish biomass can also be a result of a temporary overfishing, especially in the industrial fishing areas of Burundi and Zambia.

The standing stocks of fish in Lake Tanganyika seem to be much less than their annual production (Coulter, 1981). The P/B ratios of 4.5, 2.7 and 1.6 a^{-1} for *Stolothrissa*, *Limnothrissa* and *Lates*, respectively, were estimated now in the present data (Mannini *et al.*, 1996). According to Hanek and Coenen (1994) the total overall fish catch for 1992 was 167 000 tonnes (Burundi 24 000, Tanzania 80 000, Zaire 50 000, Zambia 13 000). These numbers are comparable with the separate estimates of fish biomass. With increasing dependence on a species with a 1-year life cycle, the fishery probably will become more seasonal and also more susceptible to environmental fluctuations.

CHAPTER 8

LAKE TANGANYIKA ECOSYSTEM ASSESSMENT

By:
Sarvala, J. K. Salonen, P. Mannini, T. Huttula, P-D. Plisnier, V. Langenberg, I. Vuorinen, H. Kurki, H. Mölsä, and O.V. Lindqvist

Abstract

The LTR Project team's assessment of the Lake Tanganyika ecosystem is based on studies of hydrodynamics and limnology, carbon and energy flows, and pelagic fish production and yield. Major hydrodynamic events affecting primary productivity are wind patterns, and secondarily the ratio of the mixing layer depth to the productive layer depth as well as transport of the nutrients to the euphotic zone through turbulence, mixing and upwelling. Interactions between the physical environment and biotic community are seemingly more dynamic and complex than previously thought, and therefore the trophic structure of lake is extremely difficult to study quantitatively with conventional field methods.

A new view of the trophic structure of Lake Tanganyika is emerging from LTR data: phytoplankton production and carbon biomass figures are higher than earlier estimates, and zooplankton data indicate lower biomass and production than previously estimated. Contrary to earlier claims the trophic efficiency between zooplankton and phytoplankton in Lake Tanganyika is not exceptionally high. Likewise, fish yield seems to be relatively low in comparison with primary production, and falls within the normal range reported from other lakes.

LTR fish biomass estimates were lower than previously published values for Lake Tanganyika, which show wide variation. The pelagic fish biomass estimate of 58 kg ha^{-1} adopted by the LTR team is close to recent acoustic estimates for Lake Malawi, however. Although present catch figures are the highest so far reported from Lake Tanganyika, they remain lower than potential yield levels cited previously. Yet recent trends suggest that sustainable catch levels are lower than previously thought. Consideration must also be taken of calculations based on the observed zooplankton production, the fact that primary production in Tanganyika is mainly dependent on internal nutrient cycling and mixing regimes, and the possibility that productivity in the large central open area may be lower than along the coasts. The realised catch of planktivorous fish in the whole lake was about 23-28%, and in the most heavily fished Burundi waters 43-52% of estimated production. For piscivorous fish in the whole lake the corresponding figure was 61-73%. These figures suggest that the present fishing pressure in Lake Tanganyika is very high.

8.1 HYDRODYNAMICS AND LIMNOLOGY

Hydrodynamic modelling and intensive field measurements indicate that wind driven forces initiate and maintain the upwelling events on Lake Tanganyika -- not only in the southern end as shown classically, but also secondarily along the eastern and western coasts. In fact the most complex and dynamic current patterns and vertical mixing events were shown in Kalemie strait. These were caused by a lake-land breeze system resulting in strong offshore winds that are influenced by mountain slope and south-easterly trade winds (Savijärvi 1997; Huttula 1997). Internal periodic wave motions of 23 days during the dry season, and 35 d during the wet season, were recorded. The typical range for dry season upwelling velocity was about 3-25 m/d.

The major hydrodynamic events that affect the primary productivity are in the first place the wind patterns, and then the ratio of the mixing layer depth to the productive layer depth as well as transport of the nutrients to the euphotic zone through turbulence, mixing and upwelling. These mechanisms are, however, very complex. Although deep mixing in principle might enhance productivity by increasing nutrient input from the hypolimnion, it simultaneously decreases primary production because light becomes limiting for phytoplankton cells forced to stay at low light conditions for most of the time. The low production levels off Mpulungu indicated by the direct *in situ* primary production measurements and the zooplankton data by LTR suggest that the negative effects of deep mixing may be dominant in southern Tanganyika. Besides direct light limitation, this may be due to the fact that the cells adapted to low-light are intermittently rapidly brought to high light intensity at the surface.

Also the horizontal currents and nutrient/ energy transport may induce the production in the three main basins, which may be locally influenced by the river inputs. The role of global climatic changes in adjusting the regional and local wind regimes has been shown, and the links of the wind and hydrophysical events with the biological production was evidenced.

Zooplankton studies demonstrate that characteristics of the pelagic ecosystem in the Lake Tanganyika to some degree reflect the different hydrophysical regimes in different parts of lake. Upwelling phenomena in the south create, together with the tilting thermocline, peculiar differences in the zooplankton behaviour, abundance, species composition and production in this part of the lake. These differences were most clearly seen in vertical migration behaviour and dynamics: the vertical range in Mpulungu extended twice as deep as in Kigoma basin or in front of Bujumbura (Kurki *et al*. 1999, Vuorinen *et al.* 1999). The effects of local off-shore driven irregular vertical mixing were, however, not that clearly seen in distribution or migration of grazer community off Kigoma as in Mpulungu. Vuorinen *et al.* (1999) concluded that the pelagic macrozooplankton community in front of Bujumbura provide evidence of more stratified conditions than in other parts of the lake. Areal differences were clearly seen even in fish diet and selective predation studies, and finally in pelagic fish ensembles too, which are dominated by clupeids in the north and by *L. stappersii* in the south (Mannini, 1998). The areal differences at any trophic level studied were, however, quite inconsistent, non-predictable, and by no means seasonally or annually stable (Bosma *et al.* 1998; Kurki 1998; Mannini 1998). The interactions between the physical environment and biotic community are seemingly more dynamic and complex than previously thought, and therefore the trophic structure of lake is extremely difficult to study quantitatively with conventional field methods.

8.2 CARBON AND ENERGY FLOWS

Our primary production estimates are based on the largest data base so far available from Tanganyika, including satisfactory seasonal coverage at three stations plus three lake-wide surveys. Although the *in situ* measurements gave somewhat lower values than the simulated *in situ* procedure, there are several methodological reasons to suggest that the true level of primary production in Tanganyika may be closer to the higher simulated *in situ* results. The clearly lower primary production estimates reported by Hecky & Fee (1981) were based on a shallower water column and included only the particulate production, while our results comprised both particulate and dissolved production.

Our results for the concentration of DOC were within the ranges given for Tanganyika by Hecky (1991) and Degens *et al.* (1971). Our new measurements thus confirmed the relatively low DOC levels in the surface waters of Tanganyika. Considering the general water quality in the lake, such DOC levels sound realistic, and do not suggest a major role for DOM in the planktonic food web.

8.2.1 Carbon flows and the trophic structure

A new view of the trophic structure of Lake Tanganyika is emerging from our data. Our phytoplankton production and carbon biomass figures (Table 8.1) are higher than the earlier estimates. In contrast, our new zooplankton data indicate lower biomass and production than previously estimated. Thus, contrary to earlier claims (Burgis 1984; Hecky 1984, 1991), our data show that, compared to lakes in general (e.g. Pauly & Christensen 1995), the trophic efficiency between zooplankton and phytoplankton in Lake Tanganyika is low -- not exceptionally high. Likewise, the fish yield seems to be relatively low in comparison with the primary production, as in many other large lakes (Oglesby 1977; Morgan *et al.* 1980). According to our estimates, fish production in Lake Tanganyika relative to primary production also falls within the normal range reported from other lakes (Morgan *et al.* 1980; Downing *et al.* 1990). The suggested role of bacterioplankton compares well with the literature (Cole *et al.*, 1988; White *et al.*, 1991).

High carbon transfer efficiency from phytoplankton to zooplankton (17%), suggested by Burgis (1984) for Tanganyika, was strongly dependent on a large correction factor for the filtration efficiency of the coarse plankton nets used, and her zooplankton production estimate may well be inflated. On the other hand, Hecky *et al.* (1981) obtained an unusually high transfer efficiency from phytoplankton production to fish yield (0.45%). However, the fish yield figure they used (125 kg ha^{-1} a^{-1} or 1.3 g C m^{-2} a^{-1}; Coulter, 1977) represented only the small intensively fished areas in the northern and southern ends of the lake. Both transfer efficiencies were also dependent on the primary production estimate of Hecky & Fee (1981: 290 g C m^{-2} a^{-1}), which may have been an underestimate, as discussed above. For the 1970s, the ECOPATH analysis of the pelagic system in the Burundi waters (Moreau *et al.* 1993, based on Moreau *et al.* 1991) likewise suggested very high transfer efficiencies from phytoplankton to zooplankton (25%), to planktivorous fish (2.4%) and to fish yield (0.36%). For the 1980s, calculated efficiencies were clearly lower (13, 1.1 and 0.2%, respectively), but still higher than our results, especially for the herbivorous zooplankton and fish yield.

It is tempting to speculate that the differences observed between the published values and our new biomass and production estimates for the different trophic groupings might represent real changes in the pelagic ecosystem over the years, owing for example to intensified fishing or climatic changes. However, none of the earlier estimates are accurate enough to allow definite conclusions about long-term changes, although at least the phytoplankton chlorophyll concentrations seem to have remained largely similar from the 1970s to the 1990s. We hope that the present LTR monitoring program can be continued for several years to produce a long-term temporal series which are so rare in the tropics.

In fact, low production efficiency of the crustacean zooplankton is not unexpected in a deep, clear water tropical lake with high epilimnion temperatures. Low efficiency would result from high respiration costs owing to the high temperatures, and/or from the costs of the long vertical migration enforced by the high predation pressure by fish in the clear pelagic waters. Low efficiency of zooplankton production was likewise found in Lake Malawi (Irvine & Waya 1999), which resembles Tanganyika in many respects. However, similarly low transfer efficiencies have been reported from Lake Michigan (Sprules *et al.* 1991), which suggests that low efficiency may be a general feature of all deep, oligotrophic lakes. Low phytoplankton densities increase feeding costs and decrease growth rates, tending to diminish the role of cladocerans that are the most productive zooplankton crustaceans. The microbial loop may also have a prominent role in the pelagic food web of oligotrophic systems (Weisse & Stockner 1993; but see Riemann & Christoffersen 1993, for opposite view). This leads to inflated respiration costs to the extent that such systems act as net sources of carbon dioxide to the atmosphere (del Giorgio *et al.* 1996). High dependence of primary production on nutrient regeneration, as in Lake Tanganyika (Hecky, 1991), implicitly suggests low efficiency of carbon transfer through the food web, because nutrients are mainly regenerated by the microzooplankton, which have high respiration rates. Thus, in Lake Tanganyika, the temporally and regionally variable nutrient inputs from the huge hypolimnetic store, through long-range transport via atmosphere, and from land runoff, are not only crucial to the absolute levels of production, but, by modulating the role of the microbial loop, may also affect the efficiency of carbon transfer through the system.

The estimated carbon transfer efficiency from crustacean zooplankton to planktivorous fish was lower than the values reported from Lake Malawi between herbivorous zooplankton and their predators (invertebrates and fish larvae; Allison *et al.*, 1995). In Tanganyika, the efficiency at this step may be partly affected by the fact that some of the fish production is based on deep-water shrimps, which may not have been caught quantitatively with the present sampling scheme. The extremely simple food web structure in the open waters of Tanganyika should enhance fish production: the food chain leading to planktivorous fish production is short. The fishery itself has simplified the food web by drastically reducing piscivorous fish stocks at an early stage of the commercial fishery (Coulter 1970). On the other hand, low production efficiency would rather be expected in a high-temperature environment (Edwards 1984). In Tanganyika, the upper, almost anoxic layers of hypolimnion may provide zooplankton with a partial refuge from fish predation. This combined with the energetic costs of extensive vertical migrations, necessary in order to avoid piscivorous fish, may lead to a relatively low energetic efficiency of planktivorous fish production.

We thus conclude that the trophic efficiencies in the pelagic food web of Lake Tanganyika are not unusually high. The crustacean zooplankton production is small, but the recorded fish yields quite normal relative to the measured primary production of pelagic phytoplankton. Thus the flourishing fisheries in Lake Tanganyika are not so much based on any exceptional productivity of the system, but on the fact that most of the pelagic production is channelled into a few fish species that have short life cycles and rapid reproduction. Those fish are furthermore easy to catch and thus suitable for an economic fishery.

8.3 PELAGIC FISH, PRODUCTION AND YIELD

The average production-to-biomass ratios of fish derived from our length-frequency analyses were roughly similar to the annual values calculated by Coulter (1981) for *Stolothrissa* (3.9 from the graphical Allen curve method, and 3.7 from mortality rate, assuming von Bertalanffy type growth). Thus, the intensified fishery seems not to have caused any changes in fish growth. Growth and mortality estimations using LFA are always somewhat suspect, although our results were in good correspondence with earlier analyses and for *Limnothrissa* were supported by otolith readings (Kimura 1995; Pakkasmaa & Sarvala 1995; H. Ahonen, unpubl.). However, the otolith studies by Kimura (1995) for *Stolothrissa* in southern Tanganyika and by H. Ahonen in central Lake Tanganyika (unpubl.) both indicated faster growth than our LFA analyses. The ontogenic migrations of juvenile and adult fish between the open lake and near shore areas, might cause errors in the LFA estimates (Mannini 1998). Further work utilising daily otolith increments is clearly needed to confirm the observed growth patterns of fish.

Our fish biomass estimates were lower than previously published values for Lake Tanganyika, which show wide variation. Biomass estimates obtained from FAO hydroacoustic surveys in 1973-1976 (Chapman *et al.* 1978; Coulter, 1991) varied from 211 to 1237 kg ha^{-1}, of which the largest value seems unrealistically high. Roest (1977), using catch samples and acoustic estimates in Burundi waters, ended up at an estimate of 160 kg ha^{-1} for *Stolothrissa* alone. Extrapolating from catch statistics in heavily exploited areas in the north and south, Coulter (1977) estimated the virgin pelagic fish biomass in the north end of Tanganyika at 32-45 kg ha^{-1}, which is only one fourth of the value of Roest (1977). Fish biomass values calculated with the ECOPATH model from a trophic analysis of the pelagic system in the Burundi sector (Moreau *et al.*, 1993) were 63-181 kg ha^{-1} for the planktivorous fish and 37-102 kg ha^{-1} for the piscivorous fish in the early 1980s and the mid-1970s, respectively. Converted to carbon units, the corresponding production estimates were 3.2-7.9 and 0.3-0.7 g C m^{-2} a^{-1}, or higher than our estimates. The P/B ratios applied by Moreau *et al.* (1993), based on Moreau *et al.* (1991), and the fish yield figures used as the starting point for the ECOPATH model were also somewhat higher than ours. Interestingly, according to recent acoustic estimates (Menz *et al.*, 1995), the average pelagic fish biomass in Lake Malawi was 70 kg ha^{-1}, i.e. close to the value adopted here for Tanganyika (58 kg ha^{-1}).

Our fish production estimates can be compared to the realised catch. It is admittedly difficult to obtain reliable statistics from a large lake like Tanganyika, where artisanal fisheries take the majority of the catch. The LTR estimates were based on estimated total fishing effort that was converted into 'traditional effort units,' number of fishing days (250 d/a), and average catch per unit (CPUE) of each gear type (Coenen *et al.* 1998). Such estimation is subject to various sources of errors or uncertainties (Francis & Shotton 1997), e.g. observation errors on catch and effort levels. Coenen *et al.* (1998) noted that the number of actual fishing days, which may vary between 225 and 275, already results in total annual lake catch estimation to range between 176 913 and 216 227 tn a^{-1}.

However, the recorded total catches from Tanganyika show a clearly increasing trend. Coulter (1977) reported an annual fish yield of 73 000 tonnes in the late 1960s and Roest (1992) estimated 85 000 tonnes for 1987. According to the most recent and probably the most accurate lake-wide statistics produced during the LTR project, the total catch was 167 000 metric tonnes (or 51 kg ha^{-1}) in 1992 (Hanek 1994; Coenen 1995), and 196 570 tonnes (60 kg ha^{-1}) in 1995 (Coenen *et al.* 1998). In areal units, the 1992 catch amounted in Burundi waters to 94.5 kg ha^{-1} yr^{-1}, in Zambia to 69, in Tanzania to 60, and in Zaire to 34 kg ha^{-1} yr^{-1} (Hanek 1994); for 1995 the corresponding figures were 111.5, 53, 40 and 62 kg ha^{-1} yr^{-1}, respectively (Coenen *et al.* 1998; the Zambian figure came from the year 1994).

8.4 CONCLUSIONS

Although the present catch figures are the highest so far reported from Lake Tanganyika, they still remain clearly lower than the potential yield levels of 380 000 - 460 000 tonnes (116-140 kg ha^{-1}) per year postulated in previous papers (e.g. Coulter 1977). However, the final potential yield estimate of Coulter (1977), 100 kg ha^{-1}yr^{-1}, is close to the present realised yield in Burundi, where the fishing pressure is highest. There, the catches per unit area have in fact decreased since 1967-1971 (Coulter, 1977). During the 1990s, Coenen *et al.* (1998) recorded declining trends in the catch per unit effort in the industrial fishery in all areas studied and in the lift net fishery in Tanzania. On the other hand, increasing unit catches were noted for apollo units in Burundi where this type of fishery was gradually replacing the industrial fishery. These trends suggest that sustainable catch levels are lower than previously thought. This is also supported by calculations based on the observed zooplankton production, which is lower than previous estimates. Moreover, because the primary production in Tanganyika is mainly dependent on internal nutrient cycling and mixing regimes, productivity in the large central open area may be lower than along the coasts (Ostrovsky *et al.* 1996). The realised catch of planktivorous fish in the whole lake was about 23-28%, and in the most heavily fished Burundi waters 43-52% of the estimated production. For piscivorous fish in the whole lake the corresponding figure was 61-73%. These figures suggest that the present fishing pressure in Lake Tanganyika is very high. Normally only 20-25 % of fish production can be taken as fisheries yield (Houde & Rutherford, 1993).

Table 8.1 Annual biomass and production at different trophic levels in Lake Tanganyika. (Sarvala *et al*., 1999)

	Biomass g C m^{-2}	Production g C m^{-2} a^{-1}	%
Phytoplankton	2.4	426-662	100
Bacterioplankton	..	..	20
Herbivorous copepods	0.81	23.0	3.5-5.4
Predatory copepods	0.20	2.2	0.3-0.5
Shrimps	0.09	1.3	0.2-0.3
Limnocnida	0.13	?	?
Fish (clupeids)	0.40	1.4-1.7	0.21-0.40
Fish (Lates etc.)	0.18	0.3	0.04-0.08
Fish yield (total)	..	0.5-0.6	0.08-0.14

CHAPTER 9.

IMPLICATIONS FOR FISHERY MANAGEMENT

By:
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Abstract

Recognising that the Tanganyika fisheries must be treated as a complex biological and anthropological reality, LTR research has been pursued with a combination of observational and analytical tools from both the natural and social sciences. In building towards a fisheries management fisheries management framework for Tanganyika particular use has been made of recent approaches that emphasise 'components of sustainability' and the FAO *Code of Conduct for Responsible Fisheries* or CCRF. A Tanganyika management framework needs to aim for the 'pursuit of sustainability' across its multiple bio-socio-economic and institutional dimensions. In CCRF terms, it needs to aim for 'responsible fisheries compliance' through simultaneous attention to basic principles of precaution (risk adverse decision making), partnership (co-management), proprietorship (local allocation of property rights), policing effective monitoring, control, and surveillance (MCS) and enforcement practices), and process (flexibility to accommodate varied or changing circumstances).

Based on sustainability and responsible fisheries paradigms, and taking into account the outcomes of the LTR Scientific Programme and complementary socio-economic/legal/institutional investigations of fisheries prospects and problems, it is proposed that policy initiatives for Lake Tanganyika be pursued along the following broad lines. 1) ***Adaptive management***: use of interactive management practices that allow for adjustments in fishing pressure, and also allow for flexible application of management treatments appropriate to different circumstances encountered around the lake shore; 2) ***Multi-disciplinary perspectives***: maintenance of monitoring capability to measure across a range of bio-physical and socio-economic parameters, as appropriate to the complexities of ecosystem – human system interactions; also, cultivation and maintenance of 'non-scientific' and 'scientific' knowledge coalitions; 3) ***Management in partnership***: promotion of local stakeholder group involvement in management decision-making and in fashioning modalities of enforcement and compliance; 4) ***Resource access and use rights***: moves to constitute control of access and fishing rights at local community levels; 5) ***Fisheries and economic diversification***: adoption of integrated development strategies and coastal area management models at the local level, to accommodate complex interactions and possible conflicts between fishing and non-fishing activities, and, at national and regional 'macro-levels,' moves to foster economic diversification to reduce pressure on the fishery resource base.

9.1 RESEARCH OUTCOMES: MULTI-DISCIPLINARY INDICATORS FOR TANGANYIKA FISHERIES

As noted in the Introduction, and as the intervening chapters fully demonstrate, LTR's Scientific Programme stands out as something rather unique in the annals of Tanganyika research. Programme activities have succeeded in being at once *innovative* and *integrative*. Scientists and fisheries personnel from all four lacustrine states and several international institutions have been brought together to work in multi-disciplinary collaboration, using standardised sampling devices and techniques from shore-based and buoy-based stations around the lake as well as from the project research vessel platform. The data collection, processing, and analysis 'yield' from these activities, all managed under often difficult technical and political circumstances, is unprecedented for Lake Tanganyika in terms of its areal and temporal comprehensiveness.

As a result, substantial progress has been made towards realising the primary purpose of the LTR Project, as reflected in its official title of 'Research ***for*** the Management of Fisheries on Lake Tanganyika' (emphasis added). Major components of the lake's hydrodynamics and its trophic structure are better understood and the whole picture of fishery resource distribution and vulnerability to fishing operations has now become clearer. Research outcomes of the Scientific Programme, in other words, have well served the intention laid out in the original LTR charter, the Project Document, in helping to provide '…an adequate reference basis for formulation of a lake-wide fisheries management policy, aiming at the maximum sustainable utilisation of the pelagic fish stocks, so as to supply high-protein food for the human populations of the four riparian States' (FAO 1992).

However, as fisheries management is as much about human behaviour and institutional arrangements as it is about hydrodynamics and trophic structure, production dynamics and stock abundance, the implications of Scientific Programme research outcomes must be considered in conjunction with various indicators derived from LTR socio-economic and legal-institutional studies. In achieving such a conjunction, the LTR team has aligned itself with what might be called 'new school' as opposed to 'conventional' approaches to management thinking. As will be seen in the following section, research implications are thus evaluated in terms of 'dimensions of sustainability' and 'responsible fisheries,' as opposed to the heavily technocratic, non-participatory, 'stock assessment driven' orientation that has characterised much of fisheries science and policy in the past.

9.2 FISHERIES PROSPECTS AND PROBLEMS: THE DIMENSIONS OF SUSTAINABILITY[2]

Many observers have pointed out how the normative concepts, analytical orientations, and application strategies that have guided much of fisheries research, development, and administration over the modern era are seriously flawed. Such diagnoses are borne out by what has aptly been termed the 'litter of failures' (Roberts 1997) across the fisheries of the world. This is manifested in repeated episodes of declining yields and economic return, stock collapse, and, ultimately, crises of social dislocation and lost biodiversity (cf. Larkin, 1977; Lindqvist 1977; Ludwig *et al.* 1993; Myers *et al.* 1997; Beverton 1998; de la Mare 1998; Holt 1998; Pauly 1998; Pitcher *et al.* 1998).

A common characteristic of conventional management systems in fisheries is their 'command and control' nature, expressed as 'top-down' directed communication channelled through highly bureaucratised structures (cf. Harris 1998). Decision-making on critical issues is seen as the preserve of state functionaries, who rely on fisheries scientists for technical advice (cf. Lindqvist & Mölsä, 1982). Minimal allowance is made for the participation of local-level resource users. Ironically, the 'objective' scientific advice that is supposed to underpin the whole process is itself open to question. Roberts (1997), for example, criticises conventional fisheries management decision-making for its over-dependence on population biology models and methods that do not take species interactions into adequate account and that allow insufficient leeway for error in circumstances that are fraught with great uncertainty.

[2] This and the following section draw in a somewhat revised and condensed fashion from Mölsä *et al.* (1999) and Reynolds (1999b).

LTR research from the very outset has been guided by recognition of the inadequacies of simple 'stock assessment driven' analyses (Lindqvist and Mikkola, 1989). Thus none of the SSP studies – whether of pelagic trophic structure (Sarvala *et al.*, 1999), bio-physical interactions (Huttula, 1997; Plisnier, 1997; Salonen *et al.*, 1999; Vuorinen *et al.*, 1999; Kurki *et al.*,, 1999), or pelagic fish stock mass (Szczucka, 1998) -- were performed with the intention to of establishing an accurate level of Maximum Sustainable Yield (MSY) and Total Allowable Catch (TAC). Use of the MSY model was deemed totally unsuitable given the highly complex, dynamic, and unpredictable conditions obtaining in the lake. The model not only neglects the significance of life-history adaptations and inter-specific relationships in multi-species stocks, but overlooks the effects of complex patterns of adaptive behaviour within the human communities that exploit them (see Larkin, 1977; Lindqvist, 1977).

In an important contribution that reviews the evolution of management paradigms and sustainability concepts over the modern era, Charles (1994) synthesises major strands of 'new school' fisheries science thinking into a unitary framework. He argues that resource conservation is a necessary but not sufficient condition for sustainability. Because sustainable fisheries development involves multiple objectives, various biological, socio-economic, culturo-communal, and institutional dimensions must be taken into account. He goes on to propose a conceptual approach through which these different dimensions or components may be ordered, evaluated, and integrated.

Another and much more extensive and programmatic synthesis of contemporary fisheries management precept and practice, though one that touches many of the same themes, is provided in the FAO *Code of Conduct for Responsible Fisheries* (hereafter CCRF). The CCRF principles (FAO, 1995), along with their accompanying series of *Technical Guidelines*, provide the basic normative orientation for LTR regional fisheries management planning (Reynolds 1998).

The CCRF first verifies the pressing need for a fundamental reorientation of global fisheries priorities and then elaborates a voluntary model framework through which such reorientation can be effected. The points of responsibility it highlights include, *inter alia*: a) use of whole ecosystem perspectives on problems of resource base and environmental preservation; b) dedication to present social welfare needs, consistent with sustainability; d) adoption of the 'precautionary approach' in management and conservation decision-making; and e) effective participation of stakeholder groups in the decision-making process, with particular attention to small-scale fisher interests.

Using the analytical approach developed by Charles (1994) in tandem with the CCRF framework, the circumstances of Lake Tanganyika fisheries and their management needs can be reviewed in terms of four principal components of sustainability – viz. ecological, socio-economic, communal, and institutional.

9.2.1 Ecological sustainability

The basic criterion for ecological sustainability in fisheries is the maintenance of the resource base (stocks and species) at viable levels – i.e., so as '…not to foreclose future options' (Charles, 1994:204). More generally, of course, this entails the need to secure the integrity and build the capacity of the overall ecosystem. Under CCRF guidelines, similar themes are expressed in terms of the 'precautionary approach,' which imposes broad obligations of 'prudent foresight' in the management of fisheries systems. Precautionary requirements include, for example, such interrelated measures as: the maintenance of system balance and productivity for the benefit of future generations; careful and constant restraint on harvesting and processing capacities in accordance with the dynamics of resource renewal; and giving automatic priority to conservation of productive capacity when the outcomes of development interventions are uncertain (FAO, 1996a, 1997).

Pelagic fish production

The ecological basis of pelagic fish production as investigated under the LTR Project and through earlier studies is reviewed in some detail by Sarvala *et al.* (Chapter 8). Salient points include the following.

Hydrophysical, limnological, food web, stock assessment, fish biology, and related studies provide a basis for reassessing the pelagic trophic structure of Lake Tanganyika, which has been claimed to be unique in the proportion of fish biomass to phytoplankton biomass (Hecky, 1984). Ecological studies and catch surveys have also evaluated the vulnerability of the fish stock to increased fishing pressure and possible over-fishing.

Hydrophysical patterns, nutrient fluxes, and related primary production of Lake Tanganyika are highly dynamic and affected by climatic, hydrological and internal factors (Huttula, 1997; Plisnier, 1997; Salonen *et al.*, 1999), all of which are non-predictable and capable of dramatic fluctuation. Various hydrophysical and biological processes regulating secondary production likewise induce fluctuations in zooplankton, medusae, and shrimp abundance and distribution. These effects are seen in high seasonality, strong daily vertical migration, and patchy horizontal distribution. Some degree of areal variation is also apparent (Vuorinen *et al.*, 1999; Kurki *et al.,* 1999, Chapter 5).

The dominant pelagic fish species (clupeids and *L. stappersii,* as distinct from the other *Lates* spp.) display an r-selected life-history strategy typified by features of high juvenile mortality, early maturity and recruitment to fishery, relatively short life cycle, and high turnover rate (Mannini *et al.,* 1996). Such features are consistent with an adaptation towards non-predictable conditions (Stearns, 1976) and, as estimated by Adams (1980) for a large number of marine fish species, provide resistance to high fishing pressure targeted even to young age classes. Great reproduction potential, multiple spawning, and migrations lead to regular recruitment and fast recovery after exposure to over-exploitation and highest actual yield and yield/ recruitment (Adams, 1980; Armstrong & Shelton, 1990; Fogerty *et al.*, 1991). Such recovery of stock was shown in Burundi after the fishing was temporarily closed in 1996.

Annual catch of planktivorous fish figures at about 23% of total estimated production for the whole lake, and as high as 66% in the case of Burundi waters, which are the most heavily fished. For piscivorous fish, the lakewide catch is reckoned to be some 70% of total estimated production. These figures suggest that the present fishing pressure in Lake Tanganyika is very high (Sarvala *et al.*, 1999). Normally it is supposed that only 20-25% of fish production can be harvested (Houde & Rutherford, 1993).

Variations in stocks and yields

Tanganyika's fish stock levels and yields are characterised by substantial year-to-year, season-to-season, and area-to-area fluctuations, often associated with dramatic shifts in the relative abundance of clupeids and *Lates*. Such fluctuations, called 'process uncertainty' by Caddy and Mahon (1995), may be caused by variable success in fish recruitment which, in turn, is regulated in complex and non-predictable way by physical, biological and fishing-related factors (for clupeoids, see Cole & McGlade, 1998). LTR researchers have established that temporal and areal variations of commercial stocks are associated with the strength and timing of nutrient upwelling and related plankton succession in Lake Tanganyika, particularly in the south. In other words, patchy and ephemeral distribution of the target pelagic species matches the patchy and ephemeral availability of their prey -- copepods for clupeids, and shrimps and clupeids for *Lates* (Plisnier & Coenen, 1997; Coenen *et al.* 1998; Mannini 1998).

Fluctuations in the relative abundance of pelagic species are also apparently linked to migrations between different sub-basins of the lake. Although not systematically studied by the LTR project, the likelihood of migration occurrence was demonstrated indirectly through catch studies (Coenen *et al.*, 1998), fish biology data (Mannini, 1998), and assessments of population genetic discreteness (Kuusipalo, 1994, 1999; Hauser *et al.*, 1998). The lack of distinct genetic population structures suggests that a significant exchange of individuals takes place between different parts of Lake Tanganyika. Mannini *et al.* (1996) claimed the same for fish biology data obtained from catch samples. Mannini (1998) later noted that although *L. stappersii* is capable of moving and mixing freely across all sub-basins of the lake, from a management perspective it is possible to discriminate a 'northern' and 'southern' stock on the basis of spawning and exploitation patterns. There are indications that the Kigoma sub-basin provides spawning and nursery areas for the 'northern' stock, and that the Moba and East Marungu sub-basins fulfil the same roles for the 'southern' stock (Chapter 6).

Localised overfishing

Signs of excess fishing pressure of *S. tanganicae* stocks (high juvenile content and smaller mean length in catches) exist for the northern end of the lake, on both west and east coasts north of Karonda (Burundi coastline, about 75 km from the northern tip of the lake). Furthermore, the highly unselective beach seine fishery, mostly prosecuted in Zambia, is heavily targeting juvenile *Limnothrissa miodon* in their shallow, inshore nursery grounds (Mannini, 1998). The seines are in addition inflicting untold damage on the mainly cichlid coastal fish community.

Although total catches show an increasing trend, CPUE for industrial units (purse seiners) have been declining. Nightly CPUE of industrial units in Burundi dropped from 166 kg in 1994 to 111 kg in 1996, and in Mpulungu from 877 kg in 1994 to 535 kg in 1996. The industrial nightly CPUE's in Congo have also decreased to 433 kg from the 780-950 kg of the early 1990's (Coenen *et al.,* 1998).

Progressive CPUE decline and increased duration of fishing trips in the industrial fishery in southern waters indicates a decrease of the catchable stock and possible over-exploitation of *L. stappersii* (Coenen *et al.,* 1998; Mannini, 1998). Indications of possibly excessive exploitation pressures on *L. stappersii* have also been noted for the northern end of the lake, as a result of the effects of successive waves of heavy industrial fishing and artisanal fishing. *L. stappersii* now make up only around 20% of the commercial catch in northern waters, with juveniles accounting for most of this contribution (Mannini, 1998).

9.2.2 Socio-economic and community sustainability

The typology proposed by Charles (1994) treats human welfare dimensions of fishery sustainability under two separate components. An analytical distinction is made between 'socio-economic sustainability' and 'community sustainability' depending respectively on whether 'individual' or 'group' perspectives are adopted.

Socio-economic sustainability pertains to the generation, distribution, and maintenance of benefits amongst individual actors or 'players' in a fishery arena. Criteria for assessing sustainability in this connection thus include, for example, the extent to which a fishery provides employment, income, and food security advantages to small-scale harvesters and traders, the extent to which different players share in these advantages, and the extent to which they will remain a viable basis of livelihood.

Community sustainability pertains to the issues of wider collective identity and welfare. It is measured with reference to such criteria as the extent to which a fishery: a) contributes to community stability in the long run; b) allows local group access to the resource base and community involvement in resource management and development decision-making; and c) affects the fortunes of various community sub-groups such as women, youth, etc.

CCRF principles likewise recognise that socio-economic and community welfare are crucial fishery issues. Management aims for maintaining resource base viability must be pursued in the context of human requirements for '…food security, poverty alleviation and sustainable development' (FAO, 1995:4). Decisions related to the regulation of fishing effort, the protection of fragile stocks, and so on, are bound to carry implications for the activities and even the basic livelihood of those who participate in a fishery system as resource users. CCRF technical guidelines therefore emphasise that an understanding of socio-economic and cultural patterns and processes is an essential component of responsible fisheries management, in order '…to anticipate the nature and extent of these impacts and to make decisions so as to optimise them' (FAO, 1997:32-33).

LTR socio-economic and community investigations

Readings on human welfare dimensions of sustainability for Lake Tanganyika fisheries are provided by findings from two major LTR investigations – the lakewide socio-economic survey that was conducted in 1997 (Reynolds and Hanek, 1997), as previously noted, and the community referenda exercise that was completed in late 1998 (Reynolds, 1999). The referenda involved a series of public meetings around the lake for the exchange of information and views between local fisheries stakeholder groups and national LTR field teams.

Socio-economic and community features of the Tanganyika fisheries have been reviewed in some detail in earlier LTR publications (Reynolds, 1997a, 1997b, 1997c, 1997d; 1999a; Reynolds and Hanek, 1997). Salient points to summarise here include the following.

Fisheries as livelihood

Communities bordering Lake Tanganyika clearly share in the conditions that, on the basis of various 'quality of life' indices, have ranked East-Central African countries amongst the world's most poverty-stricken and underdeveloped (World Bank, 1999). LTR Project SEC survey findings, for example, confirm a picture of weak and deteriorated physical infrastructure around the lake shore, and of a critical scarcity in basic social services and amenities. At the same time, however, the data show that there is considerable variation of socio-economic circumstances within local and regional settings. In some cases, estimated fishing-derived incomes in the artisanal sector rank above to well above estimated national working age population per capita annual income levels. Estimated earnings for traditional fishers, on the other hand, are substantially lower than national averages. Amongst post-harvest operators, strong gender-related discrepancy is widely apparent, with men earning at rates above national working age averages and women earning at rates well below.

In a context where the overall rural economy offers very limited opportunities for gainful employment, the attractions of fisheries work may be quite strong (cf. Skjønsberg, 1982); there is the promise of moderate remuneration, depending on the job, and conditions of entry seem relatively easy (low initial requirements for skills, working capital, or investment in productive equipment and supplies).

On the other hand, local views on the state of commercial fish stocks indicate that a degree of pessimism, or at least uncertainty, exists with regard to the ability of the lake's fisheries to sustain adequate levels of livelihood security (Reynolds and Hanek, 1997). Fishers and post-harvest operators are very pessimistic in their appraisals of catch trends over recent years: majorities in all cases take the view that they have been on the decrease.

Increasing demand for fish

Fish accounts for some 25% to 40% of total animal protein supply for the populations of the four Lake Tanganyika states (Gréboval *et al.*, 1994), so its significance for nutritional welfare is obviously considerable. At the same time, rapid population growth within the Tanganyika basin and across East-Central Africa as a whole (World Bank, 1999) fuels an ever-increasing demand for fish products, so that over the last several decades per capita supply has barely kept pace with overall fish production, despite increases in the latter (Gréboval *et al.*, 1994).

In a region already subject to severe episodes of drought, prolonged political unrest has compounded the effects of population growth in ratcheting up demand for Lake Tanganyika fishery products. Crop and livestock production capabilities, marketing infrastructure, and the general state of food security have all been severely disrupted in Burundi, eastern DRC, and Rwanda due to hostilities and attendant population displacements and breakdown of public services.

Resource access issues

Tanganyika fisheries basically operate under an open access regime. Under the broad conditions associated with national territorial partitions, everyone is free to fish. This situation is clearly untenable. Open access classically leads '…to overexploited resources and declining returns for all participants' because it is '…characterised by a race to fish in which all participants strive to catch as much of the resource… as they can, before their competitors do' (FAO, 1997:52). Rising population pressures within and without the lake basin are bound to exacerbate matters. Some form of limited access will have to be established if the fisheries are to be sustained – i.e. if the classic sequence of 'free-for-all' exploitation race to fish resource overexploitation is to be avoided (FAO, 1997).

Local participation in management decision-making

Management approaches within the four national sectors of Lake Tanganyika were established in the classic 'top-down' model, featuring a high degree of state control over all aspects of fisheries affairs from policy definition to regulation enforcement. Although existing legislation in some cases provides for consultation between administrators and local representatives of fisher interests (Cacaud, 1999), and although fisher committees are reported to exist at various landing sites (Reynolds and Hanek, 1997), *de facto* local community participation in resource management decision-making and follow-up has been very minimal. It is clear however that many local fisherfolk would be eager to embrace management responsibilities more directly (Reynolds, 1999).

Social equity

Prospects for human welfare sustainability in Tanganyika's fisheries are subject to potentially serious hindrances arising from pervasive inequalities in wealth and control of the means of production. One dimension of such socio-economic differentiation is seen in the sometimes-fraught relations between fishing unit owners and fish workers, particularly in the artisanal sector (Reynolds, 1999a).

A second is expressed in terms of educational attainment and estimated income differentials between men and women (Reynolds and Hanek, 1997). Gender-based inequality is apparent in other ways as well, as noted during the 1998 Community Referenda exercise (Reynolds, 1999a). In their exclusion from full public participation in local decision-making processes, women as a class share something of the same disadvantages as their fish worker counterparts in the harvest sector—namely, subordinate social status and poor pay.

A third dimension of socio-economic inequality can be recognised in the relations between artisanal and traditional 'small-scale' fishers on the one hand and the industrial purse seine 'large-scale' fishery on the other. Small-scale fisher antipathy towards purse seining is fairly general around the lake, but is particularly strong in the southern end, where virtually all of the industrial fleet is now based (Reynolds and Hanek, 1997; Reynolds, 1999).

9.2.3 Institutional sustainability

Charles (1994) describes institutional sustainability as playing a kind of intermediary role vis-à-vis the other three sustainability components of his typology: 'A prerequisite for …[ecological, socio-economic, and community sustainability] is the maintenance of suitable financial, administrative and organisational capability in the long-term' (*ibid*: 205). Institutional sustainability in a fisheries context thus turns on the ability of a state- or industry-supported research establishment effectively to monitor catch and effort trends, for example, or of a regulatory agency effectively to fashion management measures and ensure their enforcement.

The CCRF and its *Technical Guidelines* highlight the importance of both formal and informal institutional structures for the fisheries management process. In some contexts informal institutions may fulfil crucial management functions, as for instance where customary arrangements govern conditions of resource access or regulate fishing effort. With regard to formally constituted management authorities at regional, state, or local levels, CCRF provisions lay particular emphasis on the crucial task of fisheries monitoring, control, and surveillance, or MCS (FAO 1997).

Institutional sustainability and Lake Tanganyika fisheries

An appreciation of the problems and prospects related to institutional sustainability for Tanganyika fisheries can be gained from LTR studies of relevant organisational and legal structures within the four lacustrine states (Hanek, 1994, Maembe, 1996; Cacaud, 1996, 1999), monitoring and statistical data collection work carried out in collaboration with national research institutes and fisheries department offices around the lake shore (Coenen, 1994, 1995; Coenen *et al.*, 1998; Paffen *et al.*, 1997; Mannini, 1999), and findings of the 1997 lakewide SEC survey (Reynolds and Hanek, 1997) and 1998 community referenda exercises (Reynolds, 1999).

Institutional capabilities and legislative frameworks

All four lacustrine states are nominally committed to fisheries policies that emphasise socio-economic welfare objectives, consistent with the need to use resources in a sustainable, conservation-wise manner. Yet the institutional means provided for realising these objectives are woefully inadequate. National fisheries departments and research agencies are chronically under-funded, and in some cases disastrously so (Cacaud, 1999). As a consequence, research agencies are unable to maintain creditable scientific monitoring programmes in order to fulfil their role as technical advisors on sound management and conservation practices, except through dependence on outside sources of funding (cf. Coenen *et al.*, 1998; Mannini, 1999). Furthermore, fisheries departments are simply unable to marshal, in either qualitative or quantitative ways, adequate human and material resources for effecting their basic mission tasks of MCS and provision of extension services. Operational paralysis and lack of motivation amongst field personnel are rife.

Cacaud (1999) also identifies major fisheries legal framework deficiencies within the four lacustrine states. Existing legislation, in some cases dating back to the colonial era, is in many respects outmoded or obsolete. Comprehensive overhaul is needed in order to relate it both to current realities of territorial and administrative organisation, and contemporary management imperatives. Also, umbrella-type legislation that establishes broad regulatory powers for state authorities to exercise on a national basis needs to be augmented with specific regulations to fit the particular circumstances of Lake Tanganyika.

A second major area of legal deficiency concerns enforcement. Fisheries regulations in all four lacustrine States are widely ignored in practice, either because they are insufficiently enforced or because they are simply not enforced at all. The problem relates back to the huge financial constraints. As this situation is unlikely to improve in any dramatic way, new and viable enforcement solutions involving a much larger measure of local participation in management decision-making and in follow-up are called for.

Monitoring needs

At the beginning of the LTR project it was apparent that fisheries monitoring and information processing capabilities at some of the lake shore stations were extremely weak. Extensive collaborative work with national administrators and researchers was conducted in order to strengthen these capabilities and to assemble the sort of information base that is a first requirement of fisheries planning and management. Planning and management efforts will be impossible to pursue in future unless a regular lakewide monitoring programme is kept in place. Although monitoring activities of the same scope and intensity as achieved under LTR would clearly be impractical, any future programme would need to provide some degree of coverage over the same basic set of parameters -- physical, biological, statistical, and socio-economic – as those investigated under the project (Coenen *et. al*. 1998; Mannini, 1999).

9.3 APPLYING RESEARCH OUTCOMES: MANAGEMENT POLICY PROPOSALS FOR TANGANYIKA FISHERIES

For Lake Tanganyika as for other fisheries, management challenges not only must be met across the multiple dimensions or components of sustainability discussed above, but also met simultaneously, in an integrated fashion. A number of policy considerations have thus to be taken into account. As Charles (1994) observes, ‘If each of the [sustainability] components is viewed as crucial to overall sustainability, it follows that “sustainable development” policy must serve to maintain reasonable levels of each’ (*ibid: 205*). Policy orientation for the fisheries sector, he goes on to suggest, must therefore be such as to accommodate: a) conditions of uncertainty and complexity; b) improved local participation in management decision-making and implementation; c) clearer specification of resource property rights; and d) and actions directed internally to ensure a balanced use of resources and externally to encourage the development of non-fishing employment alternatives within the larger economic system.

In much the same terms, CCRF guidelines (FAO 1995, 1997) for responsible fishery policy and legal and institutional frameworks emphasise themes of:

1) conservative, least risk exploitation and development strategies in the face of system uncertainty, in accordance with the precautionary principle;
2) reliance on co-management approaches involving shared management responsibilities between state fisheries authorities and local stakeholders;
3) recognition of limitations on rights of resource access and use – i.e. resource 'ownership';
4) monitoring, control, and surveillance and enforcement activities to secure the regulation of fishing mortality; and
5) process, or an understanding of management as dynamic and adaptive rather than static and fixed in character.

Policy options that would help foster responsible fisheries management on Lake Tanganyika – that would, in other words, be appropriate to the effective 'pursuit of sustainability' (Charles, 1994) across its several dimensions, are summarised below under the headings of:

1.) Adaptive management;

2.) Precaution and multi-disciplinary perspectives;

3.) Co-management partnerships;

4.) Resource access and use rights;

5.) Regional fisheries, environment, and society.

9.3.1 Adaptive management

Inter-annual, seasonal, and areal variation in stock levels and yields within Lake Tanganyika, often substantial, unexpected, and marked by inverse proportions of clupeids and *Lates*, generate considerable problems for local fisherfolk and industrial operators alike, since fishing and marketing activities become difficult to plan. As earlier remarked, LTR researchers have shed some light on the mechanics of such 'process uncertainty' (cf. Caddy and Mahon 1995), by demonstrating relationships between fish stock fluctuations and migrations and the incidence of nutrient upwelling and related plankton succession. Yet such knowledge, even when coupled with findings from the wider set of hydrophysical, limnological, and related studies that have been conducted through LTR and other scientific investigations, only provides a partial understanding of pelagic fish production and distribution dynamics. It by no means allows for close 'when, where, and how much' predictions of ecosystem fluctuation. In the face of multilevel uncertainties (Francis and Shotton, 1997), a good deal of flexibility will be required to accommodate sometimes rapidly changing circumstances. Static MSY modelling and lake-wide TAC assessment are completely unequal to such a task, which is why no attempt was made to incorporate them into LTR investigations as practical management tools (Lindqvist and

Mikkola, 1989). Larkin (1996) has also pointed out how trophic ecosystem models such as ECOPATH II (Christensen and Pauly, 1993), though potential predictors of gross impacts of large-scale exploitation, are of limited utility for practical depictions of temporal and spatial dynamics. 'Adaptive' or 'interactive' management practices that allow for adjustments in fishing pressure in the short-term will also allow for fishery system sustainability in the long-term.

A policy of adaptive management is appropriate to Lake Tanganyika circumstances in other ways as well. Even though pelagic stocks seem to be distributed randomly throughout the lake, with no apparent sub-populations, the difference in target species concentration between the clupeid-based fishery of the northern areas and the *L. stappersii*-based fishery to the south might require management treatments that are somewhat distinct and separate. The same holds true with respect to the composition of national fleets and fishing units. The fisheries of the DRC and Tanzania, which respectively account for the greatest and second greatest annual take of pelagic species from the lake, are comprised mostly of traditional and artisanal units operating from landing sites distributed along vast stretches of coastline. The fisheries of Burundi and Zambia, in contrast, are limited to much more confined areas. They also feature fairly high concentrations of relatively more efficient artisanal gear – liftnet and apollo units in the case of Burundi and kapenta seines in the case of Zambia. A very high density of industrial units further distinguishes the Zambian sector.

9.3.2 Precaution and multi-disciplinary perspectives

Recognition of the inherent limitations of population biology models and methods for the task of comprehending the '…highly complex bio-socio-economic system' (Charles, 1994:207) invites a response of due care and deliberation in management decision-making. This is particularly true in the case of the Tanganyika pelagic fishery. It is a fishery of complicated 'multiples' interacting in rather unpredictable ways: multiple species, subject to multiple fluctuations of abundance, are harvested and utilised by multiple interest groups deploying multiple varieties of gear and technology. Maintaining a precautionary management orientation in the face of such complication and uncertainty requires fisheries policy and technical advisors to use a mix of observational and analytical tools from both the natural and social sciences in monitoring fishery system continuity and change. Multiple complexity and uncertainty, in short, warrants a multi-disciplined response.

Lake Tanganyika Monitoring Programme

LTR proposals for the immediate future call for the continuation of the regional monitoring activities that began under the project's Scientific Programme, though on a much reduced and revised scale and under the responsibility of national teams working in tandem (Mannini, 1999). In keeping with sustainable management needs, the extended monitoring programme will have to be capable of generating information on complex fisheries interactions involving both natural and human agencies. The design of the programme has thus made provision for collection and collation of basic data in five key indicator areas. These include:

1.) early alarms' signalled by changes in hydrodynamic patterns;
2.) density and distribution patterns in the meso- and macro-zooplankton communities

that provide prey for planktivorous fish;

3.) CPUE and fish biology data for main target species;

4.) continuities and changes in fishing communities (size, composition, and infrastructure) and the socio-economic circumstances of local harvest and post-harvest operators; and

5.) continuities and changes in local views on trends in, problems with, and regulation of the fishery sector.

Of over-riding concern for future monitoring activities on Lake Tanganyika is their practicality, given current conditions of budget, staff, and equipment limitations (Mannini, 1999). The extended programme has accordingly been designed to meet requirements of: a) feasibility (procedures commensurate with available resources); b) simplicity (use of uncomplicated equipment with minimum maintenance needs); and c) sustainability (high likelihood for regular data collection over the long run).

Apart from focusing on relevant parameters, monitoring activities in support of adaptive management strategy and decision-making for Tanganyika fisheries should be equipped to cope with observational and data modelling uncertainties (cf. Caddy and Mahon, 1995; Hilborn, 1997). An accepted method of dealing with uncertainty is to consider probabilities (McAllister *et al.*, 1994), rather than just considering single answers from deterministic projections (Cochrane *et al.*, 1998). What is basically required is that monitoring be sufficiently robust to allow for the achievement of management aims in the face of statistical uncertainty and incomplete knowledge (cf. FAO, 1996; Charles, 1985).

Robustness may be enhanced by combining information from 'non-scientific' knowledge systems into the store of multi-disciplinary data that is generated through conventional 'scientific' approaches. Working along these lines, Mackinson & Nøttestad (1998) have elaborated an 'expert system' that helps to build mutual respect and co-operation between resource users, scientists and managers. In a similar vein, de la Mare (1998) develops his idea for tidying up fisheries management with a new 'MOP' (Management Oriented Paradigm) using a whole system approach that requires collaboration between all concerned parties. O'Boyle (1993) likewise has noted the importance of interactions between managerial bodies, economists, and end-users to improve and promote more responsible management.

9.3.3 Co-management partnerships and MCS

Variously formulated as 'co-management,' 'management in partnership,' 'participatory management,' or 'community-based management,' policies to increase local involvement in resource use decision-making and regulation are based on recognition of the inherent weaknesses of 'top-down' or 'command and control' management regimes. The latter, in addition to undervaluing the potential contributions of local knowledge systems and actors to the management process just noted above, often feature a heavy measure of state intervention. This may often result in an 'us versus them' response of disassociation amongst local fisherfolk, expressed in widespread indifference and even the deliberate violation of official regulations. In CCRF language, '...the efficiency and implementability of...management measures are often highly dependent on the support gained from the interested parties' (FAO, 1997:55). Such support is most likely to exist where resource users can identify with specific measures because they have helped to craft them.

A further consideration that lends weight to the case for co-management in fisheries concerns cost-reduction and efficiency gains that might be realised in regard to MCS activities. Fisheries administrations across much of the developing world currently labour under severe financial and operational constraints (FAO, 1997), and as shown by LTR institutional studies (Maembe, 1996; Cacaud, 1996, 1999), the Tanganyika situation is no exception. If local stakeholders could be encouraged to assume a greater share of responsibility, it is conceivable that local fisheries authorities could accomplish MCS and enforcement purposes on a 'more-for-less' basis.

Because it offers such obvious long-term advantages, management partnership warrants strong emphasis in regional policy for Tanganyika fisheries. At the same time, the scope and pace with which partnership arrangements are implemented will depend on specific circumstances. Views on co-management appear to vary to some extent between countries and localities, and there are clear differences in fisheries and environmental circumstances, as well as attitudes towards specific regulatory measures (e.g. licensing, gear and space-time restrictions, etc.), that will have to be accommodated. Community outreach activities obviously must figure strongly as part of management partnership strategy, in order to build levels of environmental consciousness and receptivity to measures for the regulation of resource access and exploitation.

9.3.4 Resource access and use rights

Local control of fisheries resources is also mediated through the allocation of property rights. As noted earlier, open access regimes or regimes that, as in the case of the Tanganyika fisheries, essentially function in an open access mode under broad conditions of state resource ownership and regulation, virtually guarantee a situation of resource overexploitation. Fish harvesters, even where limited by quota and/or effort restrictions, will each race to garner as much of the resource as they can, with the ultimate result of declining returns for all. CCRF guidelines offer the reminder that the present critical status of fisheries world-wide, marked by '…a high proportion of over-exploited stocks and a general low (and often negative) profitability' (FAO, 1997:52), is in large part due to the incessant playing out of this pattern across myriad local and regional contexts. It also explains why, these days, 'Limited access is widely considered to be essential for efficient and responsible fisheries' (*ibid*). As Charles has observed, limited access arrangements in small-scale artisanal fisheries may be particularly effective when constituted as fishing rights allocated at the group or community level. There is '…an incentive for the community collectively to (a) ensure that the resource is managed wisely, (b) efficiently manage allocation of catches and fishery access (also helping to prevent the "rush to fish"…), and (c) develop local enforcement tools' (Charles, 1994:208).

The future sustainability of Tanganyika fisheries requires a transformation of the present rather loose 'open-access-within-national-jurisdictions' regime into one that allocates fishing rights to local communities and their respective territories. But here again a gradual policy move is indicated. Attitudes and circumstances that bear on access issues vary at both district or country levels, and need to be addressed on a zone-by-zone basis through careful consultation and negotiation with local stakeholder groups. Also, in the case of the southern waters particularly, the process of fishing rights reallocation will need to accommodate the interests of industrial fishing firms, possibly as stewards of special ‘offshore commercial use territories’ or directly as component parts of local community zones.

The situation with regard to industrial interests must also be considered in terms of developments within the artisanal sector. A gradual pattern seems to be emerging in which artisanal units, operating with improved technology especially in the form of the powerful ‘apollo’ liftnet configuration, are taking over the role of industrial purse seiners (Coenen *et al.*, 1998). This may well be a positive development. As Hilborn *et al.* (1995) have argued, the consolidation of small-scale community or private ownership of productive equipment, coupled with local control of resource base access and active involvement in the management thereof, are crucial ingredients for achieving true success – i.e. long term sustainability -- in the exploitation of fishery resources.

9.3.5 Regional fisheries, environment, and society

Fishing and non-fishing sector interactions

The ‘pursuit of sustainability’ as a basic policy objective cannot ignore the larger context within which local fisheries must be prosecuted, managed, and developed. Thus, the weak performance of a poorly managed fishery may have ramifications far beyond the sector, affecting a range of local, national, or even regional welfare interests. Conversely, if there is strong internal coherence in terms of ‘responsible fishing’ (FAO 1995) or ‘intelligent fishing’ (Charles 1994) practices, then optimal benefits are generated not only for sector user groups but also for the larger society of which they form a part. At the same time, developments in other, non-fishing sectors may exert far-reaching influence on the fisheries. At local ‘micro-levels’ these typically include impacts arising directly from competing demands for use of the aquatic resource base (e.g., fishing versus wildlife conservation/tourism use), or indirectly from externalities generated by non-fishing activities (e.g. fishing versus sewage disposal). At national and regional ‘macro-levels,’ impacts might arise, for instance, from declines in agricultural production due to drought, industrial stagnation, altered terms of international trade, widespread unemployment, or shifting consumer preferences.

The Tanganyika situation involves a complex of fishing and non-fishing sector interactions, at both micro- and macro- levels of socio-economic integration.

Micro-level interactions

To begin with, a variety of conflicts, existing and nascent, can be documented between fishing and other user interests around the lake shore (LTBP, 1998). Pollution impacts from waste discharge exist around urban areas like Bujumbura and Kigoma, and Mpulungu, for example. Other conflicts arise in connection with the wildlife conservation areas and development of tourism in the cases of Nsumbu National Park in Zambia, and Mahale National Park and Gombe

Stream Reserve in Tanzania. On a wider and, at present, far more serious scale is the environmental degradation and associated threats to biodiversity within the aquatic resource base linked with the activities of a rapidly expanding population of smallholder farmers. The situation is particularly acute where population density is high, as is the case in much of Burundi. Shortage of farm land for family food production leads people to cultivate on steep hillsides, leading in turn to progressive deforestation, soil erosion, and siltation of near shore waters (Coulter and Mubamba, 1993; Cohen *et al.* , 1993)

Fisheries sustainability needs to be pursued with due recognition of the reality of fishing and non-fishing sector interactions. This once again highlights the importance of multi-disciplinary approaches for the discovery and understanding of pattern and process in fisheries systems, except that here concern extends to relations between components of the fisheries and those of adjacent sectors (cf. Charles, 1994; FAO 1995). What is also indicated is the importance of policy support for 'integrated development strategies' that, '…deal with the full complexity of the fishery system *and* associated activities outside the fishery' (Charles, 1994:207).

Coastal area management

In fisheries such strategies are often associated with the 'Coastal Area Management' model (FAO 1995, 1996b) that calls for, *inter alia*: a) establishment of conflict resolution mechanisms to settle differences arising between fisheries resources users and other users of a coastal area; b) promotion of public awareness of coastal resource conservation and management needs and of public participation by affected parties in the management process; c) assessment of the economic, social, and cultural values that attach to different coastal resources; and d) use of multi-disciplinary approaches to monitor the coastal environment (*ibid*: 26-27). With regard to Tanganyika fisheries, the development of coastal area management approaches in the immediate future might best be pursued in conjunction with the work of the GEF Biodiversity Project (LTBP, 1998).

Macro-level interactions

Fishing and non-fishing sector interactions at the macro-level as they pertain to the Lake Tanganyika situation have already been characterised to a large extent in earlier discussion. Of particular note is the role of the lake as a major supplier of fish protein in a regional context marked by widespread civil turmoil, population displacements, episodes of drought, and crippled or degraded capacity in other food producing sectors. These larger events, compounded by the ever-growing load of human inhabitants within the lake basin and across East-Central Africa generally, have not only contributed to conditions of food insecurity and placed increasing pressure on the lake's fisheries resources; they have also helped to create conditions of employment insecurity. This in turn may well have the effect of attracting more rural dwellers to migrate towards the fisheries in search of a means of subsistence and employment.

Taken in conjunction with LTR evidence pointing to growing risk of over-fishing on certain stocks in certain localities in Lake Tanganyika, the effect of such a development would only be to worsen sustainability prospects for the fisheries in the short-term. Therefore, and in accordance with the strategy of integrated development advocated above, a strong dose of economic diversification would appear highly advisable as a complementary policy prescription for Tanganyika fisheries.

9.3 CONCLUSIONS

This chapter has attempted to draw out the major findings and management implications of LTR Scientific Programme research activities, as reviewed in earlier chapters. Since fisheries management fundamentally concerns the interactions between potentially renewable stocks and the human populations that exploit and depend upon them, attention was also directed to LTR socio-economic and legal-institutional studies and their outcomes.

LTR research is very much associated with recent trends in management thinking in its explicit rejection of 'stock assessment driven' approaches to fisheries resource exploitation and conservation. Such conventional approaches are simply inadequate for comprehending the complex dynamics of Tanganyika's pelagic trophic structure and the multiple uncertainties of its fisheries. Nor are they adequate as aids to understanding the complex patterns of adaptive behaviour that are played out within local fisherfolk society.

Recognising that the Tanganyika fisheries must be treated as a complex biological and anthropological reality, LTR research has been pursued with a combination of observational and analytical tools from both the natural and social sciences. In building towards a fisheries management fisheries management framework for Tanganyika particular use has been made of the 'components of sustainability' typology proposed by Charles (1994), along with themes laid out in the FAO *Code of Conduct for Responsible Fisheries* or CCRF (FAO, 1995).

What such a framework needs to aim for is the 'pursuit of sustainability' (Charles, 1994) across its multiple bio-socio-economic and institutional dimensions. In CCRF terms, it needs to aim for 'responsible fisheries compliance' through simultaneous attention to five basic principles. First, precautionary or risk-adverse thinking should inform management decision making, in the face of pervasive system uncertainty. Secondly, consensus building should be between resource users, officials, and other interested parties should be encouraged through co-management practices. Thirdly, property rights in fisheries resources should be fostered in order to avoid 'free for all' competition. Fourthly, effective monitoring, control, and surveillance (MCS) and enforcement practices must be followed. Finally, a flexible posture needs to be maintained in order to be able to accommodate varied or changing circumstances, with periodic review, renewal, or revision of existing management measures as appropriate.

Based on sustainability and responsible fisheries paradigms, and taking into account the testimony provided by LTR Scientific Programme and complementary socio-economic/legal/institutional investigations of fisheries prospects and problems, it is proposed that policy initiatives for Lake Tanganyika be pursued along the following broad lines.

- · ***Adaptive management***: use of interactive management practices that allow for adjustments in fishing pressure, and also allow for flexible application of management treatments appropriate to different circumstances encountered around the lake shore.

- ***Multi-disciplinary perspectives***: maintenance of monitoring capability to measure across a range of bio-physical and socio-economic parameters, as appropriate to the complexities of ecosystem – human system interactions; also, cultivation and maintenance of ‘non-scientific’ and ‘scientific’ knowledge coalitions.

- ***Management in partnership***: promotion of local stakeholder group involvement in management decision-making and in fashioning modalities of enforcement and compliance.

- ***Resource access and use rights***: moves to constitute control of access and fishing rights at local community levels.

- ***Fisheries and economic diversification***: adoption of integrated development strategies and coastal area management models at the local level, to accommodate complex interactions and possible conflicts between fishing and non-fishing activities, and, at national and regional ‘macro-levels,’ moves to foster economic diversification to reduce pressure on the fishery resource base.

REFERENCES CITED

Adams, P.B., 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fishery Bulletin 78 (1): 1-12.

Allen, K.R., 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28: 1573-1581.

Allison, E. H., G. Patterson, K. Irvine, A. B. Thompson & A. Menz, 1995. The pelagic ecosystem. In A. Menz (ed.), The Fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa. Natural Resources Institute, Chatham, Kent, U.K.: 351-367.

Anding, D & R.Kauth, 1970. Estimation of sea-surface temperature from space. Rem.Sensing Env. 1: 217-220.

Anderson, L.G., 1986. The Economics of Fisheries Management. Johns Hopkins Press, Baltimore, 296 pp.

Archer, D. 1995 Upper ocean physics as relevant to ecosystem dynamics: a tutorial. Ecological Applications 5:724-739.

Armstrong, M.J. & P.A. Shelton, 1990. Clupeoid life-history styles in variable environments. Environ. Biol. Fish. 28: 77-85.

Aro, E. and P. Mannini, 1995. Results of Fish Population Biology. Studies on Lake Tanganyika during July 1993-June 1994. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-TD/38 (En): 113p.

Babin, M. A. Morel & B. Gentili, 1996. Remote sensing of sea surface Sun-induced chlorophyll fluorescence: consequences of natural variations in the optical characteristics of phytoplankton and the quantum yield of chlorophyll *a* fluorescence. Int. J. Remote sensing 17 (12): 2417-2448.

Baines, S.B. & M.L. Pace, 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems. Limnol. Oceanogr. 36: 1078-1090.

Beddington & May, 1977.

Beverton, R.1998. Fish, fact and fantasy: a long view. Rev. Fish Biol. Fisheries 8, 229-250.

Beverton, R. J. H. & S. J. Holt, 1957. On the dynamics of exploited fish populations. Min Agriculture, Fisheries and Food. Fish. Invest. 2:, London.

Bosma, E., P. Paffen, V. Langenberg, D.B.R. Chitamwebwa, K.I. Katonda, F.Sobo, A.N.M. Kalangali, L. Nonde, S. Muhoza and Kadula (J.E. Reynolds, Ed.),1997. LTR Lakewide Socio-Economic Survey, 1997: Tanzania. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/68 (En): 100p.

Bosma, E., P. Paffen, N. Mulimbwa, G. Kitungano, C. Nyiringabi, A. Kwibe,C. Bulambo, E. Mukirania and I. Mbilizi, (J.E. Reynolds, Ed.), 1997. LTR Lakewide Socio-Economic Survey, 1997: Democratic Republic of Congo. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/69 (En): 56p.

Bosma, E. M., S. Muhoza & I. Zulu, 1998.The gulfnet sample results of five cruise with the *R/V Tanganyika Explorer*. FAO/FINNIDA Research for the Management of Fisheries on Lake Tanganyika GCP/RAF/271/FIN-TD/81 (En): 40 pp.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Wegle?ska, 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419-456.

Burgis, M. J. 1984. An estimate of zooplankton biomass for Lake Tanganyika. Verh. int. Ver. Limnol. 22: 1199-1203.

Cacaud, P. 1996. Institutional choices for cooperation in fisheries management and conservation on Lake Tanganyika. Mission report. Fisheries Management and Law Advisory Programme, GCP/606/NOR/INT. FAO, Rome.

Cacaud, P., 1999. Lake Tanganyika Fisheries Management Plan: institutional, legal, developmental and MCS considerations. Paper for presentation at the Eighth Session of the CIFA Sub-Committee for Lake Tanganyika. CIFA:DM/LT/99/4, FAO, Rome (In print).

Caddy, J.F. & R. Mahon, 1995. Reference points for fisheries management. FAO Fish. Tech. Pap. No. 347.

Camus, C. 1965. Fluctuations du niveau du Lac Tanganyika 1965. Bulletin dés Seances 1965:4, Academie Royale des Sciences d'Outre-Mer.

Chapman, D.W. 1976. Acoustic estimates of pelagic ichtyomass in Lake Tanganyika with an inexpensive echo sounder. Trans. Am. Fish. Soc. 105 (5): 581-587.

Chapman, D.W. & P. van Well, 1978. Observations on the biology of *Luciolates stappersii* in Lake Tanganyika (Tanzania). Trans. Am. Fish. Soc. 107: 567-573.

Chapman, D.W., J. Bayona & C. Ellis, 1974. Analysis of test fishing and limnological sampling in Tanzanian waters of Lake Tanganyika in October 1974. FAO FI/DP/URT/71/012/12. FAO, Rome.

Chapman, D. W., H. Rufli, P. van Well & F. Roest, 1978. Lake Tanganyika fishery research and development project, Tanzania. Fishery biology and stock assessment. FAO, FI:DP/URT/71/012 Technical Report 1: 37 pp.

Charles, A.T. 1992. Fishery conflicts. A unified framework. Mar. Policy. 16, 378-393.

Charles, A.T. 1994. Towards sustainability: the fishery experience. Ecol. Econ. 11: 201-211.

Charles, A.T. 1985. Fishery science: the study of fishery systems. Aquat. Living Resourc. 8, 233-239.

Chene, G., 1975. Etude des problemes relatifs aux fluctuations piscicoles du lac Tanganyika. Licentiate Thesis, Universite de Liege, Faculte des Sciences, Liege, 108 pp.

Christensen, V. & D. Pauly, 1993. Trophic models of aquatic ecosystem. ICLARM Conf. Proc. 26, 390 p.

Clark, C.W. 1990. Mathematical Bioeconomics: The Optimal Management of Renewable Resources (2nd ed.). Wiley-Interscience, New York, NY, 386 pp.

Cochrane, K. L., D.S. Butterworth, J.A.A. de Oliveira & B.A. Roel, 1998. Management procedures in a fishery based on highly variable stocks and with conflicting objectives: experiences in the South African pelagic fishery. Rev. Fish Biol. Fisheries 8: 177-214.

Coenen, E.J. (ed.),1994. Historical data report on the Fisheries, Fisheries Statistics, Fishing Gears and Water Quality of Lake Tanganyika (Tanzania). FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-TD/15 (En & Fr): 115p.

Coenen, E. J. (ed.), 1995. LTR's fisheries statistics subcomponent: March 1995 update of results for Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika GCP/RAF/271/FIN/TD/32 (En): 45 pp.

Coenen, E.J. & E. Nikomeze, 1994. Lake Tanganyika, Burundi, Results of the 1992-93 Catch Assessment Surveys. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/24 (En): 27p

Coenen, E. J., P. Paffen & E. Nikomeze, 1998. Catch per unit of effort (CPUE) study for different areas and fishing gears of Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika GCP/RAF/271/FIN-TD/80 (En): 92 pp.

Cole, J. & J. McGlade, 1998. Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. Rev. Fish Biol. Fisheries 8, 445- 471.

Cole, J. J., S. Findlay & M. L. Pace, 1988. Bacterial production in freshwater and saltwater ecosystems: a cross-system overview. Mar. Ecol. Prog. Ser. 43: 1-10.

Colwell, R.N (ed.) 1983. Manual of Remote Ensing (2nd ed.). American Society of Photogrammetry and Remote Sensing, Falls Church, Va.

Coulter, G. W. 1963. Hydrological changes in relation to biological production in southern Lake Tanganyika. Limnol. Oceanogr. 8: 463-477.

Coulter, G. W. 1968. Hydrological processes and primary production in Lake Tanganyika. Proc. Of 11th Conf. Internat. Assoc. Great Lakes Res. 1968: 609-626.

Coulter, G. W., 1970. Population changes within a group of fish species in Lake Tanganyika following their exploitation. J. Fish Biol. 2: 329-353.

Coulter, G. W., 1977. Approaches to estimating fish biomass and potential yield in Lake Tanganyika. J. Fish Biol. 11:393-408.

Coulter, G. W., 1981. Biomass, production, and potential yield of the Lake Tanganyika pelagic fish community. Trans. am. Fish. Soc. 110:325-335.

Coulter, G.W. (ed), 1991. Lake Tanganyika and its life. British Museum (Natural History) and Oxford University Press, Oxford, 354 pp.

Coulter, G. W., 1994. Lake Tanganyika. Arch. Hydrobiol. Beih. Ergebn. Limnol. 44: 13-18.

Coulter, G. W. & Spiegel, R. H. 1991. Hydrodynamics of Lake Tanganyika. In : Coulter, G. W. (Ed.): Lake Tanganyika and its life. British Museum (Natural History) and Oxford University Press, Oxford, 354 pp.
Craig, J. F., 1997. A preliminary review of the LTR scientific sampling programme. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika GCP/RAF/271/FIN-TD/74 (En): 53 pp.
Cycon, D.E., 1986. Managing fisheries in developing nations: a plea for appropriate development. Natural Resources J. 26: 1-14.
Degens, E. T. & V. Ittekkot, 1983. Dissolved organic matter in Lake Tanganyika and Lake Baikal - a brief survey. (SCOPE/UNEP Sonderband) Mitt. Geol.-paläont. Inst. Univ. Hamburg 55: 129-143.
Degens, E.T., R.P. von Herzen & H.-K. Wong, 1971. Lake Tanganyika. Water chemistry, sediments, geological structure. Naturwissenschaften 58(5): 229-241.
de la Mare, W. K. 1988. Tidier fisheries management requires a new (MOP) management-oriented paradigm. Rev. Fish Biol. Fisheries 8, 349-356.
del Giorgio, P. A., J. J. Cole & A. Cimbleris, 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385: 148-151.
Downing, J. A. & F. H. Rigler (eds), 1984. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No 17, Blackwell, Oxford, 2nd ed., 501 pp.
Downing, J.A., C. Plante & S. Lalonde, 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. aquat. Sci. 47: 1929-1936.
Dumont, H.J., 1994. The distribution and ecology of the fresh- and brackish-water medusae of the world. Hydrobiologia 272:1-12.
Edwards, R. R. C., 1984. Comparisons of growth in weight of temperate and tropical marine fish counterparts. Can. J. Fish. aquat. Sci. 41:1381-1384.
FAO, 1992. Research for the Management of Fisheries on Lake Tanganyika. GCP/RAF/271/FIN, Project document, FAO, Rome.
FAO, 1995. Code of Conduct for Responsible Fisheries, Rome, FAO, 41 pp.
FAO,1996. Precautionary Approach to Capture Fisheries and Species Introductions. Rome: FAO, FAO Technical Guidelines for Responsible Fisheries. 2, 54 pp.
Fiedler, P.C., 1984. Satellite observations of the 1982-1983 El Niño along the U.S. Pacific coast.Science (Wash. D.C.) 224: 1251-1254.
Forgarty, H.J., M.P. Sissenwine & E.B. Cohen, 1991. Recruitment variability and the dynamics of exploited marine populations. TREE 6 (8): 241-246.
Fogarty, M.J., A.A. Rosenberg & M.P. Sissenwine, 1992. Fisheries risk assessment: sources of uncertainty. Environ. Sci. Technol. 26 (3): 440-447.
Frank, K. T. & W.C. Leggett, 1994. Fisheries ecology in the context of ecological and evolutionary theory. Annu. Rev. Ecol. Syst. 25: 401-422.
Francis, R.I.C.C. & R. Shotton, 1997. "Risk" in fisheries management: a review. Can. J. Fish. Aquat. Sci. 54: 1699-1715.
Frenette, J.-J., S. Demers, L. Legendre & J. Dodson, 1993. Lack of agreement among models for estimating the photosynthetic parameters. Limnol. Oceanogr. 38: 679-687.
Gréboval, D.1990. Principles of fisheries management and legislation of relevance to the Great Lakes of East Africa: Introduction and case studies. UNDP/FAO REgional Project for Inland Fisheries Planning (IFIP). RAF/87/099/TD/05/90 (En): 39 pp.
Gréboval, D. (ed.), 1992. Report of a Regional Meeting for the Management of Lake Victoria and the Creation of a lake Victoria Fisheries Commission. UNDP/FAO Regional Project for Inland Fisheries Planning (IFIP): RAF/87/099/TD74/92 (En): 68 pp.
Gulland, J.A. (Ed.)1977. Fish Population Dynamics. Wiley Interscience, New York, NY.
Hanek, G., 1994. Management of Lake Tanganyika fisheries. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika GCP/RAF/271/FIN-TD/25 (En): 21 pp.
Hanek, G. and J.E. Reynolds (eds.), 1998. Report of the Sixth Meeting of the LTR Coordination Committee. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/82 (En): 69p.
Hanek, G. and G. V. Everett, (eds)., 1995. Report on the Workshop on theManagement and Planning of Lake Tanganyika Pelagic Stocks. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/37 (En): 79p.

Hanek, G., G.V. Everett, O.V. Lindqvist and H. Mölsä, 1996. Towards Management of Lake Tanganyika's Fisheries. In Developing and sustaining world fisheries resources: the state of science and management: 2nd World Fisheries Congress proceedings, 1996: 334-338.
Hart, R.C., 1994. Equiproportional temperature-duration responses and thermal influences on distribution and species switching in the copepods Metadiaptomus meridianus and Tropodiaptomus spectabilis. Hydrobiologia 272: 163-183.
Hauser, L. G.R. Carvalho & T.J. Pitcher, 1998. Genetic population structure in the Lake Tanganyika sardine *Limnothrissa miodon.* J. Fish Biology 53 (Suppl. A) 413-429.
Haury, L.R., Y. Hidekatsu & E.C. Itsweire, 1990. Effects of turbulent shear flow on zooplankton distribution. Deep-Sea Research. 37 (3): 447-461.
Hecky, R. E., 1984. African lakes and their trophic efficiencies: a temporal perspective. In D. G. Meyers & J. R. Strickler (eds), Trophic interactions within aquatic ecosystems. AAAS Selected Symposium 85: 405-448.
Hecky, R. E., 1991. The pelagic ecosystem. In Coulter, G. W. (ed.), Lake Tanganyika and its life. Oxford University Press, Oxford: 90-110.
Hecky, R. E. & F. W. B. Bugenyi, 1992. Hydrology and chemistry of the African Great Lakes and water quality issues: problems and solutions. Mitt. int. Ver. Limnol. 23: 45-54.
Hecky, R. E. & E. J. Fee, 1981. Primary production and rates of algal growth in Lake Tanganyika. Limnol. Oceanogr. 26: 532-547.
Hecky, R. E., E. J. Fee, H. J. Kling & J. W. Rudd, 1978. Studies on the planktonic ecology of Lake Tanganyika. Canadian Department of Fish and Environment. Fisheries and Marine Service Technical Report 816: 1-51.
Hecky, R. E., E. J. Fee, H. J. Kling & J. W. Rudd, 1981. Relationship between primary production and fish production in Lake Tanganyika. Trans. am. Fish. Soc. 110: 336-345.
Hilborn, R., 1997. Uncertainty, risk and the precautionary principle. In Pikitch, E.K., D.D. Huppert & M.P. Sissenwine (eds.), Global Trends: Fisheries Management (Proceedings of the Symposium held at Seattle, Washington, 14-16 June, 1994). Am. Fish. Soc. Symp. 20: 100-106.
Hilborn, R. & J. Sibert, 1988. Adaptive management of developing fisheries. Marine Policy 2: 112-119.
Hilborn, R. & R.M. Peterman, 1996.The development of scientific advice with incomplete informationin the context of the precautionry approach. FAO Fish. Tech. Pap. No. 350/2, pp.77-102.
Hilborn, R. C.J.Walters & D.Ludwig, 1995. Sustainable exploitation of renewable resources. Annu. Rev. Ecol. Syst. 1995 (26): 45-67.
Holt. S. J. 1998. Fifty years on. Rev. Fish Biol. Fisheries 8, 357-366.
Houde, E. D. & E. S. Rutherford, 1993. Recent trends in estuarine fisheries: predictions of fish production and yield. Estuaries 16: 161-176.
Huttula, T. (ed.) 1997. Flow, thermal regime and sediment transport studies in Lake Tanganyika. Kuopio University Publications C. Natural and Environmental Sciences 73: 173 pp. Kuopio, Finland.
Huttula, T., A. Peltonen and J. Nieminen,1993. Hydrodynamic measurements on Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-FM/02 (En): 48p.
Huttula, T. and V. Podsetchine,1994. Hydrological modelling on Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/20 (En): 19p.
Huttula, T., P. Kotilainen, V. Podsetchine and A. Peltonen, 1997. Inter Agency Agreement: Activity report in hydrodynamics during January-June 1997. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/76 (En): 18p.
Huttula, T., V. Podsetchine, A. Peltonen, P. Kotilainen & H. Mölsä, 1994. Hydrology of Lake Tanganyika. In Kern-Hansen, C., D. Rosbjerg & R. Thomsen (ed), Nordic Hydrological Conference 1994, Tórshavn, Færøerne, 2.-4. august 1994. NHP-report no. 34. Koordineringskomitéen for Hydrologi i Nordem (KOHYNO), København: 43-52.
Hyvönen, K., 1997. Study on zooplankton development time at Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika GCP/RAF/271/FIN-TD/78 (En): 12 pp.

Irvine, K., 1995. Standing biomasses, production and spatio-temporal distributions of the crustacean zooplankton. In A. Menz (ed.), The Fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa. Natural Resources Institute, Chatham, Kent, U.K.: 85-108.
Irvine, K. & R. Waya, 1995. The zooplankton: General sampling methods and estimation of biomass and development rates. In A. Menz (ed.), The Fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa. Natural Resources Institute, Chatham, Kent, U.K.: 69-84.
Irvine, K. & R. Waya, 1999. Spatial and temporal patterns of zooplankton standing biomass and production in Lake Malawi. Hydrobiologia, in print.
Jassby, A. D. & T. Platt, 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21: 540-547.
Johannes, R.E. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. TREE 13 (6): 243-246.
Johannesson, K.A., 1974. Preliminary quantitative estimates of pelagic fish stocks in Lake Tanganyika by use of echo integration methods. FAO Publ. EIFAC/74/I/Symp. 54, 15 pp.
Jensen, J.R. 1986. Introductory Digital Image Processing. Prentice-Hall, Eaglewood Cliffs, New Jersey.
Järvenoja, S., Eerola, K., Lönnberg, P. & L. Rontu, 1997. Limited area modelling at the Finnish Meteorological Institute in 1996. EWGLAM Newsletter No. 26 : 58-61.
Järvinen, M., K. Salonen & J. Sarvala, 1996. Experiments on phytoplankton and bacterial production ecology in Lake Tanganyika: results of the first lake-wide cruise on *R/V Tanganyika Explorer*. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN/TD/44 (En): 43 pp.
Järvinen, M. K.Salonen, J. Sarvala, K. Vuorio & A. Virtanen, 1999.The stoichiometry of particulate nutrients in Lake Tanganyika; implications for nutrient limitation of phytoplankton. Hydrobiologia, in print.
Kidwell, K.B. (ed.) 1995. NOAA Polar orbiter data. User's Guide. U.S. Department of Commerce. NOAA/NESDIS/NCDC/SDSC. Washington, D.C.
Kimmerer, W. J. & A. D. McKinnon, 1986. Glutaraldehyde fixation to maintain biomass of preserved plankton. J. Plankton Res. 8: 1003-1008.
Kimmerer, W. J., 1987. The theory of secondary production calculations for continuously reproducing populations. Limnol. Oceanogr. 32: 1-13.
Kimura, S., 1995. Growth of the clupeid fishes, Stolothrissa tanganicae and Limnothrissa miodon, in the Zambian waters of Lake Tanganyika. J. Fish Biol. 47: 569-575.
Kirchman, D. L., 1995. Leucine incorporation as a measure of biomass production by heterotrophic bacteria. In P. F. Kemp, B. F. Sherr, E. B. Sherr & J. J. Cole (eds), Handbook of methods in aquatic microbial ecology: 509-512.
Kirk, J. T. O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, 401 pp.
Kotilainen, P.,1993. Field notes for hydrodynamic studies. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-FM/10 (En): 32p.
Kotilainen, P., Huttula, T. & A. Peltonen, 1995. Lake Tanganyika hydrodynamics (results of March 1993-December 1994). FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/42 (En). Bujumbura, Burundi.
Kotilainen, P., T. Huttula and A. Peltonen, 1995. Results of the period of March 993 - December 1994 in Hydrodynamics on Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-TD/43 (En): 97p.
Kuikka, S. 1998. Appraisal of Lake Tanganyika Research. Finnida, Helsinki, 5 pp.
Kurki, H., 1996. The results of zooplankton at three locations in Lake Tanganyika July1993 - December 1995. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-TD/51 (En): 45p.
Kurki, H., 1998. Results of plankton net and torpedo sampling during cruises on board *R/V Tanganyika Explorer*. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/85 (En): 32 pp.
Kurki, H., I. Vuorinen, E. Bosma & D. Bwebwa, 1999a. Spatial and temporal changes in copepod zooplankton communities of Lake Tanganyika. Hydrobiologia, in print.

Kurki, H., P. Mannini, I. Vuorinen, E. Aro, H. Mölsä & O. V. Lindqvist, 1999b. Macrozooplankton communities in Lake Tanganyika indicate food chain differences between the northern part and the main basins. Hydrobiologia, in print.

Kuusipalo,L., 1994. Assessing genetic structure of pelagic fish population of LakeTanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/23 (En): 13p.

Kuusipalo, L., 1999.Genetically differentiated stocks of endemic nile perch, Lates stappersii, in Lake Tanganyika, analysed with RAPD markers. Hydrobiologia, this volume

Landry, F., T.J. Miller & W.C. Leggett, 1995. The effects pf small-scale turbulence on the ingestion rate of fathead minnow (Pimephales promelas) larvae. Can. J. Fish. aquat. Sci 52: 1714-1719.

Langenberg, V., 1996. The physical limnology of Lake Tanganyika August-December 1995. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/54 (En): 63 pp.

Larkin, P., 1977. An epitaph for the concept of maximum sutainable yield. Trans. Am. Fish. Soc. 106:1-11.

Larkin, P.A. 1996. Concepts and issues in marine ecosystem management. Rev. Fish Biol. Fisheries 6: 139-164.

Lasker, R., 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Const. int. Explor. Mer. 178: 375-388.

Lasker, R., 1985. What limits clupeoid production? Can. J. Fish. aquat. Sci. 42 (Suppl.1): 31-38.

Lensu, S., 1998. Food selection of Stolothrissa tanganicae ja Limnothrissa miodon on Lake Tanganyika. (In Finnish). MSc. Thesis, University of Kuopio, Finland.

Lillesand, T.M. & R.W. Kiefer, 1987. Remote Sensing and Image Interpretation (2nd ed.) John Wiley & Sons, 721 pp.

Lindqvist, O.V. 1977. On the principles of management strategies of crayfish and fish populations. Freshwater crayfish 3: 249-261.

Lindqvist, O.V. & H. Mölsä, 1992. Management of small-scale fisheries: is it possible? In Tvedten, I. & B. Hersoug (eds.), Fishing for Development. The Scandinavian Institute of African Studies, 191- 207.

Lindqvist, O.V., H. Mölsä, K. Salonen & J. Sarvala (eds.)Lake Tanganyika: its water and pelagic fish and other case studies'. Kluwer Acad. Publ. , in print.

Lindqvist, O. V. & H. Mikkola, 1989. Lake Tanganyika: review of limnology, stock assessment, biology of fishes and fisheries. Prepared for the Regional Project for the Management of Fisheries, Lake Tanganyika. Rome, FAO, GCP/RAF/229/FIN: 51 pp.

Lohrenz, S. E., D. A. Wiesenburg, C. R. Rein, R. A. Arnone, C. D. Taylor, G. A. Knauer & A. H. Knap, 1992. A comparison of *in situ* and simulated *in situ* methods for estimating oceanic primary production. J. Plankton Res. 14: 201-221.

Los, S.O. 1993. Calibration adjustment of the NOAA AVHRR Normalized Difference Vegetation Index without resource to component channel 1 and 2 data. Int. J. Remote Sens. 14 (10).

Lowe-McConnell, R.H., F.C. Roest, G. Ntakimazi & L. Risch, 1994. The African great lakes. Ann. Mus. r. Afr. Centr., Zool. 275: 87-94.

Ludwig, D., R. Hilborn & C. Walters, 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260:17, 36.

MacKenzie, B.R. & W.C. Legget, 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar. Ecol. Progr. Ser. 73: 149-160.

Mackinson , S. & L. Nøttestad, 1998. Combining local and scientific knowledge. Rev. Fish Biol. Fisheries 8, 481-490.

Mahon, R. 1997. Does fisheries science serve the needs of managers of small stocks in developing countries. Can. J. Fish. Aquat. Sci. 54: 2207-2213.

Malm, J., D. Mironov, A. Terzhevik & L. Jönsson, 1994. Investigation of the spring thermal regime in Lake Ladoga using field and satellite data. Limnol. Oceanogr. 39 (6): 1333-1348.

Mannini, P., 1998. Geographical distribution patterns of pelagic fish and macrozooplankton in Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/83 (En): 125 pp.

Mannini, P.,1999. Lake Tanganyika Fisheries Monitoring Programme. FAO/FINNIDA Researchfor the Management of the Fisheries of Lake Tanganayaika.GCP/RAF/271/FIN-TD/90 (En): in preparation.

Mannini, P., E. Aro, I. Katonda, B. Kissaka, C. Mambona, G. Milindi, P. Paffen & P. Verburg, 1996. Pelagic fish stocks of Lake Tanganyika: biology and exploitation. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/53 (En): 85 pp.

Maembe, T.W., 1996. Report on Fisheries Management and Institutions in the countries bodering Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/57 (En):43p.

Masundire, H. M., 1994. Mean individual dry weight and length-weight regressions of some zooplankton of Lake Kariba. Hydrobiologia 272: 231-238.

Mather, P.M. 1987. Computer processing of remotely-sensed images: an introcution. John Wiley & Sons, Chicester.

Mavuti, K. M., 1994. Durations of development and production estimates by two crustacean zooplankton species Thermocyclops oblongatus Sars (Copepoda) and Diaphanosoma excisum Sars (Cladocera), in Lake Naivasha, Kenya. Hydrobiologia 272: 185-200.

McAllister, M.K., E.K. Pikitch, A.E. Punt & R. Hilborn, 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/ importance resampling algorithm. Can. J. Fish. aquat. Sci. 51: 2673-2687.

McClain, E.P., W.G. Pichel & C.C.Walton, 1985. Comparative performance of AVHRR based multi-channel sea surface temperatures. J. Geoph. Res. 86: 11587-11601.

McMillan, L.M. & D.S.Crosby, 1984. Theory and validation of the multiple window sea surface temperature technique. J. Geoph. Res. 89 (C3): 3655-3661.

Meaden, G.J. & J.M. Kapetsky, 1991. Geographical information systems and remote sensing in inland fisheries and aquaculture. FAO Fish. Tech. Pap. 318, 262 pp.

Mengestou, S. & C. H. Fernando, 1991. Biomass and production of the major dominant crustacean zooplankton in a tropical Rift Valley lake, Awasa, Ethiopia. J. Plankton Res. 31: 831-851.

Menz, A., A. Bulirani & C. M. Goodwin, 1995. Acoustic estimation of fish biomass. In A. Menz (ed.), The Fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa. Natural Resources Institute, Chatham, Kent, U.K.: 307-349.

Mergrey, B.A., A.B. Hollowed & R.T. Baldwin, 1994. Sensitivity of optimum harves strategy estimates to alternative definitions of risk. Can. J. Fish. Aquat. Sci. 51: 2695-2704.

Mikkola, H., 1988. Some policy priorities for fisheries and aquaculture development in Africa. Aqua Fennica 18: 101-108.

Mikkola, H. & O.V.Lindqvist, 1989. Report on a Project Mobilization Mission. Lake Tanganyika Regional Fisheries Research Project.GCP/RAF/229/FIN, Rome, Italy.

Moreau, J., J. Munyandorero & B. Nyakageni, 1991. Evaluation des parametres démographiques chez Stolothrissa tanganykae et Limnothrissa miodon du lac Tanganyka. Verh. int. Ver. Limnol. 24: 2552-2558.

Moreau, J., B. Nyakageni, M. Pearce & P. Petit, 1993. Trophic relationships in the pelagic zone of Lake Tanganyika (Burundi sector). In V. Christensen & D. Pauly (eds), Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26: 138-143.

Morgan, N. C., T. Backiel, G. Bretschko, A. Duncan, A. Hillbricht-Ilkowska, Z. Kajak, J. F. Kitchell, P. Larsson, C. Lévêque, A. Nauwerck, F. Schiemer & J. E. Thorpe, 1980. Secondary production. In E. D. Le Cren & R. H. Lowe-McConnell (eds), The functioning of freshwater ecosystems. Cambridge University Press, Cambridge: 247-340.

Myers, R.A., N.J.Barrowman, J.A. Hutchings & A.A. Rosenberg, 1995. Population dynamics of exploited fish stocks at low population levels. Science 269: 1106-1108.

Myers, R.A., J.A. Hutchings & N.J. Barrowman, 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol.Appl. 7 (1): 91-106.

Mölsä, H. 1991. (ed.) Proceedings of the International symposium on Limnology and Fisheries of Lake Tanganyika, May 6-11, 1991. Publications of the Center for Training and Development, University of Kuopio, Finland, 12: 1-91.

Mölsä, H. 1995 (ed.). Symposium on Lake Tanganyika Research, Kuopio, September 11-15, 1995. Abstracts. Kuopio University Publications C. Natural and Environmental Sciences 34, 1995. 117 p.

Mölsä, H, E. Reynolds, E. Coenen & O. V. Lindqvist, 1999. Fisheries research towards resource management on Lake Tangnyika. Hydrobiologia, in press.
Nakayama, M. 1994. Application of satellite remote sensing to estimate lake water quality. Mitt. Internat. Verein. Limnol. 24: 345-347.
Niemi, M., J. Kuparinen, A. Uusi-Rauva & K. Korhonen, 1983. Preparation of 14C-labeled algal samples for liquid scintillation counting. Hydrobiologia 106: 149-156.
Nixon, S. W., 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. Limnol. Oceanogr. 33: 1005-1025.
O'Boyle, R. 1993. Fisheries management organizations: a study in uncertainty. In S.J. Smith, J.J. Hunt & D. Rivard (eds), Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. aquat. Sci 120: 423-436.
Oglesby, R. T., 1977. Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. J. Fish. Res. Board Can. 34: 2271-2279.
Ostrovsky, I., Y. Z. Yacobi, P. Walline & I. Kalikhman, 1996. Seiche-induced mixing: its impact on lake productivity. Limnol. Oceanogr. 41: 323-332.
Paffen, P., E. Coenen, S. Bambara, M. Wa Bazolana, E. Lyimo and C. Lukwesa, 1997. Synthesis of the 1995 simultaneous frame survey of Lake Tanganyika Fisheries. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/60 (En): 35p.
Paffen, P., E. Bosma, V. Langenberg, R. Chitembure, J. Chimanga, W. Chomba, C. Lukwesa and M. Mwenda (J.E. Reynolds, Ed.), 1997. 'LTR Lakewide Socio-Economic Survey, 1997: Zambia.' FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/67 (En): 67p.
Paffen, P., E. Bosma, J.M. Tumba, C. Butoyi, E. Gahungu, E. Nikomeze and B. Ndimunzigo, (J.E. Reynolds, Ed.), 1997. LTR Lakewide Socio-Economic Survey, 1997: Burundi. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/70 (En): 60p.
Pakkasmaa, S. & J. Sarvala, 1995. Preliminary study and growth of the pelagic clupeids in Lake Tanganyika estimated from daily otolith increments. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN/TD/35 (En): 29 p.
Parkkinen J., Tuomainen V., Patomäki L., Lindqvist O. V. and Mölsä H., 1994. Designing Satellite Image Analysis for the Lake Tanganyika Research Project. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/21 (En): 28p.
Pauly, D. 1997. Small-scale fisheries in the tropics: marginality,marinalization, and some implications for fisheries management. In Pikitch, E.K., Huppert, D.D. & Sissenwine, M.P. (eds.), Global trends: Fisheries Management. American Fisheries Society Symposium 20: 40-49.
Pauly, D. 1998. Beyond our original horizons: the tropicalization of Beverton-Holt. Rev. Fish Biol. Fisheries 8, 307-334.
Pauly, D. & V. Christensen, 1995. Primary production required to sustain global fisheries. Nature 374: 255-257.
Peltonen, A., Kotilainen, P., Verburg, P., Huttula, T., Makasa, L., Kagokozo, B., Kihakwi, A. & Tumba, J.-M. 1997. Data collection and analysis. In Huttula, T. (Ed.) Flow, thermal regime and sediment transport studies in Lake Tanganyika. Kuopio University Publications C. Natural and Environmental Sciences 73 : 14-105.
Peterman, R.M. & M.J. Bradford, 1987. Wind speed and mortality rate of a marine fish, the Northern anchovy (*Engraulis mordax*). Science 235: 354-356.
Pitcher T.J. & A. Bundy, 1998. The problems of estimating potential yield in data-sparse lake fisheries: a new family of approximate models withexamples from African lakes. Rev. Fish Biol. Fisheries 8, 473-480.
Plisnier P.-D., 1996.Limnological sampling during a second annual cycle 1994 - 1995 and some comparisons with year one on Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/56(En):60p.
Plisnier, P.-D., 1997. Climate, limnology and fisheries changes of Lake Tanganyika.FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/72 (En): 39p.
Plisnier, P-D. & E. Coenen, 1997. Pulsed and dampened annual limnological fluctuations in Lake Tanganyika. In Munawar, M. & R. Hecky (eds), Great Lakes of the World, Barlington,

Canada. in press.
Plisnier, P.-D., V. Langenberg, L. Mwape, D. Chitamwebwa, K. Tshibangu and E.Coenen, 1996. Limnological sampling during an annual cycle at three stations on lake Tanganyika (1993-1994). FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-TD/46 (En): 136p.
Plisnier, P.-D., V. Langenberg, L. Mwape, D. Chitamwebwa, K. Tshibangu & E. Coenen, 1999. An annual limnological cycle in Lake Tanganyika (1993-1994). Hydrobiologia, inpress.
Podsetchine, V., T. Huttula & H. Savijärvi, 1996. Modelling of hydrodynamical regime of Lake Tanganyika. In: Proc. of 2nd Int. Conf. of Hydrodynamics. Hong Kong 16-19, December 1996. ISBN90 5410 860 6. pp 661-666.
Podsetchine, V. and T. Huttula, 1995.Hydrological modelling. FAO/ FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/29 (En): 27p.
Podeschine V. and T. Huttula, 1996. Hydrological Modelling: Activity Report for the periods of 01.04-31.05.1995 and 01.09-30.09.1995. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.GCP/RAF/271/FIN-TD/45 (En): 109p.
Podsetchine, V. & Huttula, T. 1998. Numerical simulation of wind-driven circulation in Lake Tanganyika. Ecovision. World Monograph Series, in print.
Podsetchine, V., Huttula, T., Peltonen, A., Kotilainen, P., Järvenoja, S., Savijärvi, H. & Tuomainen, V. 1997. Numerical modelling. In Huttula, T. (Ed.), Flow, thermal regime and sediment transport studies in Lake Tanganyika. Kuopio University Publications C. Natural and Environmental Sciences 73 : 105-163.
Podsetchine, V., T. Huttula & S. Järvenoja, 1998 a. Applied studies of circulation and sediment transport in Lake Tanganyika. SIAM Annual Meeting, University of Toronto, July 13-17,1998. Abstract. P.87.
Podsetchine, V., T. Huttula & H. Savijärvi, 1999 b. Development of a 3D flow model of Lake Tanganyika. Hydrobiologia, in print.
Preikshot, D., E. Nsiku, T. Pitcher & D. Pauly, 1998. An interdisciplinary evaluation of the status and health of African lake fisheries using a rapid appraisal technique. J. Fish Biol. 53 (Suppl. A): 381-393.
Reynolds, C. S., 1990. Temporal scales of variability in pelagic environments and the response of phytoplankton. Freshwat. Biol. 23: 25-53.
Reynolds, J.E. and G. Hanek, 1997. Tanganyika fisheries and local stakeholders. An Overview of the LTR Lakewide Socio-economic Survey, 1997. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/71 (En): 72p.
Reynolds, J.E. and P. Paffen, LTR lakewide socio-economic survey, 1997: Notes on methods and procedures. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/66 (En): 79p.
Reynolds, J.E., 1998.Regional frameork planning for Lake Tanganyika fisheries management. Tanganyika Fisheries and local stakeholders. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/89 (En): 69p.
Reynolds, J.E.,1999. Building management partnership: local referenda on fisheries futures for Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/91 (En): 92p.
Riemann, B. & K. Christoffersen, 1993. Microbial trophodynamics in temperate lakes. Mar. micr. Food Webs 7: 69-100.
Roberts, C.M. 1997. Ecological advice for the global fisheries crisis. TREE 12(1): 35-38.
Roest, F. C., 1977. Stolothrissa tanganicae: Population dynamics, biomass evaluation and life history in the Burundi waters of Lake Tanganyika. FAO, CIFA Tech. Paper 5: 42-63.
Roest, F. C., 1992. The pelagic fisheries resources of Lake Tanganyika. Mitt. int. Ver. Limnol. 23: 11-15.
Roest, F. and J. Salo, 1997.Joint FINNIDA/FAO Evaluation Mission of GCP/RAF/ 271/FIN.FAO/FINNIDA research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/61 (En): 45 p.
Rosenberg, A.A. & v.R. Restrepo, 1994. Uncertainty and risk evaluation in stock assessment advise for U.S. marine fisheries. Can. J. Fish. aquat. Sci. 51: 2715-2720.
Salonen, K., 1979. A versatile method for the rapid and accurate determination of carbon by high temperature combustion. Limnol. Oceanogr. 24: 177-183.

Salonen, K., 1981. Rapid and precise determination of total inorganic and gaseous organic carbon in water. Water Res. 15: 403-406.
Salonen, K. & J. Sarvala, 1985. Combination of freezing and aldehyde fixation, a superior preservation method for biomass determination of aquatic invertebrates. Arch. Hydrobiol. 103: 217-230.
Salonen, K. & J. Sarvala, 1994. Sources of energy for secondary production in Lake Tanganyika. Objectives, approaches and initial experiences. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/26 (En): 30 pp.
Salonen, K. & J. Sarvala, 1995. Field manual for the determination of chlorophyll and primary production in Lake Tanganyika research. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-FM/18 (En): 24 pp**.**
Salonen, K., J. Sarvala, I. Hakala & M.-L. Viljanen, 1976. The relation of energy and organic carbon in aquatic invertebrates. Limnol. Oceanogr. 21: 724-730.
Salonen, K., J. Sarvala, M. Järvinen, V. Langenberg, M. Nuottajärvi, K. Vuorio & D. B. R. Chitamwebwa 1999. Phytoplankton in Lake Tanganyika - vertical **and horizontal distribution of *in vivo* fluorescence.** Hydrobiologia, in print.
Sanyanga, R.A., C. Machena & N. Kautsky, 1995. Abundance and distribution of inshore fish in fished and protected areas in Lake Kariba, Zimbabwe. Hydrobiologia 306: 67-78.
Sarvala, J. & K. Salonen, 1995. Preliminary experiments on phytoplankton production ecology in Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/36 (En): 38 pp.
Sarvala, J., H. Helminen & A. Hirvonen, 1994. The effect of intensive fishing on fish populations in Lake Pyhäjärvi, south-west Finland. In Cowx, I.G. (ed), Rehabilitation of freshwater fisheries. Fishing News Books, Oxford: 77-89.
Sarvala, J., T. Kairesalo, I. Koskimies, A. Lehtovaara, J. Ruuhijärvi & I. Vähä-Piikkiö, 1982. Carbon, phosphorus and nitrogen budgets of the littoral Equisetum belt in an oligotrophic lake. Hydrobiologia 86: 41-53.
Sarvala, J., H. Helminen & H. Auvinen, 1998. Portrait of a flourishing freshwater fishery: Pyhäjärvi, a lake in SW-Finland. Boreal Env. Res. 3 (in press).
Sarvala, J., K. Salonen, M Järvinen, E. Aro, T. Huttula, P. Kotilainen, H. Kurki, V. Langenberg, P. Mannini, A. Peltonen, P-D. Plisnier, I. Vuorinen, H. Mölsä & O.V. Lindqvist, 1999**.** Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. Hydrobiologia, in press.
Savijärvi , H., 1995. Sea-breeze effects on large-scale atmospheric flow. Contrib. Atmos. Physics, V. 68. P. 281-292.
Savijärvi, H., 1997. Diurnal winds around Lake Tanganyika. Q. J. R. Meteorol. Soc. Vol. 123, P. 901-918.
Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the mangagement of th ecommercial marine fisheries. Bull. Inter-Am. Trop. Tuna Comm., 1: 27-56.
Schindler, D. W., R. V. Schmidt & R. A. Reid, 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the 14C method, J. Fish Res. Bd Can. 29: 1627-1631.
Simplson, J.J., 1994. Remote sensing in fisheries: a tool for better management in the utilization of a renewable resource. Can. J. Fish . aquat. Sci. 51: 743-771.
Skjønsberg, E., 1982. Men, money and fisheries planning: The case of Northern Province of Zambia. In I. Tvedten and B. Hersoug (eds.), Fishing for Development. Small-scale fisheries in Africa. The Scandinavian Institute of African Studies, 155-172.
Smith, A.D.M., 1993. Risk assessment or management strategy evaluation: what do managers need and want? ICES CM D: 18. ICES, Copenhagen.
Sprules, W. G., S. B. Brandt, D. J. Stewart, M. Munawar, E. H. Jin & J. Love, 1991. Biomass size spectrum of the Lake Michigan pelagic food web. Can. J. Fish. aquat. Sci. 48: 105-115.
Stocker, M. V. Haist. & D. Fournier, 1985. Environmental variation and recruitment of Pacific herring (Clupea harengus pallasi) in the strait of Georgia. Can. J. Fish. aquat. Sci. 42 (Vol. 1): 174-180.
Szczucka, J., 1998. Acoustic estimation of fish abundance and their spatial distributions in Lake Tanganyika. FA/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/84 (En): 63 pp.

Tuomainen, V., H. Mölsä, J. Parkkinen, L. Patomäki and O.V. Lindqvist, 1997.The NOAA series' AVHRR radiometer's capability of reveling water features in Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/77 (En): 39p.

Twombly, S., 1983. Seasonal and short term fluctuations in zooplankton abundance in tropical lake Malawi. Limnol.Oceanogr. 28: 1214-1224.

Vandelannoote, A., Deelstra, A. & F. Ollevier, 1999. The inflow of the Rusizi River to Lake Tanganyika. Hydrobiologia, in print.

van Well, P & D.W. Chapman, 1976. Summary of limnological observatiosn in Lake Tanganyika near Kigoma 1974-75. FI:DP/URT/71/012/39. FAO, Rome, 17 pp.

Verburg, P.,1997. Lake Tanganyika hydrodynamics and meteorology diel cycle.FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/73 (En): 51p

Verburg, P., Huttula, T., Kakogozo, B., Kihakwi, A., Kotilainen, P., Makasa, L. & Peltonen, A. 1997. Hydrodynamics of Lake Tanganyika and meteorological results. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/59 (En). Bujumbura, Burundi.

Verburg, P., B. Kakogozo, L. Makasa, S. Muhoza and J-M. Tumba, 1998. Hydrodynamics of Lake Tanganyika: Results of 1996. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/86 (En): 36p.

Verburg, P., T. Huttula, B. Kakogozo, A. Kihakwi, P. Kotilainen, L. Makassa and A. Peltonen, 1997. Hydrodynamics of Lake Tanganyika and meteorological results. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika.GCP/RAF/271/FIN-TD/59 (En): 67p.

Verburg, P., B. Kakogozo, L. Makasa, S. Muhoza and J-M. Tumba,1998. Hydrodynamics of Lake Tanganyika: 1993 - 1996, Synopsis and interannual comparisons. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FIN-TD/87 (En): 50p.

Vuorinen, I. & H. Kurki, 1994. Preliminary results of zooplankton sampling in Lake Tanganyika. FAO/FINNIDA Research for the Management of the Fisheries of Lake Tanganyika. GCP/RAF/271/FINBTD/22 (En): 37 pp.

Vuorinen, I., H. Kurki, E. Bosma, A. Kalangali, H. Mölsä & O. V. Lindqvist, 1999. Vertical distribution and migration of pelagic Copepoda in Lake Tanganyika. Hydrobiologia, in print.

Weisse, T. & J.G. Stockner, 1993. Eutrophication: the role of microbial food webs. Mem. Ist. ital. Idrobiol. 52: 133-150.

Wessel, P. & W.H.F. Smith, 1991. Free software helps map and dislplay data. EOS. Trans. Amer. Geophys. U. 72: 441, 445-446.

Wetzel, R. G., 1983. Limnology. Second edition. Saunders College Publishing: 743 pp.

White, P. A., J. Kalff, J. B. Rasmussen & J. M. Gasol, 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microb. Ecol. 21: 99-118.

Wooster. M.J., C.B. Sear, G. Patterson & J.Haigh, 1994a. Tropical lake surface temperatures from locally received NOAA-11 AVHRR data - comparison with *in situ* measurements. Int. J. Remote sensing 15 (1): 183-189.

Wooster, M.J., C.B.Sear & G. Patterson, 1994 b. The use of a PC-based AVHRR receiving station for mapping tropical lake surface temperature. 2nd Thematic Conference on Remote Sensing for Marine and Coastal Environments, New Orleans, Louisiana, 21 January - 2 February 1994.

Yokoyama, R. & S.Tanaba, 1991. Estimation of sea surface temperature via AVHRR of NOAA-9 - coparison with fixed buoy data. Int. J. Remote Sens. 12: 2153-2528.

Zilioli, E., P.A. Brivio & M.A. Gomarasca, 1994. A correlation between optical properties from satellite data and some indicators of eutrophication in Lake Garda (Italy). Sci. Total Env. 158: 127-133.