Limnology and hydrology of Lakes Tanganyika and Malawi

Ruud C. M. Crul

Studies and reports in hydrology 54

Recent titles in this series

5. *Discharge of selected rivers of the world. Débit de certains cours d'eau du monde* (Multilingual English/French/Spanish/Russian).
   Vol. III (Part IV): *Mean monthly and extreme discharges (1976–1979)/Débits mensuels moyens et débits extrêmes (1976-1979).* 1985.
30. *Aquifer contamination and protection.* 1980.
    Pollution et protection des aquifères. 1986.
31. *Methods of computation of the water balance of large lakes and reservoirs.*
    Vol. I: *Methodology.* 1981.
    Vol. II: *Case studies.* 1985.
32. *Application of results from representative and experimental basins.* 1982.
33. *Groundwater in hardrocks.* 1985.
    Les eaux souterraines des roches dures du socle. 1987.
34. *Groundwater models.* Vol. I: *Concepts, problems and methods of analysis with examples of their application.* 1982.
35. *Sedimentation problems in river basins.* 1982.
    Problèmes d'érosion, transport solide et sédimentation dans les bassins versants. 1986.
36. *Methods of computation of low stream flow.* 1982.
37. *Proceedings of the Leningrad Symposium on specific aspects of hydrological computations for water projects.* 1981. (Russian only)
38. *Methods of hydrological computation for water projects.* 1982.
    Méthodes de calcul pour les études hydrologiques concernant l'aménagement des eaux. 1985.
39. *Hydrological aspects of drought.* 1985.
    Aspects hydrologiques des sécheresses. 1987.
40. *Guidebook to studies of land subsidence due to groundwater withdrawal.* 1985.
41. *Guide to the hydrology of carbonate rocks.* 1984.
42. *Water and energy: demand and effects.* 1985.
43. *Manual on drainage in urbanized areas.*
    Vol. I: *Planning and design of drainage systems.* 1987.
    Vol. II: *Data collection and analysis for drainage design.* 1987.
44. *The process of water resources project planning: a system approach.* 1987.
45. *Groundwater problems in coastal areas.* 1987.
46. *The role of water in socio-economic development.* 1987.
47. *Communication strategies for heightening awareness of water.* 1987.
48. *Casebook of methods for computing hydrological parameters for water projects.* 1987.
    Recueil de méthodes de calcul des paramètres hydrologiques pour les projets hydrauliques. 1990.
49. *Hydrology and water resources of small islands: a practical guide.* 1991.
50. *Guidelines on the study of seawater intrusion into rivers.* 1991.
51. *Use of models for river problems.* 1993.
52. *Discharge of selected rivers of Africa/Débit de certains cours d'eau d'Afrique.* 1995.
53. *Limnology and hydrology of Lake Victoria.* 1995.

Studies and reports in hydrology 54

Limnology and hydrology of Lakes Tanganyika and Malawi

Comprehensive and Comparative
Study of Great Lakes
UNESCO/IHP-IV Project M-5.1

Ruud C. M. Crul

UNESCO Publishing

The designations employed and the presentation of material throughout the publication do not imply the expression of any option whatsoever on the part of UNESCO concerning the legal status of any country, territory, city of area or of its authorities, or concerning the delimitation of its frontiers or boundaries.

Published in 1997 by the United Nations
Educational, Scientific and Cultural Organization
7 place de Fontenoy, 75352 Paris 07 SP

Printed by: Imprimerie Darantière, Quétigny (France)

ISBN 92-3-103400-6

Preface

Rivers and lakes around the world are often shared by several countries. Experience shows that it is much easier to reach consensus on the common development, management and utilization of these international water bodies when there is an agreed physical and hydrological description.

In the framework of the Fourth Phase (1900–1995) of UNESCO's International Hydrological Programme, a special theme (Theme M-5) was devoted to 'hydrological and water management aspects of international water systems' with the objective of preparing material on hydrological, ecological and water management aspects of international rivers and lakes basins.

Project M-5 was in particular devoted to the 'comprehensive and comparative study of great lakes' with the overall objective study of great lakes' with the overall objective of bringing together knowledge obtained over the last 15 years on the hydrology and limnology of psecific lakes, starting with the Great Lakes of Africa, which constitute the most improtant freshwater reserves on the African continent.

Three main lakes, namely Lakes Victoria, Tanganyika and Malawi, were selected for the preparation of monographs, to be followed by a comprehensive report on their similarities and differences.

The first monograph, published in 1995, was devoted to the limnology and hydrology of Lake Victoria, and an extensive bibliography of Lake Victoria compiled during the course of the project was published separately within UNESCO's 'Technical Documents in Hydrology' series.

Project M-5–1 was implemented with the collaboration of the African Great Lakes Working Group of the International Limnological Society (SIL), in collaboration with their professional and official contacts in the East African countries around the Great Lakes.

We are grateful to Dr F. C. Roest, from the International Agricultural Centre of Wageningen, the Netherlands, convenor of the African Great Lakes Working Group of SIL, for the supervision of the book's preparation and of course to Dr R. C. M. Crul for his major contribution to the project.

Contents

Part 2. Limnology and hydrology of Lake Malawi

List of tables and figures

Lake Tanganyika

Lake Malawi

Foreword

This final version of the monographs on the limnology and hydrology of the Lakes Tanganyika and Malawi is one of the results of the project 'Comprehensive and Comparative Study of Great Lakes (1992–1995)', a project of the fourth phase of the International Hydrological Programme (1990–1995) of the Division of Water Sciences of UNESCO (UNESCO/IHP-IV Project M-5.1).

The overall objective of this project is to bring together the knowledge obtained during the last 15 years on the hydrology, limnology and pollution of the African Great Lakes Victoria, Tanganyika and Malawi in order to contribute to the overall aim of the UNESCO IHP-IV Project M-5 to prepare material on hydrological, ecological and water management problems encountered in shared water bodies.

The African Great Lakes Working Group of the International Limnological Society (SIL) has collaborated with UNESCO in implementing the various activities of the project.

The output of the project consists of monographs on the individual Lakes Victoria, Tanganyika and Malawi and a comprehensive report on the similarities and differences between them. During the workshop in 1995, the reports formed the basis for a consensus on the hydrological and limnological descriptions of these international water systems. Consequently, from now on, it should be easier for the riparian countries to reach an agreement for the use, development, planning and management of these lakes.

Acknowledgements

Thanks are expressed to all people who assisted in the preparation of these monographs. Several scientists who have worked on the two lakes provided me with papers: R. H. Lowe-McConnell, H. A. Bootsma, and J. Halfmann. I thank R. H. Lowe-McConnell, D. Tweddle, H. Zebidi, H. A. Bootsma and A. Menz for their useful comments on the first drafts. Finally, I am indebted to F. C. Roest of the International Agricultural Centre, Wageningen, the Netherlands, for discussion and advice in the course of preparing these overviews.

Introduction

Lake Tanganyika, Lake Malawi and Lake Victoria and the other African Great Lakes are of crucial socio-economic importance to the nutrition and welfare of their riparian populations (Ntakimazi, 1992). The lakes are major sources of fish protein, reservoirs of freshwater and avenues of transportation. They have great touristic potential and offer possibilities for the development of trade between the riparian countries. Recently the oil industry has shown interest in exploring a wide area of Eastern and Central Africa and some of the concession agreements include African Great Lakes (Baker, 1992). Besides their socio-economic value to the riparian populations, the lakes have also a high scientific value to mankind as a whole due to their high biodiversity and an intrinsic value because of the unique wildlife and the exceptional scenery in and around the lakes.

Human activities in the African Great Lakes and their catchments and exploitation of the lake resources may easily damage the lakes and their resources. The threats to the lakes are diverse and include eutrophication and/or pollution caused by domestic, industrial and agricultural effluents, by oil exploration, transport and recreational activities; lake level changes and siltation due to deforestation of the watersheds; and reduction of fish stocks because of overfishing and/or introductions of exotic fish species. There are even indications of acid rain over tropical Africa (Andreae, 1991). It is therefore necessary to carefully manage the lake resources and their catchment areas (Lowe-McConnell *et al.* 1992).

Lakes Tanganyika and Malawi are, like all other African Great Lakes, shared water bodies. Mutual consultations and coordination of action between the lacustrine states are urgently needed. Only then may comprehensive programmes of scientific research supported by the international community provide the riparian states with the necessary background to take all measures for the conservation of their lakes.

One of the main disciplines involved in lake research is limnology, including hydrological research. At present, limnology covers a very broad field including aquatic, atmospheric, terrestrial, subterranean and even marine ecology (Frey, 1990). Even the past has become the subject of limnological research. Records of changes in water and nutrient budgets, productivity, eutrophication, species composition and abundance in lakes have been left in the sediments. Paleolimnology focuses on these sedimentary records in order to gain insight into the past metabolic states of lakes.

In the past fifty years, limnology has made great advances in Europe and North America and developed from a mainly descriptive discipline to a highly sophisticated science. Knowledge on lake limnology was reviewed by Ruttner (1953), Hutchinson (1957, 1967, 1975, 1993), Wetzel (1975, 1983) and Horne & Goldman (1994), and on river limnology by Hynes (1972), Whitton (1975) and Davies & Walker (1986).

An important area in limnology since the 1950s has been eutrophication, the process of progressive nutrient loading of natural waters by effluents resulting from man's activities, e.g. domestic sewage, industrial wastes and run-off water with agricultural fertilizers. It has caused large problems in temperate lakes in industrialized countries, e.g. the Laurentian Great Lakes in North America (Vollenweider, 1968; National Academy of Science, 1969; Likens, 1972; Hutchinson, 1973). Toxic pollution is another important subject of limnology. Pesticides, PCBs, heavy metals and other substances of industrial wastes have contaminated areas, including lakes, far from the source of the pollutants. In the last decade, limnologists in Norway and subsequently in North America discovered that acidification of lakes resulted from acid deposition of industrial wastes from the atmosphere. These phenomena clearly demonstrate the close interrelation between lake, watershed and atmosphere.

In the last fifty years limnological methods have developed as a result of new technologies and advances in science. Many physical and chemical parameters of water can now be measured, if necessary continuously, with sophisticated instruments, and recorded by and stored in computers. Large data sets collected in this way can be accurately analysed by statistical computer programmes. All this advanced research has only been possible thanks to large financial inputs of governments and industries in the developed countries, and has been mainly focused on temperate waters.

In sharp contrast to the sophisticated research in temperate waters, limnological studies of tropical waters have so far been more descriptive in nature. Research activities have been restricted due to limited financial budgets of most national research institutes in developing countries in the tropics and in a number of cases research was only possible with help of United Nations agencies assisting African countries in the rational exploitation of their natural resources.

African inland waters have been the subject of limnological research since the first expeditions during the 1920s and 1930s (Beadle, 1981). Textbooks which provide much information on the limnology and ecology of (African) tropical fresh waters and the African Great Lakes are Beadle (1974, 1981), Welcomme (1979, 1985), Serruya & Pollingher (1983), Taub (1984), Payne (1986), Coulter (1991) and VandenBossche & Bernacsek (1990*a*, 1990*b*, 1991). A database on the inland fisheries resources of Africa containing basic limnological data from the latter FAO publications has been developed by FAO's Fisheries Department (Crul, 1992*a*).

Recently, an outstanding, comprehensive book *Lake Tanganyika and its Life* was published (Coulter, 1991*a*) upon which the present monograph on Lake Tanganyika mainly draws. The multi-author book contains chapters on geology, hydrodynamics, nutrient dynamics, pelagic ecosystem, fisheries, flora and fauna and zoogeography of the lake and a comprehensive bibliography (Coulter & Coulter, 1991).

The first major meeting on African limnology was held in Nairobi in 1979 (Symoens *et al.* 1981). In 1989, an International Symposium on Resource Use and Conservation of the African Great Lakes was held in Bujumbura (IAC, 1990; Lowe-McConnell *et al.* 1992) followed by an International Conference on the Conservation and Biodiversity of Lake Tanganyika in 1991 (Cohen, 1991). In 1991 a symposium on the limnology and fisheries of Lake Tanganyika was held in Kuopio (Finland), and in 1992 a meeting was organized on the Impact of Species Changes in African Lakes in London (Pitcher, 1994). In 1993, a symposium on the Limnology, Climatology and Paleoclimatology of the East African Lakes was held in Uganda (IDEAL, 1993) and a Workshop on Speciation in Ancient Lakes in Belgium (SIAL, 1993). In 1994 a seminar was held to present the results of the limnological and fisheries research carried out on Lake Malawi by the UK/SADC Pelagic Fish Resource Assessment Project.

As limnology evolved in temperate regions from the beginning of this century, a theoretical framework was built upon studies of temperate lakes. Tropical lakes have unique attributes, especially in the biogeochemical cycles of nutrient elements, that make them quite different from temperate lakes (Kilham & Kilham, 1990). Lewis (1987) made an attempt to identify the features of tropical lakes that are likely to provide the most productive basis for comparison with temperate lakes.

Limnological and hydrological research may provide information on the important physical, chemical and biological events occurring in lakes. First, limnological research is important for fisheries management. It helps to elucidate the factors that determine the numbers, biomass and distribution of fish populations, such as current velocity, water temperature, dissolved oxygen and nutrient availability and food sources. Limnological data may also be used for estimating potential fish production, although the use of predictive models for African inland waters is still restricted due to the scarity and unreliability of basic limnological and fisheries data (Crul, 1992*b*). Second, water quality research is an important tool for controlling and monitoring pollution of the lakes. Finally, limnological research has its application in human health control. Water plays an important role in disseminating a number of important human diseases. In addition to many bacterial diseases (e.g. cholera, typhoid and paratyphoid) there are several widespread parasitic diseases, such as bilharzia, malaria and river blindness, linked to water.

Since long-term data sets of basic physical and chemical parameters are not available for most African Great lakes, an alternative source of information about long-term trends in tropical lakes is the study of cores of lake sediments. Paleolimnology, the multidisciplinary science that uses physical, chemical and biological information preserved in sediments, has great potential for the African Great Lakes. The lakes are among the oldest on earth and sediments may be up to 2–6 km thick in some of them. As sedimentation rates for these lakes are between 0.2 and 5 $mm.yr^{-1}$, the sediment records are resolvable to decades or in some cases even years (Johnson *et al.* 1990), and so provide important information on climatic history (Johnson *et al.* 1993).

Part 1

Limnology and hydrology of Lake Tanganyika

Section I

Research on Lake Tanganyika *a review*

1 The importance of the lake to the region and the role of limnological and hydrological research

RESOURCE USE

Lake Tanganyika is the second-largest African lake after Lake Victoria and the largest of the African rift lakes, with a surface area of 32,600 km². The lake is shared between Zaire, Burundi, Tanzania and Zambia. Its catchment lies in Tanzania, Zaire, Zambia, Burundi and Rwanda and has an area of 231,000 km² (exclusive of Lake Kivu) (Coulter & Spigel, 1991).

The lake is an important fresh water resource for people living in its vicinity. It has been an important means of transport, as most roads in the lake region are tangential to the lake and there is only a single main road along the lakeshore, in Burundi (Coulter, 1991*b*). Nearshore population densities are low around Lake Tanganyika, except for the northern end of the lake (Figure 1.1). Fishing and post-harvest activities have been important economic operations in and around the lake (Coulter, 1991*b*; Roest, 1992). In Tanzania, Zambia and Zaire the lake is remote from the major centres of population and the population in its catchment area depends largely on the lake for protein. Fish from the lake have also been a very important source of food for people in the 'Copperbelt' in Zambia, some 1000 km from the lake. This market not only absorbs dried clupieds from the Zambian sector, but also from the Tanzanian part of the lake (Coulter, 1991*b*).

Furthermore, the lake has a very rich flora and fauna (Beadle, 1981; Coulter, 1991*a*). Species checklists given by Coulter (1991*c*) provide a preliminary total of 840 floral and 1248 faunal species, but this listing is far from complete as much of the lake is still biologically unexplored. Of the 1248 faunal species described, more than 35 % are endemic (Coulter, 1991*d*). The unique fish fauna consists of more than 70 % of endemic species, of which 90 % belong to the family of Cichlidae. These have been reviewed together with those of the Lakes Malawi and Victoria by Lowe-McConnell (1987). Conservation of fish species in Lake Tanganyika is of major importance, as together with the Lakes Malawi and Victoria the lake forms one of the most spectacular examples of adaptive radiation of vertebrates in the world (Lowe-McConnell, 1991, 1993).

MAJOR ENVIRONMENTAL ISSUES

Deforestation and soil erosion

Satellite imagery analysis has revealed the effects of deforestation in the catchment area of Lake Tanganyika. In the mid 1980s uncontrolled forest clearing converted the original forest/woodland areas to grazing or agricultural land which resulted in rapid erosion. In the northernmost portion of the drainage basin of the lake, the forest is almost completely cleared and in the central portions half of the original woodland/forest has been cleared. The erosion has affected the rivers flowing into the lake and has led to a massive increase in sedimentation rates in the nearshore regions of the lake. The increase in suspended sediment load of the Ruzizi River is clearly visible by the outbuilding of the Ruzizi River Delta. Increased suspended sediment and sedimentation

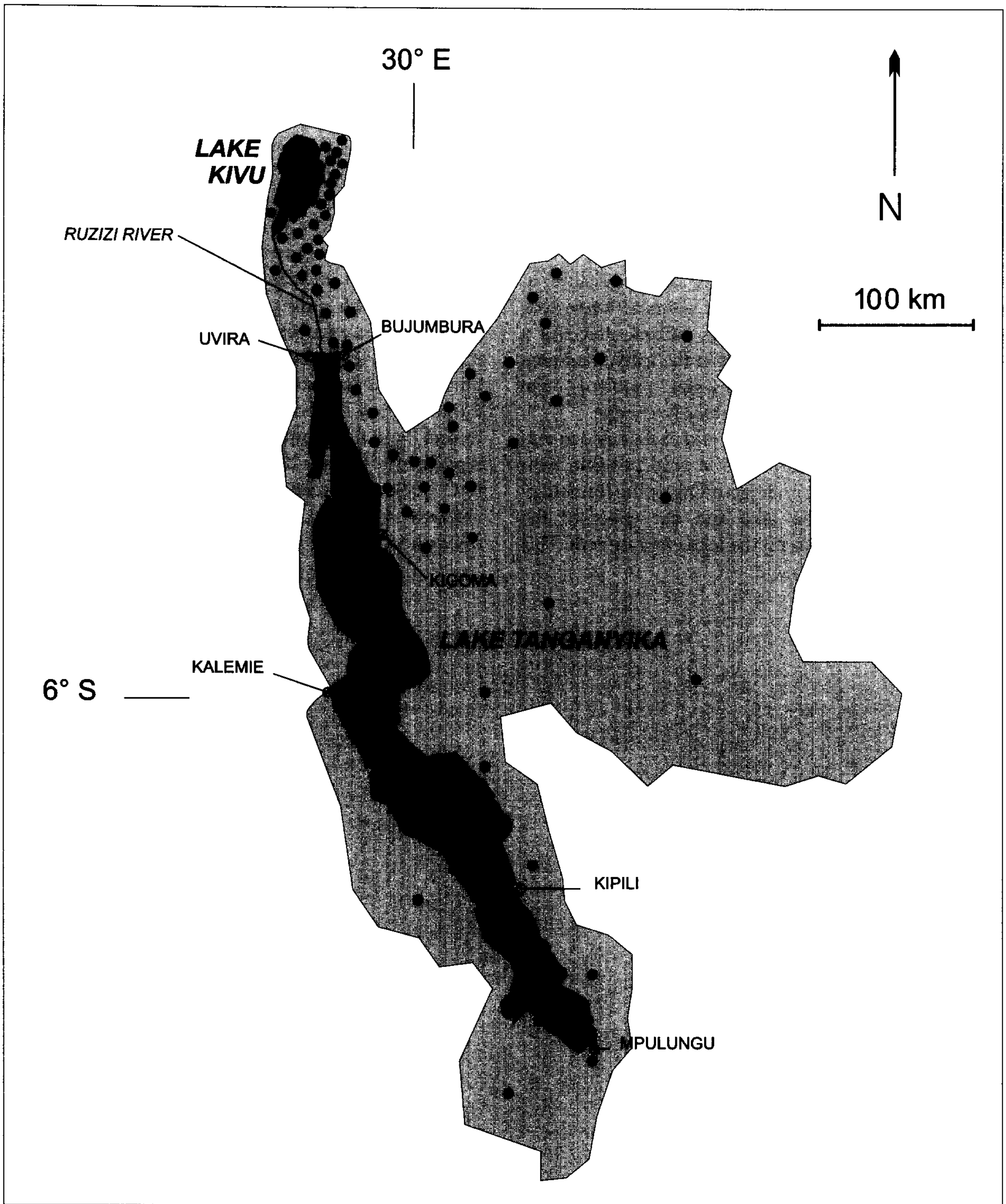


Figure 1.1 Population density in the catchment area of Lake Tanganyika. Each dot represents 100,000 persons (data extracted from Bootsma & Hecky, 1993, Fig. 4)

rates have already had a serious negative impact on biodiversity, especially in the northern part of the lake (Cohen, 1991, 1993).

Pollution

Sources of pollution into the lake are currently concentrated in the northern end of the lake near Bujumbura, where untreated, municipal, agricultural and industrial waste water is discharged into the lake. Pollution also occurs near the other harbours of Kalemie (Zaire), Kigoma (Tanzania) and Mpulungu (Zambia).

Pollution forms the greatest future threat to the ecosystem of Lake Tanganyika. Changes that have taken place in the ecosystem of Lake Victoria may be indicative of the potential impact of increasing population density and development in the catchment area of Lake Tanganyika, as it is clear that the size of the lakes does not protect them from anthropogenic influences (Bootsma & Hecky, 1993).

If positive results of oil exploration were to lead to exploitation of oil in or near the lake, pollution of the lake waters during extraction, storage and/or lake transport would clearly have negative implications for the fish stocks and water supplies of the lake (Baker, 1992).

THE ROLE OF LIMNOLOGICAL AND HYDROLOGICAL RESEARCH

In the past, population density and agricultural, industrial and fisheries activities were at levels that allowed the lake to maintain its natural state. As a result of the population growth in the catchment area and the associated environmental problems, the ecosystem of the lake will necessarily change.

Conservation of biodiversity and sustainable management of the lake's resources is only possible with an improved scientific understanding of the limnology and hydrology of the lake and the effect of the anthropogenic activities on the lake environment. This requires ecosystem monitoring, in particular information on nutrient dynamics, primary production and community structure which is useful to detect changes in the ecosystem (Bootsma & Hecky, 1993). Besides, Lake Tanganyika is a shared water body, and resource use by one of the riparian countries affects the activities in the other countries. This requires regional collaboration and co-ordination of limnological and hydrological research. The first steps towards regional co-operation in environmental research and management of the lake and conservation of its biodiversity have been taken with three projects: the newly established Regional Centre for Applied Hydrobiological research (CRRHA) in Bujumbura for the CEPGL region (Zaire, Burundi and Rwanda), the FAO/FINNIDA Regional Fisheries Project – both started in 1992 – and the GEF Project 'Pollution Control & Other Measures to Protect Biodiversity in Lake Tanganyika' started in 1994. The FAO project presently coordinates the limnological research on the lake which is carried out from the research stations of the four riparian countries.

2 History of limnological and hydrological research on Lake Tanganyika

GEOGRAPHICAL EXPLORATION AND THE EUROPEAN DISCOVERY OF THE LAKE

The first scientific research on Lake Tanganyika goes back to the explorations to find the sources of the Nile in the 1850s compellingly described by Moorehead (1960). In the early 1850s local reports of Arab slave and ivory traders spoke of three large lakes 'Ujiji', 'Nyanza' and 'Nyasa'. In 1855 J. J. Erhardt and two other German missionaries, Johann Krabf and Johann Rebmann, produced a map showing a large inland lake called 'Uniamesi Sea'. The Royal Geographical Society in London became interested and supported an expedition of Richard Burton and John Hanning Speke to the interior of East Africa in 1856 to investigate the reports on the lakes and their relation with the Nile River. In February 1858 Burton and Speke discovered 'Ujiji', the present Lake Tanganyika. They reached the lake near the mouth of the Malagarazi River from where they rowed in two canoes to the most northern trading post of the lake. There they heard reports that the Ruzizi River flowed into the lake and not out of the lake, though they did not see for themselves. Speke discovered Lake Victoria in July 1858 and Samuel Baker Lake Albert in March 1864.

In 1866 Livingstone set off from Zanzibar to finally solve the mystery of the Nile. He entered the interior of East Africa via the Ruvuma River and reached the southern end of Lake Tanganyika in 1867. He travelled west and discovered Lake Mweru and Lake Bangweulu, after which he returned to Ujiji in 1869. From there he continued to the northwest and reached the Lualaba River in 1871. At the end of that year he returned to Ujiji where the historical meeting with Stanley took place. They explored the northern part of the lake together and finally verified that the Ruzizi River flowed into the lake. Stanley left for Zanzibar in 1872, but Livingstone travelled to Lake Bangweulu where he died on 30 April 1873. Verney L. Cameron, who was sent by the Royal Geographical Society to help Livingstone, decided to go ahead with the latter's investigations after he heard of his death. He arrived in Ujiji in 1874 and sailed to the Lukuga River, the mouth of which was blocked with alluvium and vegetation. He presumed that the river had been the only one running out of the lake. When Stanley visited the Lukuga in 1876, a rise in lake level had caused a breech in the blockage and water was flowing out of the lake.

THE FIRST SCIENTIFIC INVESTIGATIONS

At a time when most of the geographical problems were being solved, European scientists became interested in the exciting new virgin area of tropical Africa. The interest in Lake Tanganyika began with the first shells taken from a beach by Speke in 1858 (Woodward, 1859). The first systematic faunal collections were made by Hore (1892), but the first purely scientific expeditions to Lake Tanganyika were those of J. E. S. Moore in 1894 and 1897, which can be regarded as the foundation of tropical African limnology (Beadle, 1981). The first comprehensive scientific account of the lake was *The Tanganyika Problem* (Moore, 1903) in which the author suggested that the lake had been connected to the sea in the Jurassic period.

LIMNOLOGICAL AND HYDROLOGICAL RESEARCH

Limnological investigations of Lake Tanganyika and other East African lakes evolved from short-term investigations at the beginning of the century focusing on the collection of specimens and the measurement of some simple physical parameters to the foundation of research institutes on the shores of the lakes, which made prolonged investigations and the use of research vessels on the lake possible (see Appendix 1). In the last decades most limnological research has been carried out in the vicinity of the four major ports of the lake, mainly for logistic reasons: Bujumbura at the north end, Kigoma on the eastern shore in the north basin, Kipili on the eastern shore in the south basin and Mpulungu at the south end. Furthermore, limnological observations have been made in the vicinity of the CNRS research station in Uvira (Zaire).

In 1909 the systematic recording of the water levels of Lake Tanganyika began. Water temperatures were first measured by Cunnington in 1904–1905 (Cunnington, 1920). Beauchamp – founder member of Freshwater Biological Association – made pioneer studies of the hydrography of Lakes Tanganyika and Malawi in 1938–1940 (Beauchamp, 1939, 1940, 1946, 1953). In 1946–1947 a Belgian expedition 'L'Exploration hydrobiologique du lac Tanganika' considerably increased the knowledge of the lake with a variety of hydrobiological studies including its bathymetry (Capart, 1949) and its phytoplankton and zooplankton (Van Meel, 1954). In 1959 the Joint Fisheries Research Organization (JFRO) of Northern Rhodesia and Nyasaland established a research station on Lake Tanganyika at Mpulungu (Zambia), and George Coulter was assigned as scientist to this station (JFRO, 1960). Studies by Coulter included hydrological and limnological observations and fisheries research (Coulter, 1960, 1962, 1963, 1964, 1968).

In the 1970s most limnological research was carried out by externally-funded fisheries projects with limnological research components, especially the UNDP/FAO 'Lake Tanganyika Fisheries Research and Development Project' from 1973 to 1977 in Tanzania, and the UNDP/FAO Project 'Fishery Research on Lake Tanganyika' in Burundi (van Well & Chapman, 1976; Ferro, 1975*a*; Ferro & Coulter, 1974). Several limnological research institutes participated in various subjects of research: Freshwater Institute, Canada (Hecky, Fee, Kling, Rudd), Scripps Institution of Oceanography, University of California, U.S.A. (Craig, Craig, Weiss, Dixon), Massachusetts Institute of Technology, Cambridge, U.S.A. (Edmond, Stallard), University of Texas, Houston, U.S.A. (Thompson, Lyon) and City of London Polytechnic, U.K. (Burgis) (see Appendix 1). In 1977 cooperative studies in ecology and limnology between Japanese and Zairian scientists were initiated in the northwestern part of the lake near Uvira and between Japanese and Zambian scientists in the southern part of the lake in 1988 (Kawanabe *et al.* 1992). The University of Burundi carried out water quality and pollution studies in the Bay of Bujumbura and the affluent rivers in the 1980s (Caljon, 1992).

In 1992 an FAO Regional Fisheries Project started, financed by the Finnish International Development Agency (FINNIDA) and the Arab Gulf Programme for UN Development Organizations (AGFUND). The project has a large limnological/hydrological component, including the rehabilitation of four research stations around the lake and lakewide research cruises (Lindqvist & Mikkola, 1989). Also in 1992 IRAZ (Institut de recherche agronomique et zootechnique de la CEPGL) created a regional centre for hydrobiological research in the CEPGL region (Zaire, Burundi and Rwanda). This new 'Centre régional de recherches en hydrobiologie appliquée' (CRRHA) focuses its research on the coastal area of Lake Tanganyika and the major northern affluents. CRRHA is at present mainly funded by the Coopération belgo-CEPGL and the project is executed by the Catholic University of Leuven (Belgium). Finally, a GEF Project 'Pollution Control & Other Measures to Protect Biodiversity in Lake Tanganyika' was scheduled to start in 1994.

Hydrological research mainly focused on lake level fluctuations and their implications for water availability (Gillman, 1933; Heinrichs, 1936; Singh, 1975; Loehnert, 1975; Sinha, 1980; Norconsult, 1980) and faunal isolation and speciation (Coulter, 1991*e*).

References on the limnology and hydrology of Lake Tanganyika are given in the Bibliography of Lake Tanganyika (Coulter & Coulter, 1991). In Appendix 1 (pp. 60–4) an overview of expeditions, limnological research programmes, projects and studies and hydrological studies on Lake Tanganyika is given.

Section II

Background

3 Geological and climatic history

GEOLOGICAL HISTORY

The African continent is one of the most ancient in the world. The rivers gradually eroded the land mass and the ancient pattern of drainage in the early Miocene which is still the basis of the hydrology of a large part of the continent, was determined by rivers flowing from a higher central region eastward and westward.

By upward earth movements and volcanic activity during the Miocene (25–12 million years B.P.) depressions and minor lake basins were created orientated approximately north-south and a wide stretch of land from Eritrea to the Zambezi River was lifted more than 1000 metres. Later the shallow basin of Lake Victoria was formed by a gradually sagging of the centre of this stretch. The two edges were raised further, forming two Great Rift Valleys. A general account of the geological development of the Rift Valleys is given by McConnell (1972). Tectonic activities in and near these valleys formed a series of splits in the earth's crust, of which some were more than 1000 metres deep and filled with water. In this way all the African Great Lakes in East Africa except Lake Victoria were formed. The Western Rift Valley comprises, from north to south, the Lakes Mobutu, Edward, George, Kivu, Tanganyika, Rukwa, Malawi, Chiuta and Chilwa. The Eastern Rift Valley extends as far north as Israel, where it contains Lake Tiberias and the Dead Sea. Other lakes in the Eastern Rift Valley are the Ethiopian Rift Lakes, Lake Turkana and a number of shallow saline lakes in Kenya and Tanzania.

The geological development of the southern part of the Tanganyika Trough is described by Haldemann (1969). The lake is the oldest of the East African lakes. In the development of Lake Tanganyika three stages are hypothesized (Tiercelin & Mondeguer, 1991; Coulter, 1991*e*). The first stage is believed to go back to the Early Miocene (20 million years B.P.), when one of the ancient river systems was situated in the area presently occupied by the Zaire River system and Lake Tanganyika. At that time this area was characterized by meandering streams with swamps, drainage was to the west and there was little tectonic activity. This stage continued till the Middle Miocene (14 million years B.P.). In the second stage tectonic activity created minor depressions and minor basins which became a series of small lakes. This stage persisted until the Miocene-Pliocene transition (6 million years B.P.).

From 6 million years B.P. to the present, subsidence of the main graben by reactivated tectonic activity combined with wetter climatic conditions created a progressively deeper lake/ lakes and this deep lake environment characterized the third and last evolutionary stage (see also Coulter, 1991*e* – *Table 10.III*).

After the final major tectonic movements in the Late Pleistocene the climate became the major force in determining the water levels in the lakes, although the rise of the Virunga volcanoes in the Holocene resulted in higher lake levels due to overflow from Lake Kivu via the Ruzizi River.

In the past 20,000–25,000 years major fluctuations in climate have occurred in Africa (Livingstone, 1975; Street & Grove, 1976; Beadle, 1981), with great implications for lake levels.

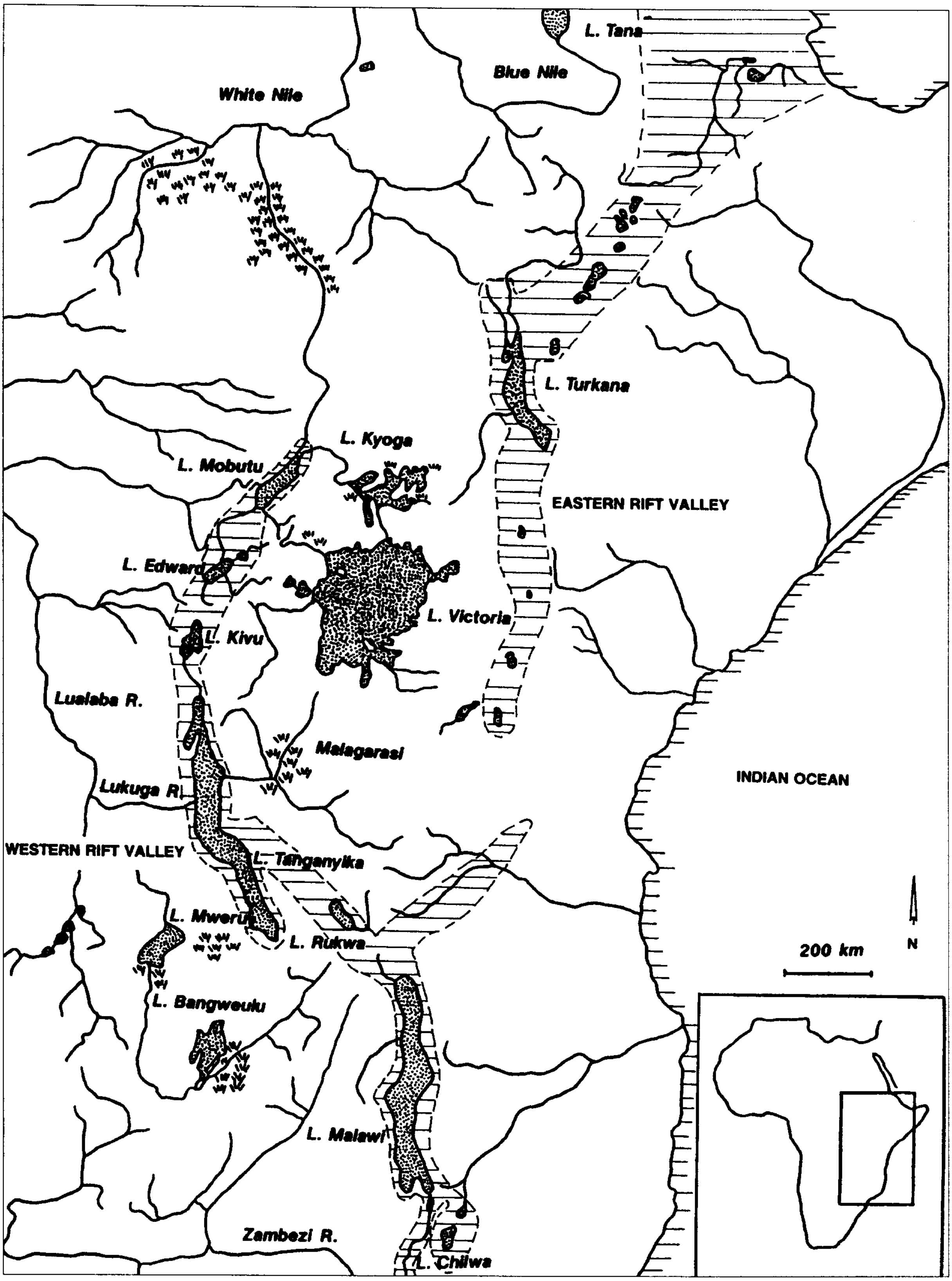


Figure 3.1 Eastern Africa showing the Rift Valleys and their lakes.

HISTORICAL LAKE LEVELS

A reconstruction of lake level variations in Lake Tanganyika was given by Tiercelin & Mondeguer (1991) and by Coulter (1991) based on information from seismic research and core studies by the PROBE and GEORIFT projects and from the earlier core studies by Livingstone (1965), Degens *et al.* (1971) and Stoffers & Hecky (1978).

Before 40,000 B.P., lake levels 600 and 400 m below the present level existed. The –600 m lake level resulted in three basins separated by interbasinal ridges.

Around 40,000 B.P., probably under the influence of a cool and humid climate in the region, the lake reached its present level. A subsequent fall of 150 m took place around 35,000 B.P., and extensive swampy zones existed in areas of the original lake above that level, such as Burton Bay, Cameron Bay and Mpulungu sub-basin and in littoral platforms in the Bujumbura and Kigoma sub-basins. The lake level continued to fall another 150 m until 22,000 B.P. and this low level persisted until 15,000 B.P. From 12,000 B.P. the lake started to rise as the climate became more humid. Around 9,500 B.P. the building of the Virunga volcanoes blocking the drainage of Lake Kivu to the Nile River system resulted in an overflow of the lake into Lake Tanganyika via the Ruzizi River. Several other East African lakes also had high lake levels between 10,000 and 8,000 B.P. (Butzer *et al.* 1972).

The introduction of Kivu water established an open system via the Lukuga River until 3,500 B.P., when cooler and drier climatic conditions closed the Ruzizi River, resulting in a lower lake level, 75 m below the present level and the closing of the Lukuga outlet.

Around 2,000 B.P. the lake was 20 m below the present level and from then to 1,400 B.P. the lake rose 14 m. From 1,400 B.P. the modern climate existed over the Kivu basin and Lake Kivu became an open system again, resulting in a rise of the level of Lake Tanganyika. Around 1,000 B.P. the level was 20 m below the present level.

OPEN/CLOSED BASIN

Lake Tanganyika was a closed basin from 35,000 to 9,500 B.P. and again from 3,500 to at least 1,400 B.P. and possibly to modern times, since in 1874 the mouth of the Lukuga River was blocked by alluvium and vegetation, as reported by Cameron.

4 Present status of Lake Tanganyika

INTRODUCTION

The present chapter will provide background information on the physical geography and climate of the catchment area of Lake Tanganyika, together with the main characteristics of the lake. A topographic map of the lake's catchment area with the major inflowing and outflowing rivers is given in Figure 4.1.

PHYSICAL GEOGRAPHY

The catchment area of Lake Tanganyika, defined as its hydrological watershed, is approximately 231,000 km^2 (exclusive of Lake Kivu) (Coulter & Spigel, 1991). It covers parts of Zaire, Burundi, Rwanda, Tanzania and Zambia, with only Rwanda not bordering the lake. The main part of the catchment area lies in Tanzania (Figure 4.1). Lake Tanganyika has a surface area (less islands) of 32,600 km^2 (Coulter & Spigel, 1991). The Zairian part of the lake is 14,000 km^2 (45% of the total surface) and the Tanzanian waters comprise 13,500 km^2 (41% of the total surface), The Burundian part is 2,600 km^2 (8%) and the Zambian portion 2,000 km^2 (VandenBossche & Bernacsek, 1990*a*). The lake's geographical boundaries are 3°20′–8°45′ S, 29°05′–31°15′ E and the altitude of the lake is 773 m above sea level. It is about 673 km long and its mean width is about 48 km. Maximum depth is 1470 m and mean depth 570 m (Coulter & Spigel, 1991). Shoreline length is 1,838 km (Hanek *et al.* 1993).

A geographical and geophysical description of Lake Tanganyika has been given by Capart (1952*a*). A more detailed description of the mountain ranges and geology of the region together with a comprehensive list of references is given in van Meel (1954). The geology of the Tanganyika Trough has been recently reviewed by Tiercelin & Mondeguer (1991).

General descriptions of the main ecological regions of the lake are provided by different members of the Belgian Mission to the lake in 1946–1947 (van Meel, 1952; Leloup, 1952*a*; and Poll, 1950) and of the main inflows by Marlier (1953, 1961). The main ecological regions of Lake Tanganyika are inflowing rivers, littoral region, benthic or sublittoral region and pelagic region (Beadle, 1981).

The main *inflowing* rivers are the Ruzizi River at the north end of the lake and the Malagarazi River, entering the lake through an extensive swampy delta, at the eastern shore (Figure 4.1). The Lukuga River at the western side of the lake is the only outlet of the lake. Fifty minor permanent rivers in the northern part of the lake in Burundi and Zaire were studied by Dubois (1958*b*). There are many short, seasonal torrents from the escarpments, especially on the west shore.

The *littoral* region is confined to a depth of about twenty metres and has a very great variety of habitats. The region is most disturbed by waves and winds, and rooted vegetation is only present in sheltered bays, small inlets and creeks. The most characteristic feature of the Lake Tanganyika littoral is the rocky shore. Long stretches of rocky shore are interspersed with long sandy or stony beaches. A field guide containing maps of the shoreline of the lake has been produced by the FAO/FINNIDA Project (Coenen, 1993). Based on the results of an aerial survey of Lake Tanganyika

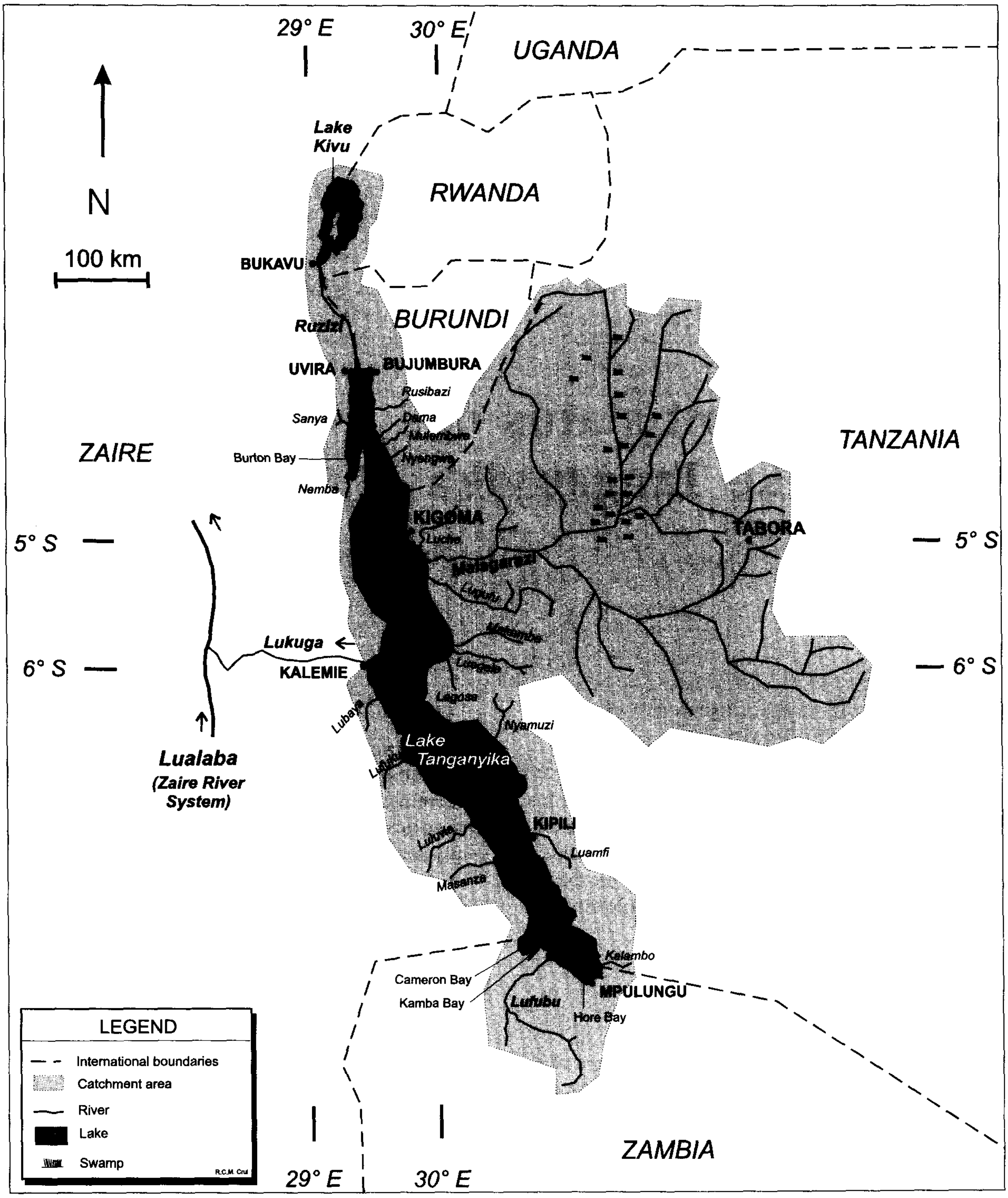


Figure 4.1 Topographic map of the catchment area of Lake Tanganyika

in 1992, the shoreline of the lake was classified (Coenen *et al.* 1993), and the main results are presented in Table 4.1

The *sublittoral* region is the area of the lake bed below 20 m depth. Its lower limit is determined by the total absence of oxygen which fluctuates seasonally (see Chapter 6). The surface of the bottom is composed of soft mud. Below 100 m depth and opposite the mouths of the larger rivers the mud is almost pure organic matter inhabited by invertebrates depending on organic detritus.

The *pelagic* zone comprises all the surface waters above the anoxic abyssal region. According to season and position in the lake this zone streches down to 100 to 200 m.

CLIMATE

General information on the climate of East Africa can be found in Griffiths (1972) and more detailed information on climatic conditions in the lake area in FAO (1984) and Balarin (1985). Meteorological data of stations around the lake are available at the national

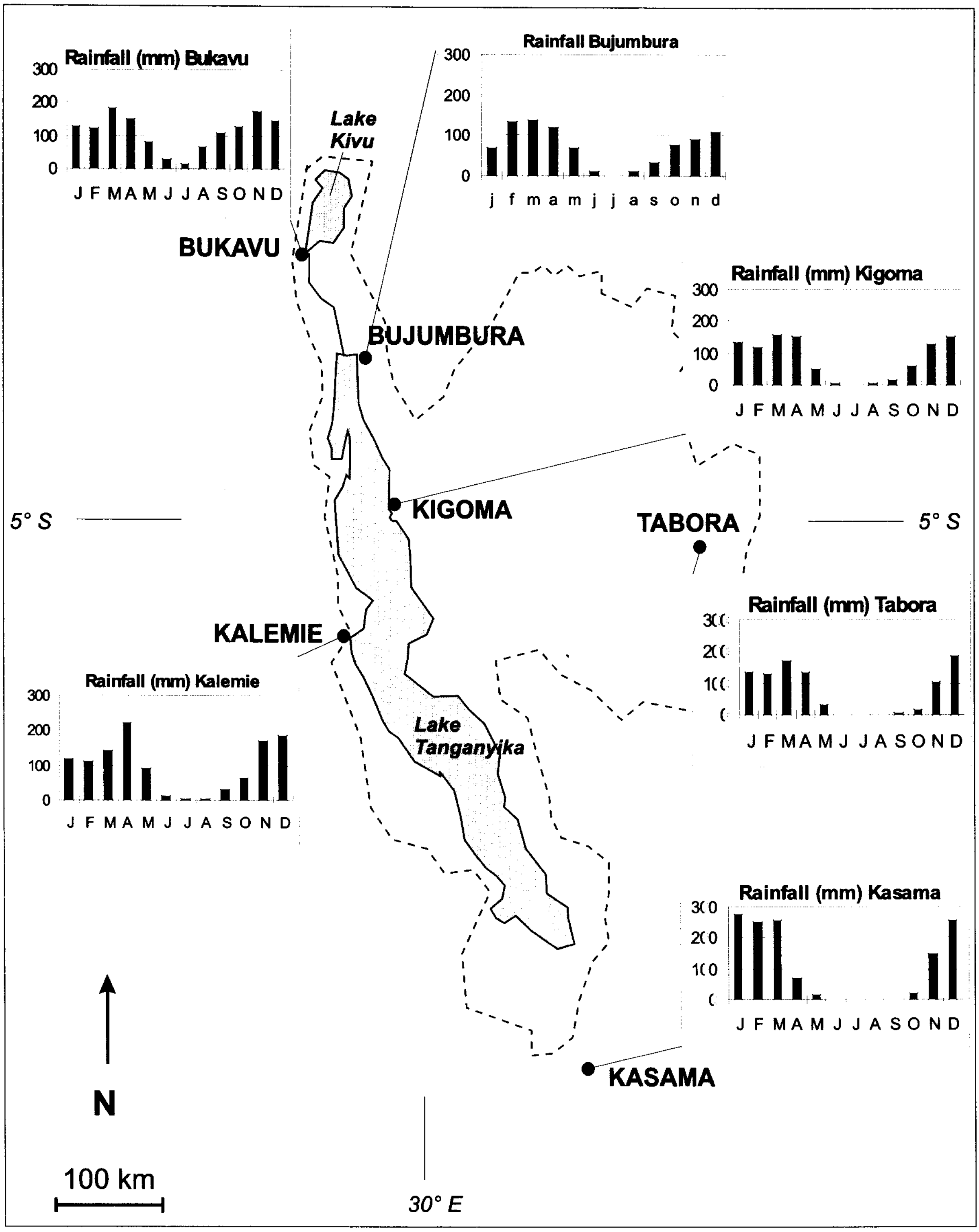


Figure 4.2 Seasonal rainfall regimes at six locations in the catchment area of Lake Tanganyika (data from FAO, 1984; Kasama outside catchment area of Lake Tanganyika)

meteorological institutes of the riparian countries. The catchment area of Lake Tanganyika lies entirely within the tropical zone. The year has two main seasons: a four-month dry season from May through August with a fairly constant southerly wind and a wet season during the rest of the year. Records from stations near the lake are used to describe the climatic conditions in the lake region.

In Table 4.2 the means of climatological elements are given for three lakeshore stations: Bujumbura (Burundi), Kigoma (Tanzania) and Kalemie (Zaire) (FAO, 1984). Records of stations in the lake's catchment area show that the conditions are not uniform and that climatic conditions vary according to topography (FAO, 1984). The main climatic elements – temperature, rainfall, wind and evaporation – are summarized below.

Table 4.2 Lake Tanganyika: means of several climatological parameters for three lakeshore stations. (Source: FAO, 1984; data are long-term (20–30 year) averages)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
a. BUJUMBURA (Burundi) [Alt. 783 m]													
rainfall (mm) - means per month/year	69	132	136	121	69	11	1	12	31	75	91	107	855
temperature (°C) - average	23.8	24.0	24.0	23.8	24.0	23.3	23.1	24.2	25.1	25.0	23.8	23.6	24.0
- means of max	28.3	28.5	28.5	28.1	28.6	28.5	28.7	30.0	30.7	30.1	28.3	28.0	28.9
- means of min	19.3	19.3	19.3	19.5	19.3	18.1	17.5	18.5	19.5	19.6	19.2	19.2	19.0
wind speed (in m.s-1 at 2 m level)	1.6	1.8	1.7	1.7	2.2	2.0	2.1	2.2	2.4	2.1	2.0	1.8	2.0
sunshine (%) (relative sunshine duration)	41	41	45	43	53	68	73	67	57	46	38	39	50
Tot.radiation (daily av.in cal.cm-1.day-1)	414	423	435	406	412	441	465	473	466	437	404	402	431
evapotransp. (mm) – (Penman method)	119	111	123	109	117	115	126	141	146	141	118	116	1482
b. KIGOMA (Tanzania) [Alt. 885 m]													
rainfall (mm) - means per month/year	134	118	155	151	51	6	2	3	15	61	130	151	977
temperature (°C) - average	23.2	23.5	23.5	23.5	23.7	23.0	22.7	23.7	24.7	24.6	23.2	22.9	23.5
- means of max	26.8	27.2	27.3	27.4	28.2	28.2	28.2	29.1	29.6	28.8	26.7	26.3	27.8
- means of min	19.6	19.7	19.6	19.6	19.3	17.8	17.2	18.4	19.8	20.4	19.7	19.4	19.2
wind speed (in m.s-1 at 2 m level)	1.6	1.6	1.6	1.7	1.9	1.9	2.0	2.2	2.3	2.7	2.5	1.9	2.0
sunshine (%) (relative sunshine duration)	45	45	56	64	76	77	70	77	80	87	71	54	66
Tot.radiation (daily av.in cal.cm-1.day-1)	459	453	471	453	439	412	402	467	534	602	559	494	478
evapotransp. (mm) – (Penman method)	138	117	134	126	117	102	109	130	155	195	182	154	1659
c. KALEMIE (Zaire) [Alt. 776 m]													
rainfall (mm) - means per month/year	117	109	144	223	91	10	3	4	32	64	168	184	1149
temperature (°C)- average	23.1	23.3	23.6	23.4	23.2	21.7	21.3	22.5	23.9	24.5	23.4	23.0	23.1
- means of max	28.0	28.4	28.2	27.8	27.9	27.3	27.0	27.9	29.1	29.7	28.0	27.4	28.1
- means of min	19.6	19.8	19.9	19.9	18.7	16.2	15.0	16.6	18.7	19.9	19.8	19.5	18.6
wind speed (in m.s-1 at 2 m level)	1.7	1.7	1.7	1.6	1.8	1.9	2.2	2.0	1.9	2.0	1.9	1.7	1.8
sunshine (%) (relative sunshine duration)	41	45	49	55	70	81	84	77	67	58	44	39	59
Tot.radiation (daily av. in cal.cm-1.day-1)	422	442	450	444	458	469	486	499	501	486	433	410	458
evapotransp. (mm) – (Penman method)	116	110	122	111	114	104	114	127	135	143	120	113	1429

Table 4.1 Lake Tanganyika: occurence (in %) of the four different types of shoreline substrate per country (Source: Coenen *et al.* 1993)

	Shoreline substrate			
Country	Rock	Sand	Rock/Sand	Marsh
Burundi	4	78	8	10
Tanzania	57	21	15	7
Zambia	57	20	21	2
Zaire	39	30	27	4
Total	43	31	21	5

Temperature

Lowest temperatures occur in the period June-July and highest temperatures in August–October (Table 4.2). Air temperatures are strongly influenced by the lake and maintained at a stable high level (Capart, 1952*a*).

Rainfall

The major tropical rains in the area are associated with an atmospheric belt of low pressure which follows the sun across the equator. Rain generally falls in heavy thunderstorms and most of it falls on the surrounding high escarpments. The amount of rainfall varies considerably with maxima in the rainy season in the period November–December and February–April, when northeastern monsoons bring heavy rains (Figure 4.2). During the 'dry' season (May–August) there is very little rainfall. Rainfall fluctuates considerably from year to year. The mean monthly rainfall at Bujumbura, Kigoma and Kalemie is given in Figure 4.3.

Wind

During the dry season (May–August) the southerly wind is the dominant feature creating dry and clear weather. It increases in strength in the period April-June, is strongest in July and August and ceases almost entirely in early September (Coulter & Spigel, 1991). The constant strong winds of this season blow more or less directly along the longitudinal axis, being channelled by the high escarpments on either side. Wind speeds occasionally reach 11 $m.s^{-1}$. Strong winds usually blow for several days interrupted by periods of reduced wind. The wind during the rainy season is mainly northerly. Wind velocities are generally much lower with long calm spells, although during thunderstorms velocities occur exceeding 25 $m.s^{-1}$ (Capart, 1952*a*). Diurnal on- and off-shore breezes (land- breeze at night and in the morning until 10 a.m. and lake-breeze in the afternoon until 5 p.m.) are prominent varying locally (Coulter & Spigel, 1991). In the southern end of the lake the offshore wind often reaches Beaufort Force 7 at night and the regular SE trade wind is frequently dominated by an offshore escarpment wind, locally named *kapata* (Coulter, 1963).

Evaporation

Seasonal variations in evaporation follow the variations in mean temperature and total radiation (Table 4.2). Lake evaporation has been estimated at 1350–1700 $mm.yr^{-1}$ (Coulter & Spigel, 1991).

PRESENT FEATURES OF LAKE TANGANYIKA

Modern geomorphology is described by Tiercelin & Mondeguer (1991). Lake Tanganyika occupies part of the western Rift Valley system and consists of two main basins, each with a number of sub-basins (see Tiercelin & Mondeguer, 1991, Fig. 3). A bathymetric map of the lake is given in Figure 4.4. Detailed maps of the northern and southern parts of the lake are given by Tiercelin & Mondeguer (1991) and a bottom profile along the north-south axis by Coulter & Spigel (1991).

General characteristics of the lake are presented in Table 4.3, together with hydrological and morphometric data. Physical and chemical parameters will be discussed in detail in the chapters that follow. Its greatest depth, the 'Alexandre Delcommune Deep' (1470 m) is located in the southern basin near the western shore (Figure 4.4). The maximum depth in the northern basin is 1310 m (The 'Baron Dhanis Deep'), also near the western shore (Figure 4.4).

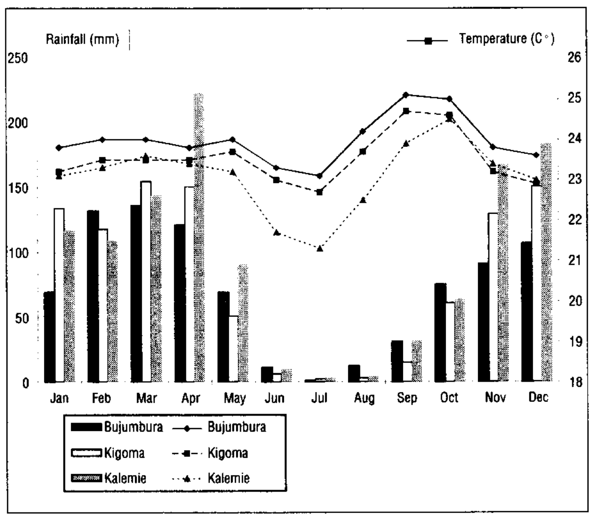


Figure 4.3 Mean monthly air temperature and rainfall at Bujumbura, Kigoma and Kalemie (data FAO, 1984)

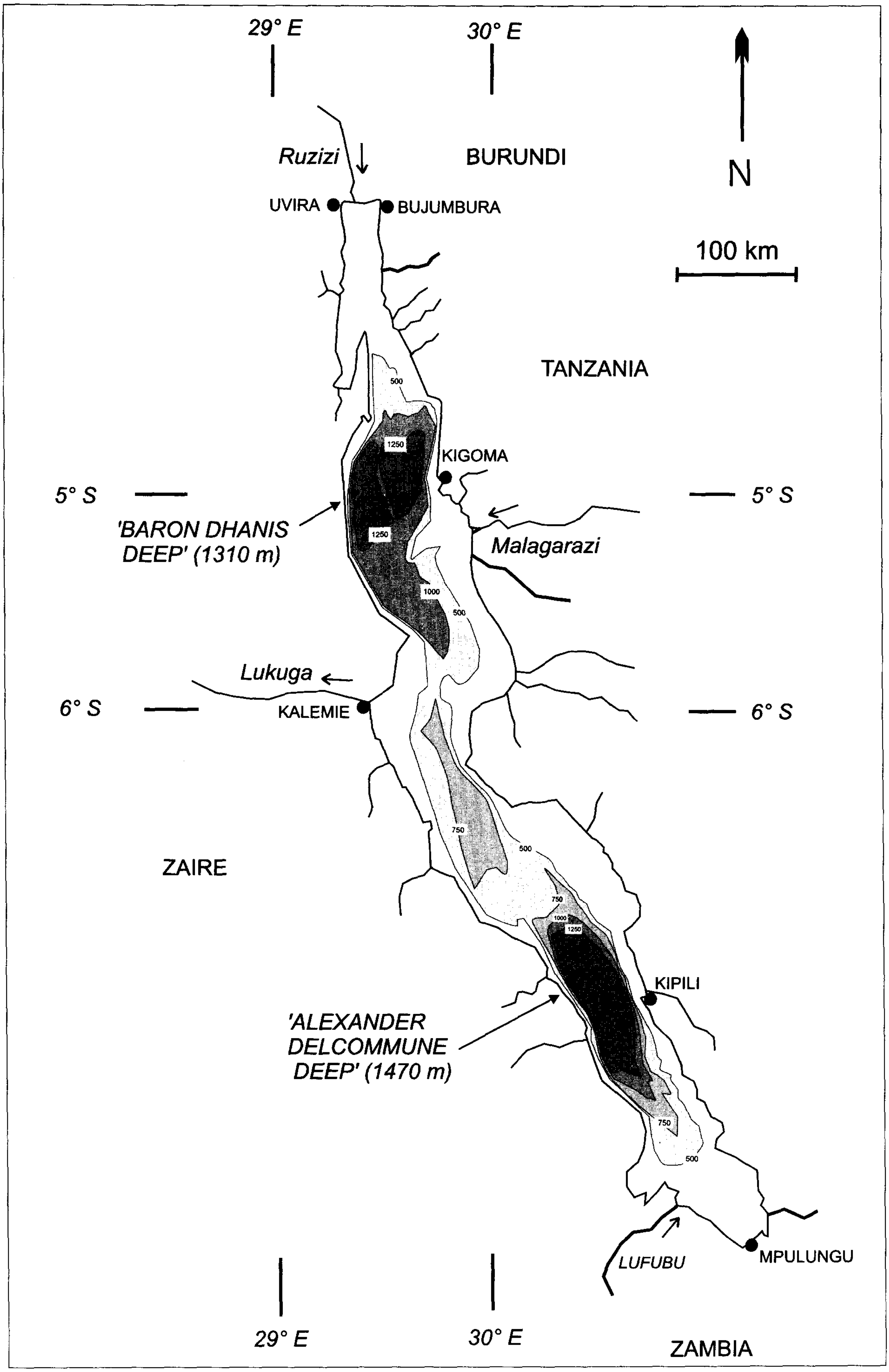


Figure 4.4 Bathymetric map of Lake Tanganyika

Table 4.3 General, hydrological, morphometric and physico-chemical characteristics of Lake Tanganyika (Source: Coulter & Spigel, 1991 (unless indicated))

a. General characteristics	
Latitude	3°20′ - 8°45′ S
Longitude	29°05 - 31°15′ E
Altitude	773 m (Beadle, 1981)
Catchment area	231,000 km^2 (exclusive of L. Kivu)
Major inflowing rivers	• Tanzania/Burundi: Malagarasi • Burundi: Ruzizi
Other inflowing rivers	• Burundi: Mpanda, Ntahangwa, Mugesa, Ruzibazi, Dama, Murembwe, Nyangwe • Tanzania: Lugufu, Luega, Kampisia, Ifume, Kalambo • Zambia: Lufubu • Zaire: Lunangwa, Lufuko, Lubaye, Lemba, (Welcomme, 1972)
Outflowing river	Lukuga River (Zaire)
b. Hydrological characteristics	
Inflow from streams (I)	14 $km^3.yr^{-1}$; 18.2 $km^3.yr^{-1}$ (Edmond *et al.* 1993)
Precipitation over lake (P)	29 $km^3.yr^{-1}$; 29 $km^3.yr^{-1}$ (Edmond *et al.* 1993)
Outflow (Lake Victoria) (O)	2.7 $km^3.yr^{-1}$; 4.2 $km^3.yr^{-1}$ (Edmond *et al.* 1993)
Evaporation	44 $km^3.yr^{-1}$; 43 $km^3.yr^{-1}$ (Edmond *et al.* 1993)
Flushing time (Volume/O)	7,000 yr (Hecky & Bugenyi, 1992)
Residence time (Vol/P+I)	440 yr (Hecky & Bugenyi, 1992)
c. Morphometric characteristics	
Type of basin	Tectonic (Hutchinson, 1957)
Surface area	32,600 km^2
Max. length	650 km (Beadle, 1981)
Mean width	50 km (Beadle, 1981)
Max. depth	1470 m
Mean depth	570 m
Volume	18,880 km^3
Shoreline	1,838 km (Hanek *et al.* 1993)
d. Physico-chemical data (See also Chapters 6 and 7)	
Surface temperature	23.75–27.5 °C
Hypolimnion temperature	23.25–23.50 °C
Conductivity (K_{20}) (surface)	610 $\mu S.m^{-1}$ (Craig, 1975)
offshore Uvira	703–765 $\mu S.cm^{-1}$ (Tshibangu, 1991)
Bay of Bujumbura	568–589 $\mu S.cm^{-1}$ (Caljon, 1992)
pH (surface) offshore Uvira	9–9.1 (Tshibangu, 1991)
(100 m) offshore Uvira	8.4–8.5 (Tshibangu, 1991)
Transparency (Secchi disk) – offshore	22 m (Capart, 1952*a*)
offshore outer Mwela	5–17.5 m (Coulter, 1968)
inshore Nera Mpulungu	3-12 m (Coulter, 1968)
offshore	8–18 m (Hecky & Fee, 1981)
off Uvira	11.3–15.3 m (Tshibangu, 1991)
Bay of Bujumbura	1.0–12.0 m (Caljon, 1992)
Depth of euphotic zone (m) (mean all stations in 1975)	28 m (Hecky & Fee, 1981)
Ionic composition	see Table 7.1

Section III

State of knowledge on limnology and hydrology of Lake Tanganyika

5 Water balance

INTRODUCTION

Information on the water balance of Lake Tanganyika is very scarce. Lake levels up to 1949 are given by Devroey (1949) and Edmond *et al.* (1993). More recent information is given by Kite (1981), Lema (1990) and Tiercelin & Mondeguer (1991). Data on the water budget given by Coulter & Spigel (1991) and Edmond *et al.* (1993) are rough estimates based mainly on the work of Gillman (1933).

HYDROLOGY OF LAKE TANGANYIKA

Lake Tanganyika forms a reservoir of 18,800 km^3 of fresh water (Coulter & Spigel, 1991). Due to its large volume and relatively small outflow, the lake has a flushing time of 7,000 years, which is long compared to Lakes Malawi (750 years) and Victoria (140 years) (Hecky & Bugenyi, 1992). Lake Tanganyika has only one outlet, the Lukuga River, halfway at the western shore. A rock sill at the mouth of the Kukuga River plays an important role in the hydrology of the lake, although the outflow only represents 6% of the total water input of the lake (Coulter & Spigel, 1991).

There are two main inflowing rivers, the Ruzizi River and the Malagarazi River, both entering the lake in the northern basin. A large number of smaller rivers also flow out into the lake, of which the Lufubu River in the south is the most important (Figure 4.1). Due to its large surface area the major factors affecting the water balance of Lake Tanganyika are precipitation on the water surface and evaporation from it.

LAKE LEVELS

Annual variations in rainfall have caused large fluctuations in lake levels. Information on lake levels goes back to 1846. The mean lake level increased from 777.6 m in 1846 to a maximum of 783.6 m in 1878, after which the lake overflowed (Devroey, 1949). The level then fell to 775 m in 1884 and reached a minimum of 772.5 m in 1894 and 1902 (Devroey, 1949).

In 1909 the systematic recording of the water level of Lake Tanganyika was started (Devroey, 1949). The lowest lake level, just below 773 m, was recorded in 1929, after which the level increased until 1939. From then the lake level dropped steadily, reaching a minimum in 1950 (Devroey, 1949). Water levels for the period 1909–1992 are given in Figure 5.1. In the early 1960s the lake level rose more than 2 m. In 1965 the lake reached its highest level since 1878 of 776.5 m. At that time the other East African Lakes Victoria, Mobutu Sese Seko and Malawi showed a similar rise in water level (Kite, 1981; Lema, 1990).

Besides these variations from year to year there is a seasonal fluctuation of about 80 cm following the rainfall pattern within the year. The seasonal low-water level is reached in October and the high-water level in the period April-June (Devroey, 1949).

WATER BALANCE

The main components of the water balance of Lake Tanganyika are rainfall over the lake, evaporation from the lake surface, inflows and outflow. A first estimate

Table 5.1 Estimates of annual water balance of Lake Tanganyika

Water balance components	Water balance (in mm over lake area)	Water balance (in $km^3.yr^{-1}$) (lake area: 32,600 km^2)	
		Coulter & Spigel	Edmond *et al.*
Rainfall over lake	900	29	29
Inflow	430	14	18.2
Evaporation	1350	44	43
Outflow	80	2.7	4.2

of the annual water balance of Lake Tanganyika is given by Coulter & Spigel (1991), based on Gillman (1933). Edmond *et al.* (1993) presented different data (given below) on the water balance based on the same work of Gillman (1933) and Degens *et al.* (1973).

The average inflow from the Ruzizi River was estimated as 3.2 $km^3.yr^{-1}$ based on the outflow from Lake Kivu at the dam at Bukavu (Zaire). The average inflows of the Malagarazi River and the other streams entering the lake were estimated at 6.9 and 8.1 $km^3.yr^{-1}$ respectively (Gillman, 1993). Total inflow was therefore estimated at 18.2 $km^3.yr^{-1}$. With an estimated precipitation and evaporation of 43 and 29 $km^3.yr^{-1}$ respectively, the outflow to the Lukuga averages 4.2 $km^3.yr^{-1}$, which is in agreement with observations (Edmond *et al.* 1993).

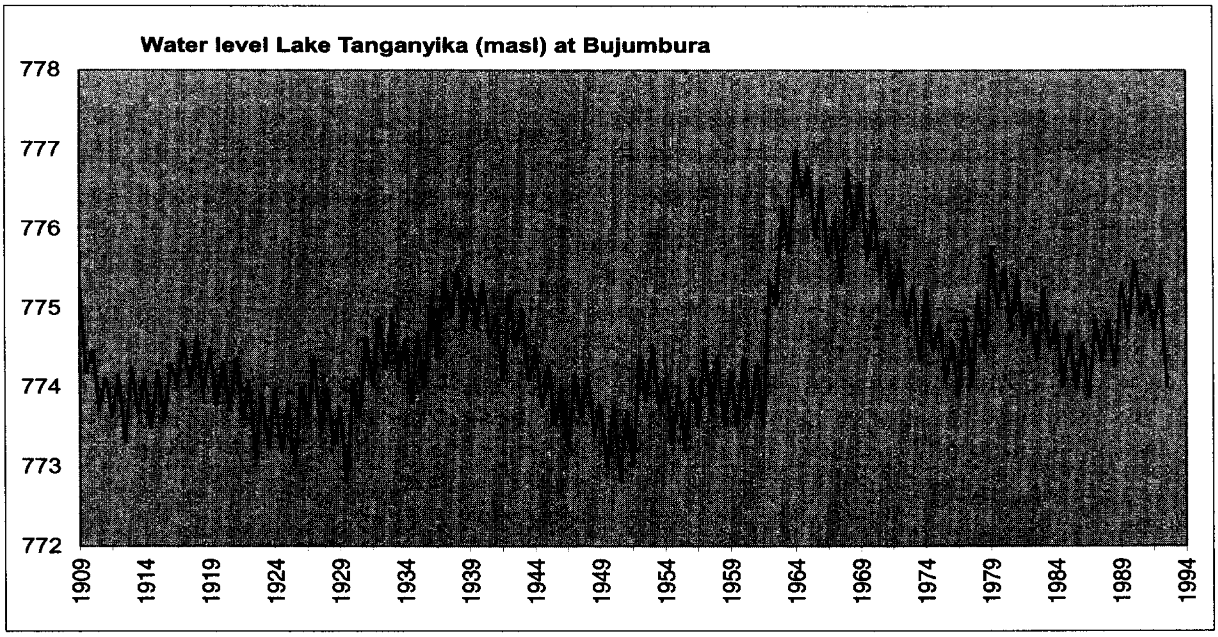


Figure 5.1 Lake levels between 1909 and 1992 (data from National Centre of Hydrometeorology, Bujumbura)

6 Hydrodynamics

INTRODUCTION

In this chapter a description of the lake's stratification cycle will be given on the basis of temperature distribution, water movements, mixing and oxygen distribution.

Climatic conditions in the lake region affecting the water balance and distribution of the water temperature in the lake are summarized in Chapter 4 together with the bathymetric features of Lake Tanganyika (Figure 4.4) and maps of the northern and southern parts of the lake (Figures 4.5 and 4.6). Data on the physical limnology of a tropical lake like Lake Tanganyika are limited compared with the information available on physical phenomena in temperate lakes such as the North American Great Lakes. Most of the limnological observations have been made in the vicinity of the three lakeshore ports of Bujumbura, Kigoma and Mpulungu, with occasional measurements near Kipili and Uvira. Research has been discontinuous in time and carried out in separate programmes by the four countries around the lake (Coulter & Spigel, 1991). The earliest information on the temperature distribution in the lake was provided by Cunnington (1920), who measured surface temperatures in 1904–1905 during the third Tanganyika Expedition. During the bathymetric survey of Stappers (1913*a*) in 1912–1913 the first deep-water temperatures were taken. In 1938 Beauchamp (1939) carried out temperature and dissolved oxygen measurements in the lake. The Belgian expedition 'L'exploration hydrobiologique du Lac Tanganika' in 1946–1947 resulted in a considerable increase in knowledge of the lake. A detailed bathymetric map became available (Capart, 1949) and temperatures were measured at the bottom with greater accuracy. The first temperature and dissolved oxygen depth-time series were measured by Dubois (1958*a*) at a station near Uvira in the period November 1955–February 1957. In 1959 regular temperature measurements and plankton observations were started at the south end station near Mpulungu by Coulter (Coulter, 1962) which continued in the 1960s. In May 1964 the first temperature transect to a depth of 150 m was made longitudinally along the lake by Coulter (1968). In 1970 Degens *et al.* (1971) made a two-month expedition which collected data on temperature, dissolved oxygen, water chemistry, sediments and geological structure.

In the 1970s limnological research, including temperature and dissolved oxygen observations, was carried out as part of two UNDP/FAO Fisheries Research projects in Tanzania and Burundi. In Tanzania the main research station was near Kigoma and in Burundi near Bujumbura. Occasional lakewide surveys were made with regularly spaced stations.

Appendix 2 (p. 65) provides an overview of papers with data on physics and related chemistry of Lake Tanganyika. The locations of the main sampling stations are shown in Figure 4.4.

TEMPERATURE DISTRIBUTION

Lake Tanganyika is permanently stratified and has exhibited stable behaviour over the period since 1939 for which systematic measurements are available (Edmond *et al.* 1993). The water mass does not become isothermal and a deeper, cooler water mass (hypolimnion) with an invariant temperature lies below an upper water mass which undergoes seasonal temperature change annually.

Stratification is characterized by the vertical temperature structure which ranges from 23.25 °C to about 27.25 °C (Coulter, 1988). Craig (1975) observed a small thermal discontinuity at 300 m depth. From there to the bottom the water temperature slowly decreased to a minimum of 23.25 °C at 900 m (Craig, 1975). The deep water layers below 300 m are permanently anoxic and contain free H_2S (Hecky *et al.* 1991). The lake can be classified as meromictic. The water column in the lake can be divided into three layers: an 'epilimnion' up to 50–80 m thick in the north basin and 150 m in the south basin, a 'metalimnion' to 200–300 m and a 'hypolimnion' below 300 m (Coulter & Spigel, 1991). The hypolimnion is equivalent to the monimolimnion and the upper water layers of epilimnion and metalimnion to mixolimnion in the terminology for meromixis by Hutchinson (1957).

The stratification cycle of Lake Tanganyika can be divided into three phases (Coulter & Spigel, 1991):

Phase 1 [Sept. to Nov.]

Warming phase – heating of the lake in September through November resulting in an increase of the surface temperature of 23.75–25 °C in August to 27.5 °C in December; almost the entire annual heat budget – estimated at 11,650 cal.cm^{-2} – is gained in this period.

Phase 2 [Dec. to April/May]

Phase of maximum stability – surface temperatures remain at the same level reached in December; internal wave oscillations are most prominent during this period.

Phase 3 [May to Sept.]

Cooling phase – cooling of the epilimnion with the onset of the dry season and the south winds resulting in a decrease of the surface temperature to 23.75–25 °C in August.

Loss of heat from the lake resulting in a decrease in surface temperature is mainly determined by wind-driven evaporative cooling. The saturation deficit (=100% humidity) is highest and minimum temperatures are lowest in the dry season (Beadle, 1981 – *Fig. 3.7*).

Differences in stratification pattern between the north and south basin of the lake are caused by different responses to the wind action over the lake. In the dry season upwelling of cooler water occurs in the south end of the lake which is dispersed towards the north. The thermocline in the southern part of the lake becomes diffuse and mixing extends to about 150 m depth. The thermocline is tilted downwards towards the north and persists in the north basin confining the vertical mixing there to 50–80 m depth (Coulter & Spigel, 1991).

Annual cycle of stratification in the northern part of the lake

In Figure 6.1*a* the annual variation in temperature at the surface and at 110 m depth at Uvira at the north end of the lake is depicted (data from Dubois, 1958*a*). The temperature difference between surface and 110 m deep water is least in August and vertical mixing occurs to a depth of approximately 80 m. A permanent thermocline fluctuated in depth from 25 m in October to 105 m in August (Dubois, 1958*a*). This permanent thermocline was confirmed by other observations near the north end (Bujumbura Station) in 1973 by Ferro & Coulter (1974) and Ferro (1975*a*) (see also Coulter & Spigel, 1991, Fig. 3.3). Further south in the north basin (Kigoma Station) a similar pattern was found to that of the north end of the lake, although the thermocline was generally weaker (van Well & Chapman, 1976).

Annual cycle of stratification in the southern part of the lake

Because of the upwelling in the south end of the lake in the dry windy season, vertical mixing occurs to a depth of 150 m (Coulter, 1968*a*). In Figure 6.1*b* the annual variation in temperature at the surface and at 110 m depth at the south end of the lake is given (Data from Coulter, 1968*a*, Fig. 6). The thermocline disappears at the surface at the south end of the lake in May–June and becomes weak throughout the south basin and the water column mixes freely to at least 150 m depth in August (Coulter, 1968*a*).

Mixing

Deep lakes like Lake Tanganyika show a tendency to mix deeply once a year. Mixing in lakes in Africa is mainly caused by loss of stability resulting from evaporative cooling of the upper water column, although influx of cool rainwater and reduced insolation can be also significant (Livingstone & Melack, 1984). During stratification mixing is confined to the upper water layers. Thickness of the upper mixed layer fluctuates strongly in tropical lakes (Talling, 1969; Lewis, 1973, 1983, 1984). During storms and windy weather the upper mixed layer will thicken, while calm and sunny periods will result in a thin mixed layer superimposed on the old mixed layer. In this way multi-layer stratification may occur. Variability of the thickness of the upper mixed layer will have great implications for the productivity and composition of phytoplankton. As stratification in the epilimnion does not break down completely in the northern part of the lake, the internal waves play a very important role in mixing epilimnion with metalimnion water and so returning nutrients from the deeper layers to the epilimnion.

At the south end nutrient regeneration from the deeper water layers occurs under strong wind stress by upwelling of cooler water (Coulter, 1963).

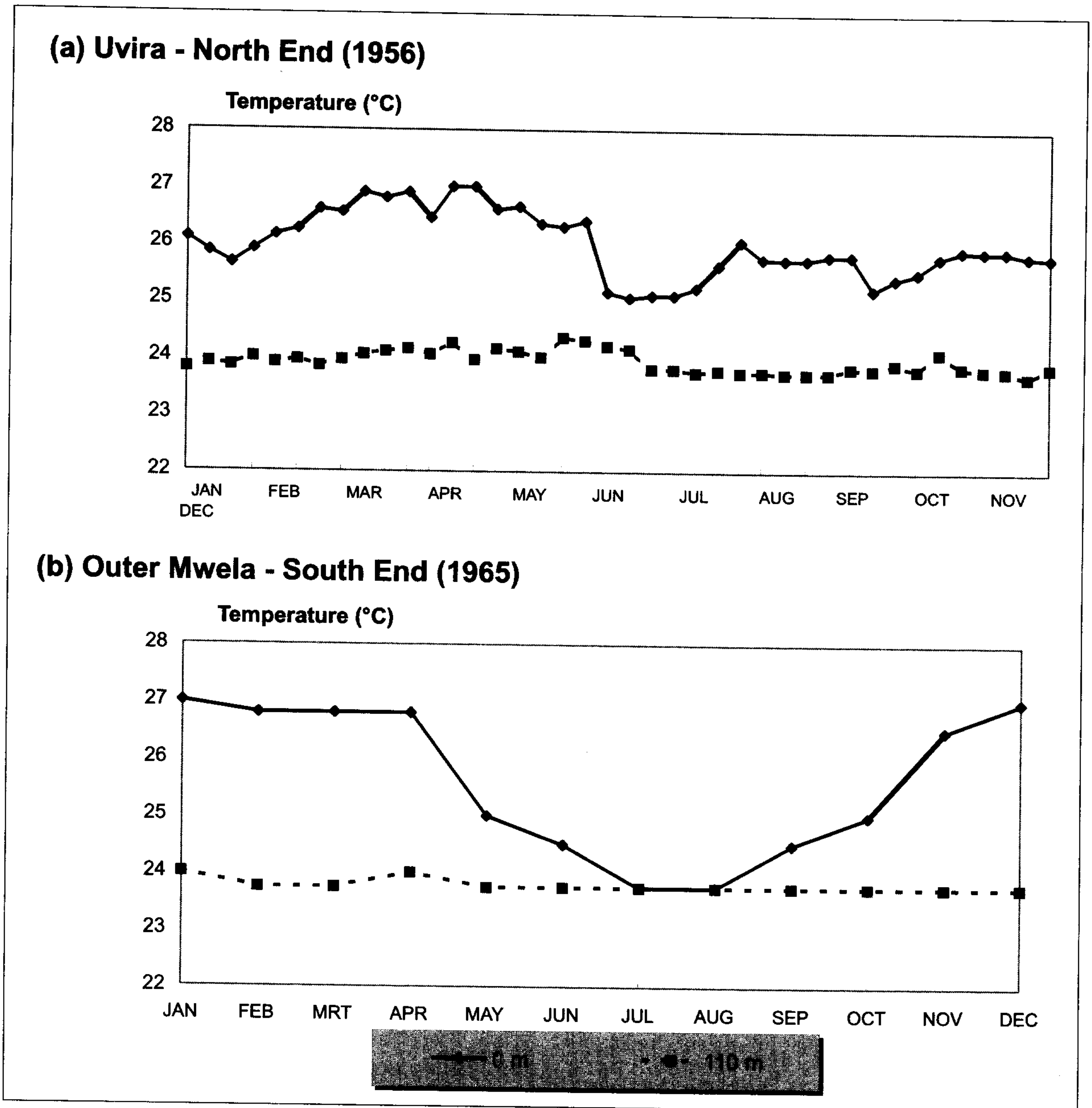


Figure 6.1 Annual variation in temperature at the surface of Lake Tanganyika and at 110 m depth at (a) Uvira (north end station) and (b) Outer Mwela (south end station)

Currents and water movements

Winds move water masses. Wind strength and direction determine the currents in the lake in addition to their effects on the vertical and horizontal temperature distribution.

The wind regime on Lake Tanganyika is dominated by south winds, especially in the dry season from May to September (see Chapter 4). Although the current systems of the lake have not extensively been studied, there appears to be a clockwise current (Coulter & Spigel, 1991). A generally north to south current along the east coast has been observed by van Well & Chapman (1976*b*) and Coulter (1968*a*) observed a westward swing of the Lufubu River at the south-western side of the lake, as it enters the lake. Nearshore currents may explain the absence of biogenic sediment on the bottom in shallow water as observed by Livingstone (1965). Profile-bound density currents may also play a role; these may occur due to nocturnal cooling causing water temperature differences at the lake margins of up to 3 °C (Capart, 1952*a*) and due to inflowing streams in the rainy season which may have water temperatures up to 6 °C lower than those in the lake (Coulter, 1968*b*).

Internal waves play an important role in the hydrodynamics and nutrient dynamics in Lake Tanganyika, as turbulence associated with these currents will result in mixing between epilimnion and the deeper water layers and in returning nutrients to the epilimnion. Internal waves were extensively studied in the 1960s and 1970s by Coulter (1963, 1968*a*, 1988). Temperature-depth observations in the lake revealed regular internal wave oscillations with fundamental modes of

25–30 days and amplitudes of 30–40 m (Coulter, 1988, Fig.3). The seiche appears to persist during the rainy season without major interruptions until the onset of the south wind in the following dry season (Coulter & Spigel, 1991). More detailed calculations on the internal waves in Lake Tanganyika can be found in Coulter & Spigel (1991).

DISSOLVED OXYGEN DISTRIBUTION

Surface water is generally well oxygenated throughout the year. Dissolved oxygen levels in the euphotic zone generally range between 7 and 9 $mgO_2.l^{-1}$ and occasionally are as high as 9.5 mg $O_2.l^{-1}$ in the surface layers (Dubois, 1958*a*; Coulter, 1963; Tshibangu, 1992). The distribution of dissolved oxygen in the water column is closely coupled with the stratification regime. Oscillations in the temperature profiles were also observed in the oxygen distribution in the water column (Coulter & Spigel, 1991). The different stratification patterns in the north and south basin in the lake are reflected in the dissolved oxygen distribution in the epilimnion. Throughout the year the depth limit of dissolved oxygen is less in the north than in the south (Degens *et al.* 1971; Hecky *et al.* 1978). At the north end of the lake the anoxic interface closely follows the thermocline fluctuations (Dubois, 1958*a*; Ferro & Coulter, 1974). Further south in the north basin (Kigoma Station) oxygen is found at 100 m far below the thermocline in the period August–December, when temperature gradients are weaker (van Well & Chapman, 1976*b*). In the south fluctuations in oxygen and temperature were also nearly parallel. However, oxygen is found well below the thermocline during stratification.

In the mixing period (June–August) low oxygen levels in the lower part of the water column between 80–120 m depth indicating upwelling of anoxic hypolimnion water alternate with relatively high oxygen levels up to 100 m depth indicating deep vertical mixing (Coulter, 1963).

HYPOLIMNION

The deep water profiles made by Capart (1952*a*) and Craig (1975) at the north basin station revealed a deeper, cooler water mass (hypolimnion) with an invariant temperature below an upper water mass which undergoes seasonal temperature change. Capart (1952*a*) found that temperatures varied between 23.43 °C and 23.48 °C at 200 m depth. He observed the lowest temperatures in the depth range between 500 and 800 m (23.25–23.28 °C) and somewhat higher temperature at depths below 1000 m. Thus the variation in water temperature below 200 m was approximately 0.25 °C. The causes of the temperature distribution in the hypolimnion were examined and an hypothesis on water circulation was formulated by Coulter (1968*b*). Craig (1975) found a slight temperature break at 300 m and regarded the water below it as the hypolimnion. They observed the lowest hypolimnion temperature at 900 m (23.25 °C). Kufferath (1952) observed fairly homogeneous distribution of the major ions and also a conductivity which varied only slightly within the hypolimnion. Therefore stratification seems to depend upon thermal gradients. Isotopes were used to estimate downward mixing in the water column as well as transfer rates between density layers (Craig, 1975). The very low tritium (hydrogen-3) concentrations in the hypolimnion indicate that the rate of mixing with the epilimnion is extremely slow in Lake Tanganyika. Craig (1975) observed high enrichment of the isotopes deuterium and oxygen-18 in deep water and suggested that the hypolimnion is a product of a colder drier climate.

7 Nutrient dynamics

INTRODUCTION

Light, temperature and nutrients may all limit algal productivity in aquatic ecosystems. As Lake Tanganyika is situated near the equator at 3–9 °S, temperature (23.5–27 °C) and solar radiation (400–560 cal.cm^2.dy^{-1}) are adequate for photosynthetic growth all year around.

Nutrients are generally considered to limit algal productivity, although the high temperature prevailing in the tropics allows rapid nutrient recycling. The elements required in largest amounts for plant production are carbon, phosphorus and nitrogen, while silicon is of importance to diatoms, being a major component of the cell wall. Nutrients most likely to be limiting in African lakes are nitrogen (Talling & Talling, 1965; Moss, 1969; Lehman & Branstrator, 1993) and phosphorus (Melack *et al.* 1982; Kalff, 1983). Furthermore silicon may limit diatoms growth. Sulphates may also play a role in limiting phytoplankton productivity, as suggested for Lake Victoria by Hecky (1993). It appears that in Lakes Tanganyika, Malawi and Victoria concentrations of many nutrients are low, and that no single nutrient is continuously dominant in controlling algal growth (Bootsma & Hecky, 1993). The hydrodynamics of the lake play a major role in the nutrient dynamics. One of the most important aspects is the permanent stratification of the lake. The lake is meromictic with only the upper water layers mixing every year in the period June-August and a deeper, cooler water mass below it. Because of this permanent stratification, mixing and internal seiches control the annual cycle of nutrient concentrations in the mixed layer of the lake. In this chapter, the ionic composition and its possible effects on the algal growth is summarized and a description given of the nutrient cycles and the main forces controlling them, as well as their nutrient sources.

IONIC COMPOSITION

Together with the other great lakes of the western Rift Valley, Lake Tanganyika belongs to the sodium-potassium-magnesium bicarbonate water type (low chloride subtype) (Kilham & Hecky, 1973). The lake and the inflowing Ruzizi River have a striking resemblance in water chemistry (Degens *et al.* 1971). The mineral-rich Rizizi River came into existence when the Virunga volcanoes blocked the Nile drainage of Lake Kivu and this lake overflowed to the south into Lake Tanganyika. Factors responsible for the relatively high ionic concentrations of the lake are the mineral-rich Ruzizi River and evaporative concentration within the lake. The water budget of Lake Tanganyika is dominated by direct rainfall on the lake and evaporation (see Chapter 5). The lake is deep and meromictic, only mixing down to a depth of 80–150 m in the period June-August (see Chapter 6). Data on ionic composition and/or nutrients concentrations have been provided by Craig (1975) and recently by Edmond *et al.* (1993) (Table 7.1).

Table 7.1 Chemistry of Lake Tanganyika at the surface and at 400 m depth (Craig 1975) (all concentrations in μM)

	Surface	400 m
Na	2700	2900
K	820	900
Ca	270	310
Mg	1650	1740
DIC	5880	6720
Cl	750	780
SO_4	37	–
SRSi	9.5	244
NO_3-N	0.3	0.0
NH^{4+}	–	–
PO_4-P (SRP)	0.15	5.73
Total P		–
Alkalinity ($meq.l^{-1}$)	6.52	6.91
Conductivity ($mS.cm^{-1}$)	610	–

DISTRIBUTION OF NUTRIENTS

Distribution of the main plant nutrients nitrate (NO_3-N), ammonia (NH_4-N), phosphate (PO_4-P) and silicon is governed by physical factors (upwelling, mixing and diffusion) and by biological processes such as algal photosynthesis. Information on the vertical distribution of inorganic nutrients has become available through the research of Beauchamp (1939), Kufferath (1952), Degens *et al.* (1971), Hecky and co-workers (Hecky *et al.* 1978; Hecky & Kling, 1981) and Craig and co-workers (Craig, 1975; Edmond *et al.* 1993). These studies clearly revealed that strong vertical gradients of nutrient concentrations are caused by the meromictic condition of the lake. Increasing plant nutrient concentrations are found with increasing depth. Concentrations of phosphate, nitrate, ammonia and silica are low in the epilimnion due to their uptake by photosynthetic organisms, but they increase in the metalimnion and hypolimnion. In the deep anoxic water layers of the hypolimnion ammonia is the dominant form of inorganic nitrogen (Hecky *et al.* 1991). Data on distribution of inorganic nutrients in the epilimnion are scant. Dissolved silicon concentrations ranged between 8 and 10 mM, phosphate between 0.05 and 0.16 mM and total fixed nitrogen between 'not detectable' and 0.31 mM in two profiles from Kigoma and Kipili in April 1975 (Edmond *et al.* 1993). Hecky & Kling (1981) observed higher dissolved nutrient concentrations in surface waters in the south than in the central and north of the lake during a transect in 1975.

The most prominent feature of vertical distibution of nutrients in the metalimnion is the minimum in dissolved fixed nitrogen between 160 and 200 m depth at the oxic-anoxic interface due to intense denitrification and other heterothrophic microbial processes (Hecky *et al.* 1991).

In the upper hypolimnion (or monimolimnion) between 200 and 700 m, nutrient concentrations are simular in both the north and south basin. They gradually increase with depth and concentrations of NH_4-N and PO_4-P are slightly higher in the north basin. At 700 m concentrations of N and P significantly increase, particularly in the north basin (Hecky *et al.* 1991).

NUTRIENT LOADING

Possible sources of nutrients for phytoplankton in Lake Tanganyika are atmospheric deposition, riverine inputs, *in situ* biological nitrogen fixation, recycling in the upper mixed layer and the nutrient-rich waters below the epilimnion. In the case of Lake Tanganyika the nutrient sources have not been studied, but internal loading should play a more important role than nutrient loading from external sources because of the lake's long residence time (440 year) and high nutrient concentrations in the deeper layers (Hecky *et al.* 1991).

An exception is nitrogen loading as the denitrification around the oxic-anoxic boundary acts as a sink for fixed nitrogen (Hecky *et al.* 1991; Edmond *et al.* 1993). The nitrogen balance of the mixolimnion will therefore totally depend on inputs from rain, rivers and *in situ* nitrogen fixation. Hecky *et al.* (1991) constructed putative nutrient budgets (dissolved inorganic nutrients only) for the mixolimnion and the whole lake. The monimolimnion is the most important source of phosphorus and silicon to the surface waters. It supplies 90% of the total annual input of inorganic phosphate and all the silicon. Biological nitrogen fixation dominates the nitrogen budget with a small additional input from rain.

8 The biotic environment

INTRODUCTION

The pelagic zone is by far the most important zone in the lake. Because of the steep slopes a depth of 100 m is found everywhere in the lake within 10 km of the shore. Information on the littoral and sub-littoral zone is mainly confined to taxonomic studies on collections (Coulter, 1991*d*) and taxonomic and ecological studies on fish (Poll, 1956; Coulter, 1991*c*; Kawanabe, 1992) and evolutionary studies on gastropods (Michel *et al.* 1992). Almost all other limnological studies are focused on the pelagic ecosystem.

THE PHYTOPLANKTON COMMUNITY

Phytoplankton studies

The phytoplankton of Lake Tanganyika has been studied floristically since 1904–1905 when the first phytoplankton collections were made. During the Belgian expedition 'L'exploration hydrobiologique du Lac Tanganika' in 1946–1947 new extensive collections were made (Van Meel, 1954). Phytoplankton blooms of *Anabaena* were observed by Beauchamp (1939) in 1938 near Kigoma, by Symoens (1956*a*) and Dubois (1958*a*) at the north end of the lake and at the south end in the early 1960s by Coulter (1962), but all these studies and observations were qualitative, as all collections were made with plankton nets (Hecky, 1991).

The first 'quantitative' phytoplankton observations were carried out in 1975 by Hecky and co-workers (Hecky *et al.* 1978; Hecky & Kling, 1981, 1987) who observed the seasonal cycle of phytoplankton and protozooplankton biomass at two stations from February through November 1975. Primary productivity measurements were carried out in April 1971 by Melack (1980) and in April-May and in September-October 1975 by Hecky & Fee (1981) both using the radiocarbon method. A first measurement of primary production of epilithic algae in the lake was carried out in 1986 near Uvira by Takamura (1988).

More recent research concerns the influence of pollution on water quality and phytoplankton composition of the lake by Caljon (1992) in the Bay of Bujumbura in 1986–1987 and limnological observations made by the Zairian-Japanese project near Uvira (Tshibangu, 1991).

Species composition

Coulter (1991*b*) compiled a checklist of 759 algae from various sources. Hecky & Kling (1987) selected and illustrated the 44 most prominent phytoplankters. The early net samples revealed a dominance of *Anabaena* and *Nitzschia* when phytoplankton was abundant and van Meel (1954) characterized the pelagic phytoplankton as an association of *Oocystis-Nitzschia-Anabaena-Anabaenopsis*. Hecky & Kling (1981) observed that these species were sometimes present in high densities, but quite sparse throughout much of the year. The quantitative sampling of Hecky & Kling (1981) revealed that nanoplankton shared dominance with *Anabaena* and *Nitzschia* at biomass maxima and that at all other times the nanoplankton dominated the biomass.

They found 21 species of Cyanophyta, 36 Chlorophyta, 13 Crysophyceae, 18 Diatomeae, 5 Cryptophyceae, 9 Peridineae, 1 Euglenophyta and 16 species of Protozoa (for complete species list see Hecky *et al.* 1978). The dominant groups in pelagic phytoplankton were Cyanophyta, Chlorophyta and Chrysophyceae. A special feature of the pelagic phytoplankton in Lake Tanganyika is the importance of Chrysophyceae. No other tropical lake has that many species, nor the biomass that the Crysophyceae achieve in Lake Tanganyika (Hecky, 1991). Cryptophyceans are always present, but of secondary importance. The distribution of nitrogen-fixing *Anabaena flos-aquae* may indicate the relative importance of biological nitrogen fixation which plays an important role in the nitrogen balance of the lake (Hecky *et al.* 1991).

Horizontal and vertical distribution

Spatial variability of the phytoplankton in Lake Tanganyika was already observed by earlier researchers (West, 1907; van Meel, 1954). In April/May and October/November 1975 phytoplankton studies in the lake by Hecky & Kling (1981) showed great differences in the horizontal distribution of the phytoplankton both in biomass and species composition, as not had also been observed in other large East African lakes (Talling, 1966, 1987; Hecky & Kling, 1987; Bootsma, 1993). In April/May 1975 at the end of the stratification period, the highest regional biomass was found near the Malagarazi River. In this region perideans made up a large portion of the biomass. In the other parts of the lake the biomass was consistently low, generally between 50 and 170 $mg.m^{-3}$, with somewhat higher biomasses in the north and the south of the lake. In October/ November 1975 after the mixing period higher biomasses, primarily of diatoms, occurred in the northern part of the lake, while in the southern part biomasses were low, consisting primarily of chlorophytes.

Differences in species composition was most conspicuous in the Cyanophyta: Chroococcus spp. were dominant in the northern waters and Anabaena flos-aquae fa. aptekariana in the southern waters. A single station near the Malagarazi river had abundant Glenodinium pulvisculus. Vertical distribution of net plankton was recorded by van Meel (1954) who found maximum concentrations in the upper 30–40 m. Hecky et al. (1978) observed rather uniform vertical distributions in the top 30 metres with somewhat higher concentrations in the upper 20 m.

Seasonal fluctuations

The seasonal cycle of phytoplankton can be divided into three periods which correspond quite well with the stratification cycle of the lake (Hecky & Kling, 1987). At the sampling station of Bujumbura, low biomass and stable species composition occurred from mid-February through April. Intermediate biomass with species replacements especially among the chrysophytes and diatoms was observed from May through mid-September. Highest biomass with large fluctuations of several species, especially Anabaena sp., occurred from mid-September through November (Hecky & Kling, 1981).

Each period had a characteristic phytoplankton community (Hecky & Kling, 1987):

- in March-April there was a dominance of small chlorophytes and cyanophytes (Chroococcus limneticus)
- in the mixing period May–September the first chrysophytes appeared followed by the diatoms Nitzschia and Stephanodiscus, while cyanophytes were extremely sparse;
- in the mid-September–November period the species composition was dynamic, with dominance of diatoms and chlorophytes, while all species except *Stephanodiscus* and *Chroococcus* had their annual maximum biomasses; a species of *Anabaena* showed the most dramatic increase and formed surface scums which are characteristic of the north end of the lake, as observed by Symoens (1956*a*) and Dubois (1958*a*).

Stratified conditions in the lake clearly favour cyanophytes and chlorophytes and mixing diatoms and chrysophytes.

Light regime

Its large volume and steep basin slopes make Lake Tanganyika quite transparent. Secchi disk readings up to 22 m were observed in the lake by Capart (1952*a*). Secchi disk measurements in 1964–1965 ranged between 5 and 17.5 at the offshore station Mwela and the observed fluctuations in transparency were associated with periodic changes in phytoplankton abundance, as turbidity is negligible offshore (Coulter, 1968*a*). Hecky & Kling (1981) observed reduced Secchi disk readings during higher plankton abundance, although they did not found such an effect on the vertical extinction of light. The mean depth of the euphotic zone was calculated to be 28 m based on all extinction measurements in the pelagic waters in 1975 (Hecky, 1991). Solar irradiance is relatively constant through the year and the vertical extinction appears to be nearly constant in space and time (Hecky, 1991).

The depth of mixing varies considerably with the annual cycle of stratification. During the stratification period the mean depth of mixing is 50 m ranging between 30 and 60 m due to internal wave fluctuations. During the mixing period the epilimnion in the lake may be isothermal to 100 m in the northern part and to 150 m in the southern part (Hecky *et al.* 1991). Therefore, despite the high transparency of Lake Tanganyika in all seasons the algal cells may circulate far below the euphotic zone and light may be insufficient for growth (Hecky, 1991).

Photosynthesis

In April 1971 the first direct *in-situ* measurements of photosynthetic productivity were carried out with the ^{14}C technique and the oxygen light- and dark-bottle method (Melack, 1980). A photosynthetic rate of 0.5 g $C.m^{-2}dy^{-1}$ was measured at an offshore station in the northern part of the lake and of 1.2 g $C.m^{-2}dy^{-1}$ at a nearshore station.

Phytoplankton photosynthesis measurements with the radiocarbon method were carried out by Hecky & Fee (1981) during the two surveys in April/May and October/November 1975. In April/ May the photosynthetic uptake was unmeasurable by the methods applied. In October/November, when conditions for algal growth were much better, the mean rate of primary production was 1.4 g $C.m^{-2}dy^{-1}$ for the euphotic zone with a mean chlorophyll concentration of 1.7 $mg.m^{-3}$. With a mean chlorophyll concentration in April/May of 0.7 $mg.m^{-3}$ and the assumption of a constant assimilation rate the mean rate of primary production for that period would be 0.6 g $C.m^{-2}dy^{-1}$. The mean annual rate was estimated at 0.8 g $C.m^{-2}dy^{-1}$ assuming two seasons of equal duration.

Hecky & Fee (1981) calculated a mean algal growth rate of 1.2 dy^{-1} for Lake Tanganyika which appeared to be very high compared to other tropical lakes. These growth rates could easily generate the high biomasses observed during blooms in October/November.

The observed seasonality in the lake's primary production is the result of changes in light availability and in nutrient supply to the epilimnion.

During the wet season, the period of stable stratification (September to May), nutrients are lost from the epilimnion and accumulate in the metalimnion. The thermocline will be a barrier to the upward diffusion of nutrients. Vertical diffusion and boundary mixing are the only physical processes responsible for the supply of nutrients to the epilimnion and both processes would only supply 20–30% of the demand for primary productivity. During the wet season nutrient regeneration in the epilimnion itself must play an important role to reduce losses of nutrients to sedimentation.

In the dry season vertical mixing plays a more prominent role in the whole lake and upward transport of nutrients is at least 3 to 10 times higher than in the wet season. Upwelling occurs only at the south end of the lake resulting in much higher nutrient supply rates than in the north during the dry season (Hecky *et al.* 1991).

The higher growth rates observed in October/ November are the result of higher nutrient concentrations due to the increased mixing and the improved light conditions after the restratification (Hecky, 1991). The most important cause of phytoplankton loss is probably grazing by zooplankton, as efficient grazing keeps algal biomass low, growth rates high, and assures that fixed carbon accumulates as fish biomass (Hecky, 1991).

ZOOPLANKTON

The zooplankton is the least studied component of the pelagic ecosystem. Research is confined to taxonomic work in the first half of this century and the studies done by the FAO fisheries projects and associated research.

Species composition

The pelagic zooplankton community consists of protozoans, crustaceans, coelenterates and fish larvae, and each of these groups have relatively few species. The zooplankton community is dominated in biomass and numbers by crustacean copepods.

Grouping by size results in:

- microzooplankton (10–50 mm): protozoans and nauplii
- mesozooplankton (0.5–5.0 mm): copepoda and decapoda
- macrozooplanktom (1–2 cm): coelenterates (with mean densities of 22 m^{-3} (Rufli & Chapman, 1976) and fish larvae (with densities less than 1 to 10 m^{-3}).

Special features of the pelagic zooplankton community of Lake Tanganyika are the prominence of protozoa, the presence of *Limnocnida tanganyicae,* endemic Atyidae, paucity of crustacean species and the absence of Cladocera (Hecky, 1991).

Because of the absence of Rotifera and Cladocera the small particle-feeding role must be fulfilled by Protozoa (Hecky, 1991). Protozooplankton was studied by Hecky & Kling (1981) in 1975. Sixteen species of Protozoans were found, of which the ciliate *Strombidium* cf. *viride* was the most important species (Hecky *et al.* 1978). Although 68 copepod species are known from the Tanganyika basin (Coulter, 1991*d*), the crustacean zooplankton in the pelagic zone consists of one calanoid copepod *Tropodiaptomus simplex* and two cyclopods *Mesocyclops aequatorialis* and *Tropocyclops tenellus*. Furthermore, some endemic decapods of the genus *Limnocaridina* may occur. *Limnocnida tanganyicae* medusae commonly occur near the water surface, when the water is calm and in the evening (Leloup, 1951) and there is some circumstantial evidence that they migrate vertically (Coulter, 1991*d*).

Seasonal fluctuations

There are only a few quantitative studies of abundance of zooplankton available. Hecky & Kling (1981) made observations on protozooplankton together with their phytoplankton studies in 1975, and this provided information on seasonal fluctuations in abundance at two stations Bujumbura and Kigoma respectively from February to November 1975 and March to October 1975. The ciliate *Strombidium* cf. *viride* was the dominant protozoan throughout the year and maximum densities occurred in the wet season. *Strombidium* always occurred with zoochlorellae in its cell in Tanganyika and Hecky & Kling (1981) considered them symbiotic. On the basis of several sets of zooplankton collections Burgis (1984) estimated a mean zooplankton biomass of 480 $mg.m^{-2}$ with a range between 32 and 1,245 $mg.m^{-2}$.

Horizontal distribution

Rufli & Chapman (1976) and Rufli (1976) sampled zooplankton quantitatively at respectively 17 and 15 stations at two partly overlapping transects. Crustacean abundances appeared to be quite variable in space and time (see Hecky, 1991, Table 5III): mean abundances in October 1975 were eight times higher than in April 1976 (3,387 versus 412.m^{-3}) and there were large differences between the sampling stations.

Vertical distribution

Vertical distribution of zooplankton was studied by Van Meel (1954). He observed vertical migration of the crustacean zooplankton towards the surface at night. Zooplankton was found throughout the water column to 200 m depth with a oxygen content of 0.16 mg.l^{-1}, but copepods concentrated in the upper 40 m in the daytime and especially the upper 20 m at night.

Van Meel (1954) observed at a station near Kigoma (sampled in the daytime) a distinct secondary maximum in the vertical distribution of zooplankton between 100 and 175 m with an oxygen content of 0.2 mg.l^{-1}. This aggregation might indicate migration to feed upon bacterial production near the oxic-anoxic layer or to avoid predators, as clupeids do not enter depths where the oxygen content is lower than 2 mg.l^{-1} (Hecky, 1991).

TROPHIC DYNAMICS

The lake has high annual fish yields which consist of two clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon*, and four species of centropomid predators *Lates stappersii*, *L. mariae*, *L. angustifrons* and *L. microlepis* (Coulter, 1991*b*; Roest, 1992).

Based on the primary production measurements carried out in the lake in 1975, Hecky & Fee (1981) concluded that the conversion of photosynthetic carbon to fish carbon must be extremely efficient. Fish yield-primary productivity equations (Melack, 1976; Oglesby, 1977) appeared to be inappropriate for Lake Tanganyika. Possible other sources of organic carbon like periphyton, macrophytes, allochthonous organic carbon and bacterial production were examined by Hecky & Fee (1981). The potential littoral production was estimated at approximately 15% of the phytoplankton production, annual river discharge appearing to be too small to increase the organic carbon by more than a few percent. Therefore, the only possible organic carbon source was bacterial production. The enormous reservoir of reduced substances in the hypolimnion could sustain a significant bacterial production. Van Meel (1954) already suggested that bacteria might play a major role in the trophic dynamics of the lake.

Hecky & Kling (1981) observed that bacteria were reasonably abundant in the lake. The mean estimated biomass of bacteria in the euphotic zone in October/November 1975 exceeded the phytoplankton biomass. The density of the bacteria ranged between 140,000.ml^{-1} and 1,400,000.ml^{-1} and the mean density was 760,000.ml^{-1}. Rudd (1980) estimated methane oxidation equivalent to 10% of the annual primary production, but other possible contributions of bacterial production (e.g. NH_3, H_2S, DOC) were not available.

Hecky *et al.* (1981) proposed two hypotheses to explain the high fish yields: other sources of organic production in the lake recycling fixed carbon for the hypolimnion and a highly efficient trophic structure.

The high trophic efficiency of the lake may be explained by the trophic structure. Lake Tanganyika's pelagic food web is of marine nature. The primary grazer is a calanoid copepod also common in productive marine systems. The primary planktivores are clupeids which are of marine origin and the piscivores are all Centropomidae, a predominantly marine family (Hecky, 1991). A trophic structure of Lake Tanganyika is given by Hecky (1984).

9 Sediments

BOTTOM STRUCTURE AND GENERAL COMPOSITION OF SEDIMENTS

Bottom sediments were first studied by Capart (1949) during 'L'exploration hydrobiologique du lac Tanganika' in 1946–1947 by echosounding and sediment dredging. The first coring in the lake was carried out by Livingstone (1965) and Degens *et al.* (1971). Recently the research on sedimentation in the lake was done by the PROBE and GEORIFT projects of which Tiercelin & Mondeguer (1991) summarize the main results. Multifold seismic profile studies by the PROBE project revealed 6000 m of fluviatile, marshy and lacustrine sediments (Scholz & Rosendahl, 1988).

Modern sediments of the lake have two main origins: allochthonous linked to the whole Tanganyika catchment and autochthonous linked to the lacustrine basin. In addition to these two main categories various depositional systems can be recognized in the onshore and offshore areas of the lake (Tiercelin & Mondeguer, 1991). Allochthonous sediments are mainly formed by clastic debris originating from weathering and erosion of geological formations in the catchment area which is mainly composed of granites, gneisses, micaschists, amphibolites and quartzites of Precambrian age and of lavas of the Ruzizi-Kivu troughs. Allochthonous-type sedimentation is represented by conglomerates, sands and silts. Autochthonous sediments are characterized by components from the lacustrine environment and include organic oozes, carbonite deposits and iron-rich sediments. These sediments are found in the deeper parts of the lake and are composed of homogeneous or laminated dark-green or black muds. Diatoms are the main component of the organic matter and other components present are: Cyanophyta (mainly *Anabaena*), chrysophyceans, cryptophytes and chlorophytes.

Preservation of this organic material can be explained by the anoxic conditions over most of the lake sediments of which a maximum area of 20% of the lake bottom is oxygenated during the period of mixing. Most of the oxygenated bottom is steep and composed of rock. A littoral substrate map of parts of the lake is provided by Cohen (1992).

PALEOLIMNOLOGY

Sediments accumulated in lake basins consist of various organic and inorganic substances providing information on the history of the lake, e.g. pollen, diatoms, and inorganic compounds. Paleolimnology is a multidisciplinary science using information preserved in sediments to reconstruct past environmental conditions in aquatic systems. Tremendous progress has been made in the development of paleolimnological techniques and approaches over the last decade. Advances include increased knowledge of indicator organisms, better use and combining of indicators and refinements in sampling techniques (Smol, 1992).

In Lake Tanganyika permanently anoxic conditions in the deep waters and a seasonal pattern in the primary production in the pelagic zone of the lake are very favourable to deposition and preservation of finely laminated mud. These layers contain detailed information on seasonal, annual and longer term climatic fluctuations. Studies on sediment cores provided information on diatom succession. Among the sediments deposited over the last 2,000 years in the lake *Nitzschia* is the most common species, while prior to this date *Stephanodiscus* and *Melosira* were the major fossil components (Degens *et al.* 1971). Evidence of regional climatic change and fluctuations in lake level are also apparent in the sediment records (Livingstone, 1965; Haberyan & Hecky, 1987). The surface of sandy lakeshore deposits observed in the high-resolution seismic profiles made in the lake indicated low water level stands (Scholz & Rosendahl, 1988).

References

ANCEY, C. F. 1894. Sur quelques espèces de mollusques et sur un genre nouveau du lac Tanganika. *Bulletin de la Société zoologique de France,* 19: 28–29.

——. 1898. Notes malacologiques: Descriptions d'espèces nouvelles du centre de l'Afrique. *Bulletin Muséum Marseille,* 1: 142.

——. 1906*a*. Réflexions sur la faune ichthyologique du lac Tanganika. *Bulletin scientifique de la France et de la Belgique,* 5(9): 229.

——. 1906*b*. Réflexions sur la faune malacologique de lac Tanganika et catalogue des mollusques de ce lac. *Bulletin scientifique de la France et de la Belgique,* 5(9).

ANDREAE, M. O. 1991. Biomass burning: Its history, use and distribution and its impact on environmental quality and global warming. *In*: *Global biomass burning: Atmospheric, climatic and biospheric implications*. Proceedings of the Chapman Conference, 12–23 March 1990, Williamsburg, VA, USA.

BAKER, J. M. 1992. Oil and African Great Lakes. pp. 71–78. *In*: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes,* Bujumbura 1989. SIL Mitteilungen No. 23.

BALARIN, J. D. 1985. *National Reviews for Aquaculture Development in Africa. 11. Tanzania.* FAO Fish. Circ. 770.11. 105 pp.

BASILEWSKY, P. 1951. Coleoptera Carabidae. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Institut Royal des Sciences Naturelles de Belgique,* 3(2): 13–19.

BAYLIS, H. A. 1927. Turbellaria from Lake Tanganyika. *Annals and Magazine of Natural History, London,* Series 9, 20: 380–385

——. 1928. Some parasitic worms mainly from fishes from Lake Tanganyika. *Annals and Magazine of Natural History, London,* Series 10, 1: 552–652.

BEADLE, L. C. 1974. *The inland waters of tropical Africa: an introduction to tropical limnology.* 365 pp. London: Longman.

——. 1981. *The inland waters of tropical Africa: an introduction to tropical limnology.* 2nd edition, 475 pp. London: Longman.

BEAUCHAMP, P. M. de. 1914. Sur quelques parasites provenant du Congo belge. *Revue de zoologie et de botanique africaines,* 4: 109–116.

BEAUCHAMP, R. S. A. 1939. Hydrology of Lake Tanganyika. *Int. Revue ges. Oceanogr.,* 10: 510–520.

——. 1940. Chemistry and hydrography of Lakes Tanganyika and Nyasa. *Nature, London,* 146: 253–256.

——. 1946. Lake Tanganyika. *Nature, London,* 157: 183–184.

——. 1953. Hydrological data from Lake Nyasa. *J. Ecol.,* 41: 226–239.

BEDDARD, F. E. 1906. Report on the Oligochaeta, Zoological results of the Third Tanganyika Expedition, 1904–1905. *Proceedings of the Zoological Society of London,* 1(15): 206–218.

BOOTSMA, H. A. 1993. Spatio-temporal variation of phytoplankton biomass in Lake Malawi, Central Africa. *Verh. Internat. Verein. Limnol.,* 25: 882–886.

BOOTSMA, H. A.; HECKY, R. E. 1993. Conservation of the African Great Lakes: A Limnological Perspective. *Conservation Biology,* 7(3): 644–656.

BORG, F. 1936. Über die Süsswasser-Bryosoen Afrikas. *Senckenbergiana,* 18: 20–36.

BOURGUIGNAT, J. R. B. 1890. Histoire malacologique du lac Tanganika. *Annales des sciences naturelles, Paris.* Zoologie Série 7, 10: 1–267.

BOUVIER, E. L. 1913. *Sur les Caractères, les Affinités et les Origines de la Faune atyienne du lac Tanganika.* 9th International congress of Zoology, Monaco, Section 4: 572–578.

BROOKS, J. L. 1950. Speciation in ancient lakes. *Quarterly Review of Biology,* Baltimore 25(2): 30–36, 131–176.

BURGIS, M. J. 1984. An estimate of zooplankton biomass for Lake Tanganyika. *Verh. Internat. Verein. Limnol.,* 22: 1199–1203.

——. 1986. Food chain efficiency in the open water of Lake Tanganyika. Bulletin des séances. *Académie r. des sciences d'outre mer,* 30(3): 283–284

BURTON, R. F. 1860. *The lake Region of Central Africa.* 2 vols. London: Longmans Green.

BUTZER, K. W.; ISAAC, G. L.; RICHARDSON, J. L.; WASHBOURN-KAMAU, C. 1972. Radiocarbon dating of East African lake levels. New observations provide fresh insights into late Quaternary paleoclimates. *Science,* 175: 1069–1076.

CALJON, A. G. 1992. Water quality in the Bay of Bujumbura. pp. 55–65. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura 1989.* SIL Mitteilungen No. 23.

CALMAN, W. T. 1899. On two species of Macrurous Crustaceans from Lake Tanganyika. *Proceedings of the Zoological Society of London,* 704–712.

——. 1906. Report on the Macrurous Crustacea. Zoological results of the Third Tanganyika Expedition, 1904–1905. *Proceedings of the Zoological Society of London,* 187–206.

——. 1910. The researches of Bouvier and Bordage on mutations in Crustacea of the Family Atyidae. *Quarterly Journal of Microscopical Science,* 55(4): 785–797.

——. 1928. On prawns of the family Atyidae from Tanganika. *Proceedings of the Zoological Society of London,* 49: 737–741.

CAMUS, C. 1965. Fluctuations du niveau du lac Tanganika. *Bulletin des séances. Académie roy. des sciences coloniales (d'outre mer).* Série 11: 1242–1256.

CAPART, A. 1949. Sondages et carte bathymétrique du lac Tanganika. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 2(2): 1–16.

——. 1952*a*. Le milieu géographique et géophysique. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 1: 3–27.

——. 1952*b*. Crustacés Décapodes Brachyures. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Institut Roy. des Sc. Nat. de Belgique,* 3(3): 41–67.

——. 1952*c*. Le lac Tanganika et sa faune. *Bulletin de la Société zoologique de France,* 77(4): 245–251.

COHEN, A. 1982. *Ecological and Paleoecological Aspects of the Rift Valley Lakes of East Africa.* Unpublished thesis, University of California at Berkeley. 314 p.

COHEN, A. S. 1987. Skeletal accumulations and the taphonomy of lacustrine coquinites: Evidence from modern lakes. The Geological Society of America, 40th Annual Abstract with Programs, p. 267.

——. 1988. Modern and late Holocene distribution of the endemic genus *Paramelania* in Lake Tanganyika: Implications of taphonomic complexity for the study of species flock evolution. American Malacological Union meeting. Charleston S.C., Abstract.

——. 1989*a*. The taphonomy of gastroped shell accumulations in large lakes: an example from Lake Tanganyika, Africa. *Paleobiology,* 15(1): 26–45

——. 1989*b*. Facies relationships and sedimentation in large rift lakes: examples from Lakes Turkana and Tanganyika. *Paleogeography, Paleoclimatology and Paleoecology,* 70: 65–80.

——. 1991. *Report on the first International Conference on the Conservation and Biodiversity of Lake Tanganyika, Bujumbura, Burundi, 11–13 March 1991. Compte rendu de la première conférence internationale sur la conservation et la biodiversité du lac Tanganika, Bujumbura, Burundi, 11–13 Mars 1991.* 128 pp.

——. 1992. Underwater natural reserves in Lake Tanganyika. pp. 109–116. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.). *Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura 1989.* SIL Mitteilungen No. 23.

COHEN, A. S.; BILLS, R.; COCQUYT, C. Z.; CALJON, A. G. 1993. The Impact of Sediment Pollution on Biodiversity in Lake Tanganyika. *Conserv. Biol.,* 7(3): 667–677.

COULTER, G. W. 1960. Preliminary research on Lake Tanganyika. pp. 4–6. In: *Joint Fisheries Research Organisation, Annual Report No. 9, 1959.* Government Printer, Lusaka.

——. 1962. Lake Tanganyika Research. pp. 7–30. *In: Joint Fisheries Research Organisation Annual Report No. 10, 1960.* Government Printer, Lusaka.

——. 1963. Hydrobiological changes in relation to biological production in southern Lake Tanganyika. *Limnol. Oceanogr.,* 8: 463–477.

——. 1964. Research on Lake Tanganyika. pp. 22–25. In: *Joint Fisheries Research Organisation Annual Report No. 11, 1962.* Government Printer, Lusaka.

——. 1966. *Hydrobiological processes and the deep-water fish community in Lake Tanganyika,* vols 1 and 2. Ph.D. Thesis. Queens University, Belfast.

——. 1967*a*. Hydrological processes in Lake Tanganyika. *Fisheries Research Bulletin,* Zambia, 4: 53–56.

——. 1967*b*. Low apparent oxygen requirements of deepwater fishes in Lake Tanganyika. *Nature,* London, 215: 317–318.

——. 1968*a*. Hydrological processes and primary production in Lake Tanganyika. Proc. 11th Confer. Great Lakes Res., *Int. Ass. Great Lakes Research,* 609–626.

——. 1968*b*. Thermal stratification in the deep hypolimnion of Lake Tanganyika. *Limnol. Oceanogr.,* 13(2): 385–387.

——. 1988. Seasonal hydrodynamics in Lake Tanganyika. *Verh. Internat. Verein. limnol.*, 23: 86–89.

——. (ed.) 1991*a*. *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press. 354 pp.

——. 1991*b*. Fisheries. pp. 139–150. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

——. 1991*c*. Benthic fish community. pp. 151–199. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

——. 1991d. Composition of the flora and fauna. pp. 200–274. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

——. 1991*e*. Zoogeography, affinities and evolution with special regard to the fish. pp. 275–305. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

COULTER, G. W.; SPIGEL, R. H. 1991. Hydrodynamics. pp. 49–75. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

COULTER, M. R.; COULTER, G.W. 1991. A comprehensive bibliography of Lake Tanganyika. pp. 306–336. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

CRAIG, H. 1975. Lake Tanganyika geochemical and hydrographic study: 1973 expedition. *Publ. Scripps Inst. of Oceanogr.*, Series 75–5: 1–83.

CROSSE, H. 1881*a*. Faune malacologique du lac Tanganika. *Journal de conchyliologie*, Paris 29: 105–272

——. 1881*b*. Supplément à la faune malacologique du lac Tanganika. *Journal de conchyliologie*, Paris 29: 277.

CRUL, R. C. M. 1992*a*. *Database on the inland fisheries resources of Africa (DIFRA). A description.* FAO/CIFA Occ. Pap. No. 17. Rome, FAO. 21p.

——. 1992*b*. *Models for estimating potential fish yields of African inland waters.* FAO/CIFA Occ. Pap. No. 16 Rome, FAO. 22p.

CUNNINGTON, W. A. 1906. Tanganyika or Tanganika. *Geographical Journal*, London 27: 411–412

CUNNINGTON, W. A. 1920. The fauna of the African lakes: A study in comparative limnology with special reference to Lake Tanganyika. *Proc. Zool. Soc.*, 3: 507–622.

DADAY, E. VON. 1910. Untersuchungen über die Süsswasser-Mikrofauna Deutsch-ost-Afrikas. *Zoologica*, Stuttgart 23: 1–314

DARTEVELLE, E.; SCHWETZ, J. 1946. Sur la faune malacologique du lac Tanganika. *Bulletin du Musée r. d'histoire naturelle de Belgique, Zoologie*, 76: 73.

——. 1947. Sur l'origine des mollusques thalassoïdes du lac Tanganika. Mémoires de l'Institut roy. colonial belge. Classe des sciences naturelles et médicales (8^{0}) 16(7): 1–58.

——. 1948. Contribution à l'étude de la faune malacologique des grands Lacs Africains II: le lac Tanganika. Mémoires de l'Institut roy. colonial belge. Classe des sciences naturelles et médicales. (8^{0}) 17: 4–118.

DAVIES, B. R.; Walker, K. F. 1986. *The Ecology of River Systems*. Monographiae Biologicae No. 60. Dordrecht, Junk Publ.

DEELSTRA, H. 1970. Le lac Tanganika: nouvelle source d'approvisionnement en eau potable de la ville de Bujumbura: la teneur en fluor. *Bulletin de la Société belge des études géographiques*, Bruxelles 39: 307.

——. 1972. Contribution à l'étude de la composition en acides gras des poissons du lac Tanganika. *Revue de l'Université de Burundi*, 1(2): 39–49.

——. 1974. Étude d'orientation des effets secondaires de l'utilisation des pesticides autour du lac Tanganika. *Bulletin Centre belge d'études et de documentation des eaux*, Liège 27(363): 93–96.

——. 1977*a*. Danger de pollution dans le lac Tanganika (Bassin de Bujumbura). *Bulletin de la Société belge des études géographiques*, Bruxelles 46(1): 23–35.

——. 1977*b*. Organochlorine insecticide levels in various fish species in Lake Tanganyika. *Medische Faculteit Landbouwwet, Rijksuniversiteit, Gent, Belgium* 42(2): 869–882.

——. 1983. Problèmes d'environnement dans les pays en voie de développement. Pollution chimique en Afrique. *Bulletin des séances, Academie roy. des sciences d'outre-mer. Mededelingen der Zittingen*, 29(2): 179–194.

DEGENS, E. T., VON HERZEN, R. P.; WONG, H.-K. 1971. Lake Tanganyika. Water Chemistry, Sediments, Geological Structure. *Naturwissenschaften*, 58(5): 229–241

DEMOULIN, G. 1956. Ephemeroptera. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Institut Royal des Sciences Naturelles de Belgique*, 3(7): 3–24.

DIGBY, L. 1902. On the structure and affinities of the Tanganyika gastropods *Chytra* and *Limmotrochus*. *Journal of the Linnean Society (Zoology)*, 28(185): 434–442.

DUBOIS, J. T. 1958*a*. Évolution de la température et de l'oxygène dissous et de la transparence dans la baie Nord du lac Tanganika. *Hydrobiologia*, 10: 215–240.

——. 1958*b*. Composition chimique des affluents du nord du lac Tanganika. *Bulletin des Séances Académie roy. des sciences coloniales (d'outre mer)*, Bruxelles, 4: 1226–1237.

EDMOND, J. 1975*a*. Report on a study of nutrient chemistry, Lake Tanganyika, March-April 1975. FAO FI:DP/BDI/70/508. Rome, FAO.

——. 1975*b*. Lake chemistry. pp 65–75. In: Craig, E. (ed.), *Lake Tanganyika geochemical and hydrographic study, 1973 expedition*. Publication of Scripps Institute of Oceanography, Series 75–5.

EDMOND, J. M.; STALLARD, R. F.; CRAIG, H.; CRAIG, V.; WEISS, R. F.; COULTER, G. W.. 1993. Nutrient chemistry of the water column of Lake Tanganyika. *Limnol. Oceanogr.*, 38(4): 725–738.

ESAKI, T.; CHINA, W. E.. 1927. A new family of aquatic Heteroptera. *Transactions of the Royal Entomological Society of London*, 2(2): 279–295.

EVANS, R. 1899. A description of two new species of *Spongilla* from Lake Tanganyika. *Quarterly Journal of Microscopical Science*, London, 41: 471–488.

FAO. 1977. *Recherches halieutiques sur le lac Tanganika, Burundi, Rapport terminal.* FAO FI:DP/BDI/73/020. Rome, FAO. 30 p.

FAO. 1984. *Agroclimatological Data for Africa, vol. 2. Countries south of the equator.* FAO Plant Production and Protection Series No. 22. Rome, FAO.

FERRO, W. 1974*a*. *Étude limnologique de la partie nord du lac Tanganika.* FAO FI:DP/BDI/73/020/7: 1–7.

——. 1974*b*. *Note on surface temperature measurements at Lake Tanganyika.* FAO FI:DP/BDI/73/020: 1–2.

——. 1974*c*. *Limnological note on the acoustic survey of November 1973 on Lake Tanganyika.* FAO FI:DP/BDI/73/020: 2–3.

——. 1975*a*. *Observations limnologiques dans le nord du lac Tanganika.* FAO Report FI:DP/BDI/73/020/7. 29 pp.

——. 1975*b*. *Some statistics from the Kitaza fishing centre.* FAO FI:DP/BDI/73/020: 1–7.

——. 1975*c*. *Data files limnology – Lake Tanganyika Northern Bay. Data collected 1972–1975.* FAO FI:DP/BDI/73/020: 1–5.

FERRO, W.; COULTER, G. W. 1974. *Limnological data from the north of Lake Tanganyika.* FAO Report FI:DP/BDI/73/020/10. 19 pp.

FREY, D. G. 1990. What is a lake? *Verh. Internat. Verein. limnol.*, 24: 1–5.

FUHRMANN, O.; BEAR, J. G. 1925. Report on the Cestoda. Zoological results of the Third Tanganyika Expedition (1904–1905). *Proceeding of the Zoological Society of London*, 1(6–7): 79–100.

GILLMANN, C. 1933. The hydrology of Lake Tanganyika. *Bull. Geol. Surv., Tanganyika Territory, Dar es Salaam*, 5: 1–25.

GIRAUD, V. 1885. Description du nouveau genre *Bourguignatia* du Tanganika. *Bulletin de la Sociéte Malacologique*, France 2: 193

GRAVIER, C. 1907. La méduse du Tanganika et du Victoria Nyanza; sa dispersion en Afrique. *Bulletin du Muséum d'histoire naturelle*, Paris, 13(3): 218–224.

GREENE, C.; JONES, E. N. 1970. Physical and chemical properties of Lake Tanganyika. Technical memorandum No. 2213-331-70. New London Laboratory Naval Underwater Systems Center. U.S.A. 17 p.

GRIFFITHS, J. F. 1972. Eastern Africa. pp. 313–348. In: J.F. Griffiths (ed.), *Climates of Africa. World Survey of Climatology*. Vol. 10.

GROVES, H. ; GROVES, J. 1907. Characeae. General report upon the botanical results of the third Tanganyika Expedition, (1904–1905). *Journal of the Linnean Society, (Botany)*, London, 38: 26–27.

GUERNE, J. DE. 1893. La méduse du lac Tanganika. *La Nature*, 21: 51–52

GÜNTHER, A. 1893. Descriptions of the reptiles and fishes collected by Mr. F. Coode-Hore on Lake Tanganyika. *Proceedings of the Zoological Society of London*: 628–632

GÜNTHER, R. T. 1864. On the reptiles and fishes obtained by Capt. Speke during the East African expedition. *Proceedings of the Zoological Society of London*: 115

——. 1893. Preliminary account of the freshwater medusa of Lake Tanganyika. *Annals and Magazine of Natural History*, London, Series 6 11: 269–275.

——. 1894. A futher contribution to the anatomy of *Limnocnida tanganyicae. Quarterly Journal of Microscopical Science*, 36: 271–293.

——. 1906. Présentation de *Limnocnida tanganyicae* du lac Tanganika. *Proceedings of the Zoological Society of London*, 1: 179–180.

GURNEY, R. 1928. Some Copepoda from Tanganyika collected by Mr. Pask. *Proceedings of the Zoological Society of London*, 22: 317–332.

HABERYAN, K. A. 1984. *Copepod fecal pellets and microfossil deposition in Lake Tanganyika.* M.Sc.Thesis, University of Georgia, Athens: 1–151.

——. 1985. The role of copepod fecal pellets in the deposition of diatoms in Lake Tanganyika. *Limnology and Oceanography* 30(5): 1010–1023.

HABERYAN, K. A.; HECKY, R. E. 1987. The late Pleistocene and Holocene stratigraphy and paleolimnology of the Lakes Kivu and Tanganyika. *Palaeogeogr. Palaeoclim. Palaeooecol.* 61: 169–197.

HALDEMANN, E. G. 1969. Geology. pp. 20–46. In: J. D. Clark (ed.), *Kalambo Fall Prehistoric Site.* Cambridge University Press.

HANEK, G.; COENEN, E. J.; KOTILAINEN, P. 1993. *Aerial Frame Survey of Lake Tanganyika Fisheries.* FAO/FINNIDA research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/09 (En): 34 p.

HARDING, J. P. 1957. Crusacea: Cladocera. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 3(6): 53–89.

HECKY, R. E. 1984. African lakes and their trophic efficiencies: a temporal perspective. pp. 405–448. In: D.G. Meyers and J.R. Strickler, *Trophic Interactions within Aquatic Ecosystems.* 1981 AAAS Symposium 85. Westview Press, Boulder (USA).

——. 1991. The pelagic ecosystem. pp. 90–110. In: G. Coulter (ed.), *Lake Tanganyika and its life.* British Museum (Natural History) and Oxford Univ. Press.

HECKY, R. E.; BUGENYI, F. W. B. 1992. Hydrology and chemistry of the African Great Lakes and water quality issues: Problems and solutions. pp. 45–54. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium* *on Resource Use and Conservation of the African Great Lakes, Bujumbura 1989*. SIL Mitteilungen No. 23.

HECKY, R. E.; DEGENS, E. T. 1973. *Late Pleistocene-Holocene chemical stratigraphy and paleolimnology in the Rift Valley Lakes of Central Africa*. Technical Report, Woods Hole Oceanographic Institution 1-73-28: 1–144.

HECKY, R. E.; FEE, E. J. 1981. Primary production and rates of algal growth in Lake Tanganyika. *Limnol. Oceanogr.*, 26: 532–547.

HECKY, R. E.; FEE, E. J.; KLING, H. J.; RUDD, J. W.. 1978. *Studies on the planktonic ecology of Lake Tanganyika*. Can. Dep. of Fish and Environment. Fisheries and Marine Service Techn. Pap. 816: 1–51.

——.; ——.; ——.; ——. 1981. Relationship between primary production and fish production in Lake Tanganyika. *Trans. Am. Fish. Soc.*, 110: 336–345.

HECKY, R. E.; KLING, H.J. 1981. Phytoplankton ecology and zooplankton of the euphotic zone of Lake Tanganyika: species composition, biomass, chlorophyll content, and spatio-temporal distribution. *Limnol. Oceanogr.*, 26: 548–564.

——.; ——. 1987. Phytoplankton ecology of the great lakes in the rift valleys of Central Africa. *Arch. Hydrobiol. Beih.*, 25: 197–228.

HECKY, R. E.; SPIGEL, R. H.; COULTER, G. W. 1991. The nutrient regime. pp. 76–89. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

HEINRICHS, G. 1936. Les fluctuations du niveau du lac Tanganika. *Bull. Inst. roy. Col. Belge*, 7: 366–385.

HETT, M. L. 1924. Report on the Linguatulidae. Zoological Results of the 3rd Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London* 11: 161.

HORE, E. C. 1892. *Tanganyika: Eleven years in Central Africa*. London, Clarke.

HORNE, A. J.,GOLDMAN, C. R. 1994. *Limnology*. 2nd. ed. McGraw-Hill, Inc. New York. 576 pp.

HUTCHINSON, G. E. 1930. On the chemical ecology of Lake Tanganyika. *Science*, 71(1850): 616.

——. 1957. *A Treatise on Limnology*. Vol. 1: Geography, Physics and Chemistry. Wiley, New York. 1015 pp.

——. 1967. *A Treatise on Limnology*. Vol. 2: Introduction to Lake Biology and Limnoplankton. Wiley, New York. 1115 pp.

——. 1973. Eutrophication. The scientific background of a contemporary practical problem. *Amer. Sci.*, 61: 269–279.

——. 1975. *A Treatise on Limnology*. Vol. 3: Limnological Botany. Wiley, New York. 660 pp.

——. 1993. *A Treatise on Limnology*. Vol. 4: The Zoobenthos. Wiley, New York. 944 pp.

HYNES, H. B. N. 1972. *The Ecology of Running Waters*. Liverpool University Press, Liverpool. 555 pp.

IAC 1990. Report on the International Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura, Burundi, November 29–December 2, 1989. Fisheries and Aquaculture Unit, IAC Wageningen, The Netherlands. Occasional Paper No. 2. 71 pp.

JAFFE, G. 1916. Zwei Schwämme aus dem Tanganjikasee. *Zoologischer Anzeiger*, 48: 5–14.

JOHNSON, T. C.; KITAKA, G.; ODADA, E. 1993. The International Decade for the East African Lakes. The IDEAL Symposium on the Limnology, Climatology and Paleoclimatology of the East African Lakes. Jinja, Uganda, 18–23 February 1993. Program with Abstracts. 30 pp.

JOHNSON, T. C.; TALBOT, M. R.; KELTS, K.; COHEN, A. S.; LEHMAN, J. T.; LIVINGSTONE, D. A.; ODADA, E. O.; TAMBALA, A. F.; MCGILL, J.; ARQUIT, A.; TIERCELIN, J.-J. 1990. An International Decade for the East African Lakes. Workshop Report 1 on the Paleoclimatology of African Rift lakes, Bern, Switzerland, March 29–31 1990. Duke University Marine Lab. Technical Paper. Duke University, Beaufort (USA). 37 pp.

JFRO. 1960. *Joint Fisheries Research Organization. Annual Report No. 9, 1959*. Government Printer, Lusaka.

KALFF, J. 1983. Phosphorus limitation in some tropical African lakes. *Hydrobiologia*, 100: 101–112.

KAWANABE, H.; KWETUENDA, M. K.; GASHAGASA, M. M. 1992. Ecological and limnological studies of Lake Tanganyika and its adjacent regions between African and Japanese scientists: An introduction. pp. 79–83. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes*, Bujumbura 1989. SIL Mitteilungen No. 23.

KIEFER, F. 1956. Ruderfüsskrebse aus dem Tanganjika-See (Crustacea: Copepoda). *Revue de zoologie et de botanique africaines*, 54(3–4): 241–266.

——. 1957*a*. Ein neuer Cyclopide (Crustacea: Copepoda) aus dem Tanganjika-See. *Zoologische Anzeiger*, Leipzig, 160(1–2): 28–31.

——. 1957*b*. Ein seltener Cyclopide (Crustacea: Copepoda) aus dem Tanganjika-See. *Revue de zoologie et de botanique africaines*, 56(1–2): 4–8.

KILHAM, P. 1990. Mechanisms controlling the chemical composition of lakes and rivers: Data from Africa. *Limnol. Oceanogr.*, 35: 80–83.

KILHAM, P.; HECKY, R. E. 1973. Fluoride: geochemical and ecological significance in East African waters and sediments. *Limnol. Oceanogr.*, 18: 932–945.

KILHAM, S. S.; KILHAM, P. 1990. Tropical limnology: Do African lakes violate the 'first law' of limnology? *Verh. Internat. Verein. Limnol.*, 24: 111–120.

KIRKPATRICK, R. 1906. Report on the Porifera, with notes on species from the Nile and Zambesi. Zoological Results of the Third Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London*, 1: 218–227.

KISS, R. 1959*a*. Quelques ostracodes nouveaux et intéressants de la région de l'extrémité nord du lac Tanganika. *Revue de zoologie et de botanique africaines*, 59(1–2): 81–105.

——. 1959*b*. Ostracodes de l'Afrique tropicale. *Revue de zoologie et de botanique africaines*, 60(1–2): 1–16

——. 1960*a*. Technique nouvelle pour la pêche quantitative du zooplancton des Lacs Tanganika et Kivu. *Folia Scientifica Africae centralis*, 6(2–4): 19

——. 1960*b*. Entomostracés de la plaine de la Rusizi. 1. Entomostracés de la région d'Usumbura (Burundi). Mémoire des séances. *Académie roy. des sciences d'Outre mer. Classe des sciences naturelles et médicales Bruxelles*, 11(5): 1–49.

——. 1961. Un nouvel Ostracode du lac Tanganika *Tanganyikacypris matthesi*. *Bulletin de l'Institut francaise d'Afrique Noire*, Série A, 23(1): 18–24.

KITE, G. W. 1981. Recent changes in level of Lake Victoria. *Hydrol. Sci. Bull.*, 26(3): 233–243.

KUFFERATH, J. 1952. Le mileu biochimique. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 1: 31–47.

——. 1956. Organismes trouvés dans les carottes de sondages et les vases prélevées au fond du lac Tanganika. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 4(3): 1–74.

LAWALRÉE, A. 1955. Compositae, Leeaceae, Lemnaceae et Vitaceae. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 4(2): 53–82.

LEHMAN, J. T.; BRANSTRATOR, D. K. 1993. Effects of nutrients and grazing on phytoplankton of Lake Victoria. *Verh. Internat. Verein. Limnol.*, 25: 850–855.

LELOUP, E. 1949*a*. Relevé des stations. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 2(1): 1–119.

——. 1949*b*. Une mission hydrobiologique belge au lac Tanganika, (1946–1947). *Les naturalistes belges*, 30(1): 2–9 and 30(2): 22–27.

—— 1950*a*. Lamellibranches. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 3(1): 1–153.

——. 1950*b*. Relation entre la consistance du fond et de la forme des coquilles chez les lamellibranches du lac Tanganika. *Journal de Conchyliologie*, Paris 90(1).

——. 1951. Méduses. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 3(2): 27–43.

—— 1952*a*. Les invertébrés. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 1: 71–100.

——. 1952*b*. Avant-propos. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 1: 3–6

——. 1953. Gastéropodes. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 3(4): 1–272.

LEMA, A. J. 1990. East African climate: 1880–1980. *Water Resources Development*, 6: 270–277.

LESTAGE, J. A. 1917. Mission Stappers au Tanganyika-Moero. Deuxième contribution à l'étude des larves des Ephémères et Perlides (Pseudo-Névroptères) du Congo Belge. *Revue de zoologie et de botanique africaines*, 5: 121–140.

LEWIS, W. M. 1973. The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. *Limnol. Oceanogr.*, 18: 200-217.

——. 1983. Temperature, heat, and mixing in Lake Valencia. *Limnol. Oceanogr.*, 28: 273-286.

——. 1984. A five-year record of the thermal and mixing properties for a tropical lake (Lake Valencia, Venezuela). *Arch. Hydrobiol.*, 99: 340-346.

——. 1987. Tropical limnology. *Ann. Rev. Ecol. Syst.*, 18: 159–184.

LIKENS, G. E. (ed.). 1972. Nutrients and eutrophication: The Limiting-Nutrients Controversy. Special Symposium, *Amer. Soc. Limnol. Oceanogr.*, 1, 328 pp.

LINDBERG, K. 1951. Cyclopides (Crustacés: Copépodes). Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 3(2): 47–91.

LINDQVIST, O. V.; MIKKOLA, H. 1989. Lake Tanganyika: review of limnology, fisheries, stock assessment, biology of fishes and fisheries. FAO Report, CGP/RAF/229/FIN. 51 pp.

LIVINGSTONE, D. 1965. Sedimentation and the history of water level change in Lake Tanganyika. *Limnol. Oceanogr.,*, 10(4): 607–610.

——. 1975. Late Quaternary climate change in Africa. *Ann. Rev. Ecol. Syst.*, 6: 249–280.

LIVINGSTONE, D.; MELACK, J. M. 1984. Some lakes of subsaharan Africa. pp. 467–497. In: F. B. Taub (ed.), *Lakes and Reservoirs Ecosystems of the World*. Elsevier Publ., Amsterdam.

LOEHNERT, E. P. 1975. Some observations on water composition and groundwater potential in the Lake Tanganyika and Kivu basins. Economic Commission for Africa, Addis Ababa, May 1975: 1–12.

LOWE-MCCONNELL, R. H. 1991. Lake Tanganyika's unique fish fauna: its international importance for evolutionary studies and the special opportunities it offers for biological research. pp. 72–75. In: A. S. Cohen (ed.), 1991. *Report on the first International Conference on the Conservation and Biodiversity of Lake Tanganyika*, Bujumbura, Burundi, 11–13 March 1991.

——. 1993. Fish Faunas of the African Great Lakes: Origins, Diversity and Vulnerability. *Conservation Biology*, 7(3): 634–643.

LOWE-MCCONNELL, R. H.; CRUL, R.C.M.; ROEST, F. C. (eds.). 1992. *Symposium on resource use and conservation of the African Great Lakes*, Bujumbura 1989. SIL Mitteilungen No. 23. 128 pp. With 46 figures and 18 tables in the text.

MARLIER, G. 1953. Étude biogéographique du Bassin de la Ruzizi, basée sur la distribution des poissons. *Ann. Soc. Roy. Zool. de Belgique*, 84(1): 175–224.

——. 1961. Recherches hydrobiologiques dans les rivières du Congo Oriental. I. La conductivité électrique. II. Études écologiques. *Hydrobiologia,* 3: 225–264.

Martens, E. von. 1883. Über eine von Dr. Böhm im Tanganjika-See gefundene Qualle. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin: 97.

Matthiessen, P. 1977. *A visit to Tanzania with reference to the problem of pesticide run-off into Lake Tanganyika.* London, Centre for Overseas Pest Research. 9 p (mimeo).

Melack, J. M. 1976. Primary productivity and fish yields in tropical lakes. *Trans. Am. Fish. Soc.,* 105: 575–580.

——. 1980. An initial measurement of photosynthetic production in Lake Tanganyika. *Hydrobiologia,* 72: 243–247.

Melack, J. M.; Kilham, P.; Fischer, T. R. 1982. Responses of phytoplankton to experimental fertilization with ammonium and phosphate in an African soda lake. *Oecologia,* 52: 321–326.

Meyl, A. H. 1955. Nematoden aus dem Psammon des Tanganjika-Sees. *Zoologischer Anzeiger,* Leipzig, 155: 135–138.

——. 1956. Freeliving nematodes. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 3(7): 27–51.

Michel, A. E.; Cohen, A. S.; West, K.; Johnston, M. R.; Kat, P. W. 1992. Large African Lakes as natural laboratories for evolution: Examples from the endemic gastropod fauna of Lake Tanganyika. pp. 85–99. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on resource use and conservation of the African Great Lakes,* Bujumbura 1989. SIL Mitteilungen No. 23.

Moore, J. E. S. 1898*a*. On the zoological evidence for the connection of Lake Tanganyika with the sea. *Proceedings of the Royal Society,* 62: 451–458.

——. 1898*b*. The marine fauna in Lake Tanganyika and the advisability of further exploration in the Great African Lakes. *Nature,* London, 58(1504): 404–408.

——. 1903. *The Tanganyika Problem.* London: Hurts and Blackett Ltd. 356 pp.

——. 1938. Additions to our knowledge of African leeches (Hirudinea). *Proceedings of the Academy of Natural Sciences,* Philadelphia, 90: 297–360.

Moorehead, A. 1960. *The White Nile.* Hamish Hamilton, London. 385 pp.

Moss, B. 1969. Limitation of algal growth in some central African waters. *Limnol. Oceanogr.,* 14: 591–601.

National Academy of Sciences. 1969. *Eutrophication: Causes, Consequences, Correctives.* Washington D.C., National Academy of Sciences. 661 pp.

Ndayizeye, P. 1985. *Influence des déchets industriels sur la qualité de l'eau du lac Tanganika.* Mémoire de Maîtrise en biologie, Université du Burundi, Bujumbura.

Norconsult, 1980. *Hydrological research in the Kigoma region.* Oslo, Norconsult. Vol. 1–7.

Ntakimazi, G. 1992. Conservation of the resources of the African great lakes. Why? An overview. pp. 5–9. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on resource use and conservation of the African Great Lakes,* Bujumbura, 1989. SIL Mitteilungen No. 23.

Oglesby, R. T. 1977. Relationships of fish yields to lake phytoplankton standing crops, production and morphoedaphic factors. *J. Fish. Res. Board Can.,* 34: 2271–2279.

Payne, A. I. 1986. *The Ecology of Tropical Lakes and Rivers.* 301 pp. Chichester: John Wiley & Sons.

Peters, R. H.; MacIntyre, S. 1976. Orthophosphate turnover in East African lakes. *Oecologia,* 25: 313–319.

Pilsbry, H. J.; Bequaert, J. 1927. The aquatic mollusks of the Belgian Congo with a geographical and ecological account of Congo malacology. *Bulletin of the American Museum of Natural History,* 53: 69–602.

Pitcher, T. J. 1994. Impact of Species Changes in African Lakes.Fish Management Science Research Programme. Revised Final Report on ODA Research Project R4683. 169 pp.

Poll, M. 1950. Histoire du peuplement et origine des espèces de la faune ichtyologique du lac Tanganika. *Ann. Soc. Roy. Zool. Belg.,* 81: 111–140.

——. 1953. Poissons non Cichlidae. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 3(5a): 1–251.

——. 1956. Poissons Cichlidae. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 3: 1–619.

Prudhoe, S. 1951. Trematoda, Cestoda and Acanthocephala. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946– 1947). *Inst. Roy. Sc. Nat. Belgique,* 3(2): 3–10.

Reinhold, T. 1937–1938. La flore fossile à Diatomées de Moliro (lac Tanganika, Katanga). *Mémoires de la Société géologique de Belgique,* 61(1): 39–47.

Rendle, A. B. 1907. Botanical Results of the Third Tanganyika Expedition (1904–1905). *Journal of the Linnean Society,* 38: 18–28.

Roest, F. C. 1992. The pelagic fisheries resources of Lake Tanganyika. pp. 11–15. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes,* Bujumbura 1989. SIL Mitteilungen No. 23.

Rome, R. 1962. Ostracodes. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 3(8): 1–305.

Rosendahl, B. R.; Versfelt, J. W.; Schloz, C. A.;Woods, L. D. (eds.). 1988. *Seismic Atlas of Lake Tanganyika.* Project Probe, Duke University Durham, N.C.

Rousselet, C. F. 1907. Report on the Polyzoa. Zoological results of the Third Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London,* 250–257.

——. 1910. Report on the Rotifera. Zoological results of the Third Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London,* 792–796.

RUDD, J. W. M. 1980. Methane oxidation in Lake Tanganyika (East Africa). *Limnology and Oceanography,* 25: 958–963.

RUFLI, H. 1976. *Preliminary analysis on zooplankton sampling in Lake Tanganyika in May 1976.* FAO Report FI:DP/URT/71/012/44. 10 pp.

——. 1978. *Bibliography of fisheries and limnology for Lake Tanganyika.* FAO CIFA Occasional Paper 5: 1–12.

RUFLI, H.; CHAPMAN, D. W. 1976. *Preliminary analysis on zooplankton sampling and estimates of fish abundance in Lake Tanganyika in October 1975.* FAO Report FI:DP/URT/71/012/31. 14 pp.

RUTTNER, F. 1953. *Grundriss der Limnologie.* Walter de Gruyter, Berlin. 232 pp.

SARS, G. O. 1909. Report on the Copepoda. Zoological Results of the Third Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London,* 1: 31–77.

——. 1910. Report on the Ostracoda. Zoological Results of The Third Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London,* 2: 732–760.

——. 1912. Report on some larval and youg stages of prawns from Lake Tanganyika. Zoological Results of the Tanganyika Expedition (1904–1905). *Proceedings of the Zoological Society of London,* 1: 426–440.

SCHOLZ, C. A.; ROSENDAHL, B. R. 1988. Low Lake Stands in Lakes Malawi and Tanganyika, Delineated with Multifold Seismic Data. *Science,* 240: 1645–1648.

SCIACCHITANO, I. 1935. Sanguisughe del Congo belga. *Revue de zoologie et de botanique africaines,* 26: 448–460.

——. 1937. Irudinei del Congo Belga. *Revue de zoologie et de botanique africaines,* 29(4): 426–469.

——. 1952. Irudinei del Congo belga. *Annales du Musée r. du Congo belge.* Tervuren, Sciences Zoologiques (8)16: 1–87.

——. 1958. Gordioidea del Congo belga. *Annales du Musée r. du Congo belge.* Tervuren, Sciences Zoologiques (8)67: 1–111.

——. 1960. Contributo alla conoscenza degli Irudinei del Congo belga (Nota terza). *Revue de zoologie et de botanique africaines,* 61(3–4): 287–309.

——. 1962. Contributo alla conoscenza degli Irudinei dell'Africa Centrale. *Revue de zoologie et de botanique africaines,* 65(3–4): 276–381.

SERRUYA, C.; POLLINGHER, U. 1983. *Lakes of the Warm Belt.* Cambridge: Cambridge University Press.

SERVAIS, F. 1957. Étude théorique des oscillations libres (sèiches) du lac Tanganika. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique,* 2(3): 1–311.

SINGH, H. 1975. *A brief review of the hydrology of Tanganyika and Kivu Lakes.* Economic Commission for Africa, Addis Ababa (May 1975) 4: 1–9.

SINHA, B. 1980. *Studies on Behaviour of Lake Tanganyika and Notes on Hydro-meteorological Conditions around Kigoma.* Min. of Water, Energy and Minerals, Dar-es-Salaam, Tanzania.

SMITH, E. A. 1906. Report on the Mollusca. Zoological Results of the Third Tanganyika Expedition 1904–1905. *Proceedings of the Zoological Society of London,* 1: 180–186.

SMOL, J. P. 1992. Paleolimnology: an important tool for effective ecosystem management. *J. of Aquatic Ecosystem Health,* 1: 49–58.

STAPPERS, L. 1911. Rapport de la mission d'exploration des eaux intérieures de Congo belge. Renseignements de l'Office Colonial Belge, Bruxelles 12: 396–414.

——. 1913*a*. Mission Stappers 1911–1913. Exploration hydrographique et biologique des lacs Tanganika et Moero. Répertoire général des échantillons d'histoire naturelle recueillis, Bruxelles. 80 pp.

——. 1913*b*. Sondages dans le lac Tanganika. *Revue congolaise,* Bruxelles: 116.

——. 1913*c*. Note sur les variations saisonnières de l'embouchure de la Lobozi, affluent du lac Tanganika. *Revue congolaise,* Bruxelles 4(2): 100–110.

——. 1914*a*. Recherches bathymétriques sur les lacs Moero et Tanganika. *Annales de biologie lacustre,* Bruxelles 7: 83–114.

——. 1914*b*. Composition chimique de l'eaux de surface des lacs Moëro et Tanganika. Renseignements de l'Office Colonial Belge, Bruxelles: 1–4.

STOFFERS, P.; HECKY, R. E. 1978. Late Pleistocene-Holocene evolution of the Kivu-Tanganyika basin. pp. 43–54. In: A. Matler & M.E. Tucker (eds.), *Modern and Ancient lake sediments.* Intern. Ass. Sediment., Special Publication 2, Oxford, Blackwell.

STREET, F. A.; GROVE, A. T. 1976. Environmental and climatological implications of late Quaternary lake level fluctuations in Africa. *Nature,* London, 261: 385–390.

SYMOENS, J. J. 1955*a*. Observation d'une fleur d'eau à Cyanophycées au lac Tanganika. *Folia scientifica Africae centralis,* 1(3): 17

——. 1955*b*. Sur le maximum planctonique observé en fin de saison sèche dans le bassin nord du lac Tanganika. *Folia scientifica Africae centralis,* 1(4): 12.

——. 1956*a*. Sur la formation de 'fleurs d'eau' à Cyanophycées (*Anabaena flos-aquae*) dans le bassin nord du lac Tanganika. *Bull. des séances, Académie roy. des Sciences Coloniales,* Bruxelles 2: 414–429.

——. 1956*b*. Le lac Tanganika. *Bulletin les Naturalistes Belges,* 37(11–12): 288–316.

——. 1959. Le développement massif de Cyanophycées planctoniques dans le lac Tanganika. 9th International Botanical Congress, Montreal 2A: 37.

SYMOENS, J. J.; BURGIS, M.; GAUDET, J. J. 1981. *The Ecology and Utilization of African Inland Waters.* UNEP Reports and Proceedings Series No. 1, 191 pp. Nairobi, UNEP.

TAKAMURA, K. 1988. The first measurement of the primary production of epilithic algae in Lake Tanganyika. *Physiol. Ecol.* , Japan 25: 1–7.

TALLING, J. F. 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Int. Rev. ges. Hydrobiol.*, 51: 545–621.

——. 1969. The incident of vertical mixing, and some biological and chemical consequences in tropical African Lakes. *Verh. Int. Ver. Limnol.*, 17: 998–1012.

——. 1987. The phytoplankton of Lake Victoria (East Africa). pp. 229–256. In: M. Munawar (ed.), Phycology of Large Lakes of the World. Arch. *Hydrobiol. Beih. Ergebn. Limnol.*, 25.

TALLING, J. F.; TALLING, I. B. 1965. The chemical composition of African lake waters. *Int. Rev. ges. Limnol.* 25: 229–256.

TAUB, F. B. 1984. *Lakes and reservoirs*. Amsterdam: Elsevier Publ. 643 pp.

TEALE, R. 1932. The eastern shore of Lake Tanganyika and its vicinity. *Annual Report Geological Survey Tanganyika:* 22–24.

THOMPSON, J. 1882. On the geographical evolution of the Tanganyika basin. *Report of the British Association for the Advancement of Science:* 662

TIERCELIN, J.-J.; Mondeguer, A. 1991. The geology of the Tanganyika Trough. pp. 7–48. In: G. Coulter (ed.), *Lake Tanganyika and its life*. British Museum (Natural History) and Oxford Univ. Press.

TSHIBANGU, K. K. 1991. Annual fluctuations of limnological parameters in the northwestern part of Lake Tanganyika from 1986 to 1990. *Ecol. Limnol. Tanganyika VII:* 98–99.

VANDEN BERGHEN, C. 1955. Hepaticae. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). Inst. Roy. Sc. Nat. Belgique, 4(2): 23–27.

VANDENBOSSCHE, J.-P.; BERNACSEK, G. M. 1990*a*. *Source book for the inland fisheries resources of Africa: 1.* CIFA Technical Paper 18.1. Rome, FAO. 411 pp.

——.; ——. 1990*b*. *Source book for the inland fisheries resources of Africa: 2.* CIFA Technical Paper 18.2. Rome, FAO. 240 pp.

——.; ——. 1991. *Source book for the inland fisheries resources of Africa: 3.* CIFA Technical Paper 18.3. Rome, FAO. 219 pp.

VAN MEEL, L. 1952. Le Milieu Végétal. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). Inst. Roy. Sc. Nat. Belgique, 1: 51–48.

——. 1954. Le phytoplancton. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). Inst. Roy. Sc. Nat. Belgique, 4 (1)A: 1–681.

VAN WELL, P.; CHAPMAN, D. W. 1976. *Summary of limnological observations in Lake Tanganyika near Kigoma, 1974–1975.* FAO Report FI:/DP/URT/71/012/39. 24 pp.

VOLLENWEIDER, R. A. 1968. *Scientific fundamentals of the Eutrophication of Lakes and Flowing Waters, with special Reference to Nitrogen and Phosphorus as Factors in Eutrophication.* Paris, Rep. Organisation for Economic Cooperation and Development, DAS/CSI/68.27, 192 pp., Annex, 21 pp., Bibliography, 61 pp.

WELCOMME, R. L. 1979. *The fisheries ecology of floodplain rivers*. 317 pp. London: Longman.

——. 1985. *River fisheries*. FAO Tech. Pap. 262, 330 pp. Rome, FAO.

WEST, G. S. 1907. Report on the freshwater algae, including phytoplankton of the Third Tanganyika Expedition (1904–1905). *Journal of the Linnean Society*, 38(264): 81–197.

WEST, K.; COHEN, A. S. 1987. Experimental studies of decapod-gastropod interactions at Lake Tanganyika: implications for predator-prey coevolution. Geological Society of America, 1987 Annual meeting (Abstract).

WETZEL, R. G. 1975. *Limnology*. Philadelphia, W. B. Saunders Comp. 743 pp.

——. 1983. *Limnology*. 2nd edition. Philadelphia, W. B. Saunders Comp. 860 pp.

WHITTON, B. A. (ed.). 1975. *River ecology*. Studies in Ecology. Vol. 2. Univ. of California Press, Berkeley. 725 pp.

WITTE, G. de. 1952. Amphibiens et reptiles. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 3(3): 1–22.

WOOD, R. D. 1955. Characea. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belgique*, 4(2): 5–13.

WOODWARD, S. P. 1859. On some new freshwater shells from Central Africa. *Proc. Zool. Soc.* London: 348–349.

Appendices

APPENDIX 1. Overview of limnological research on Lake Tanganyika

Sources: Coulter, 1991a; Beadle, 1981

RESEARCH	RESEARCHER(S)	LOCALITY	PERIOD	REFERENCES	SCOPE/SUBJECT(S)
1856–1960					
EXPEDITIONS					
Burton & Speke	Speke (collector)	northeastern shore near Ujiji	1859–1860	Burton, 1860	Geography; collection of shells
Thomson	Thomson	southern part	1880	Thomson, 1882	Geography
Tanganyika expeditions	Moore		1st: 1894	Moore, 1903 (1897–1906)	Collections; molluscs
	Moore		2nd: 1897	Moore, 1903 (1897–1906)	Collections; molluscs
	Cunnington		3rd: 1904–5	Cunnington, 1906, 1920	Collections; comparative limnology
	Rendle		1904–05	Rendle, 1907	Botanic results 3rd Expedition
	Rousselet		1904–05	Rousselet, 1907,10	Polyzoa, Rotifera
	Sars		1904–05	Sars, 1909,10,12	Copepoda, Ostracoda
	Smith		1904–05	Smith, 1906	Mollusca
	West		1904–05	West, 1907	Phyto-/zooplankton
Mission Stappers	Stappers		1911–1913	Stappers, sev refs	Bathymetry, water chemistry
	Lestage		1911–1913	Lestage, 1917	Ephemeroptera
Mission belge L'exploration hydrobiologique du lac Tanganika	Leloup	lakewide	1946–1947	Leloupe, 1949*ab*,50–53	Collections; Gastropoda, bivalvae
	van Meel			van Meel 1952,1954	Phytoplankton
	Poll			Poll, 1953, 1956*b*	Fishes
	Capart			Capart, 1949–52	Bathymetry, geography, Decapoda
	Kufferath			Kufferath, 1952, 1956	Water chemistry; phytoplankton
	Sevais			Servais, 1957	Hydrodynamics
	Harding			Harding, 1957	Cladocera
	Lindberg			Lindberg, 1951	Copepoda
	Rome			Rome, 1962	Ostracoda
	Demoulin			Demoulin, 1956	Ephemeroptera
	Basilewsky			Basilewsky, 1951	Coleoptera
	Lawalrée			Lawalrée, 1955	Macrophytes
	De Witte			de Witte, 1952	Amphibia, Reptilia
	VandenBerghen			VandenBerghen, 1955	Hepaticae

	Wood		Wood, 1955	Characeae
Taxonomic and ecological studies	Woodward	1858	Woodward, 1859	Shells collected by Speke
	Giraud		Giraud, 1885	Mollusca
	Crosse		Crosse, 1881*a,b*	Mollusca
	van Martens		van Martens, 1883	*Limnocnida tanganyicae*
	Bourguignat		Bourguignat, 1890	Mollusca
	Hore		Hore, 1892	Collection fauna
	de Guerne		de Guerne, 1893	Cnidaria
	Ancey		Ancey, 1894 & sev. refs.	Mollusca
	Günther		Günther, 1864	Reptiles & fishes collected by Speke
			Günther, 1893–1907	*Limnocnida tanganyicae*
	Moore		Moore, 1898, 1903	Marine fauna ('The Tanganyika problem')
	Evans		Evans, 1899	Porifera
	Calman		Calman, 1899–1928	Decapoda
	Cunnington		Cunnington, 1899	Crustacea
			Cunnington, 1906	Surface temperatures
			Cunnington, 1920	Study comparative limnology
	Digby		Digby, 1902	Gastropoda
	Kirkpatrick		Kirkpatrick, 1906	Porifera
	Beddard		Beddard, 1906	Oligochaeta
	Gravier		Gravier, 1907	Cnidaria
	Groves	1904–1905	Groves & Groves, 1907	Characeae
	West		West, 1907	Algae including phytoplankton
	Von Daday		Von Daday, 1910	plankton
	Bouvier		Bouvier, 1913	Decapoda
	De Beauchamp		De Beauchamp, 1914	Cestoda
	Jaffe		Jaffe, 1916	Porifera
	Hett	1904–1905	Hett, 1924	Linguatulidae
	Fuhrmann & Baer	1904–1905	Fuhrmann & Baer, 1925	Cestoda
	Pilsbry & Bequaert		Pilsbry & Bequaert, 1927	Mollusca
	Baylis		Baylis, 1927, 1928	Turbellaria, parasitic worms
	Esaki & China		Esaki & China, 1927	Hemiptera
	Gurney		Gurney, 1928	Copepoda
	Hutchinson		Hutchinson, 1930	Water chemistry
	Teale		Teale, 1932	Geology
	Gillman		Gillman, 1933	Hydrology

Appendix 1 (contd)

RESEARCH	RESEARCHER(S)	LOCALITY	PERIOD	REFERENCES	SCOPE/SUBJECT(S)
	Kiefer			Kiefer, 1956,57*a,b*	Copepoda
	Sciacchitano			Sciacchitano, 1935,sev refs	Hirudinea
	Heinrichs			Heinrichs, 1936	Hydrology, water levels
	Borg			Borg, 1936	Bryozoa
	Reinhold			Reinhold, 1937–38	Fossil diatoms
	Moore			Moore, 1938	Hirudinea
	Beauchamp	lakewide	1938	Beauchamp, 1939,1940,1946	Physical limnology
	Dartevelle			Dartevelle, & Schwetz 1946,7,8	Gastropoda
	Brooks			Brooks, 1950	Speciation
	Prudhoe			Prudhoe, 1951	Cestoda, Trematoda
	Meyl			Meyl, 1955, 1956	Nematoda
	Symoens			Symoens, 1955*a,b*,56*a,b*,59	Cyanophyta, macrophytes
	Marlier			Marlier, 1956–1962	Trichoptera
	Dubois	Uvira	1955–57	Dubois, 1957, 1958	T and D.O. observations (depth-time)
	Kiss			Kiss, 1959–1961	Ostracoda
1960–1985					
JFRO	Coulter	Mpulungu (Zamb.)	7/59 – 66	JFRO, 1960,62,64 Coulter, 1966, 67	Limnological observations, Plankton, clupeids
FAO Lake Tanganyika Fishery Res. and Dev. Project Tanzania (URT/71/012)	Chapman van Well Rufli	Kigoma (Tanz.), lakewide surveys	1973–1977	FAO reports: Van Well & Chapman, 1976 Rufli (sev refs) Coulter *et al.*, 1975	 Limnological observations Zooplankton observations Reports limn. work
	Craig Edmond	off Kigoma	2/73	Craig, 1975; Edmond, 1975*a*	Geochemical/hydrographic survey
UNDP/FAO Fish. Res. Project Burundi (BDI/73/020) & (BDI/70/508)	Ferro Coulter	Bujumbura (Bur.)	1973–1977	FAO, 1977 Ferro (sev refs) Ferro & Coulter, 1974	Limnological observations Limnological observations Limnological observations
	Edmond	off Kigoma/Kipili shallow/deep waters	3–4/1975	Edmond, 1975*b* Edmond *et al.*, 1993	Nutrient chemistry Nutrient chemistry

Other studies:					
	Camus			Camus, 1965	Water levels
	Greene & Jones	longitud. transect		Greene & Jones, 1970	Temperature observations
	Melack	Burundi waters	1971	Melack, 1980	Primary productivity
	Deelstra	Burundi, rivers	1970–90	Deelstra, sev refs	Pollution
	Singh	lakewide		Singh, 1975	Hydrology
	Loehnert	lakewide		Loehnert, 1975	Hydrology
	Matthiessen	Tanzania		Matthiessen, 1977	Pollution, pesticides
Freshwater	Hecky, Degens	lakewide	1973	Hecky & Degens, 1973	Paleolimnology/chem. stratigraphy
Institute (Canada)	Hecky, Fee	lakewide	1975	Hecky & Fee, 1981	Primary production, algal growth rates
	Hecky, Kling	lakewide	1975	Hecky & Kling, 1981	Phytoplankton/ protozooplankton
	Hecky	lakewide		Hecky (et al.) (sev refs)	Trophic dynamics
	Rudd	longitud. transect	1975	Rudd, 1980	Methane oxidation
	Burgis	lakewide	1974–5	Burgis, 1984,1986	Zooplankton, trophic dynamics
	Norconsult	Kigoma		Norconsult 1980	Hydrology
RECENT AND ONGOING LIMNOLOGICAL RESEARCH					
GEOLOGY & PALEOLIMNOLOGY					
CEGAL project	Livingstone	lakewide surveys	1980–1982	Livingstone & Melack, 1984	Geology, sedimentology
PROBE project (Duke Univ.)	Rosendahl & others	lakewide	1982–	Rosendahl *et al.*, 1988 Tiercelin & Mondeguer, 1991	Geology, paleolimnology, sediments
GEORIFT Project (French Univs., CNRS and local geologists)	Mondeguer Tiercelin & others		1982–	Tiercelin & Mondeguer, 1991	Geology, sediments
'Livingstone core'	Livingstone			Livingstone, 1965	Core stratigraphy, water levels
	Stoffers & Hecky			Stoffers & Hecky, 1978	Core mineralogy
	Haberyan	lakewide		Haberyan, 1984,85	Diatom deposition by faecal pellets
				Haberyan & Hecky, 1987	Core analysis: diatoms, chemistry,
Woods Hole Expedition	Degens, von Herzen & Wong	lakewide	1970	Degens *et al.*, 1971	Chemistry, sediments, Geological structure Sedimentology

Appendix 1 (contd)

RESEARCH	RESEARCHER(S)	LOCALITY	PERIOD	REFERENCES	SCOPE/SUBJECT(S)
RECENT AND ONGOING LIMNOLOGICAL AND ECOLOGICAL RESEARCH					
University of Burundi	Ndayizeye	Bay of Bujumbura		Ndayizeye, 1985	Water quality
/Univ. of Ghent	Ndabigengesere			Ndabigengesere, 1986	Pollution
/Free Univ. Brussel	Niyibona			Niyibona, 1988	Pollution
	Gasana			Gasana, 1988	Pollution
	Rwimo			Rwimo	Phytoplankton
	Caljon		1986–87	Caljon, 1992	Water quality, phytoplankton
Univ. of Burundi/	Cohen,	eastern shore		Cohen, sev refs	Endemic gastropods, conservation
Univ.of Arizona	Johnston,Kat			Michel *et al.*, 1992	Lacustrine speciation
(USA)	Michel, West			West *et al.*, 1991	
Coop. Study	Kawanabe	near Uvira	1982 –	Kawanabe *et al.*, 1992	Overview of ecological
Ecology Lake	Kwetuenda		present		and limnological studies
Tanganyika	Gashagaza				
CNRS/Uvira – Japan					
FAO Regional	Lindqvist	lakewide	1992–1997	Lindqvist &	Limnological/hydrological
Fisheries Project	Hanek			Mikkola, 1989	research (also using remote
(FINNIDA/AGFUND)					sensing techniques)
(GCP/RAF/271/FIN)					
Belgium/CEPGL	Risch	northern part	1992–1996	Risch (pers. comm)	Limnological studies, water chemistry,
Hydrobiological	De Vos	Lake, rivers			Pollution, faunal studies,
Project	Vandelannoote				*Limnocnida tanganyicae*
(CRRHA-Burundi/	Ntakimazi				
Univ. of Burundi/	Dumont				
Univ of Leuven/					
Univ. of Ghent/					
CNRS-Uvira)					

APPENDIX 2. **Data on physical limnology of Lake Tanganyika**

RESEARCHER	DATA	LOCATION	TIME SPAN	FREQUENCY	DATE	REFERENCE(S)
Beauchamp	Temperature/D.O. (0 – 400 m)	off Kigoma sev. stations Kigoma-southend	–	–	1938	Beauchamp, 1939,40,46,53
Capart	Temperature profile (0 – >1000 m)	off Kigoma	–	–	8/47	Capart, 1949
Dubois	Temperature/D.O.	Station 4 km off Uvira	14 months	weekly	11/55–2/57	Dubois, 1958
Coulter	Temperature/ D.O.	station 'mid–Mwela' (inshore) & 'outer-Mwela (offshore) off Mpulungu longitud. transect	11 months 20 months 24 months 4 days	occasionally weekly weekly –	7/59—6/60 6/60–2/62 4/64–4/66 5/64	JFRO, 1960 JFRO, 1962,64, Coulter, 1963 Coulter, 1968 Coulter, 1968
Degens, von Herzen, & Wong	Temperature/D.O.	several stations	2 months	–	3/70–4/70	Degens *et al.*, 1971
Greene & Jones	Temperature	transect	–	–	–	Greene & Jones, 1970
Ferro Ferro & Coulter	Temperature/D.O.	northern part near Bujumbura north basin transect to 150 m depth	2 years –	regularly	73–75 74	Ferro, 1975 Ferro & Coulter, 1974
Van Well & Chapman	Temperature/D.O.	off Kigoma	1 year	regularly	75	Van Well & Chapman, 1976
Craig	Temperature/D.O.	off Kigoma	1 month	–	2/73	Craig, 1975; Edmond, 1975*a*
Edmond *et al.*	Temperature/D.O.	shallow/deep stations off Kigoma/off Kipili	2 months	–	3–4/75	Edmond, 1975b Edmond *et al.*, 1993
Tshibangu	Temperature	off Uvira	4 years	twice a month	7/86–12/90	Tshibangu, 1991
FAO L. Tanganyika Research Project	Temperature/D.O.	lakewide			1992–1997	FAO L. Tanganyika Research Project Series

Part 2

Limnology and hydrology of Lake Malawi

Section I

Research on Lake Malawi

a review

1 The importance of the lake to the region and the role of limnological and hydrological research

RESOURCE USE

Lake Malawi/Niassa, the third largest African lake after Lakes Victoria and Tanganyika, has a surface area of 28,800 km^2. The lake is shared between Malawi, Tanzania and Mozambique. Approximately 80% of its catchment lies in Malawi, one of the most densely populated countries in Africa with a land area of 94,052 km^2 (Eccles, 1984) and a population of 9.1 million in 1992 (World Bank, 1994). The lake is an important fresh water resource for people living in its vicinity. It has been an important means of transport since the Arabs first put their sailing dhows on the lake at the end of the nineteenth century. It is vital for electricity generation by hydro-electric power stations on the outflowing Shire River (Tweddle, 1992). Furthermore, water is diverted from major affluents of Lake Malawi such as Dwangwa and Bua River for irrigation purposes (Tweddle, 1992). The lake, with its spectacular scenery, white beaches and beautiful fish, is a tourist attraction.

Fishing and post-harvest activities have been important economic operations in and around the lake. The most important fisheries activities take place in the south-east arm of the lake in Malawi (Tweddle & Magasa, 1989; Alimoso *et al.* 1990; FAO, 1992). In Tanzania and Mozambique the lake is remote from the major centres of population. The population in the catchment area of the lake in these countries largely depends on the lake for protein. Fish has always been a very important source of food for the people around the lake.

Considerable investments have been made into development of the infrastructure of water supplies, electricity generation, irrigation, and harbour facilities, which are dependent on stable lake levels (Tweddle, 1992). Changes in lake levels in the past have occurred through purely natural causes. Between 500 and 125 years ago the lake receded more than 100 m below its present level, which implied reduced rainfall for a prolonged period (Owen *et al.* 1989). The relatively stable lake levels of the last 30 years have probably been fairly unusual.

Next to these economic uses the lake has a tremendous diversity in fish species, with an estimated 1,000 species which exceeds that of any other lake in the world (Fryer & Iles, 1972; Lowe-McConnell, 1987; Eccles & Trewavas, 1989). Conservation of fish species in Lake Malawi is of major importance, as the lake is one of the most spectacular examples of adaptive radiation of vertebrates in the world (Tweddle, 1992). The Government of Malawi made a major contribution towards conservation by the establishment of the Lake Malawi National Park in 1980, which UNESCO has designated as a World Heritage Site (Bootsma, 1992).

MAJOR ENVIRONMENTAL ISSUES

Deforestation and soil erosion

Deforestation in the catchment area is of major concern to Lake Malawi. It has already affected the rivers flowing into the lake and consequently the potamodromous fish migration (Tweddle, 1992).

As the shoreline of Lake Malawi is steep at many places, deforestation will increase soil erosion.

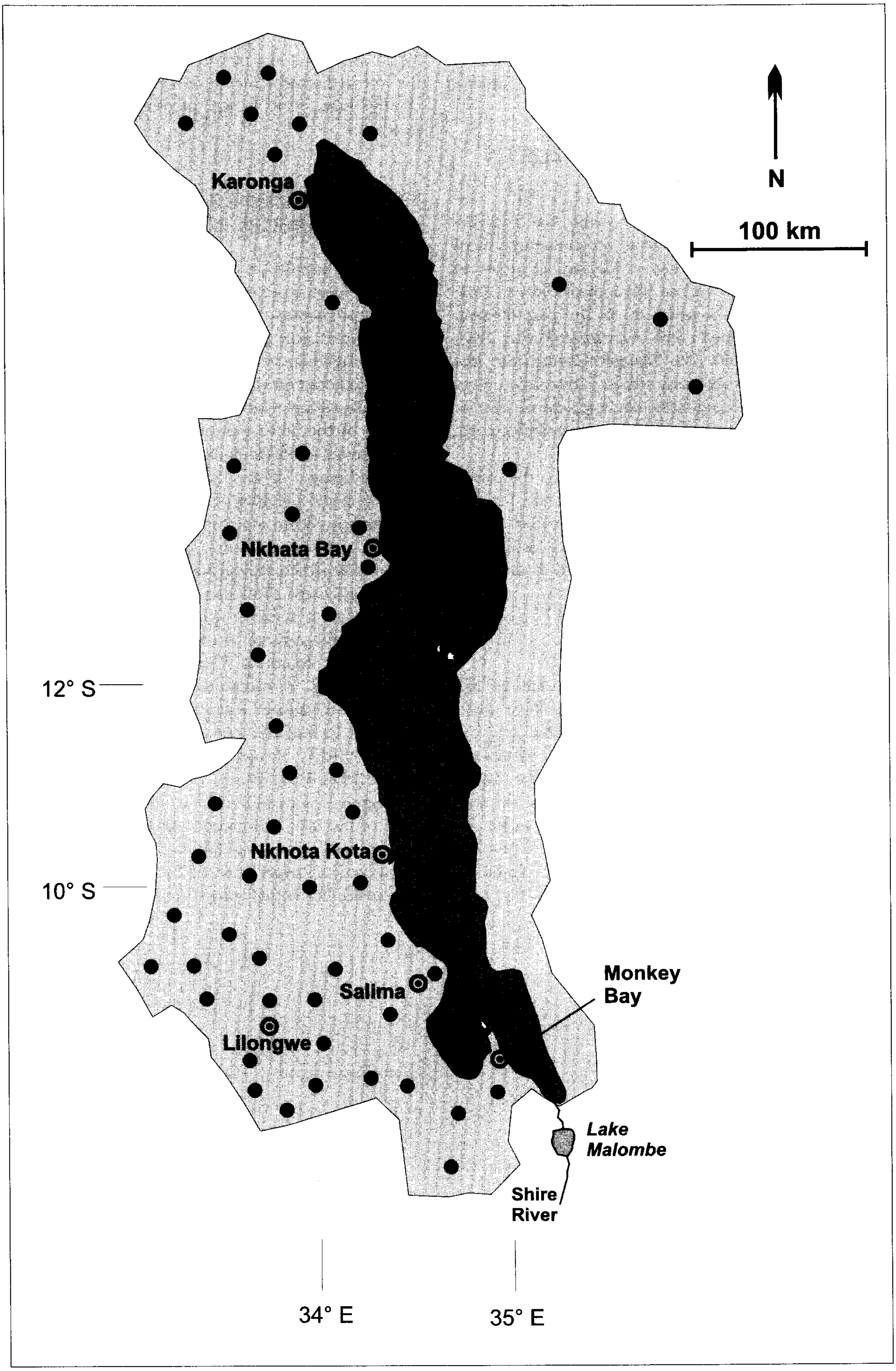


Figure 1.1 Population density in the catchment area of Lake Malawi. Each dot represents 100,000 persons (redrawn after Bootsma & Hecky, 1993).

Especially in the vicinity of villages deforestation is intense, as observed in the Lake Malawi National Park (Bootsma, 1992). Siltation has already been observed at rocky habitats at depths deeper than 12 m (Ribbink *et al.* 1983).

Overexploitation of fish stocks and reduction of biodiversity

As the human population is growing fast and fish catches remain relatively stable, the consumption of fish per capita is declining in Malawi. In order to compensate for this decline, the introduction of alien fish species has been proposed in the past (Turner, 1982) and has aroused much discussion (Eccles, 1985; McKaye *et al.* 1985). The Malawi Government has stated that no introductions will ever be made unless conclusive scientific evidence can be produced that an introduction will boost catches on a sustainable basis (Nongwa, 1986).

Another threat to the lake's ecology is the exotic water hyacinth *Eichhornia crassipes*. It has become already a prominent feature of the vegetation of the lower Shire River system and continuous monitoring is necessary to restrict the further spread of the plant (Tweddle, 1992).

Pollution

Pollution forms the greatest future threat to the ecosystem of Lake Malawi. Changes that have taken place in the ecosystem of Lake Victoria may be indicative of the potential impact of increasing population density and development in the catchment area of Lake Malawi, as it is clear that the size of the lakes does not protect them from anthropogenic influences (Bootsma & Hecky, 1993). If positive results of oil exploration were to lead to exploitation of oil in or near the lake, pollution of the lake waters during extraction, storage and/or lake transport would have negative implications for the fish stocks and water supplies of the lake. Development of the tourist industry may also have a negative impact on the lake, if it is not properly developed and managed.

THE ROLE OF LIMNOLOGICAL AND HYDROLOGICAL RESEARCH

In the past, population density and agricultural, industrial and fisheries activities were at levels that allowed the lake to maintain its natural conditions. As a result of the population growth in the catchment area and the associated environmental problems, the ecosystem of the lake necessarily will change.

Conservation of biodiversity and sustainable management of the lake's resources is only possible with an improved scientific understanding of the limnology and hydrology of the lake and the effect of the anthropogenic activities on the lake environment. This requires ecosystem monitoring, in particular information on nutrient dynamics, primary production and community structure which is useful to detect changes in the ecosystem (Bootsma & Hecky, 1993). Besides, Lake Malawi is a shared water body, and resource use by one of the riparian countries affects the activities in the other countries. This requires regional collaboration and co-ordination of limnological and hydrological research. A first step towards regional cooperation in research and resource management was the UK/SADC Pelagic Fish Resource Assessment Project (1990–1994) (Menz, 1995).

Regional co-operation in environmental management of the lake and conservation of its biodiversity is proposed in the Lake Malawi/Niassa Biodiversity Conservation Project financed by the Global Environmental Facility which started in 1995.

2 History of limnological and hydrological research on Lake Malawi

GEOGRAPHICAL EXPLORATION AND THE EUROPEAN DISCOVERY OF THE LAKE

The first scientific research on Lake Malawi – formerly Lake Nyasa – goes back to the expeditions to find the sources of the Nile in the 1850s, compellingly described by Moorehead (1960). In the early 1850s local reports of Arab slave and ivory traders spoke of a third large lake, 'Nyasa', further south than the two large lakes 'Ujiji' and 'Nyanza'. The existence of the lake, however, had been known to the Portuguese for more than a century previously. The discovery of Lake Nyasa was preceded by the discovery of Lakes Tanganyika and Victoria in 1858, the year that David Livingstone started his second Zambezi Expedition (1858–1863) in Quelimane. From the Zambezi River Livingstone followed the Shire River upstream with a steamboat, the *Ma Robert*, and in September 1859 he discovered Lake Nyasa. In 1860 Livingstone went more than half-way up the lake in a four-oared row-boat which he took along. Arab dhows were already sailing on the lake at that time. After Livingstone returned to England from his second Zambezi Expedition in 1864 the Royal Geographical Society sent him on a new expedition to Africa to solve the catchments of the rivers of Southern Africa. He started this expedition from Zanzibar in March 1866, went into the interior at the mouth of the Ruvuma River. He reached Lake Nyasa at the south-eastern side a few months later, went on in a north-western direction to Lake Tanganyika, where he arrived almost a year after his departure from Zanzibar. He went on and discovered Lakes Mweru and Bangweulu. In the years after Livingstone's expeditions other expeditions were conducted to the lake or past it. In 1878–1880 and in 1890–1891 the Scottish explorer Joseph Thomson passed Lake Nyasa to the north and to the south respectively, on his way to other Central African lakes.

THE FIRST SCIENTIFIC INVESTIGATIONS

John Kirk, a naturalist and physician who accompanied Livingstone during his second Zambezi Expedition (1858–1863), was the first European to collect fish from Lake Malawi. At the time most of the geographical problems had been solved, and European scientists were becoming interested in the exciting new virgin area of tropical Africa. The first purely scientific expeditions in the region were those of J. W. Gregory, a Scottish geologist who worked in the East African Rift Valley, and J. E. S. Moore whose journeys to Lake Tanganyika in 1894 and 1897 can be regarded as the foundation of tropical African limnology (Beadle, 1981). Both studies were of obvious importance to research on Lake Malawi.

LIMNOLOGICAL AND HYDROLOGICAL RESEARCH

Limnological investigations of Lake Malawi and other East African lakes evolved from rather short-term investigations carried out at the beginning of the century focusing on collecting specimens and measurement of some simple physical parameters into the foundation of research institutes on the shores of the lakes which made prolonged investigations and the use of research vessels on the lake possible. In recent decades limnological research has been carried out mainly by limnologists based in Malawi, at the National Fisheries Research Institute, other government institutes or in projects related to the lake's fisheries development (Tweddle, 1991*a*; Menz, 1995).

From 1896 onwards systematic recording of the water levels of Lake Malawi was carried out. For the period between 1860 and 1896 some information on the water levels of the lake is available through the occasional measurements of Livingstone and several missionaries (Beadle, 1981). The lake was first surveyed at the end of the nineteenth century by Commander Rhoades (Rhoades, 1902) and the soundings that he carried out with line and winch appear to have been quite accurate (Jackson *et al.* 1963). The first limnological information from Lake Malawi came from Fuelleborn (1900) who was the first to observe a thermocline in a tropical lake.

The Freshwater Biological Association (FBA) has made an important contribution to the limnology of Lake Malawi and African limnology in general (Fryer & Talling, 1986). During 1939–1940 Beauchamp – founder member of FBA – made pioneer studies of the hydrography of Lakes Malawi and Tanganyika (Beauchamp, 1939, 1940, 1953). In 1939 the first fisheries survey was conducted on Lake Malawi by Ricardo-Bertram, Borley and Trewavas (Ricardo-Bertram *et al.* 1942). In 1945–1947 further studies on Tilapia ('Chambo') fisheries of the South-east arm of Lake Malawi were carried out (Lowe, 1952). At the end of the 1950s Fryer was engaged in research on crustacean parasites, invertebrates and cichlids of the lake (Fryer & Talling, 1986).

In 1954 the Joint Fisheries Research Organization (JFRO) of Northern Rhodesia and Nyasaland established a research station at Nkhata Bay and research focused on northern Lake Malawi. Initial studies by JFRO in 1954–1955 included hydrological and limnological observations in the lake off Nkhata Bay and the affluent rivers, invertebrate studies, research on fishes, fish ecology, and fisheries (Jackson *et al.* 1963). Results of further limnological sampling carried out at Nkhata Bay were presented in the JFRO Annual Reports (JFRO, 1960, 1962, 1964). A list of JFRO Annual Reports is given in the limnological bibliography of Malawi (Tweddle & Mkoko, 1986). In 1962 the focus of research shifted to southern Lake Malawi, as new laboratories were established in Monkey Bay. Since the independence of Malawi in 1966 the Fisheries Department research section has carried out limnological studies, most of them in co-operation with fisheries projects.

Several externally-funded projects have contributed to the limnology of Lake Malawi. Two UNDP/FAO Fisheries projects in the 1970s included limnological research components, notably the Fisheries Expansion Project from 1972 to 1982 (Tweddle, 1991*a*). The Bangula Lagoon Study, an ODA-funded project in 1975–1976, examined the limnology of the lagoon ecosystem (Shepherd, 1976). Recently, a UK/SADC fisheries research project carried out an extensive limnological research programme in the pelagic waters of the lake as part of a research programme to assess the productivity and fishery potential of the lake (Menz, 1995).

Hydrological research provided information on lake level fluctuations and their implications for water availability (Kidd, 1983) and speciation of the cichlid fauna of the lake (Owen *et al.* 1990).

References on the limnology and hydrology of Lake Malawi are given by Tweddle & Mkoko (1986), Tweddle (1991*b*) and Patterson & Kachinjika (1995). In Appendix 1 (pp. 108–10) an overview of expeditions, surveys, limnological research programmes, projects and studies on Lake Malawi is presented.

Section II

Background

3 Geological and climatic history

Fryer & Iles (1972) and Beadle (1981) have reviewed the geological and palaeontological evidence on the origins of Lake Malawi. Work on the historical geography of the Malawi basin started in 1920 with the pioneering geological work of Dixey (1926, 1941).

The African continent is one of the most ancient in the world. The rivers gradually eroded the land mass and the ancient pattern of drainage – rivers flowing from a higher central region eastward and westward – is still the basis of most of the continent. In East Africa this drainage pattern began to change by upward earth movements and volcanic activity in Miocene times (starting some 25 million years ago). A wide stretch of land from Eritrea to the Zambezi has been lifted more than 1000 metres since the Miocene. Later the shallow basin of Lake Victoria was formed by a gradually sagging of the centre of this stretch. The two edges were raised further, forming two Great Rift Valleys. Tectonic activities in and near these valleys formed a series of splits in the earth's crust, some of which were more than 1000 metres deep and filled with water.

In this way all the African Great Lakes in East Africa except Lake Victoria were formed. It is the Western Rift Valley, which comprises from north to south the Lakes Mobutu, Edward, George, Kivu, Tanganyika, Rukwa, Malawi, Chiuta and Chilwa (Figure 3.1). The Eastern Rift Valley extends as far north as Israel, where it includes Lake Tiberias and the Dead Sea. Other lakes in the Eastern Rift Valley are the Ethiopian Rift Lakes, Lake Turkana and a number of shallow saline lakes in Kenya and Tanzania. Lakes existed in the early Miocene; these eventually dried out or drained completely during the Miocene itself (Fryer & Iles, 1972).

Lake Malawi, a tectonic lake, may be several million years old (Owen *et al.* 1990), which means that in Africa only Lake Tanganyika is older. Geological evidence indicates that Lake Malawi originally occupied the northern part of its present basin and that it stood at a considerably higher elevation than it does today. Its present form and level were arrived at after much complex faulting and collapse (Fryer & Iles, 1972). First, the rift trough deepened and the lake extended south, capturing rivers from the west and flooding the former head of the Shire River. The lake level was then still higher than at present and faulting brought the lake to its present level, depth and width, with the Shire River as its only outlet.

HISTORICAL LAKE LEVELS

In the late Pleistocene Lake Malawi underwent considerable changes in level, as did all East African lakes. A major recession was reported by Scholz and Rosendahl (1988) based on seismic data before 25,000 years B.P. when the level of the lake was 250–500 m lower than today. This recession has been attributed to a drier climate, although tectonic tilting may have been a contributing factor (Scholz & Rosendahl, 1988). Owen *et al.* (1990) reported another major recession at 10,740 ± 130 years B.P. based on a hard reflector in geopulse recordings. More recently, they reported lake level falls between 1150 and 1250 A.D. and between 1500 and 1850 A.D. These events

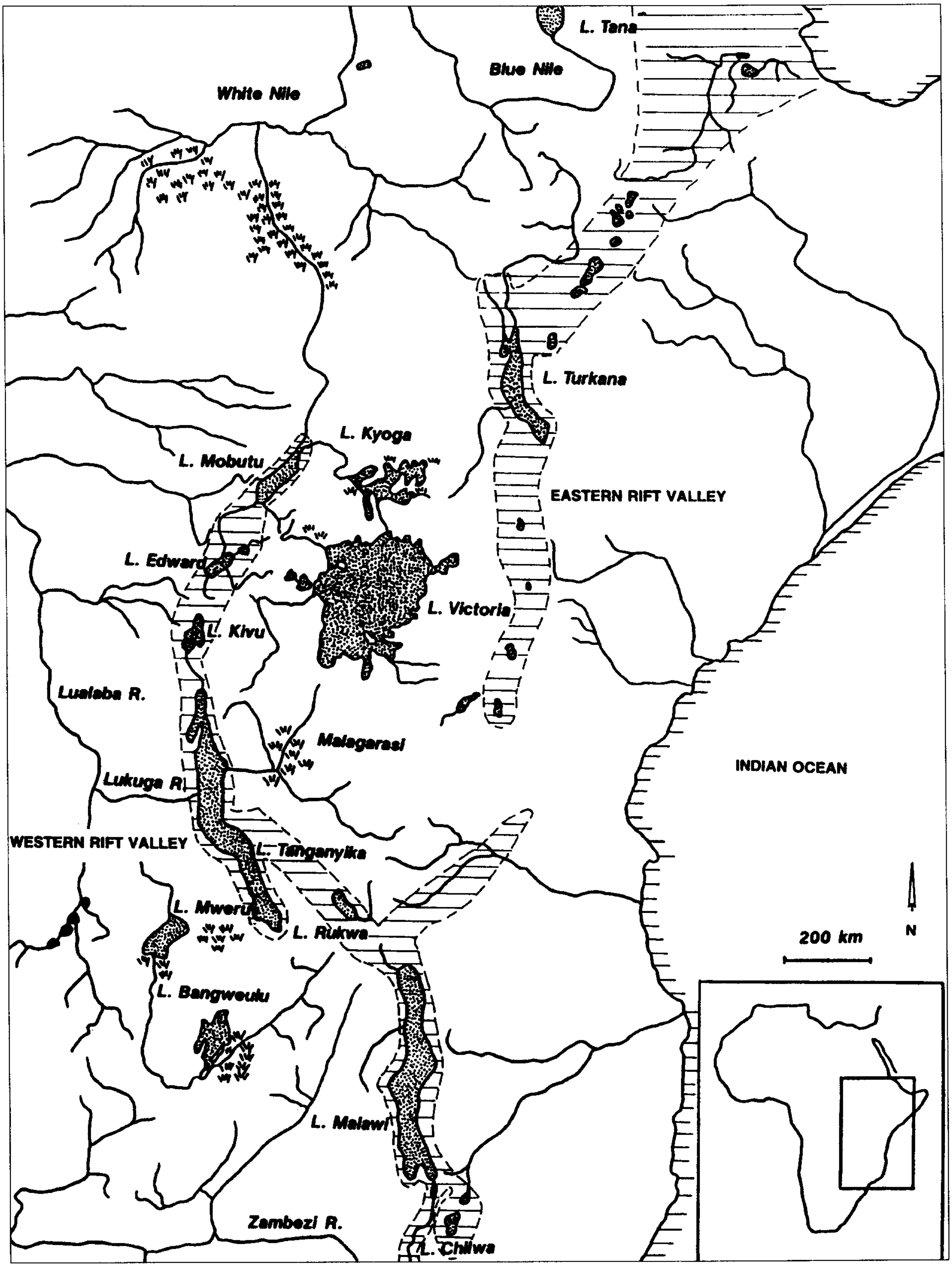


Figure 3.1 Eastern Africa showing the Rift Valleys and their lakes

seem to be climatically controlled given the lack of beach ridge lifting (Crossley *et al.* 1984). The 1500–1850 lake recession and refilling cycle has been extensively documented by Owen *et al.* (1990). The climatic history of (East) Africa has been discussed by Nicholson (1980) and Street & Grove (1976).

4 Present status of Lake Malawi

INTRODUCTION

The present chapter will provide background information on the physical geography and climate of the catchment area of Lake Malawi, together with the main characteristics of the lake. A topographic map of the lake's catchment area with the inflowing and outflowing rivers is given in Figure 4.1.

PHYSICAL GEOGRAPHY

The catchment area of Lake Malawi including the lake, is approximately 126,500 km2. It covers parts of Malawi, Mozambique and Tanzania, all three countries bordering the lake. The main part of the catchment area is on Malawian territory (Figure 4.1). Lake Malawi is the third-largest lake of Africa after Lake Victoria and Lake Tanganyika, its surface area being approximately 28,800 km2 (Gonfiantini *et al.* 1979). The lake's geographical boundaries are 9°30′ - 14°30′ S, 33°50′ - 35°20′ E and the altitude of the lake is 471 m above sea level. The lake is the most southerly of the African Rift Valley lakes. The majority of the lake (± 80%) is Malawian territory and the remaining part (± 20%) is Mozambican.

A good description of the shoreline is given by Ricardo-Bertram *et al.* (1942). One-third of the shores of the lake are rocky, and two-thirds are gently sloping sandy beaches or swampy river estuaries.

The main inflowing rivers are the Ruhuhu River and the North and South Rukuru Rivers flowing into the northern part of the lake. The eastern coast south of the Ruhuhu River has only minor inflowing rivers (Figure 4.1). A map showing the main inflowing rivers and their catchment areas in Mozambique is given by Massinga (1990). Sediment-laden high-volume runoff occurs along the steep lake shore of the northern reaches of the lake (Pilskaln & Johnson, 1991). The Shire River is the only outlet of the lake.

Since the pioneer work of Gregory (1896,1921) on the geology of East African Rifts geological maps have been available for most parts of East Africa. The foundation of the whole region mainly consists of Eozoic rocks. These rocks form high mountains which surround the lake and are especially prominent in the north. A map showing the geological structure is given by Dixey (1926). A simplified geological sketch map of the catchment of Lake Malawi based on maps of East Africa in Furon (1963) is given in Figure 4.2. The predominant lithologies consist of Pre-Cambrian metamorphic rocks with less common Pre-Cambrian and Lower Paleozoic granitic and syenitic plutons. The only volcanic rocks present are at the northern end of the lake in the Rungwe volcanic field (Owen *et al.* 1990). A brief description of the coastal terrain is given by Jackson *et al.* (1963). A more detailed description of the mountain ranges and geology of the region together with a comprehensive list of references is given in Van Meel (1954). Information on soils and vegetation of the catchment area of Lake Malawi in Tanzania and Malawi is given by Balarin (1985,1987). References to other publications on soils are presented by Smith-Carington & Chilton (1983).

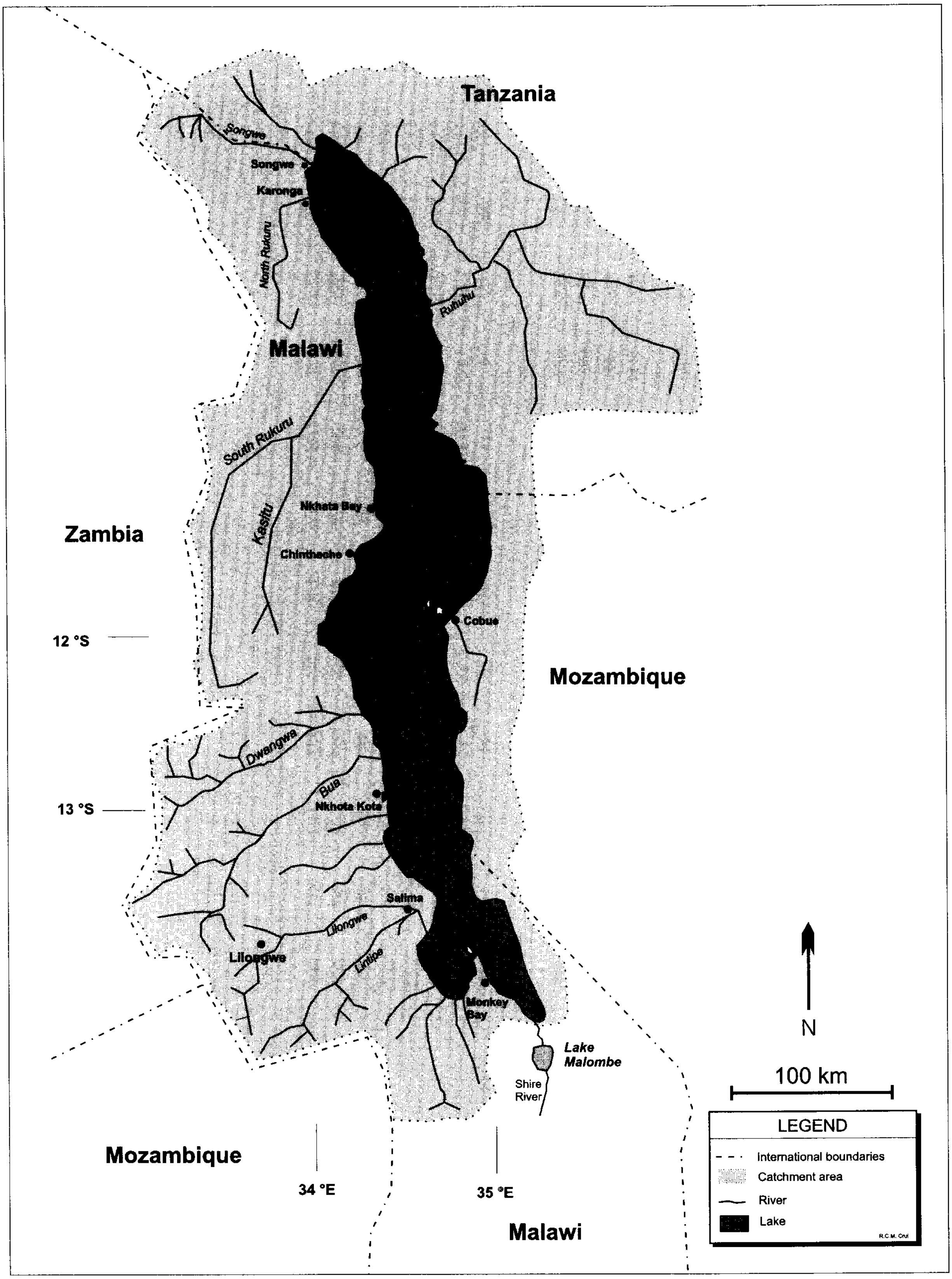


Figure 4.1 Topographic map of the catchment area of Lake Malawi

CLIMATE

General information on the climate of East Africa can be found in Griffiths (1972), and more detailed information on meteorological conditions in the lake area in FAO (1984), Balarin (1987) and the Meteorological Department of Malawi (1982). Monthly temperature and wind observations from Salima station obtained from the Meteorological Department of Malawi from 1980 to 1994 are given by Patterson & Kachinjika (1995).

The catchment area of Lake Malawi lies entirely within the tropical zone. Lying far enough south of

Table 4.1 Lake Malawi: Means of various climatological elements for two lakeshore stations (Source: FAO, 1984; data long-term averages (20–30 years)).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
a. NKHATA BAY (Malawi) [Alt. 480 m]													
rainfall (mm) - means per month/year	273	214	376	273	65	40	23	6	4	18	88	217	1597
temperature (°C) - average	23.7	24.0	23.5	22.9	21.0	19.3	19.2	20.1	22.0	24.3	25.0	24.5	22.5
- means of max	28.5	27.8	28.3	28.1	27.1	25.2	25.1	26.3	28.6	30.6	31.5	29.3	28.0
- means of min	21.1	21.1	20.6	20.0	17.6	15.6	14.1	15.2	17.1	19.0	21.1	21.2	18.6
wind speed (in $m.s^{-1}$ at 2 m level)	0.7	0.7	0.8	0.9	1.1	1.2	1.3	1.3	1.4	1.4	1.2	1.0	1.1
sunshine (%) (relative sunshine duration)	33	50	52	70	78	86	81	88	90	90	71	48	69
Tot. radiation (daily average in $cm^{-1}.day^{-1}$)	410	473	457	475	448	442	438	505	569	613	557	469	488
evapotransp. (mm) – (Penman method)	110	109	113	106	91	77	84	102	125	152	142	126	1337
b. COBUÈ (Mozambique) [Alt. 502 m]													
rainfall (mm) - means per month/year	287	361	203	66	11	3	1	1	1	7	44	192	1177
temperature (°C) - average	25.3	25.0	25.2	25.3	23.8	22.4	21.8	22.6	24.9	27.3	27.6	26.0	24.8
- means of max	28.6	28.3	28.7	29.1	28.1	27.0	26.2	27.2	29.3	31.0	31.1	29.4	28.7
- means of min	22.1	21.7	21.7	21.6	19.5	17.9	17.4	18.1	20.6	23.7	24.1	22.7	20.9
wind speed (in $m.s^{-1}$ at 2 m level)	1.7	1.5	1.5	1.7	1.8	1.9	2.0	2.2	2.3	2.7	2.5	1.9	2.0
sunshine (%) (relative sunshine duration)	45	45	56	64	76	77	70	77	80	87	71	54	66
Tot. radiation (daily average in $cm^{-1}.day^{-1}$)	459	453	471	453	439	412	402	467	534	602	559	494	478
evapotransp. (mm) – (Penman method)	138	117	134	126	117	102	109	130	155	195	182	154	1659

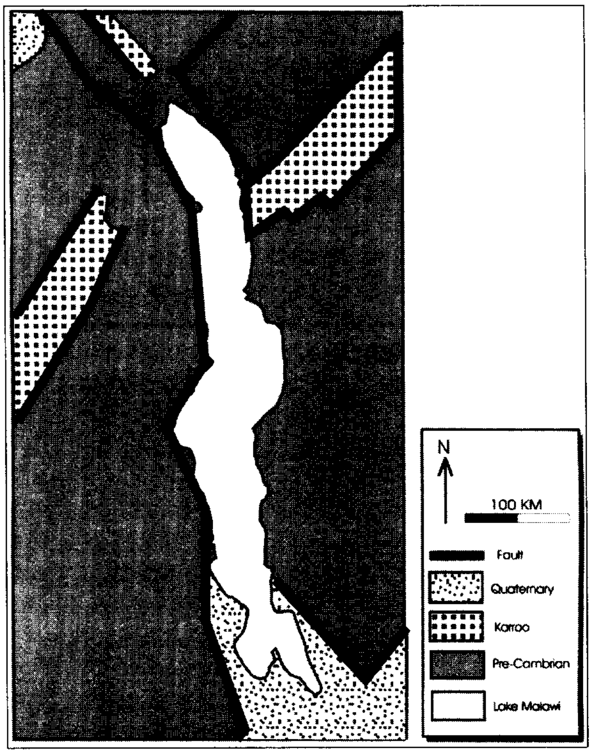


Figure 4.2 Geological sketch map of the catchment area of Lake Malawi (data from Furon, 1963)

the equator, it has marked seasonal variations in temperature and rainfall. The prevailing winds are the South-east Trade winds and North-east Monsoons. The year may be divided into a rainy and a dry season and also into a hot and a cold season. The hot season commences in October and almost coincides with the rainy season which begins somewhat later, in December. There are consequently three main seasons:

- April to September: dry season (cool dry) South-east Trade winds
- October to December: dry season (hot dry) East/North-east winds
- December to April: rainy season (hot wet) North-east Monsoons

Records from stations in the catchment area are used to describe the climatic conditions.

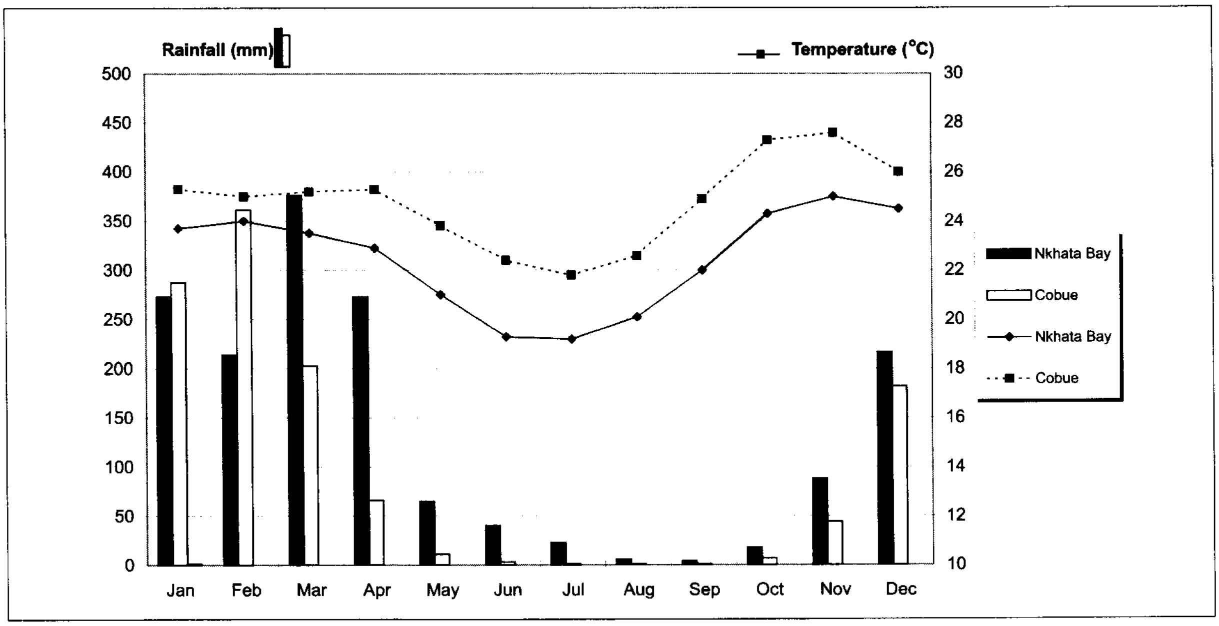
In Table 4.1, the means of climatological elements are given for two lake-shore stations: Nkhata Bay (Malawi) and Cobué (Mozambique). Records of several stations in Malawi show that the conditions in the catchment area are not uniform and that climatic conditions vary according to topography (Table 4.2). Comparison of five lake-shore stations over a 20-year period reveals that conditions were fairly similar for all stations (Patterson & Kachinjika, 1995). Detailed meteorological observations from Salima station for the period January 1991–January 1994 obtained from the Meteorological Department of Malawi are given by Patterson & Kachinjika (1995).

The main climatic elements – temperature, rainfall, wind and evaporation – are summarized below.

Temperature

Temperature recordings in Malawi date back to 1890, but more reliable records have been available since 1946 (Balarin, 1987). Mean monthly air temperature at Nkhata Bay (Malawi) and Cobué (Mozambique) is given in Figure 4.3. Maximum temperatures occur in November. Cloud cover in the rainy season after November has a cooling effect. The lake has a warming influence and the surrounding region tends to be warmer (Balarin, 1987). Air temperature (7-day running average) from Salima meteorological station for the period January 1991–January 1994 is given by Patterson & Kachinjika (1995).

Figure 4.3. Mean monthly air temperature and rainfall at Nkhata Bay (Malawi) and Cobue (Mozambique)



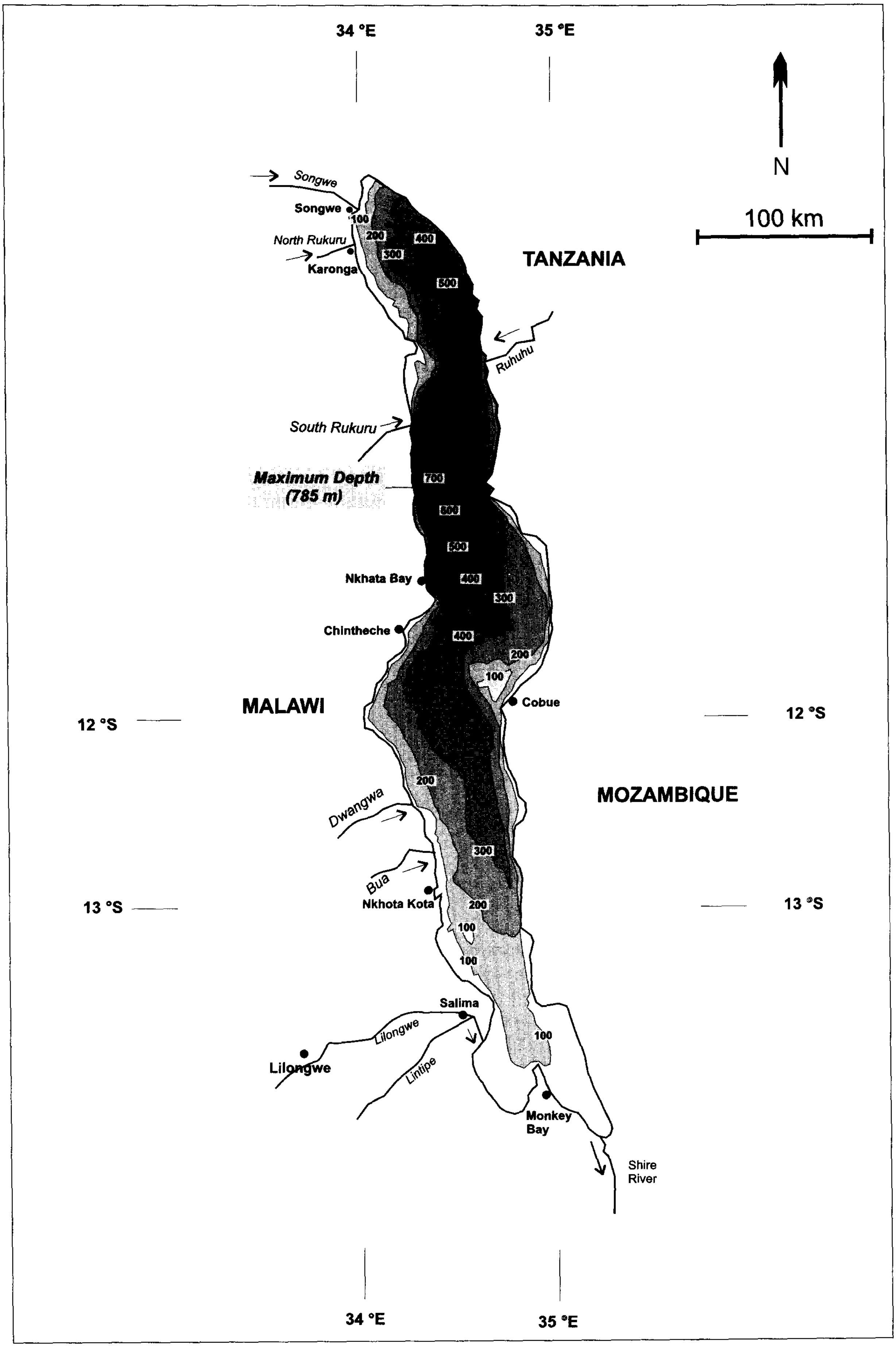


Figure 4.4 Bathymetric map of Lake Malawi

Table 4.2 Annual mean temperature and rainfall from several stations in Malawi (Source: FAO, 1984)

	Alt.	Temp (°C)	Rainfall (mm)
Nkhata Bay*	480	28.0	1597
Chitedzi	1149	19.4	848
Mzimba	1350	19.0	870
Mzuzu	1253	17.6	1344
Chitipa	1278	19.9	975
Karonga*	529	23.7	1121
Mulanje	628	21.0	1908
Bvumbwe	1146	18.3	1248
Lilongwe	1136	19.4	840
Chileka	767	21.9	847

* lake-shore station

Rainfall

The major tropical rains in the area are associated with an atmospheric belt of low pressure which follows the sun across the equator. The amount of rainfall varies considerably per season, with maxima in the period November–March/April when North-east Monsoons bring heavy rains. During the remaining part of the year (May–October) there is very little rainfall with South-east Trade winds. Fluctuations in rainfall are considerable from year to year. Rainfall is strongly related to topography. Highlands and exposed slopes facing prevailing winds during the rainy season have a much higher rainfall. Over 90% of Malawi receives more than 800 mm of rain per year (Balarin, 1987). Mean monthly rainfall at Nkhata Bay (Malawi) and Cobué (Mozambique) is given in Figure 4.3. Detailed information on rainfall in the catchment of Lake Malawi is given by Eccles (1984). Daily rainfall observations from Salima meteorological station for the period January 1991–January 1994 are given by Patterson & Kachinjika (1995).

Wind

During the dry season (May–October) the South-east Trade winds, known locally as 'Mwera', prevail creating dry and clear weather. The constant strong winds of the Mwera season blow more or less directly up the lake, being funnelled along the length by the mountains on either side. The N.E. Monsoon winds ('Mpoto') during the rainy season (November–March/April) are less strong and bring the rains. There are seasonal variations in wind speed with an increase in windspeed in the dry season (see Table 4.1). The southerly winds can blow with considerably force for several days, with speeds up to 40 km.hr^{-1} (Eccles, 1974). The lake generates diurnal on- and off-shore breezes (land-breeze in the morning and lake-breeze in the afternoon) and exerts a considerable moderating effect on the winds in its vicinity. Land breezes may be strong in the vicinity of high grounds (Eccles, 1974). Wind speed (21 days running average) from the Salima meteorological station for the period January 1991–January 1994 are given by Patterson & Kachinjika (1995). Comparison of wind speed at four lake-shore stations (Karonga, Nhota Kota, Salima and Monkey Bay) revealed that Karonga had higher wind speeds than the three other stations (Patterson & Kachinjika, 1995).

Evaporation

Evaporation rates vary and reach higher values on the eastern shore of the lake: 1337 mm.yr^{-1} at Nkhata Bay and 1659 mm.yr^{-1} at Cobué (Table 4.1). Evaporation rates are highest on the lake shore, reaching 2200 mm at Dwangwa and Karonga (Balarin, 1987). Seasonal variations in evaporation follow the variations in mean temperature (Table 4.1). Annual lake evaporation has been estimated at 1872 mm by Owen *et al.* (1990) based on an estimation of the annual lake level recession during the dry season (Harrison *et al.* 1976) and lake-shore Penman evaporation figures of Kidd (1983). Evaporation rates (7-day running average) from Salima meteorological station for the period January 1991–January 1994 are given by Patterson & Kachinjika (1995).

PRESENT FEATURES OF LAKE MALAWI

Lake Malawi consists of a single basin. It occupies part of the southern Rift Valley system and is to a large extent delimited by faults, in particular in the northern part of the lake, where depths over 200 m can be found close to the lake shore. In the south the lake divides into two arms round the Nankumba Peninsula. The lake is relatively shallow in these arms at less than 100 m.

The southern part of the lake is less deep, with the 200 m depth line at 110 km from the southern end. The lake is about 560 km long and has a maximum width of about 75 km. Its greatest reported depth is 785 metres in the northern part of the lake (Gonfiantini *et al.* 1979). General geography of the lake and the shoreline habitat types have been described by Mayland (1982).

In Figure 4.4 the outline of the lake and the 100 to 700 m depth lines are given. A map of the southern part of the lake is given by Owen *et al.* (1989). General characteristics of the lake are given in Table 4.3, together with hydrological and morphometric data. Physical and chemical parameters will be discussed in detail in the chapters that follow. Lake Malawi has a flushing time of 750 years, which is intermediate compared to the lakes Tanganyika (7,000 years) and Victoria (140 years) (Hecky & Bugenyi, 1992).

Table 4.3 **General, hydrological, morphometric and physico-chemical characteristics of Lake Malawi (Main sources: *a* – Vanden Bossche & Bernacsek, 1990*a*; *b* – Owen *et al.*, 1990; *c* – Gonfiantini *et al.* 1979) (otherwise reference given)**

a. General characteristics	
Latitude	9°30′–14°30′ S
Longitude	33°50′–35°20′ E
Altitude	471 m
Catchment area	126,500 km^2 (the lake included) (Drayton, 1979)
Vegetation catchment area	*Brachystegia* woodlands, tropical forests, savanna woodlands and open savanna grassland (Balarin, 1987)
Major inflowing rivers	• Malawi: Songwe River (International), Lufira, North Rukuru, South Rukuru, Dwangwa, Bua, Lilongwe • Tanzania: Songwe, Ruhuhu • Mozambique: Cobue, Lunho, Luaice, Luangua (Massinga, 1990)
Outflowing river	Shire River (international river)
b. Hydrological characteristics	
Inflow from streams (I)	29 $km^3.yr^{-1}$
Precipitation over lake (P)	41 $km^3.yr^{-1}$
Outflow (O)	12 $km^3.yr^{-1}$
Evaporation	54 $km^3.yr^{-1}$
Annual lake level fluctuations	0.7–1.8 m (Eccles, 1974)
Flushing time (Volume/O)	750 yr (Hecky & Bugenyi, 1992)
Residence time (Vol/P+I)	140 yr (Hecky & Bugenyi, 1992)
c. Morphometric characteristics	
Type of basin	Tectonic (Hutchinson, 1957)
Surface area	28,800 km^2
Max. length	560 km
Max. width	75 km
Max. depth	785 m; ± 700 m (Patterson & Kachinjika, 1995)
Mean depth	292 m
Volume	8,400 km^3
Shoreline	1,500 km (VandenBossche & Bernacsek, 1990*a*)
d. Physico-chemical data	
Nkhata Station offshore	
Surface temperature	23–29 °C (JFRO 1962, 1964)
Hypolimnion temperature	22.1 °C in 1939 (Beauchamp, 1953) 22.45 °C in 1955 (Jackson *et al.* 1963) 22.65 °C in 1964 (Eccles, 1974) 22.5 °C in 1980 (Degnbol & Mapila, 1982)
Conductivity (K_{20}) (surface)	215–225 $\mu S.cm^{-1}$
(300 m)	220–230 $\mu S.cm^{-1}$ (Jackson *et al.* 1963)
pH (surface)	7.9–9.1
(300 m)	7.8 (Jackson *et al.* 1963)
Secchi disk transparency	12–20 m (Ferro, 1977)
Ionic composition	see Table 7.1

Section III

State of knowledge on limnology and hydrology of Lake Malawi

5 Water balance

INTRODUCTION

Information on the water balance of Lake Malawi is scant. Lake levels are given by Drayton (1979), Eccles (1984) and the Water Resources Department of Malawi. Estimates on the water balance components are given by Owen *et al.* (1990).

HYDROLOGY OF LAKE MALAWI

Lake Malawi forms a reservoir of 8,400 km^3 of fresh water. Due to its large volume and relatively small outflow the lake has a flushing time of 750 years (Bootsma & Hecky, 1993). Lake Malawi has only one outlet, the Shire River leaving the lake at its southernmost point. In the first 20 km of its course the river has a slight gradient, on its way flowing into Lake Malombe; for the next 80 km the river has a steep gradient of about 280 m with a number of cataracts, the Murchinson Rapids. In the lower course the river has a floodplain/swamp, the Elephant Marsh, of which 500 km^2 is permanently flooded and up to 1,000 km^2 flooded during the rainy season (VandenBossche & Bernacsek, 1991*a*) and discharges into the Zambezi River. There are several inflowing rivers, of which the largest are the North and South Rukuru, Bua River and Lilongwe River in Malawi, the Songwe River on the border of Malawi and Tanzania and the Ruhuhu River in Tanzania. In Mozambique only short coastal streams flow into the lake. The Dwangwa River in Malawi is completely closed off during the dry season and diverted to irrigate the sugar fields of the Dwangwa Sugar Corporation. Besides, water is diverted from the Bua River for irrigation of a rice scheme (Tweddle, 1992). Due to its large surface area the major factors affecting the water balance of Lake Malawi are precipitation on the water surface and evaporation from it. The lake is highly sensitive to changes in the rainfall-evaporation ratio.

LAKE LEVELS

Annual variations in rainfall have caused large fluctuations in lake level from year to year. Lake levels for the period 1950–1993 are given in Figure 5.1. Regular lake levels are available from 1894. Information on water levels in the period 1865–1894 is available through measurements by Livingstone and several missionaries and a tentative curve for that period was drawn by Pike and Rimmington (1965). A historic sequence of lake levels from 1900 to 1982 is given by Eccles (1984). The water level records revealed a progressive fall from 1900 to a minimum in 1915, when the outflow via the Shire River ceased. From then the water level rose more than five metres to a maximum in 1937. In the period 1915–1935 the outflow was not resumed because of a combined blockage of sandbanks across the bed of the outlet, silt deposits by small tributaries and growth of vegetation in the river bed. In 1935 the lake reached a water level sufficient to wash away the obstructions at the outlet. In the period 1937–1964 the lake level remained below the maximum level of 1937. In 1964 the level of 1937 was exceeded by 0.08 m. During the following years

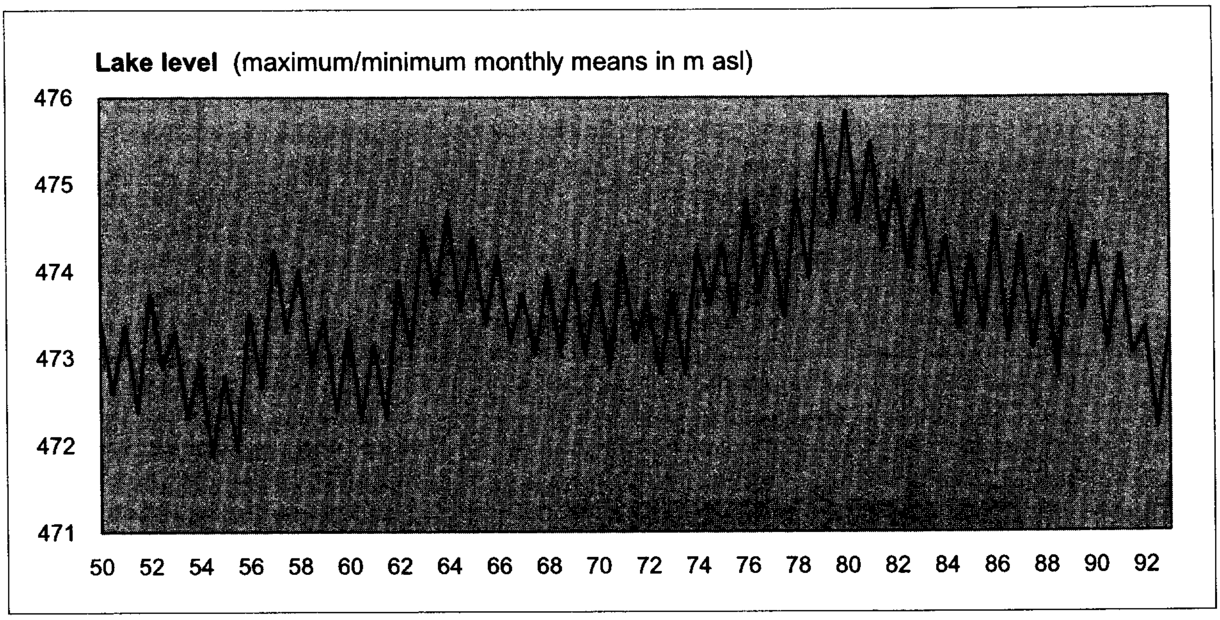


Figure 5.1 Lake levels between 1950 and 1993 (data from Water Resources Division of Malawi).

the water level gradually decreased until 1974, after which it rose again with maximum levels in 1979 and 1980 (at approximately 476 masl, 1.41 and 1.43 m respectively above the level of 1937). During the period 1980–1993 the level gradually decreased 3 metres (Figure 5.1).

The 1964 high level of Lake Malawi coincided with exceptionally high levels in Lakes Victoria, Mobutu and Tanganyika (Kite, 1981; Eccles, 1984). All four lakes also showed rises in water level in the late 1970s, but that in Lake Malawi was disproportionately greater than in the other lakes (Eccles, 1984). The high lake levels in the late 1970s caused considerable difficulties to lake-shore dwellers and inundated large areas of productive land; many properties had to be abandoned, and roads, harbours and lake-shore hotels were adversely affected (Eccles, 1984).

In addition to these variations from year to year there are seasonal fluctuations according to the rainfall pattern within the year. The seasonal low-water level is usually reached at the end of November. The lake level rises during the rainy season (November–April) reaching a maximum after the end of the rains in the south of the catchment, usually in May (Eccles, 1984). In the period 1948–1982 annual lake level fluctuations ranged between 0.25 m (in 1948–49) and 1.83 m in 1978–79, with a average annual fluctuation of approximately one metre (Eccles, 1984).

WATER BALANCE

The main components of the water balance of Lake Malawi are rainfall over the lake, evaporation from the lake surface, inflows and outflow. Groundwater inflow has been estimated at between 7 and 19 mm over the lake area (0.2 and 0.6 $km^3.yr^{-1}$) (Owen *et al.* 1990). A mean annual water balance of Lake Malawi was determined by Owen *et al.* (1990) using mean hydrological statistics for the period 1954–1980.

Table 5.1 Mean annual water balance of Lake Malawi (Owen *et al.* 1900)

Water balance components	Water balance (in mm over lake area)	Water balance (in $km^3.yr^{-1}$) (lake area: 28,750 km^2)
Rainfall over lake	1414	41
Inflow	1000	29
Evaporation	1872	54
Outflow	418	12
Increase in storage	112	3

6 Hydrodynamics

INTRODUCTION

In this chapter a description of the lake's stratification cycle will be given on the basis of temperature distribution, water movements, mixing and oxygen distribution.

Climatic conditions in the lake region affecting the water balance and distribution of the water temperature are summarized in Chapter 4, together with the bathymetric features of Lake Malawi (Figure 4.4). Data on the physical limnology of a tropical lake like Lake Malawi are limited compared with the information available on physical phenomena in temperate lakes such as the North American Great Lakes. The earliest information on the temperature distribution in the lake was provided by Fuellenborn (1900) who presented a temperature profile. It was the first observation of a thermocline in a tropical lake. From July 1939 to March 1940, Beauchamp (1939, 1940, 1953) carried out temperature and dissolved oxygen measurements which demonstrated a stratification cycle governed by wind and the existence of internal seiches with amplitudes of up to 50 m and periods of around 20 days. Since 1954 regular limnological observations have been carried out in Lake Malawi. Between 1954 and 1962 data on physical phenomena of the lake were collected on a regular basis in the vicinity of the research station of the JFRO at Nkhata Bay in the northern part of the lake. This 'standard station' was located some 5.5 km offshore from Nkhata Bay with a depth of approximately 400 m. In August 1962 the research station was moved to Monkey Bay, on the peninsula between the two southern arms of the lake. In the 1960s regular observations were made at a sampling point some 4.5 km offshore from Monkey Bay with a depth of about 98 m (Eccles, 1974). In 1976 a limnological study of the Chintheche area was conducted as part of the UNDP/FAO Fisheries project (1972–1976) (Ferro, 1977). From April 1978 to February 1981 limnological studies were carried out as part of the UNDP/FAO Fisheries Expansion project at a station two miles offshore and northeast of Nkhata Bay with a depth of 360 m.

Occasional lakewide surveys were made with regularly spaced stations. The first longitudinal run was made by Eccles (1965, 1974) in May 1964 which measured temperature profiles to a depth of 120 m at stations 10 km apart. Lakewide surveys were also carried out by the UNDP/FAO Fisheries Expansion Survey in October 1979 and April–May 1980 (FAO, 1982).

Recently in the period January 1992–January 1994 the UK/SADC Pelagic Fish Resource Assessment Project carried out a large limnological sampling programme which consisted of ten full-lake cruises and an intensive sampling of two stations (Nkhotakota and Nhkata Bay Stations) (Patterson & Kachinjika, 1995).

Appendix 2 provides an overview of papers providing data on physics and related chemistry of Lake Malawi.

TEMPERATURE DISTRIBUTION

Lake Malawi is permanently stratified. The water column can be divided into three layers: an epilimnion from the surface down to 125 m depth, a metalimnion

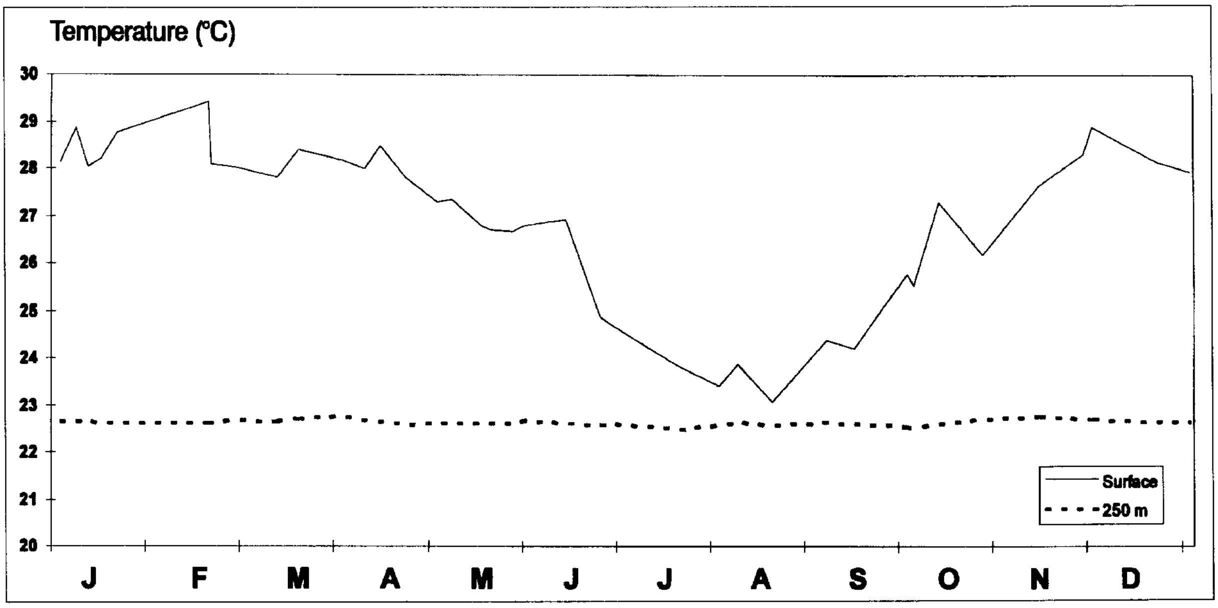


Figure 6.1 Annual variation in temperature of surface and deep water (250 m) in 1958 (data from JFRO, 1960)

from 125 to 230 m and a hypolimnion below 230 m (Gonfiantini *et al.* 1979). The metalimnion/hypolimnion boundary in the lake is maintained by a density difference caused by a higher salinity in the hypolimnion and the epilimnion/metalimnion boundary by a density difference caused by the higher temperature in the epilimnion. Observations by Patterson & Kachinjika (1995) confirmed the existence of a chemocline at about 230 m depth marked with a conductivity discontinuity. In the terminology for meromixis (Hutchinson, 1957) the hypolimnion is equivalent to monimolimnion and the water layers of the epilimnion and metalimnion to mixolimnion.

Beauchamp (1953) had already observed in 1939–1940 that the lake was meromictic with a warmer upper water layer overlying cooler water. Eccles (1974) observed in temperature profiles that there was a small but consistent density discontinuity at approximately 230 m. Below this depth the water has had a temperature of about 22.5 °C, has been anoxic and has contained free H_2S since at least 1954.

Annual cycle of stratification in the northern part of the lake

In the upper 230 m of the water layers of epilimnion and metalimnion an annual cycle of stratification occurs. A thermocline persists throughout the year in the upper 50–100 m of the water column. In Figure 6.1 the annual variation in temperature of the surface and the deep water (250 m) of Lake Malawi is given. The difference between deep and surface water is least in August, but complete mixing of the upper 250 m water column has never been observed since the earliest regular temperature observations in 1939–1940 by Beauchamp (1953). In 1958 the minimal temperature difference (0.18 °C) was observed between the surface water and 200 m, while the upper 80 m was homothermal at 23.08 °C (JFRO, 1960). In August 1992 and 1993 the temperature difference between surface water and 200 m was 0.6 °C (Patterson & Kachinjika, 1995).

The general pattern of the stratification cycle is (Eccles, 1974):

Phase 1 (Sept.–Dec.)

Warming up of the epilimnion; the surface temperature rises from approximately 23 °C to 28 °C; a developing stratification with a series of gradients separated by more or less homothermal layers.

Phase 2 (Dec.–May)

Development of one major thermocline which moves deeper as the season progresses. By the beginning of May the upper 60 m may be homothermal at about 27 °C.

Phase 3 (May–Sept.)

Cooling of the epilimnion with the onset of the dry season and of the south east trade winds resulting in decrease of the surface temperature to approximately 23 °C in August and a deeper thermocline.

Comparison of time-depth plots of temperature for the deep stations samples by Jackson *et al.* (1963), Eccles (1974) and Degnbol & Mapila (1982) with that of the offshore Nhkotakota station sampled in 1992–1993 revealed that all plots showed the general pattern of stratification as described above, but that the plot for the offshore Nhkotakota station was not subject to large short-term vertical shifts of isotherms as observed in the other plots (Patterson & Kachinjika, 1995).

Characteristic temperature profiles of the stratification cycle are shown in Figure 6.2.

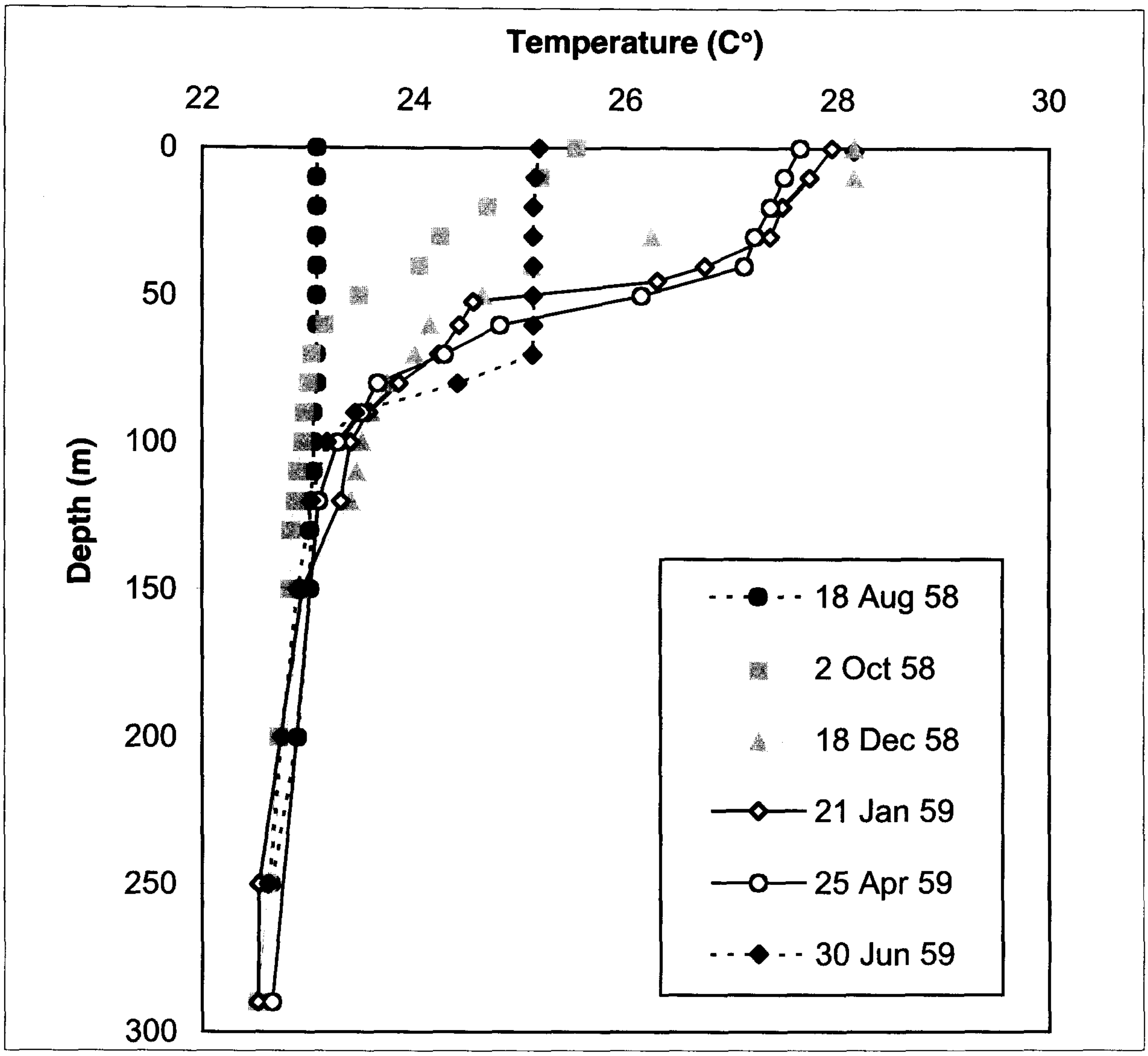


Figure 6.2. Characteristic temperature profiles of the stratification cycle in 1958–1959 (data from JFRO, 1960)

Annual cycle of stratification in southern arms of the lake

The southern arms of the lake with depths down to 100 m have basically the same pattern of stratification as the first 100 m of the deeper northern part (Eccles, 1974). The main difference between the two parts of the lake is that the temperature of the bottom water of the shallow southern arms often falls below the temperature of the deep water of the open lake in the cool season due to the cooling effect of the strong dry south-eastern trade winds (Eccles, 1974). The water chilled at the south is sinking and running along the bottom as a profile-bound density current.

Currents and water movements

Winds move water masses. Wind strength and direction determine the currents in the lake in addition to their effects on the vertical temperature distribution. The wind regime on Lake Malawi is dominated by South-east Trade winds, especially from May to September. Although the current systems of the lake have not been extensively studied, there appears to be a northerly drift of surface water on the western shore with a southerly return current on the eastern shore of about 0.5 $km.hr^{-1}$ (Eccles, 1974). In addition, profile-bound density currents in the south-east arm have been observed from temperature data (Eccles, 1974). Observations in the bay at Chintheche in 1975–1976 revealed currents along the shore to the north-east with velocities at the surface between 100 and 300 $m.hr^{-1}$, occasionally up to 600 $m.hr^{-1}$ (Ferro, 1977). Internal waves appear to play an important role in nutrient dynamics in Lake Malawi and turbulence associated with the waves will result in mixing between epilimnion and the deeper water layers and returning nutrients to the epilimnion. Internal waves were observed in 1954 by Jackson *et al.* (1963), and in 1967 by Eccles (1974). Patterson & Kachinjika (1995) found evidence that seiching occurred in the lake during the period September–November in 1992 and 1993.

Mixing

Deep lakes like Lake Malawi and Tanganyika show a tendency to mix deeply once a year. Mixing in lakes in Africa is mainly caused by loss of stability resulting from evaporative cooling of the upper water column, although influx of cool rainwater and reduced insolation can also be significant (Livingstone & Melack, 1984). During stratification mixing is confined to the upper water layers. Thickness of the upper mixed layer fluctuates strongly in tropical lakes (Lewis, 1973, 1983, 1984). During storms and windy weather the upper mixed layer will thicken, while calm and sunny periods will result in a thin mixed layer superimposed on the old mixed layer. In this way multi-layer stratification may occur. Variability of the thickness of the upper mixed layer will have great implications for productivity and composition of phytoplankton.

In meromictic lakes, such as Lake Malawi, nutrient concentrations increase with depth. Because the thermocline in the upper water layers of Lake Malawi does not break down completely, the return of nutrients from the metalimnion to the epilimnion is limited. Nutrient regeneration from the deeper water layers may, however, occur in different ways. In the open lake seiching along the north-south axis, especially in the period from September to November, may play an important role in mixing epilimnion with metalimnion water. A downward tilt of the thermocline towards the north of the lake and upwelling at the southern part of the lake was observed in July 1992 and 1993 (Patterson & Kachinjika, 1995). Local upwelling or partial mixing may occur in Lake Malawi under the influence of wind in the cold season, especially when the thermocline approaches the surface under the influence of an internal wave (Eccles, 1974). An isolated upwelling event occurred in the northern part of the lake in July 1993 when a notable plume of cold water was observed at the surface (Patterson & Kachinjika, 1995). Similar local upwelling events were observed in Lake Tanganyika (Coulter, 1968) and Lake Victoria (Kitaka, 1972). Kitaka (1972) suggested that the upwelling event in Lake Victoria was caused by cyclonic circulation.

In areas near lake margins with a gently sloping bottom, small oscillations of the thermocline were observed to involve large horizontal water displacements in the south-east arm of the lake in April 1964 (Eccles, 1974). Resulting currents along the bottom may cause mixing between metalimnion and epilimnion water and sweeping of the sediments (Eccles, 1974). Gonfiantini *et al.* (1979) showed by means of isotope analysis of tritium profiles in the lake that annually 25% of the metalimnion water is exchanged with the epilimnion.

DISSOLVED OXYGEN DISTRIBUTION

Observations by JFRO in 1978–1981 (1960, 1962, 1964), and those of Degnbol & Mapila (1982) and Patterson & Kachinjika (1995) at offshore stations revealed that the distribution of dissolved oxygen in the water column is coupled with the stratification regime. Dissolved oxygen gradually decreased with depth until it was virtually absent at 250 m and a sharp oxycline was only rarely observed. During the stratification period oxygen was generally present at concentrations of 7–8 mg $O_2.l^{-1}$ and occasionally up to 9.5 mg $O_2.l^{-1}$ (JFRO, 1960) down to the thermocline. Oxygen levels of 5–6 mg.l^{-1} were found below the thermocline and of 1 mg.l^{-1} at a depth of 200 m. During mixing oxygen levels increased in the water layers below 100 m depth, e.g. in June-August 1980 when a sharp oxycline was found between 100 and 275 m, and oxygen levels of 6 mg.l^{-1} were found down to a depth of 200 m (Degnbol & Mapila, 1982). Within 100 km of the southern end of the lake depth is less than 250 m and the south-east and south-west arms of the lake are shallower than 100 m. The lake bottom in the southern part of the lake is therefore exposed to metalimnetic water with oxygen levels decreasing from 6 mg.l^{-1} at 100 m to 1 mg.l^{-1} at 200 m (Eccles, 1986).

HYPOLIMNION

Gonfiantini *et al.* (1979) estimated by means of tritium isotope analysis that 20% of the metalimnion water is exchanged with the hypolimnion water annually. Cooling of deep water below a 250 m depth during the middle part of the year in 1993 also suggests some mixing at the metalimnion/hypolimnion boundary (Patterson & Kachinjika, 1995). The regular occurrence of chilling and profile-bound density currents in the south-east arm of the lake means that large volumes of cold water must enter the hypolimnion every year and this will contribute to the deep stratification of the lake (Eccles, 1974).

Eccles (1974, 1988) suggested a gradual warming of the hypolimnion in the period between 1939 and 1976 which was contested by Johnson & Ng'ang'a (1990). Measurements of the water column below 350 m in 1992–1994 indicated that the temperatures of the hypolimnion were 22.68 °C ± 0.01 (Patterson & Kachinjika, 1995). A comparison with the temperature of the hypolimnion in 1976 obtained by Gonfiantini *et al.* (1979) revealed that there was no hypolimnion warming between 1976 and 1993.

7 Nutrient dynamics

INTRODUCTION

As Lake Malawi is situated at 10–14° S, temperature and solar radiation – ranging between 400 and 600 $cal.cm^{-2}.dy^{-1}$ – are adequate for photosynthetic growth all year round. In Lake Malawi light may still be limiting, however, as deep mixing will carry the phytoplankton below the euphotic zone of approximately 50 m (see also Chapter 8). In general, nutrients are considered to limit algal productivity in the tropics, although the high temperature prevailing there allows rapid nutrient recycling. The elements required in largest amounts for plant production are carbon, phosphorus and nitrogen, while silicon is of importance to diatoms as a major component of the cell wall. Nutrients most likely to be limiting in African lakes are nitrogen (Talling & Talling, 1965; Moss, 1969; Lehman & Branstator, 1993) and phosphorus (Melack *et al.* 1982; Kalff, 1983) while silicon may limit diatom growth. Sulphates may also play a role in limiting phytoplankton productivity, as suggested for Lake Victoria by Hecky (1993). It appears that in Lakes Malawi, Tanganyika and Victoria concentrations of nutrients are generally low, and that not one nutrient is continuously controlling algal growth (Bootsma & Hecky, 1993).

The hydrodynamics of the lake play a major role in the nutrient dynamics. One of the most important aspects is the permanent stratification of the lake. The lake is meromictic with only the upper water layers mixing every year in the period June–August and a deeper, cooler, anoxic water mass below it. Because of this permanent stratification mixing and internal seiches play an important role in the annual cycle of nutrient concentrations in the upper layers of the lake. Another important process is the denitrification at the oxic-anoxic boundary which results in low NO_3 concentrations in the upper water layers (Bootsma & Hecky, 1993).

In this chapter the ionic composition and its possible effects on the algal growth is summarized, followed by a description of the nutrient cycles and the main forces controlling them, and of the nutrient sources.

IONIC COMPOSITION

Lake Malawi has a 'common' water type. The ionic composition is a product of deep weathering profiles of granitic and metamorphic rocks of the African plateau and is hardly influenced by volcanic terrain (Kilham & Hecky, 1973). The chemical composition of the dilute African waters with less than 600 ppm is largely controlled by rock weathering (Kilham, 1990). The water budget of Lake Malawi is dominated by direct rainfall on the lake (see Chapter 5). The lake is deep and meromictic and it only mixes down to a depth of 100 m once a year in the period June-August (see Chapter 6). Data on ionic composition and/or nutrients concentrations have been provided by Talling & Talling (1965), Hecky (1993), Bootsma & Hecky (1993), (Patterson & Kachinjika, 1995) and Bootsma *et al.* (in prep). Measurements of a number of chemical variables in 1992 and 1993 showed no evidence for a difference between the chemical characteristics of water in the north and south (Patterson & Kachinjika, 1995).

Table 7.1 **Chemistry of Lake Malawi at the surface and at 400 m depth (Hecky & Bugenyi, 1992 after Gonfiantini *et al.* 1979), and chemical composition of rain in 1990–1991 (Bootsma *et al.* in prep.). (All concentrations in μM)**

	L. Malawi surface	L. Malawi 400 m	Rain
Na	80	900	2.9
K	160	500	5
Mg	310	320	1.1
DIC [1]	2360	2510	–
Cl	130	140	1.5
SO_4	27	–	2.5
SRSi [2]	21.8	177.5	–
NO_3-N	>0.1	>0.1	3.2
NH^{4+}-N	–	–	5.4
PO_4-P (SRP) [3]	0.13	1.25	0.18
Total P	0.53	3.23	0.1
Alkalinity ($meq.l^{-1}$)	2.45	–	
Conductivity ($\mu S.cm^{-1}$)	285	–	

[1] dissolved inorganic carbon
[2] soluble reactive silicon (1μmol Si $(OH)_4$ l^{-1} = 28 μg Si (or SRSi) l^{-1}= 60 μg SiO_2 l^{-1})
[3] soluble reactive phosphorus

DISTRIBUTION OF NUTRIENTS

Distributions of the main plant nutrients nitrate (NO_3-N), phosphate (PO_4-P) and silicon strongly depend on the stratification processes, and are governed by physical factors (upwelling, mixing and diffusion) and biological processes, e.g. photosynthesis. Information on the vertical silicon distribution (cited as equivalent silica (SiO_2) concentrations) at the offshore station near Nkhata Bay in 1939 was provided by Beauchamp (1953). Studies by Jackson *et al.* (1963) and JFRO (1960, 1962, 1964) provided the first data on the distribution of nutrients. Studies in the early 1990s provided information on the present distribution of nutrients (Bootsma & Hecky, 1993; Patterson & Kachinjika, 1993, 1995).

Nutrient concentrations tend to increase with depth. Concentrations of phosphate, nitrate and silica are low in the epilimnion, especially in the euphotic zone where they are taken up by photosynthetic organisms. Concentrations increase in the metalimnion and hypolimnion. In the deep anoxic water layers of the hypolimnion ammonia is the dominant form of inorganic nitrogen resulting from denitrification at the oxic-anoxic boundary.

Concentration–depth profiles of nitrate, ammonia, soluble reactive phosphorus (SRP) and silicate together with dissolved oxygen given by Bootsma & Hecky (1993) clearly show low concentrations in the surface waters. Time–depth distributions of N, P and Si were strongly related to water temperature at the offshore station Nkhotakota in 1992 and 1993 and nutrient concentrations increased with depth (Patterson & Kachinjika, 1995). Nutrient concentrations appeared to be higher in the extreme south of the lake which can be explained by thermocline tilting and upwelling (Patterson & Kachinjika, 1995).

The N:P molar ratio appeared to be up to 8 in the epilimnion, higher (between 8 and 32) in the metalimnion and around 8 in the hypolimnion (Patterson & Kachinjika, 1995). This pattern was also observed in Lake Tanganyika by Hecky *et al.* (1991). Low ratios in the hypolimnion can be explained by denitrification at the oxic-anoxic boundary.

NUTRIENT LOADING

Possible sources of nutrients for phytoplankton in Lake Malawi are atmospheric deposition, riverine inputs, *in-situ* biological nitrogen fixation, recycling in the upper mixed layer and the nutrient-rich waters below the epilimnion. Groundwater inflow is likely to be negligible in Lake Malawi (Owen *et al.* 1990). Rain falling directly onto the lake may contribute significant quantities of minerals and nutrients. The ionic composition of rainwater in Malawi is given in Table 7.1.

Preliminary estimates of nutrient inputs into the mixed surface layer of Lake Malawi are given by Bootsma & Hecky (1993). Phosphate inputs to the upper layers of Lake Malawi are dominated by vertical mixing and diffusion from below the oxic-anoxic boundary while atmospheric deposition and river inputs account for the remaining 10% of the estimated total phosphate input. Because of denitrification around the oxic-anoxic interface there is no internal nitrogen loading from below this zone in Lake Malawi and nitrogen demands must be met by inputs from rivers, rain and dry fallout and nitrogen fixation. A recent study to determine the anthropogenic influence on precipitation chemistry in Malawi and the significance of atmospheric nutrient deposition in Lake Malawi's nutrient cycle (Bootsma *et al.* in prep.) revealed that atmospheric deposition accounted for 71 % of the nitrogen input into the lake, excluding nitrogen fixation. Nitrogen fixation of the gaseous nitrogen (N_2) by blue-green algae (e.g. *Anabaena*) and bacteria may be an important source of nitrogen. In Lake Malawi blue-green algae are an important component of the phytoplankton, although nitrogen-fixing algae are generally low in abundance (Hecky & Kling, 1987). In the littoral zone of the lake large aggregations of heterocystous cyanobacteria (cf. *Rivularia*) were often observed, which may indicate that nitrogen fixation in shallow waters is a substantial source of nitrogen for the lake (Bootsma, 1993).

8 The biotic environment

INTRODUCTION

Most limnological observations were made in the pelagic zone which is the most important area of the lake. Studies of the littoral zone have mainly been confined to taxonomic and ecological work on invertebrates and fish (e.g. Lowe, 1952 and Fryer, 1959). The present chapter deals mainly with the pelagic ecosystem.

THE PHYTOPLANKTON COMMUNITY

Phytoplankton studies

The phytoplankton of the lake has been studied floristically since 1899 (see Appendix 1).

Phytoplankton blooms of *Anabaena* were first observed by Lowe (1952) during her Tilapia research in the south-eastern arm of the lake, notably in September and October 1946 and blooms of *Melosira* (*Melosira* has been recently renamed *Aulacoseira*) and *Anabaena* in the 1960s (JFRO, 1964; Talling, 1969; Eccles, 1974). The first 'quantitative' phytoplankton observations were carried out by Jackson *et al.* (1963), who measured monthly plankton volumes (in cm^3, sedimented from 7070 litres of lake water) at the offshore station near Nkhata Bay from March 1954 to October 1955. Counts of phytoplankton from net hauls were made from July 1957 to November 1959 (JFRO, 1960).

In the last two decades phytoplankton investigations were carried out with modern quantitative ecological methods. Degnbol & Mapila (1982) carried out primary productivity and chlorophyll-*a* measurements at the offshore station near Nkhata Bay in 1980. Hecky and Kling (1987) provided data on temporal and spatial distribution of the phytoplankton in 1980. Haberyan (1988) and Haberyan & Mhone (1991) reported on phytoplankton studies from stations in the southern part of the lake near Cape Maclear. Recently Bootsma (1993) studied seasonal, vertical and horizontal distributions of phytoplankton in 1990. Phytoplankton and chlorophyll-*a* distribution have been studied during a number of lakewide surveys and at a station in the open water located at 12°43′ S, 34°30′ E in 1992–1993 by Patterson & Kachinjika (1993, 1995). In 1991 a preliminary study was carried out on taxonomy and ecology of phytobenthos in the northern part of the lake (Vyverman & Cocquyt, 1993).

Species composition

Observations on net plankton by JFRO (1960) at the offshore station near Nkhata Bay in 1957–1958 revealed that *Nitzschia* sp. was the dominant species, followed by *Melosira, Surirella, Microsystis, Pediastrum* and *Stephanodiscus*. *Botryococcus* was relatively abundant near the surface probably due to its buoyancy.

In 1980, phytoplankton was collected by taking samples of equal volume from evenly spaced depths over the euphotic zone (Hecky & Kling, 1987). Their collections differed substantially from earlier collections taken by nets. At the offshore station the phytoplankton was largely made up of blue-green algae, green algae and diatoms, while chrysophytes and peridineans were always rare. Prominent species were the blue-greens *Lyngbya circumcreta, L. bipunctata* and *Anabaena flosaquae. Nitzschia* sp. and *Stephanodiscus* sp. were the most abundant diatoms, while the genus *Melosira* was rarely found in the samples of the offshore station in 1980. The lack of a *Melosira* bloom in 1980, as reported by Hecky & Kling (1987), correlated well with the lack of *Melosira* in the 1980 diatomaceous laminae of a 26-year depositional record (Owen, 1989; Owen & Crossley, 1992). The year 1980 appeared to have been atypical of the long-term pattern for the area, which showed considerable variability from year to year, but with a general dominance of either *Melosira* or *Stephanodiscus* (Owen, 1989). The most important chlorophyte was *Coenococcus*, while *Mougeotia, Ankyra, Elakatothrix* and *Monoraphidium* appeared in the plankton in every season. Cryptomonads peaked in June and July).

The general pattern of phytoplankton composition observed by Hecky & Kling (1987) in 1980 was also found in 1990 by Bootsma (1993). The main factors controlling the different diatom assemblages in the lake have been summarized by Haberyan & Hecky (1987) and by Kilham *et al.* (1986). *Melosira* dominates where nutrients, and in particular Si, are abundant and turbulence is high. Low Si:P ratios favour *Stephanodiscus* and somewhat higher ratios *Nitzschia.*

The plankton composition observed by Patterson & Kachinjika (1995) in 1992–1993 closely resembled that of earlier studies by Hecky & Kling (1987), Haberyan & Mhone (1991) and Bootsma (1993), although there were some differences. Cryptomonads reported common by Hecky & Kling (1987) and Bootsma (1993) were absent in 1992–1993. Chrysophytes recorded by Hecky & Kling (1987) and Haberyan & Mhone (1991) as uncommon in the phytoplankton were not recorded in 1992–1993 and not by Bootsma (1993). The high densities of protozoans recorded by Bootsma (1993) were absent in 1992–1993 and also not recorded by the other studies. The two years 1992 and 1993 (Patterson & Kachinjika, 1995) appeared to have been somewhat atypical of the long-term pattern for the lake (Owen & Crosley, 1992) like the year 1980 studied by Hecky & Kling (1987).

Seasonal fluctuations

Stratified conditions in the lake favour cyanophytes and chlorophytes. Periods of mixing clearly favour diatoms and chrysophytes, as diatom abundance clearly followed the increased nutrient flux into the mixed layers in the period June-August (Hecky & Kling, 1987). Hecky & Kling (1987) observed a complete annual cycle at selected stations in 1980. Phytoplankton biomass was highest in January-March with a secondary peak in June-August. Maximum biomass values ranged between 100 and 200 mg.m^{-3}. Minimum values of 20–30 mg.m^{-3} were observed in April-May and October-November. Phytoplankton composition showed a dominance of Cyanophyta and Chlorophyta from October through March when the lake is thermally stratified, followed by a dominance of diatoms from April to September during the mixing period (Hecky & Kling, 1987).

In 1990 peaks in biovolume were observed in March and December, although maxima were not reported at all stations. Cyanophyta and in particular *Chroococcus limneticus* dominated the major peaks in biovolume reaching approximately 70% of the total biovolume. Diatom biovolume was dominated by *Stephanodiscus* and by *Aulacoseira* in October-December, although the latter only in the southern part of the lake. Chlorophyta biovolume was dominated by *Botryococcus braunii* at three of the five stations sampled in March 1991. However, the lake was calm in March and the high abundance may also have been the result of its buoyancy (Bootsma, 1993).

In 1992–1993 the highest biovolumes were found in the middle part of each year, with subsidiary peaks during the wet season. The phytoplankton was dominated by diatoms, specifically *Stephanodiscus* and *Cyclostephanos*, while blue-green algae were common throughout the year, with highest abundance in November 1993. Comparison of the phytoplankton composition in the lake during 1992–1993 with recent fossil records have revealed that the two years were not typical and that much longer time series are required to identify the factors which dictate changes in composition and production of phytoplankton (Patterson & Kachinjika, 1995).

Chorophyll-*a* 'concentrations in 1980–1981 varied between 0.1 and 2.1 mg.m^{-3} with a mean value of 0.73 mg.m^{-3} at 10 m and 0.65 mg.m^{-3} at 50 m and were generally highest between 30 and 50 m. The highest values between 1 and 2 mg.m^{-3} were found from June to August and December to February (Degnbol & Mapila, 1982). The average chorophyll-*a* concentration of all samples taken in 1992 and 1993 was 0.68 mg.m^{-3} (Patterson & Kachinjika, 1995).

Horizontal and vertical distribution

The phytoplankton studies in Lake Malawi in 1980 and the early 1990s (Hecky & Kling, 1987; Bootsma, 1993; Patterson & Kachinjika, 1995) showed no large differences in horizontal distribution of the phytoplankton both in biomass/biovolume and composition, like those observed in other large East African lakes (Talling, 1969, 1987; Coulter, 1963, 1991; Hecky & Kling, 1981). The relatively shallow south-east arm of the lake may have a somewhat higher phytoplankton biomass.

Based on the distribution of diatoms in the bottom sediments Lake Malawi can be divided into four sectors (Owen, 1989; Owen & Crossley, 1992):

- *the southern sector* characterized by *Melosira* dominance with variations at the species lèvel and by the presence of other less common taxa
- *the Nkhotakota sector* dominated by *Stephanodiscus,* and occasional blooms of *Melosira* and *Nitzschia*
- *the Central sector* showing the most varied pattern of diatom dominance at the generic level, with *Stephanodiscus, Melosira* and *Nitzschia* all becoming dominant or co-dominant at different times

- *the northern sector* characterized by *Melosira* dominance and extreme stability over time.

Vertical distribution pattern of the phytoplankton is important in relation to the euphotic zone. Phytoplankton densities in 1993 often showed sub-surface maxima made up of diatoms near the thermocline. These may reflect the slowing of the sinking rate caused by the increased water density. Blue-green algae showed some tendency to be shallower in the water column in the beginning of the year and were concentrated near the surface at the end of the year (Patterson & Kachinjika, 1995).

Light regime

Its large volume and steep basin slopes make Lake Malawi quite transparent and the euphotic zone can be in the order of 50 m (Hecky & Kling, 1987). During maximum circulation the mixed layer in Lake Malawi may be isothermal to 200 m (Eccles, 1974), which means that algal cells may circulate far below the euphotic zone. Light measurements carried out in 1980 appeared to be relatively constant through the year (Degnbol & Mapila, 1982). Light measurements carried out in 1992 and 1993 (Patterson & Kachinjika, 1995) confirmed the estimate of a euphotic zone of 50 m by Hecky and Kling (1987).

Photosynthesis

Primary productivity measurements with the ^{14}C method were carried out from March 1980 to February 1981 (Degnbol & Mapila, 1982). Light inhibition of photosynthesis close to the surface was often observed and maximum values were found between 5 and 15 m, except for two occasions in October and November when a peak was found at 20–25 m. Integrated production from March 1980 to February 1981 was 271 g $C.m^{-2}.yr^{-1}$, giving a daily average of 740 mg $C.m^{-2}$. Daily production was maximum in the period from June to September with levels of 920–1140 mg $C.m^{-2}$, and low levels were observed in December (380 mg $C.m^{-2}$) and February (240 mg $C.m^{-2}$). Bootsma (pers. comm.) found an average photosynthetic rate of 656 mg $C.m^{-2}.dy^{-1}$ for the whole lake and an average rate of 403 mg $C.m^{-2}.dy^{-1}$ for a station near the station that Degnbol & Mapila (1982) sampled. Average annual photosynthetic rates for the Nkhotakota station in 1992 and 1993 were 329.4 and 518.3 g $C.m^{-2}.yr^{-1}$ respectively (Patterson & Kachinjika, 1995). The large difference in productivity between these two years can be explained by the more pronounced seiching pattern in the mixing season of 1993 which resulted in greater amounts of nutrients in the epilimnion in that year compared to 1992 (Patterson & Kachinjika, 1995).

Periphyton photosynthesis has been measured in the south-east arm of Lake Malawi on seven dates between March and December 1992 (Bootsma & Hecky, in review). An estimate of benthic primary production within the south-east arm suggests that it may represent a significant proportion (between 19 and 38%) of total primary production in that area.

ZOOPLANKTON

Species composition

Studies on the zooplankton in Lake Malawi were carried out by Jackson *et al.* (1963), Degnbol & Mapila (1982), Twombly (1983), McKaye *et al.* (1985) and recently Irvine & Waya (1993, 1995) and Irvine (1995*a*, *b*). All studies have revealed that the pelagic zooplankton community consists of a small number of calanoid and cyclopoid copepods, a few Cladocera and larvae of the chaoborid *Chaoborus edulis* and the cyprinid *Engraulicypris sardella*. Zooplankton nomenclature has changed over the years and changes in the names of the main species are given in Table 8.1.

The post-naupliar *Tropodiaptomus cunningtoni* dominated the mean crustacean zooplankton biomass in 1992–1993. The two cyclopoid species, *Mesocyclops aequatoralis aequatoralis* and *Thermocyclops neglectus*, were common, while the latter was generally the more abundant of the two. *Thermodiaptomus mixtus* was generally uncommon, and only found in the southern part of the lake (south of latitude 13°08′ S). The cladoceran populations contributing little to the total zooplankton biomass were dominated by *Diaphanosoma excisum* and tended to be more abundant in the extreme south of the lake (Irvine, 1995*a*). *Chaoborus edulis* larval instars showed a high degree of variation in numbers of animals sampled and there was no consistent pattern of abundance over the lake (Irvine, 1995*b*). Larvae of the cyprinid *Engraulicypris sardella* appeared to be more abundant in the south, probably as a result of a higher adult biomass there (Thompson, 1995).

Previous studies revealed similar species composition and patterns of abundance of the crustacean zooplankton. In 1954–1955 crustaceans were by far the most important component of the zooplankton. Other groups were less important with the exception of the lake fly larvae *Corethra edulis* (= *Chaoborus edulis*) (Jackson *et al.* 1963). In the northern part of the lake the zooplankton consisted of *Diaptomus (Tropodiaptomus) kraepelini* and *Mesocyclops leuckarti*, which were the dominant species during the survey, and *Mesocyclops (Thermocyclops) neglectus*, the cladocerans *Diaphanosoma excisum, Bosmina longirostris, Bosminopsis deitersi* and the larvae of *Chaoborus edulis*. In the southern part the cladoceran *Daphnia lumholtzi* and *Diaptomus (Thermodiaptomus) mixtus* occurred together with all species recorded from the northern part of the lake. In 1978–1980 the zooplankton community was studied by Twombly (1983) at two stations (one offshore and one inshore) in the southern part of the lake near Cape Maclear during a period of 2.5 years. The most important zooplankton species – also observed in the southern part of the lake in the 1950s – were present throughout the year: *T. kraepelini, T. mixtus, M. leuckarti,*

Table 8.1 Nomenclature of main zooplankton species of Lake Malawi used by the UK/SADC project (Irvine & Waya, 1995) and in previous studies (Twombly, 1983; Degnbol & Mapila, 1982; Jackson *et al.* 1963; Fryer, 1957)

Irvine & Waya, 1995	Previous studies
Tropodiaptomus cunningtoni Sars	*T. kraepelini* Kiefer, *Diaptomus kraepelini*
Thermodiaptomus mixtus Sars	*Thermodiaptomus mixtus* Sars
Mesocyclops aequatoralis aequatoralis	*M. leuckarti aequatoralis, M. leuckarti*
Thermocyclops neglectus	*M. neglectus*
Diaphanosoma excisum	*Diaphanosoma excisum*
Bosmina longirostris	*Bosmina longirostris*
Chaoborus edulis (larvae)	*Corethra edulis* (larvae)
Engraulicypris sardella (larvae)	*Engraulicypris sardella* (larvae)

T. neglectus and the Cladocera *D. excisum and B. longirostris*. Copepod nauplii composed the largest proportion (30–80%) of the total crustacean zooplankton during the study period at both stations. The zooplankton community had its seasonal maximum in population size in the period July–October and its minimum in the period December–February. In the same period zooplankton abundance was estimated at several inshore stations near Cape Maclear (McKaye *et al.* 1985). Mean abundance in numbers per m^3 for the most important species were: *D. kraepelini* + *D. mixtus* (4,573); *M. leuckarti* (2,827); *D. excisum* (1,754); *M. neglectus* (3,386); *C. edulis* (5) and Nauplii (40,630). In 1980–1981 the pelagic zooplankton community in the offshore waters in the northern part of the lake consisted of five species (mean abundance and range in numbers per m^3 given between brackets): *D. kraepelini* (7,300 / 2,000–46,000); *M. leuckarti* (4,200 / 600–14,000); *D. excisum* (1,000 / 10–13,000); *B. longirostris* (14 / 0–500); *C. edulis* (19 / 2–1,000) (Degnbol & Mapila, 1982).

Seasonal fluctuations

Observations on the zooplankton at a station off Senga Bay (13°44′ S, 34°40′ E) from August 1991 to December 1993 revealed a maximum abundance of all crustacean zooplankton species between July and December and minimum abundance between February and May (Irvine, 1995*a*) which was in agreement with previous studies of Degnbol & Mapila (1982) and Twombly (1983). *C. edulis* larvae showed maximum abundance in the latter part of 1993 (Irvine, 1995*b*). The larvae of *E. sardella* showed well-defined seasonal patterns of abundance being more abundant from August to October and low in number from December to March (Thompson, 1995).

Twombly (1983) studied the seasonal variations in the abundance of crustacean zooplankton populations in the lake in the period 1979–1981. Four of the six most common zooplankton species showed clear seasonal maxima in population size. Only *T. mixtus* and *B. longirostris* lacked a clear seasonal pattern. *T. kraepelini*, nauplii and diaptomid copepods showed maximum abundance in the period of mixing (July–September) and *T. neglectus* in September-November when the epilimnion restratifies. The total number of crustacean zooplankton increased similarly to a maximum in the period July-September. In addition, the zooplankton exhibited aseasonal short-term fluctuations. Both seasonal and aseasonal fluctuations in abundance resulted in marked variations in abundance which differed considerably between years. Similar observations on the seasonal abundance of the common zooplankton species including *C. edulis* were made by Degnbol & Mapila (1982). *D. kraepelini, M. leuckarti, D. excisum* and nauplii were abundant in January and early March, and peaked in mid-March except for *D. excisum*. In early May *M. leuckarti, D. excisum* and nauplii increased in number and levels were maintained through early September. Abundance increased again in October and December–February. *D. kraepelini* reached its maximum abundance not before early July and after a decrease in September abundance increased in October and December–February, although to lower levels than before. Changes in the abundance of *B. longirostris* and *C. edulis* were greater than those observed in the other species. *C. edulis* peaked in January and remained low and variable from May 1980 until February 1981 except for a maximum in September–October. The maximum in population size of copepods and *D. excisum* during the period of mixing in June-August seems to be a response to the increased phytoplankton abundance, while the maxima during the stratification period are irregular and of shorter duration and may be related to varying mixing conditions (Degnbol & Mapila, 1982).

Spatial distribution

Distribution of crustacean zooplankton biomasses appeared to be homogeneous over the lake in 1992–1993 (Irvine 1995*a*), while *C. edulis* larvae were generally lower in abundance in the extreme south except for the latter part of 1993 (Irvine, 1995*b*). Average densities of *E. sardella* larvae appeared to be twice as high in the south as in the north (Thompson, 1995). Degnbol & Mapila (1982) did not observe a clear horizontal variation in crustacean zooplankton abundance between inshore and offshore stations.

Irvine (1995*a*) observed that crustacean zooplankton inhabited the upper 60–80 m of the water column with a greater depth of maximum abundance during the day than the night. Upward migration during the night was most obvious in *T .cunningtoni*. This species moved upwards in the water column over distances of 10–20 m (occasionally up to 40 m) and came close to the surface during the night as a possible response to predation pressure by the larger instars of *C. edulis* (Irvine, 1995*b*). The early larval instars of *C. edulis* showed diel vertical migration of relatively low amplitude probably in order to maintain themselves amongst their food supply, the crustacean zooplankton (Irvine, 1995*b*). The larger (especially the fourth) instars of *C. edulis* showed the ability to inhabit deeper, low oxygenated water layers during daytime and perform large diel vertical migrations of up to 200 m to the water layers near the surface at night. The reason for these large migrations is almost certainly to avoid the visually hunting planktivorous fish which could not follow the larvae into the low oxygenated water layers during daytime (Irvine, 1995*b*). Abundance of the *E. sardella* larvae was low in the upper 50 m at night with a maximum around 100 m depth and the larvae exhibited migrations of up to 50 m during daytime (Thompson, 1995; Turner *et al.* 1982).

Vertical distribution of the zooplankton was studied on three occasions by Degnbol & Mapila (1982): during moderate (June 1979) and maximum (February 1980) stratification and during the time of maximum mixing (August 1980). In June 1979 upward migration by *C. edulis* and *D. kraepelini* was observed during the night. Abundance of these species was low in the upper 10 m during daytime and generally maximum abundance was found between 10 and 25 m. *M. leuckarti* and *D. excisum* also avoided the upper 10 m during daytime with maximum abundance somewhat lower between 25 m and 50 m. In February 1980 during strong stratification all species showed an avoidance of the surface during daytime. At night abundance increased in the top 10 m. In August 1980 the same daytime avoidance of surface was noted as in the previous occasions. Residence time during the day was significantly deeper during daytime than at night for *D. kraepelini, D. excisum* and *B. longirostris.*

Zooplankton production

The UK/SADC research project estimated standing biomasses and productions of the main zooplankton groups. Total means of crustacean zooplankton standing biomass for the whole lake ranged between 886 ±106 and 2424 ± 344 mg dry wt.m^{-2} with an overall mean of 1608 ± 528 mg dry wt.m^{-2}.yr^{-1} . Average total annual copepod production was 49.5 g dry wt.m^{-2} (Irvine, 1995*a*). Total mean standing biomass of *C. edulis* was estimated as 72 ± 10 mg dry wt.m^{-2} and 201± 23 mg dry wt.m^{-2} and total production as 2.4 and 8.2 g dry wt.m^{-2} in 1992 and 1993 respectively (Irvine, 1995*b*). The average annual standing biomasses of *E. sardella* larvae for 1992 and 1993 were 15.0 and 34.8 mg dry wt.m^{-2} and average annual productions 0.96 and 2.08 g dry wt.m^{-2} respectively (Thompson, 1995).

TROPHIC DYNAMICS

The trophic relationships in the pelagic zone of Lake Malawi are relatively simple (Degnbol & Mapila, 1982; Allison *et al.* 1995) compared with the very complex interrelationships of communities in the inshore waters (Fryer, 1959; Ribbink *et al.* 1983; Reinthal, 1990).

Five crustacean zooplankton species are quantitatively important to the pelagic ecosystem: one calanoid copepod, *Tropodiaptomus cunningtoni,* and two cyclopoid copepods, *Mesocyclops aequatorialis aequatorialis* and *Thermocyclops neglectus;* two cladocerans, *Diaphanosoma excisum* and *Bosmina longirostris;* and larvae of *Chaoborus edulis* and *Engraulicypris sardella* and only eight fish species or species groups: *Diplotaxodon* 'elongata', *Diplotaxodon* 'bigeye', *Synodontis njassae, Rhamphonochromis longiceps, Rhamphochromis ferox, Engraulicypris sardella, Copadichromis quadrimaculatus* and *Opsaridium* spp. Information on the identification of these fish species is given by Allison, Ngatunga & Thompson (1995).

The food web of the pelagic zone of the lake comprises five trophic levels: phytoplankton, herbivorous zooplankton (*T. cunningtoni, T. neglectus, D. excisum* and *B. longirostris),* predatory zooplankton *(M. aequatorialis aequatorialis, C. edulis* and *E. sardella* larvae), zooplanktivorous fish (*E. sardella, C. quadrimaculatus* and *D.* 'elongata' feeding on herbivorous zooplankton and *D.* 'elongata', *D.* 'bigeye', *S. njassae, R.. longiceps* feeding on predatory zooplankton) and piscivorous fish (large *Rhamphochromis* spp. and *Opsaridium* spp. feeding on *E. sardella* and to a lesser extent on *R. longiceps, D.* 'bigeye' and *D.* 'elongata'). In the food web *C. edulis* appears to be a very important link between the herbivorous zooplankton and the fish. The diet of *C. edulis* larvae is estimated to consist of 72% herbivorous zooplankton, 10% *M. aequatorialis aequatorialis* and 8% algae. The larvae themselves form an important component of the diet of a number of fish species in the pelagic zone, although more than 50% of the *C. edulis* production does not pass to higher levels (Irvine, 1995*b*; Allison *et al.* 1995). This is in contrast to previous studies by Turner (1982) and Degnbol (1990) which have implied that *C. edulis* is not heavily preyed upon by fish. Detritus does not seem to be a significant source of energy to the higher trophic levels nor a significant source of organic carbon to the base of the food web (Allison *et al.* 1995).

Allison *et al.* (1995) used estimates of biomass, production and consumption for the main trophic groups to summarize the trophic structure of the pelagic ecosystem using the steady- state ECOPATH model (for details on the ECOPATH model and the ICLARM software package of the ECOPATH model see Polovina (1984*a,b*) and Christensen & Pauly (1991) respectively). Based on the ECOPATH modelling and all other studies on the trophic groups Allison *et al.* (1995) categorize the pelagic zone of the lake as a food limited system without vacant niches. They conclude therefore that an introduced zooplanktivorous fish would probably not be successful and that an elimination of the lakefly *C. edulis* would probably have large implications for the pelagic ecosystem of the lake.

9 Sediments

BOTTOM STRUCTURE AND GENERAL COMPOSITION OF SEDIMENTS

Several sediment types occur on the floor of Lake Malawi. Distribution of the main sediment types is given in Figure 9.1 and main characteristics of the major sediment types in Lake Malawi identified by Owen (1989) are given below:

1. *Diatomites*. This sediment type occurs in the shallowest rift settings. The main area lies in the southern part of the lake with water depths less than 150 m and minimal input of clastic material due to the relatively small catchment.
2. *Laminated muds* are composed of diatomites formed by cold season diatom blooms and clastic inputs of the rainy season. This sediment type mainly occurs in the northern deep water basins of the lake. The deposits owe their preservation to the anoxic bottom conditions.
3. *Homogeneous muds* of diatomaceous clays and silts at intermediate depths. Lamination has been destroyed due to oxygenated bottom waters which allow bioturbation The main areas of this sediment type lie between Salima and Likoma Island and smaller areas lie in the northern part of the lake off Karonga.
4. *Turbitides*. Series of micaceous and quartzo-feldspathic turbitides interbedded with pelagic sediments occur along the well defined axes of major boundary faults. Areas with this sediment type are found along the north-east lake shore and along the western lake shore near Nhkata Bay.
5. *Sand*. Sands of fluvial, colluvial and beach origins occur in areas on submerged tilt block surfaces at Mbenje, Likoma and Chisumulu Islands and in marginal locations down to about 150 m depth which have been maintained by strong bottom currents.
6. *Ferric oolites*. Ferro-manganous oolites and pisolites occur between 100 and 160 m depth at the boundary between sands and muds in the southern part of the lake.

PALEOLIMNOLOGY

Sediments accumulated in lake basins consist of various organic and inorganic substances providing information on the history of the lake, e.g. pollen, diatoms and inorganic compounds. Paleolimnology is a multidisciplinary science using information preserved in sediments to reconstruct past environmental conditions in aquatic systems.

Tremendous progress has been made in the development of paleolimnological techniques and approaches over the last decade. Advances include increased knowledge on indicator organisms, better use and combining of indicators and refinements in sampling techniques (Smol, 1992).

In Lake Malawi permanent anoxic conditions in the deep waters and a seasonal pattern in the supply of the major autochthonous and allochthonous sedimentary components to the lake basin are very favourable to deposition and preservation of finely laminated sedimentary sequences containing detailed information on seasonal, annual and longer term environmental conditions.

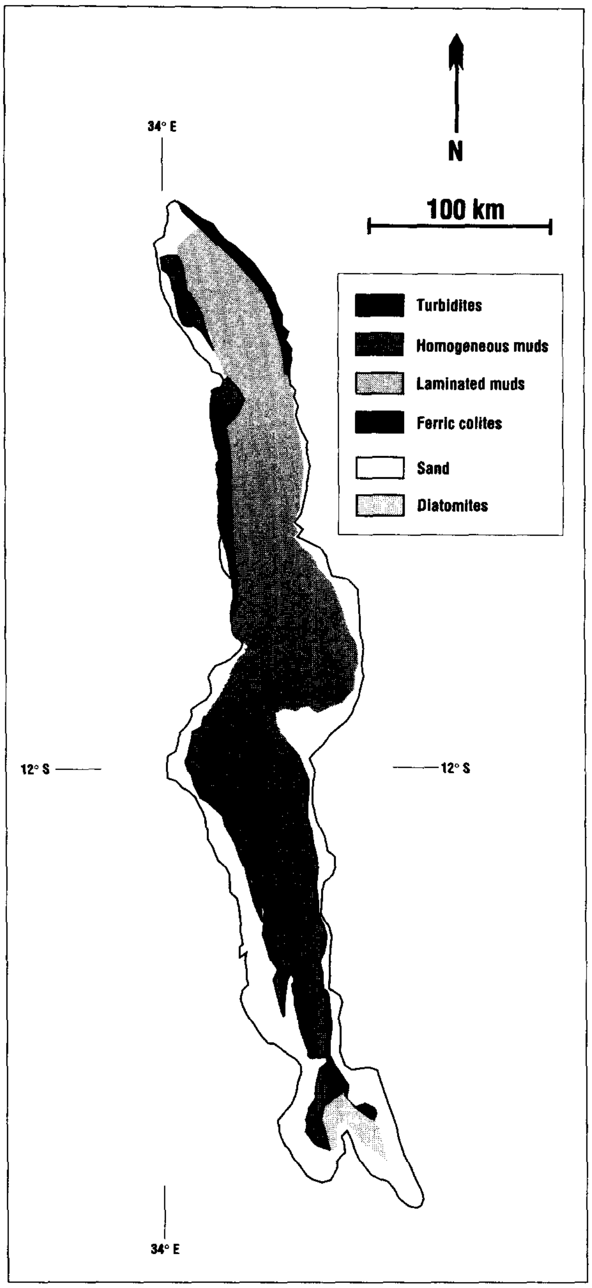


Figure 9.1 Distribution of major sediment types in Lake Malawi (Redrawn after Owen, 1989).

The presence of these conditions throughout a significant part of the lake's history has resulted in the deposition of thick laminated sequences consisting of light-dark laminae couplets with an average thickness of 1 mm representing biannual sedimentation sequences (Pilskaln & Johnson, 1991). The light laminae are completely dominated by diatoms resulting from diatom blooms during the dry, windy season and the dark laminae consist of 50% diatoms and 50% terrestrial plant debris, mineral grains, clay and organic material sedimented in the rainy season (November–March) (Pilskaln & Johnson, 1991).

Studies on sediment cores (Owen, 1989; Owen *et al.* 1990; Pilskaln & Johnson, 1991; Owen & Crossley, 1992) revealed that *Melosira* was the dominant diatom in the Lake Malawi sediments throughout the 10,000-year depositional history of the lake, which indicates persistence of strong, seasonal wind stress and resultant turbulent mixing and nutrient upwelling conditions in this period.

Evidence of regional climatic change and fluctuations in lake level were also apparent in the sediment records. The laminated sequences indicating periods of high lake levels are frequently interrupted by diatom-rich, nonlaminated layers reflecting fluctuations in local climate and lake level (Pilskaln & Johnson, 1991). Periods of low lake level are associated with a marked increase in littoral diatom species and coarse sand in the sediments and an increase of allochthonous inputs (Johnson *et al.* 1988; Owen, 1989). The surface of sandy lake shore deposits were also observed in the high-resolution seismic profiles made in the lake (Scholz & Rosendahl, 1988; Johnson & Davies, 1989).

References

ALIMOSO, S. B.; MAGASA, J. H.; VAN ZALINGE. N. P. 1990. Exploitation and management of fish resources in Lake Malawi. pp. 83–95. In: IAC, Fisheries research papers of the International Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura, Burundi. Fisheries and Aquaculture Unit, IAC Wageningen, The Netherlands. Occasional Paper No. 3.

ALLISON, E. H.; NGATUNGA, B. P.: THOMPSON, A. B. 1995. Identification of the pelagic fish. Chapter 6. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa.* Natural Resources Institute, Chatham, U.K. (In press).

ALLISON, E. H.; PATTERSON, G.; IRVINE, K.; THOMPSON, A. B.; MENZ, A. 1995. The pelagic ecosystem. Chapter 12. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa.* Natural Resources Institute, Chatham, U.K. (In press).

ANDREAE, M. O. 1991. Biomass burning: Its history, use and distribution and its impact on environmental quality and global warming. In: *Global Biomass Burning: Atmospheric, Climatic and Biospheric Implications.* Proceedings of the Chapman Conference, 12–23 March 1990, Williamsburg, VA, USA.

BAKER, J. M. 1992. Oil and African Great Lakes. pp. 71–78. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes,* Bujumbura 1989. SIL Mitteilungen No. 23.

BALARIN, J. D. 1985. *National Reviews for Aquaculture Development in Africa. 11.* Tanzania. FAO Fish. Circ. 770.11. 105 pp.

——. 1987. *National Reviews for Aquaculture Development in Africa. 12.* Malawi. FAO Fish. Circ. 770.12. 82 pp.

BEADLE, L. C. 1974. *The Inland Waters of Tropical Africa: an Introduction to Tropical Limnology.* 365 pp. London: Longman.

——. 1981. *The Inland Waters of Tropical Africa: an Introduction to Tropical Limnology.* 2nd edition, 475 pp. London: Longman.

BEAUCHAMP, R. S. A. 1939. Hydrology of Lake Tanganyika. *Int. Revue ges. Oceanogr.,* 10: 510–520.

——. 1940. Chemistry and Hydrography of Lakes Tanganyika and Nyasa. *Nature,* London, 146: 253–256.

——. 1953. Hydrological data from Lake Nyasa. *J. Ecol.,* 41: 226–239.

BOOTSMA, H. A. 1992. Lake Malawi National Park. pp. 125–128. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes,* Bujumbura 1989. SIL Mitteilungen No. 23.

——. 1993. *Algal Dynamics in an African Great Lake and their Relation to Hydrographic and Meteorological Conditions.* Ph.D. thesis. University of Manitoba, Canada.

——. 1993. Spatio-temporal Variation of Phytoplankton Biomass in Lake Malawi, Central Africa. *Verh. Internat. Verein. limnol.,* 25: 882–886.

BOOTSMA, H. A.; HECKY, R.E. 1993. Conservation of the African Great Lakes: A Limnological Perspective. *Conservation Biology,* 7(3):644–656.

——. In review. Initial measurements of benthic photosynthesis in an African Great Lake. (Submitted to *Limnology and Oceanography*)

BOOTSMA, H. A.; BOOTSMA, M. J.; HECKY, R. E. In prep. The chemical composition of precipitation and its significance to the nutrient budget of tropical Lake Malawi.

CHRISTENSEN, V.; PAULY, D. 1991. A guide to ECOPATH II software system (Version 2.0). *ICLARM Software,* 6: 71pp.

COULTER, G. 1963. Hydrobiological changes in relation to biological production in southern Lake Tanganyika. *Limnol. Oceanogr.*, 8: 463–477.

——. 1968. *Hydrological processes and primary production in Lake Tanganyika.* Proc. 11th Conf. Great Lakes Res. 609–626.

——. 1991. *Lake Tanganyika and its life.* British Museum (Natural History) and Oxford Univ. Press. 354 pp.

CROSSLEY, R.; DAVISON-HIRSCHMANN, S.; OWEN, R.B.; SHAW, P. 1984. Lake level fluctuations during the last 2000 years in Malawi. pp. 305–316. In: J. C. Vogel (ed.), *Late Cainozoic palaeoclimates of the southern hemisphere.* Sasqua International Symposium (Swaziland), 29 August–2 September 1983. Rotterdam, A. A. Balkema.

CRUL, R.C.M. 1992*a*. *Database on the inland fisheries resources of Africa (DIFRA). A description.* FAO/CIFA Occ. Pap. No. 17. Rome, FAO. 21p.

——. 1992*b*. *Models for estimating potential fish yields of African inland waters.* FAO/CIFA Occ. Pap. No. 16 Rome, FAO. 22p.

DAVIES, B. R.; WALKER, K. F. 1986. *The Ecology of River Systems.* Monographiae Biologicae No. 60. Dordrecht: Junk Publ.

DEGNBOL, P. 1990. *The pelagic zone of central Lake Malawi – A trophic box model.* ICES CM 90 /L:30. 7 pp.

DEGNBOL, P.; MAPILA, S. 1982. Limnological observations on the pelagic zone of Lake Malawi from 1970 to 1981. pp. 5–47. In: FAO, *Biological studies on the pelagic ecosystem of Lake Malawi.* FI:DP/MLW/75/019 Technical Report 1. FAO, Rome.

DIXEY, F. 1926. The Nyasaland section of the Great Rift Valley. *Geogr. J..*, 68: 117–140.

DRAYTON, R. S. 1979. *A study of the causes of the abnormally high levels of Lake Malawi in 1979.* Lilongwe, Water Resources Division. Report No. TP.5. 46p.

ECCLES, D. H. 1974. An outline of the physical limnology of Lake Malawi (Lake Nyasa). *Limnol. Oceanogr.*, 19(5): 730–42.

——. 1984. On the recent high levels of Lake Malawi. *S. Afr. J. Sci.*, 80: 461–468.

——. 1985. Lake flies and sardines – a cautionary note. *Biol. Conserv.*, 33(4):301–333.

FAO. 1984. *Agroclimatological Data for Africa Volume 2. Countries south of the equator.* FAO Plant Production and Protection Series No. 22. FAO. Rome.

——. *Fisheries management in the south-east arm of Lake Malawi, the Upper Shire river and Lake Malombe with special reference to the fisheries on chambo* (Oreochromis spp.). Report on the Workshop held at Mangochi, 8–11 July 1992. FI:DP/MLW/86/013, Technical Paper 1, 106 pp.

FERRO, W. 1977. *A limnological baseline survey of the Chintheche area of Lake Malawi.* FAO FI:MLW/71/516/13. FAO, Rome. 23 pp.

FREY, D. G. 1990. What is a lake? *Verh. Internat. Verein. limnol.*, 24: 1–5.

FRYER, G. 1959. The trophic interrelationship and ecology of some littoral communities of Lake Nyasa with special reference to the fishes, and a discussion of the evolution of a group of rock-frequenting cichlidae. *Proc. Zool. Soc. Lond.*, 132, Part 2, pp. 153–281.

FRYER, G.; ILES, T. D. 1972. *The Cichlid Fishes of the Great Lakes of Africa.* Edinburgh: Oliver & Boyd, 642 pp.

FRYER, G.; TALLING, J. F. 1986. Africa: The FBA Connection. *Rep. Freshwat. Biol. Ass.*, 1986, No. 54, 97–122.

FUELLEBORN, F. 1900. Über Untersuchungen in Nyassa-See und in den Seen im nördlichen Nyassa-Land. *Verh. Ges. Erdkd. Berl.*, 28: 332–338.

FURON, R. 1963. *Geology of Africa.* English edition. Edinburgh and London, Oliver & Boyd. 377 p.

GONFIANTINI, R.; ZUPPI, G. M.; ECCLES, D. H.; FERRO, W. 1979. Isotope investigation of Lake Malawi. pp. 195–205. In: IAEA, *Proceedings on the application of nuclear techniques to the study of lake dynamics,* Vienna, 29 August- 2 September 1977. Vienna, IAEA.

GREGORY, J. W. 1896. *The great Rift Valley, being the narrative of a journey to Mount Kenya and Lake Baringo.* London, John Murray.

——. 1921. *The rift valleys and geology of East Africa.* London, Seeley Service and Company.

GRIFFITHS, J. F. 1972. Eastern Africa. pp. 313–348. In: J. F. Griffiths (ed.), *Climates of Africa. World Survey of Climatology,* Vol. 10.

HABERYAN, K. A. 1988. *Phycology, sedimentology and paleolimnology near Cape Maclear, Lake Malawi, Africa.* Ph.D. thesis, Duke University. 246 pp.

——. 1990. The misrepresentation of the planktonic diatom community in traps and sediments: southern Lake Malawi, Africa. *Africa J. Paleolimnol.*, 3:35–44.

HABERYAN, K. A.; HECKY, R. E. 1987. The late Pleistocene and Holocene stratigraphy and paleolimnology of the Lakes Kivu and Tanganyika. *Palaeogeogr. Palaeoclim. Palaeooecol.*, 61: 169–197.

HABERYAN, K. A.; MHONE, O. K. 1991. Algal communities near Cape Maclear, southern Lake Malawi, Africa. *Hydrobiologia,* 215: 175–188.

HARRISON, K. P.; LORUM , L. E.; MATTICK, A. K. 1976. A water resources assessment of Lake Malawi. WMO/UNDP project report MLW/71/518. 167 pp.

HALFMAN, J. D. 1993. Water characteristics from modern CTD data, Lake Malawi, Africa. *J. Great Lakes Res.*, 19: 512–520.

HALFMAN, J. D.; Scholz, C.A. 1993. Suspended sediments in Lake Malawi, Africa: A reconnaissance study. *J. Great Lakes Res.*, 19:499–511.

HECKY, R. E.; BUGENYI, F. W. B. 1992. Hydrology and chemistry of the African Great Lakes and water quality issues: Problems and solutions.

pp. 45–54. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes,* Bujumbura 1989. SIL Mitteilungen No. 23.

HECKY, R. E.; KLING, H. J. 1981. Phytoplankton ecology and zooplankton of the euphotic zone of Lake Tanganyika: species composition, biomass, chlorophyll content, and spatio-temporal distribution. *Limnol. Oceanogr.,* 26: 548–564.

——. 1987. Phytoplankton ecology of the great lakes in the rift valleys of Central Africa. *Arch. Hydrobiol. Beih.,* 25: 197–228.

HECKY., R. E.; SPIGEL, R. H.; COULTER, G. W. 1991. The nutrient regime. pp. 76–89. In: G. Coulter (ed.), *Lake Tanganyika and its life.* British Museum (Natural History) and Oxford Univ. Press.

HUTCHINSON, G. E. 1957. *A Treatise on Limnology.* Vol. 1. Wiley, New York. 1016 pp.

——. 1967. *A Treatise on Limnology.* Vol. 2. Wiley, New York. 1115 pp.

——. 1973. Eutrophication. The scientific background of a contemporary practical problem. *Americ. Sci.,* 61: 269–279.

——. 1975. *A Treatise on Limnology.* Vol. 3. Wiley, New York. 660 pp.

HYNES, H. B. N. 1972. *The Ecology of Running Waters.* Liverpool University Press, Liverpool. 555 pp.

IAC 1990. Report on the International Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura, Burundi, November 29–December 2, 1989. Fisheries and Aquaculture Unit, IAC Wageningen, The Netherlands. Occasional Paper No. 2. 71 pp.

IDEAL 1990. An International Decade for the East African Lakes. Workshop Report 1 on the Paleoclimatology of African Rift lakes, Bern, Switzerland, March 29–31 1990. Duke University Marine Lab. Technical Paper. Duke University, Beaufort (USA). 37 pp.

—— 1993. The International Decade for the East African Lakes. The IDEAL Symposium on the Limnology, Climatology and Paleoclimatology of the East African Lakes. Jinja, Uganda, 18–23 February 1993. Program with Abstracts. 30 pp.

IRVINE, K. 1995*a*. Standing biomasses, production and spatio-temporal distributions of the crustacean zooplankton. Chapter 3. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa.* Natural Resources Institute, Chatham, U.K. (In press).

——. 1995*b*. Ecology of the lakefly, *Chaoborus edulis.* Chapter 4. *In* A. Menz (ed.) The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa. Natural Resources Institute, Chatham, U.K. (In press).

IRVINE, K.; WAYA, R. 1993. Predatory behaviour of the cyclopoid copepod *Mesocyclops aequatorialis aequatorialis* in Lake Malawi, a deep tropical lake. *Verh. Internat. Verein. Limnol.,* 25: 877–881.

——. 1995. The zooplankton: general sampling methods and estimation of biomass and development rates. Chapter 2. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa.* Natural Resources Institute, Chatham, U.K. (In press).

IRVINE, K.; WAYA, R.; HART, R. C. 1995. Additional studies into the ecology of *Tropodiaptomus cunningtoni.* Chapter 5. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa.* Natural Resources Institute, Chatham, U.K. (In press).

JOHNSON, T. C.; Halfman, B. M.; VAUGHAN, N. D. 1988. Sediment core descriptions: Malawi '86: Lake Malawi, East Africa. Duke Univ. Mar.Lab. Project PROBE Techn. Report.

JOHNSON, T. C.; DAVIES, T. W. 1989. High resolution seismic profiles from Lake Malawi, East Africa. *African Earth Sci.,* 8: 383–392.

JOHNSON, T. C.; NG'ANG'A, P. 1990. Reflections on a rift lake. In: B. J. Katz (ed.), Lacustrine basin exploration: case studies and modern analogs. *Assoc. Petrol. Geol. Mem.* , 50:113–115.

JACKSON, P. B. N.; ILES, T. D.; HARDING, D.; FRYER, G. 1963. *Report on the survey of northern Lake Nyasa 1954–55.* Zomba, Government Printer. 171 pp.

JFRO. 1960. *Joint Fisheries Research Organisation Annual Report No. 9, 1959.* Government Printer, Lusaka.

——. 1962. *Joint Fisheries Research Organisation Annual Report No. 10, 1960.* Government Printer, Lusaka.

——. 1964. *Joint Fisheries Research Organisation Annual Report No. 11, 1962.* Government Printer, Lusaka.

KALFF, J. 1983. Phosphorus limitation in some tropical African lakes. *Hydrobiologia* , 100:101–112.

KILHAM, P. 1990. Mechanisms controlling the chemical composition of lakes and rivers: Data from Africa. *Limnol. Oceanogr.,* 35: 80–83.

KILHAM, P.; Hecky, R. E. 1973. Fluoride: geochemical and ecological significance in East African waters and sediments. *Limnol. Oceanogr.,* 18: 932–945.

KILHAM, P.; KILHAM, S. S.; HECKY, R. E. 1986. Hypothesized resource relationships among African planktonic diatoms. *Limnol. Oceanogr.,* 31: 1169–1181.

KILHAM, S. S.; KILHAM, P. 1990. Tropical limnology: Do African lakes violate the 'first law' of limnology? *Verh. Internat. Verein. Limnol.,* 24: 111–120.

KIDD, C. H. R. 1983. *A water resources evaluation of Lake Malawi and the Shire River.* UNDP project report MLW/77/012. 135 pp.

KITAKA, G. E. B. 1972. An instance of cyclonic upwelling in the southern offshore waters of Lake Victoria. *Afr. J. Trop. Hydrobiol. Fish.,* 2(1): 85–92

KITE, G. W. 1981. Recent changes in level of Lake Victoria. *Hydrol. Sci. Bull.,* 26(3): 233–243.

LEHMAN, J. T.; BRANSTRATOR, D. K. 1993. Effects of nutrients and grazing on phytoplankton of Lake Victoria. *Verh. Internat. Verein. Limnol.,* 25:850–855.

LEWIS, W. M. 1973. The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. *Limnol. Oceanogr.,* 18: 200-217.

——. 1983. Temperature, heat, and mixing in Lake Valencia. *Limnol. Oceanogr.,* 28: 273-286.

——. 1984. A five-year record of the thermal and mixing properties for a tropical lake (Lake Valencia, Venezuela). *Arch. Hydrobiol.*, 99: 340-346.

——. 1987. Tropical limnology. *Ann. Rev. Ecol. Syst.* 18: 159–184.

LIKENS, G. E. (ed.). 1972. Nutrients and eutrophication: The limiting-Nutrients Controversy. Special Symposium. *Amer. Soc. Limnol. Oceanogr.,*, 1, 328 pp.

LOWE, R. H. 1952. *Report on the Tilapia and other fish and fisheries of Lake Nyasa 1945–47*. Part 2. Fish. Publ. Colon. Off. Lond. 1(2): 126 pp.

LOWE-MCCONNELL, R. H.; CRUL, R. C. M.; ROEST, F. C. (eds.). 1992. *Symposium on Resource Use and Conservation of the African Great Lakes*, Bujumbura 1989. SIL Mitteilungen No. 23. 128 pp. With 46 figures and 18 tables in the text.

MASSINGA, A. V. R. 1990. River impact on the cyprinid fishery of the Mozambiquean side of Lake Niassa/Malawi with particular reference to the genus *Opsaridium* and the importance of long-term data collection. pp. 96–108. In: SIL, *Fisheries of the African Great Lakes*. Research papers presented at the International Symposium on Resource Use and Conservation of the African Great Lakes Bujumbura 1989. Fisheries and Aquaculture Unit, IAC Wageningen, The Netherlands. Occasional Paper No.3. 134 pp.

MAYLAND, H. J. 1982. *Der Malawi-See und seine Fische*. Hannover, Landbuch Verlag. 336 pp.

MCKAY, K. R.; MAKWINJA, R. D.; MENYANI, W. W.; MHONE, O. K. 1985. On the Possible Introduction of Non-indigenous Zooplankton-feeding Fishes into Lake Malawi, Africa. *Biol. Conserv.*, 33: 289–307.

VAN MEEL, L. 1954. Le phytoplancton. Résultats scientifiques de l'exploration hydrobiologique du Lac Tanganika (1946–1947). *Inst. Roy. Sc. Nat. Belg.*, 4 (1)A: 1–681.

MELACK, J. M.; KILHAM, P.; FISCHER, T. R. 1982. Responses of phytoplankton to experimental fertilization with ammonium and phosphate in an African soda lake. *Oecologia*, 52: 321–326.

MENZ, A. (ed.). 1995. *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Natural Resources Institutes, Chatham, U.K. (In press).

MOOREHEAD, A. 1960. *The White Nile*. Hamish Hamilton, London.

MOSS, B. 1969. Limitation of algal growth in some central African waters. *Limnol. Oceanogr.*, 14: 591–601.

NATIONAL ACADEMY OF SCIENCES. 1969. *Eutrophication: Causes, Consequences, Correctives*. Washington D.C., National Academy of Sciences. 661 pp.

NONGWA, G.M. 1986. African lakes. *Nature*, London, 322: 679.

NTAKIMAZI, G. 1992. Conservation of the resources of the African great lakes. Why? An overview. pp. 71–78. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on resource use and conservation of the African Great Lakes*, Bujumbura 1989. SIL Mitteilungen No. 23.

OWEN, R. B. 1989. Pelagic Fisheries Potential of Lake Malawi – Palaeolimnology and palaeoproductivity of Lake Malawi and its implications for fisheries management. ODA project R4370. ODA, London. 300 pp.

OWEN, R. B.; CROSSLEY, R. 1992. Spatial and temporal distribution of diatoms in sediments of Lake Malawi. *J. of Paleolimnology* 7:55–71.

OWEN, R. B.;CROSSLEY, R.; JOHNSON, T. C.; TWEDDLE, D.; KORNFIELD, I.; DAVISON, S.; ECCLES, D. H.; ENGSTROM, D. E. 1990. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proc. R. Soc. Lond.*, B 240: 519–553.

PATTERSON, G.; KACHINJIKA, O. 1993. Effect of wind-induced mixing on the vertical distribution of nutrients and phytoplankton in Lake Malawi. *Verh. Internat. Verein. limnol.* , 25: 872–876.

——. 1995. Limnology and Phytoplankton Ecology. Chapter 1. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa*. Natural Resources Institute, Chatham, U.K. (In press).

PAYNE, A. I. 1986. *The Ecology of Tropical Lakes and Rivers*. 301 pp. Chichester: John Wiley & Sons.

PETERS, R. H., MACINTYRE, S. 1976. Orthophosphate turnover in East African lakes. *Oecologia*, 25: 313–319.

PHILIP, G. 1980. *Altasi Mpya kwa Shule za Tanzania*. London, George Philip and Son, Transafrica Book Distr. 48 pp.

POLOVINA, J. J. 1984*a*. Models of coral reefs ecosystems. I. The ECOPATH model and its application to French Frigate shoal. *Coral Reefs*, 3: 1–11.

——. 1984*b*. An overview of the ECOPATH model. *Fishbyte*, 2: 5–7.

REINTHAL, P. N. 1990. The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, *Africa. Environm. Biol. Fish.*, 27: 215–233.

RHOADES, E. L. 1902. Lieutenant Rhoades' survey of Lake Nyasa. *Geogr. J.*, 20: 68–70.

PILSKALN, C. H.; JOHNSON, T. C. 1991. Seasonal signals in Lake Malawi sediments. *Limnol. Oceanogr.*, 36(3): 544–557.

RIBBINK, A. J.; MARSH, B. A.; MARSH, A. C.; RIBBINK, A. C.; SHARP, A. J. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S. Afr. J. Zool.*, 18(3): 149–310.

RICARDO-BERTRAM, C. K.; BORLEY, H. J. H.; TREWAVAS, E. 1942. *Report on the fish and fisheries of Lake Nyasa*. London, Crown Agents. 181 pp.

RUTTNER, F. 1953. *Grundriss der Limnologie*. Walter de Gruyter, Berlin. 232 pp.

SERRUYA, C.; POLLINGHER, U. 1983. *Lakes of the Warm Belt*. Cambridge: Cambridge University press.

SCHOLZ, C. A.; ROSENDAHL, B. R. 1988. Low stands on Lakes Malawi and Tanganyika, delineated with multifold seismic data. *Science*, 240: 1645–1648.

SHEPHERD, C. J. (ed.). 1976. *Investigations into fish productivity in a shallow freshwater lagoon in Malawi 1975/1976*. London, ODM 90 p.

SMITH-CARINGTON, A. K.; CHILTON, P. J. 1983. *Groundwater resources of Malawi.* Dep. Lands, Valuation and Water / ODA, Inst. Geol. Sci. 172 pp.

STREET, F. A.; GROVE, A. T. 1976. Environmental and climatological implications of late Quaternary lake level fluctuations in Africa. *Nature*, London, 261: 385–390.

SMOL, J. P. 1992. Paleolimnology: an important tool for effective ecosystem management. *J. of Aquatic Ecosystem Health*, 1: 49–58.

SYMOENS, J. J.; BURGIS, M.; GAUDET, J. J. 1981. *The Ecology and Utilization of African Inland Waters.* UNEP reports and proceedings series No. 1, 191 pp. Nairobi: UNEP.

TALLING, J. F. 1969. The incident of vertical mixing, and some biological and chemical consequences in tropical African Lakes. *Verh. Int. Ver. Limnol.*, 17: 998–1012.

——. 1987. The phytoplankton of Lake Victoria (East Africa). In: M. Munawar (ed.), Phycology of Large Lakes of the World. Arch. *Hydrobiol. Beih. Ergebn. Limnol.*, 25: 229–256.

TALLING, J. F.; TALLING, I. B. 1965. The chemical composition of African lake waters. *Int. Rev. ges. Limnol.*, 25: 229–256.

TAUB, F. B. 1984. *Lakes and reservoirs.* 643 pp. Amsterdam: Elsevier Publ.

THOMPSON, A. B. 1995. Eggs and larvae of *Engraulicypris sardella.* Chapter 7. In: A. Menz (ed.), *The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa.* Natural Resources Institute, Chatham, U.K. (In press).

TURNER, J. L. 1982. Lake flies, water fleas and sardines. pp. 165–173. In: FAO, *Biological studies on the pelagic ecosystem of Lake Malawi.* FI:DP/MLW/75/019, Technical Report 1. FAO, Rome.

TURNER, J. L.; MAGASA, J. H.; DEGNBOL, P. 1982. Distribution and abundance of larval *Engraulicypris sardella* in Lake Malawi from 1978 to 1980. pp. 68–82. In: *FAO, Biological studies on the pelagic ecosystem of Lake Malawi.* FI:DP/MLW/75/019 Tech. Rep. 1. FAO, Rome.

TWEDDLE, D. 1991*a*. *Twenty years of fisheries research in Malawi.* Fisheries Department, Fisheries Bull., No. 7. 43 pp.

——. 1991*b*. *A limnological Bibliography of Malawi.* Supplement One. FAO/CIFA Occasional Paper No. 13, Suppl. 1. FAO, Rome. 18 pp.

——. 1992. Conservation and threats to the resources of lake Malawi. pp. 17–24. In: R. H. Lowe-McConnell, R. C. M. Crul and F. C. Roest (eds.), *Symposium on Resource Use and Conservation of the African Great Lakes*, Bujumbura 1989. SIL Mitteilungen No. 23.

TWEDDLE, D.; MAGASA, J. H. 1989. Assessment of yield in multi-species cichlid fisheries in the Southeast Arm of Lake Malawi, Africa. *J. Cons. int. Explor. Mer*, 45(2):209–222.

TWEDDLE, D.; MKOKO, B. J. 1986. *A limnological bibliography of Malawi.* CIFA Occ. Pap. 13. 75 pp.

TWOMBLY, S. 1983. Seasonal and short term fluctuations in zooplankton abundance in tropical Lake Malawi. *Limnol. Oceanogr.*, 28(6): 1214–1224.

VANDENBOSSCHE, J.-P.; BERNACSEK, G. M. 1990*a*. *Source book for the inland fisheries resources of Africa: 1.* CIFA Technical Paper 18.1. Rome, FAO. 411 pp.

——. 1990*b*. *Source book for the inland fisheries resources of Africa: 2.* CIFA Technical Paper 18.2. Rome, FAO. 240 pp.

——. 1991. *Source book for the inland fisheries resources of Africa: 3.* CIFA Technical Paper 18.3. Rome, FAO. 219 pp.

VOLLENWEIDER, R. A. 1968. *Scientific fundamentals of the Eutrophication of Lakes and Flowing Waters, with special Reference to Nitrogen and Phosphorus as Factors in Eutrophication.* Paris, Rep. Organisation for Economic Co-operation and Development, DAS/CSI/68.27, 192 pp., Annex, 21 pp., Bibliography, 61 pp.

VYVERMAN, W.; COCQUYT , C. 1993. Living and nonliving diatoms in Lake Nyasa. *Verh. Internat. Verein. Limnol.*, 25:866–871.

WELCOMME, R. L. 1979. *The fisheries ecology of floodplain rivers.* 317 pp. London: Longman.

——. 1985. *River fisheries.* FAO Tech. Pap., 262, 330 pp. Rome: FAO.

WETZEL, R. G. 1975. *Limnology.* Philadelphia, W. B. Saunders Comp. 743 pp.

——. 1983. *Limnology.* 2nd edition. Philadelphia, W. B. Saunders Comp. 860 pp.

WHITTON, B. A. (ed.). 1975. *River ecology.* Studies in Ecology. Vol. 2. Univ. of California Press, Berkeley. 725 pp.

WORLD BANK. 1994. *Annual Report 1994.* Washington D.C., The World Bank. 254 pp.

Appendices

APPENDIX 1. Overview of limnological research on Lake Malawi

Sources: Beadle, 1981; Fryer & Talling, 1986; Tweddle & Mkoko, 1986; Tweddle, 1991a,b; Menz, 1995

RESEARCH	RESEARCHER(S)	LOCALITY	PERIOD	REFERENCES	SCOPE/SUBJECT(S)
1859–1950					
EXPEDITIONS					
Livingstone	Livingstone, Kirk	southern part of the lake	1859–1860	Livingstone (sev. ref.)	Geography ; collection of fish, shells, reptiles
Young	Young		1877	Young, 1877	Geography
Thomson	Thomson	northern part	1878	Thomson, 1881	Geography
		southern part	1890		Geography
SURVEYS	Rhoades	lakewide	1897	Rhoades, 1902	bathymetric survey
STUDIES	Günther			Günther, 1864 (and other refs)	Taxonomy fishes and reptiles (collected by Kirk)
	Lea			Lea, 1864	Molluscs
	Dorhn			Dohrn, 1865	Molluscs (collected by Kirk)
	Frauenfeld			Frauenfelt, 1865	Molluscs
	Schmith			Schmith, 1877 (and other refs)	Shells, snails
	Bourguignat			Bourguignat, 1889	Molluscs
	Ancey			Ancey, 1894	Molluscs
	Kirby			Kirby, 1898	Dragonflies
	Moore			Moore, 1898, 1903	Marine fauna (Tanganyika problem)
	Schmidle			Schmidle, 1899,1902*a,b*	Phytoplankton
	Thiele			Tiele, 1900, 1904	Crustacea (parasitic Branchiura)
	Fuelleborn			Fuelleborn, 1900	Limnological observations (thermocline), collection of insects
	Gruenberg			Gruenberg, 1902, 1903	Taxonomy Odonata (collected by Fuelleborn)
	Müller			Müller (sev.refs)	Phytoplankton (Diatoms)
	Cunnington			Cunnington, 1907,13	Plankton, Crustacea
	Rousselet			Rousselet, 1907,10	Polyzoa, Rotifera
	West			West, 1907	Algae including phytoplankton
	Beddard			Beddard, 1908	Oligochaeta
	Calman			Calman, 1908	Crustacea
	Newton			Newton, 1910	Mollusca

	Preston			Preston, 1910	Mollusca
	Sars		1904–05	Sars 1910*a,b*	Copepoda, Ostracoda
	Von Daday			Von Daday, 1910	Invertebrates
	Gregory		1923–56	Gregory, 1921	
	Dixey			Dixey (sev.refs)	Geology, lake levels, sediments
	Lamborn			Lamborn, 1925	*Anopheles*
	Connolly			Connolly, 1925,27,39	Fossil molluscs
	Kiefer			Kiefer, 1934	Copepoda
SURVEY	Ricardo, Borley & Trewavas	whole lake	1939	Ricardo *et al.* 1942	Fish, fisheries
STUDIES	Beauchamp	whole lake	7/39–3/40	Beauchamp, 1940, 1953	T and DO observations
	Lowe	southeast arm	1945–1947	Lowe, 1952 (and several other references)	*Tilapia* ecology
	Ransford			Ransford, 1948	Schistosomiasis
	Johnston			Johnston, 1949	Meteorology
	Kanthack			Kanthack, 1942, 1948	Hydrology, lake levels
1950 – 1985					
JFRO	Harding, Iles	off Nkhata Bay (and affluent rivers)	3/54–10/55	Jackson *et al.* 1963	Limnological observations, Plankton observations
	Eccles	off Nkhata bay	9/57–11/59 9/59–1/61	JFRO, 1959,1960,1962	Phyto- and zooplankton T, D.O. and silica observations
	Fryer		1955–60	Fryer (sev. refs)	Invertebrates
	Eccles	off Nkhata Bay off Monkey bay lakewide transects	1961–70	Eccles, 1962, 1974, 1988	Physical limnology
Others studies	Mandahl-Barth			Mandahl-Barth, 1954,1972	Molluscs, bilharzia
	Whitehouse			Whitehouse, 1952	Water levels
	Van Meel			Van Meel, 1954	Phytoplankton
	Mattingley			Mattingley, 1954	Distribution mosquitoes
	Kimmins			Kimmins, 1955	Ephemeroptera
	Jollyman			Jollyman, 1955	Tides and seiches
	Omer-Cooper			Omer-Cooper (sev. refs.)	Coleoptera
	King			King, 1957	Geology (Seismicity)
	Pike			Pike (sev. refs)	Hydrology, geology
	Tetley			Tetley, 1959	Rainfall characteristics
	Lewis			Lewis, 1961	Diptera (*Simulium neavei* complex)
UNDP/FAO	Ferro	Chintheche bay	1976	Ferro, 1977	T, D.O., Conduct., pH, Secchi

Appendix 1 (contd)

RESEARCH	RESEARCHER(S)	LOCALITY	PERIOD	REFERENCES	SCOPE/SUBJECT(S)
Fish. Dev. Proj. (1972–76)	Gonfiantini			Gonfiantini *et al.* 1979	Isotope analysis/deep profile
UNDP/FAO	Degnbol	pelagic zone	4/78–2/81	Degnbol & Mapila, 1982	Limnological studies of pelagic
Fisheries	& Mapila	off Nkhata Bay			ecosystem
Expansion	Turner,			Turner, 1982	Lake flies
Project	Van Lissa			Van Lissa, 1982	Food habits *Engraulicypris sardella*
(1977–82)	Degnbol			Degnbol, 1982	Food habits larvae *E. sardella*
ODA project	Shepherd	Bangula Lagoon	1975–76	Shepherd, 1976	Limnological observ., phytoplankton
-	Hecky & Kling	lakewide	1981	Hecky & Kling, 1987	Phytoplankton
RECENT AND ONGOING LIMNOLOGICAL RESEARCH					
PROBE project	Johnson	lakewide	1985–90	Johnson *et al.* 1988	Paleolimnology, sediments
				Johnson & Davis, 1989	Seismic profiles
				Johnson & Ng'ang'a, 1990	Paleolimnology
	Pilskaln	lakewide		Pilskaln & Johnson, 1991	Paleolimnology, sediments
	Haberyan	southern part		Haberyan (sev. refs.)	Paleolimnology, phycology,
				sediments	
	Owen	lakewide		Owen, 1989	sediments, paleolimnology
				Owen *et al.* 1990	Water levels, water balance
				Owen & Crossley, 1992	Paleolimnology
	Halfman	lakewide	1992	Halfman, 1993	Geological limnology,
				Halfman & Scholz, 1993	suspended sediments
Un. Manitoba/IDRC	Bootsma	southern part	1988–92	Bootsma, 1993	Phytoplankton, nutrient,
		lakewide survey		and several other refs	dynamics, conservation
CASIMIR/SIAL	Vyverman	northern part	1991	Vyverman &	Phytoplankton
	& Cocquyt			Cocquyt, 1993	
UK/SADC	Patterson	lakewide	1992–94	Patterson &	Limnology, nutrient dynamics
Pelagic Fish	& Kachinjika			Kachinjika, 1993, 1995	phytoplankton ecology
Resources					
Assessment	Irvine	lakewide	1992–94	Irvine & Waya, 1993, 1995	Zooplankton
Project	& Waya			Irvine, 1995	*Chaoborus edulis*
				Irvine *et al.* 1995	*Tropodiaptomus cunningtoni*
	Thompson	lakewide	1992–94	Thompson, 1995	Egg/larvae *E. sardella*
	Allison *et al.*	lakewide	1992–94	Allison *et al.* 1995	Food web pelagic ecosystem

APPENDIX 2. Data on physical limnology of Lake Malawi

RESEARCHER	DATA	LOCATION	TIME SPAN	FREQUENCY	DATE	REFERENCE(S)
Beauchamp	Temp/D.O.	open lake station (4 miles offshore from Nkhata Bay)	9 months	weekly	7/39–3/40	Beauchamp, 1940, 1953
Ricardo Bertram	Temp/D.O.	open lake and inshore stations during lakewide fishery survey	5 months	–	3/39–8/39	Ricardo Bertram *et al.* 1942
Lowe	Temperature	Station in Domira Bay (depth 80 m)	11 months	monthly	4/46–3/47	Lowe, 1952
Harding	Temperature/D.O.	open lake station (3 miles N.E. of Nkhata Bay)	18 months	weekly	3/54–9/55	Jackson *et al.* 1963
		other stations lakewide	18 months	irregular	3/54–9/55	
Iles Eccles	Temperature/ heat content	open lake station (3 miles N.E. of Nkhata Bay)	4 years	weekly	9/57–12/61	JFRO, 1960, 1962, 1964, 1965 Eccles, 1962
Eccles	Temperature	standard station near Monkey Bay			1963–1969	Eccles, 1974, 1988
Ferro	Temperature	inshore/offshore Chintheche area	9 months	weekly/monthly	10/75–6/76	Ferro, 1977
Patterson & Kachinjika	Temperature/D.O.	10 full-lake cruises	2 years	bimonthly	1992–1993	Patterson & Kachinjika, 1995
Patterson & Kachinjika	Temperature/D.O. light	Nkhota Kota Station (12°43′S, 34°30′E)	2 years	monthly	1992–1994	Patterson & Kachinjika, 1995
Patterson & Kachinjika	Temperature/D.O. light	Nhkata Bay Station (11°36′S, 34°30′E)	1 month	every two days	7 June–1 July 1993	Patterson & Kachinjika, 1995
Patterson & Kachinjika	Temperature/light	Cruise in SE arm	2 days	–	May 1993	Patterson & Kachinjika, 1995

Limnology and hydrology of Lakes Tanganyika and Malawi

Lakes Tanganyika and Malawi are of great socio-economic importance to the region, and are vital to the well-being of the people living on or near their banks. They are major sources of fish protein, reservoirs of fresh water and important avenues of transportation. They also have great touristic potential and offer possibilities for the development of trade between countries in the area.

In addition, the two lakes have a high scientific value due to their wide biodiversity and unique wildlife, and conservation of fish species is of major importance since the African Great Lakes offer one of the most spectacular examples of adaptive radiation of vertebrates anywhere in the world.

This book brings together in an accessible form knowledge obtained during recent decades on the limnology and hydrology of Lakes Tanganyika and Malawi, providing background on important physical, chemical and biological events occurring in the lakes that will be of interest to all those involved in the science, development and management of African inland waters.

Cover: Lake Tanganyika
(photo by Ruud C. M. Crul)

92-3-103400-6
9 789231 034008