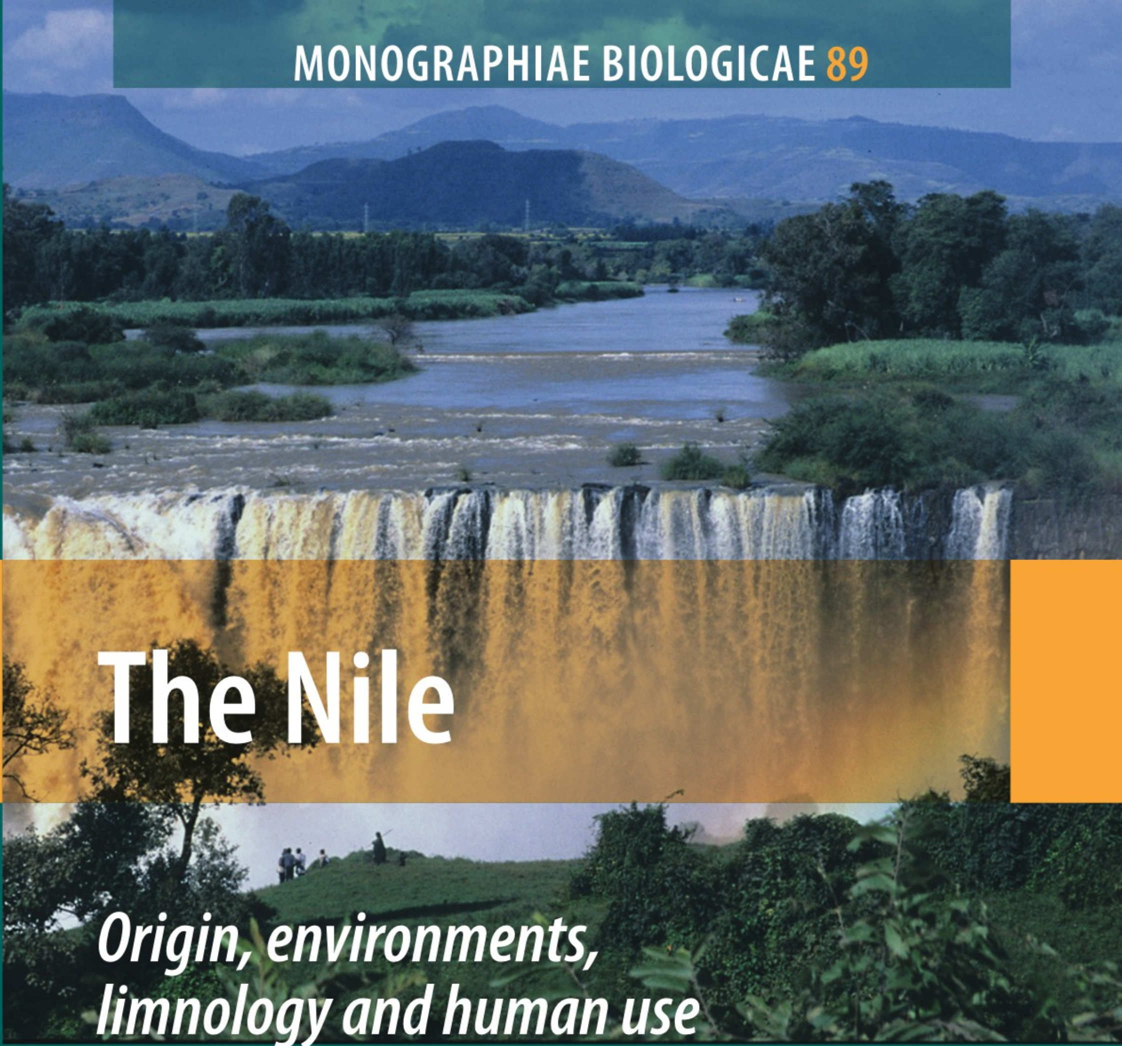

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The Nile

Origin, environments, limnology and human use

Henri J. Dumont
Editor

Springer

The Nile

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The Nile

Origin, Environments, Limnology and Human Use

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Front cover: Tissisat Falls on the Upper Blue Nile in Ethiopia, isolating Lake Tana from the rest of the Blue Nile System (Photograph by Ferdinand Sibbing).
Back Cover: Photo 1: Fish traps opposite a papyrus swamp on Lake Victoria (Photograph by Frans Witte).
Photo 2: The Shoebill, a large piscivorous bird typical of the Upper Nile Swamps (Photograph by Pat Morris).
Photo 3: The Equatorial Nile in Southern Sudan, meandering through a savanna landscape (Photograph by Jack Talling)

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Preface

What have we learnt about the Nile since the mid-1970s, the moment when Julian Rzóska decided that the time had come to publish a comprehensive volume about the biology, and the geological and cultural history of that great river?

And what changes have meanwhile occurred in the basin? The human population has more than doubled, especially in Egypt, but also in East Africa. Locally, industrial development has taken place, and the Aswan High Dam was clearly not the last major infrastructure work that was carried out. More dams have been built, and some water diversions, like the Toshka lakes, have created new expanses of water in the middle of the Sahara desert. What are the effects of all this on the ecology and economy of the Basin?

That is what the present book sets out to explore, 33 years after the publication of "The Nile: Biology of an Ancient River". Thirty-seven authors have taken up the challenge, and have written the "new" book. They come from 13 different countries, and 15 among them represent the largest Nilotic states (Egypt, Sudan, Ethiopia, Uganda, and Kenya). Julian Rzóska died in 1984, and most of the co-authors of his book have now either disappeared or retired from research. Only Jack Talling and Samir Ghabbour were still available to participate again. With his huge Nilotic experience of more than half a century, Talling offered to write a brief overview of (biological) research on the Nile. But his chapters in Rzóska's book turned out to be still remarkably up to date. His 1976 paper on the physical and chemical limnology of the Nile is here reprinted with minimal changes. His second contribution, on Nile phytoplankton, required more updating. It was revised with the assistance of colleagues from Egypt and the Sudan, mainly to accommodate the effects of eutrophication, now increasingly affecting the basin, but especially Egypt and Lake Victoria.

Samir Ghabbour preferred to write a new paper, although 30 years of time had changed little to his insights in the origin of Nilotic oligochaetes.

I tried to save some of the structure that Rzóska had imposed on his book, though not necessarily giving all subjects the same weight, and not in the same order. Thus, the geological development of the basin is treated immediately after my introductory chapter. One of the two contributors to that section, Martin Williams, was not among the authors of Rzóska's monograph. Martin had spent 2 early years of his carrier (1962–1964) mapping soils along the Nile in the Sudan. In 1975, he spent a year in the CNRS lab of Hugues Faure in Paris, when Julian Rzóska came on a visit. Julian probably judged him "too young" to be a contributor to his book. Instead, he asked him to review drafts of the geological chapters. Only 4 years later, Martin published his influential book "The Sahara and the Nile", with Hugues Faure as a co-editor. With a number of his students, he has continued to work on the Nile Basin ever since.

I have tried to single out a number of building blocks of the Nile system, and asked experts of each of them to write a synoptic paper about them. Eleven such environments, either specific lakes, or groups of lakes, or swamps, or even mountain chains supplying runoff to the Nile, have been included. As to chapters dealing with biota, their ecology and biogeography, my choice has perhaps been idiosyncratic, but it was also dictated by available expertise and level of background knowledge. I hope that the reader will find it easy to come to the conclusion that the Nile, more than other rivers like the Niger, Congo, and even the Logone-Chari, has had a tumultuous history, and, after the drying up of the Sahara, continued to link "deep" Africa to the Mediterranean. Biologically, it may not be the richest and most diverse of African river basins, but it is certainly the most fascinating!

The Nile is also the home of millions of people, and as their number keeps increasing, so does their influence on the river. Aspects related to that could not be neglected in this book, and so Tony Allan, winner of the 2008 Stockholm Water Prize, made an updated analysis of what John Waterbury had called "the Hydropolitics of the Nile" in the early 1970s. Martin Williams concludes the volume with a brief paper on what he perceives to be man's long-term impact on the river.

Ghent, Belgium and Guangzhou, China Henri J. Dumont

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A Description of the Nile Basin, and a Synopsis of Its History, Ecology, Biogeography, Hydrology, and Natural Resources

Henri J. Dumont

Abstract Following a description of the Nile, the longest river of the world (ca 6,800 km) and its basin (2.9×10^6 km^2), including its various "source" lakes, some brief notes on its main neighbours (Congo and Logone-Chari) and their history are given. The biota of the basin are moderately diverse, and endemism tends to be low, except in some of the "old" source lakes. The situation is complicated by the fact that at least two of these lakes (Victoria and Tana) dried out around or slightly before the beginning of the Holocene, and thereafter, speciation (especially of cichlid fish) may have happened at an unusually great speed.

In general, the Nile offers a pathway for African species to extend from the tropics to a Mediterranean climate and spill over into the Levant and Arabia. Such incursions may have happened many times across history, with some of the older "waves" using the Red Sea (before its opening to the Indian Ocean) rather than the Nile.

Currently, as elsewhere in the world, invasive species in the Nile are becoming more and more common, although the oldest cases (some Ponto-Caspian cnidarians) may date back to the end of the nineteenth century. The water hyacinth *Eichhornia* has invaded the Nile basin in at least three different zones.

Since early pharaonic times, man has interfered with the river and its flow regime, in an effort to control the yearly "flood of a hundred days", but large-scale damming only started in the nineteenth century, and culminated with the construction of the Aswan High Dam in the 1960s, reducing the river to a giant irrigation canal. More recent developments include the construction of the Toshka lakes diverticle to Lake Nasser, a project with an uncertain future.

The river and its lakes are important fisheries resources; the various dams are generating large amounts of power, and fossil hydrocarbon deposits are under development in at least three zones of the basin. This may contribute to river pollution, which is still a local phenomenon, except in Lake Victoria, which suffers from eutrophication, and in Egypt, that combines a population explosion (almost four doublings in the last century) with a substantial industrial development.

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1 Introduction

The Nile monograph by Rzóska (1976) was entitled "biology of an ancient river". Whether the Nile is indeed an ancient river is, however, a matter of taste. Rather, one could conceive the Nile as a puzzle, to which at times pieces were added, while at other times pieces were subtracted. This happened all along its history, including the late Pleistocene. In its present form, the delta, for example, is not much more than 6,000 years old. On the other hand, surely a river (or a series of consecutive rivers) existed in North-East Africa since it emerged from the Tethys Sea at the end of the Mesozoicum. Talbot & Williams and Williams & Talbot (2009) summarize the current views on the various stages of the drainage systems that ultimately became the Nile as we know it.

As usual, we know more as we approach the present, and the Pleistocene history of the River is, in broad lines, well established even if some parts of the basin (e.g. the evacuation pathway of the Blue Nile across geological time) still invites more research work (Talbot & Williams; Williams & Talbot, 2009).

The twentieth century stood witness to the progressive, and ultimately, the complete regulation of the Nile. Population growth and economic expansion, especially in the lower Nile valley, continue to increase the demand on the water resource, a process that has been underway for about five millennia, but risks to reach a climax soon. The river is therefore more than a complex ecological jewel: it is a multi-purpose renewable resource that should be wisely managed, however difficult this may be.

2 A Description of the Nile Basin (Fig. 1)

With an approximate length of ca 6,800 km (Said, 1981), the Nile is the longest river in the world (Ibrahim, 1984). The nineteenth century quest for the source(s) of the Nile is a heroic chapter in the history of the exploration of the African continent, and it was long thought that Lake Victoria (see further) was its ultimate source. Yet, that lake itself is fed by rivers that arise further south, the most important of which is the Kagera. Until recently, it was believed that its tributary, the Luvironza, that springs in Tanzania at ca 4° S, was the Nile's ultimate "source". However, a revised length estimate of 6,718 km was established in 2006, when a British–New Zealand expedition found that the tributary of the Kagera River arising furthest to the south is the Rukarara. It springs in the Nyungwe forest, Rwanda.

The Nile is the only permanent river that manages to cross the Sahara, the largest desert in the world, and reach the Mediterranean Sea, yet its early beginnings are in a montane equatorial climate, and it traverses a series of climatic zones before reaching its delta. Its basin orientation is unique among the major rivers in the world in that it runs almost perfectly from south to north, discharging at 31° N (Fig. 1). Each climate zone which it crosses shows considerable variability in precipitation and run-off (Camberlin, 2009), but over more than half its length

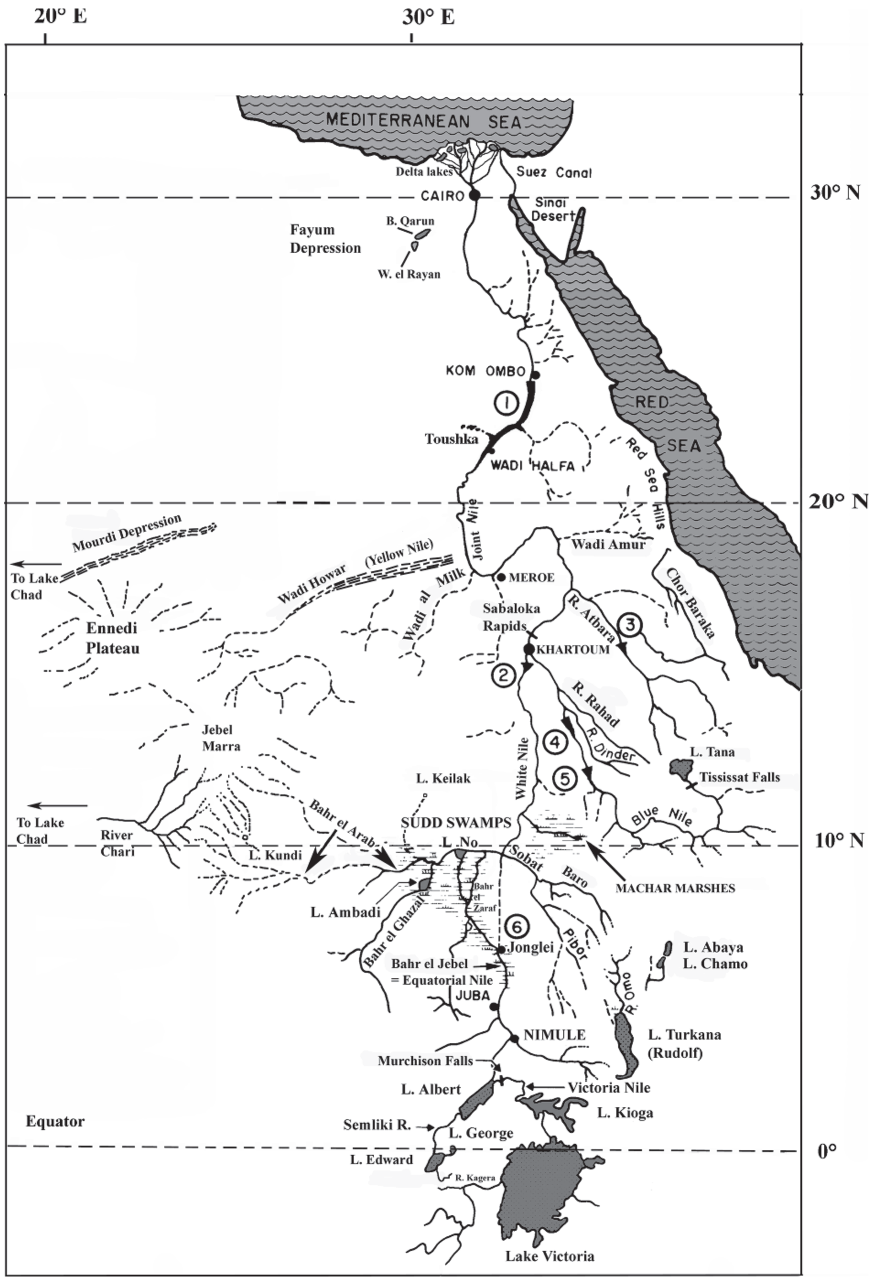

Fig. 1 The Nile Basin. All specific environments dealt with in this volume are shown. The possible zones of contact between Nile and Chad, north and south of Jebel Marra, are also indicated

it receives less than 150 mm of rain per annum. Its basin is relatively narrow and small (2.9×10^6 km^2) compared to that of most other large rivers of the world (the Congo, ca 4×10^6 km^2 according to Bailey, 1986; the Amazon, ca 7×10^6 km^2 according to Sioli, 1984).

The Nile basin covers the whole of Egypt and the Sudan, except for the short rivers that drain the Red Sea Hills towards the red Sea. Most of these are wadis that only discharge water for few days after rare desert rains. For both countries, the Nile is a vital economic resource (see further) and the need to secure access to sufficient water has dominated their political agenda since times immemorial (Allan, 2009). The basin also covers about one third of Ethiopia (Tudorancea & Taylor, 2002), the whole of Uganda, and part of Kenya, Tanzania, Congo, Rwanda and Burundi.

Conventionally, the Nile is divided into a number of sub-basins: the White or Equatorial Nile and its source lakes, the Blue Nile and Lake Tana, and the Main Nile. The River Atbara is often considered a separate, although small, sub-basin. Presently not or hardly active is the so-called Yellow or Desert Nile, comprised of the valleys of the Wadi Howar and the Wadi El Milk. Around 6,000 BP, these watercourses significantly augmented the total discharge with water coming from the Nile-Chad divide (Jebel Marra, the Tabago and Meidob hills, and the Eastern Ennedi – see further) (Kuper & Kröpelin, 2006).

The entire White Nile sub-basin has a surface area of ca 3.8×10^5 km^2. It is best known for the large, reputedly ancient lakes on the plateau in the south of its drainage area. Of these, Lake Victoria is the largest. With a surface area of 7×10^4 km^2, it is second in size only to the Caspian Lake in West Asia and Lake Superior in North America (Lehman, 2009). The White Nile also drains a sizeable part of the Western Rift, including lakes Albert and Edward (Green, 2009). Both obtain much of their water from the high mountains of the Rwenzori (Eggermont et al., 2009). A second source of water are the Virunga highlands, which rose as a volcanic plug across the rift valley between 9 and less than 3 million years ago (Kampunzu et al., 1998). This deleted Lake Kivu from the Nile basin. The Virunga volcanoes also blocked the course of a number of smaller rivers (Beadle, 1981), and created the Kigezi lakes to the north. They are renowned for their scenic beauty, but are also of great biological interest (Green, 2009). The outflow of these lakes eventually finds its way to either Lake Victoria or Lakes Albert-Edward.

Lake Victoria is not a rift lake, but a huge, saucer-shaped depression with marshy shores (Beadle, 1981; Lehman, 2009). Its maximum depth (ca 70 m) is modest and it is therefore sensitive to fluctuations in precipitation, to the point of occasionally drying out, as happened around 12,500 BP (Johnson et al., 1996, 2000). Historical deviations in lake level with an amplitude of more than 4 m have been recorded, and fluctuations of 2 m within less than a decade are not exceptional (Beadle, 1981; Lehman, 2009).

The origin of the lake is described by Lehman (2009). It is about 400,000 years old, and was created by uplift of the western side of the East African Rift valley. Uplifting and tilting reversed the direction of flow of the previously westwards flowing rivers Kagera, Katonga and Kafu, that began to fill the Victoria depression and transformed the Kyoga area from a river to a river-lake. Probably, for some time, a series of river-lakes existed in the Victoria cuvette too, together forming the cradle for the speciation of an endemic fauna. For the overflow to the north (at Jinja) to function, a precipitation threshold is required that was not reached at several occasions in the late Pleistocene. Johnson et al. (1996) show that the basin was closed around 18,000 BP and again at 14,200 BP (Stager & Johnson, 2008), and fell dry completely about two millennia later. Lake Victoria is famous for an "endemic" flock of haplochromine cichlid fish (Witte et al., 2009). The number of species is still debated, because many are so closely related as to raise doubts about their full species status. Lévêque (1997) estimates their number at about 200, but according to Witte et al. (2009), there might be as many as 500.

A man-made ecological disaster made Lake Victoria a global news item in the 1990s, viz. the consequences of the intentional introduction of the Nile perch, a large carnivorous centropomid fish that contributed to the collapse of many endemic haplochromines as they fell prey to it (for details, see Lehman, 2009; Witte et al., 2009).

The Victoria Nile leaves the lake near Jinja in the north, crossing the Owen falls (now Nalubaale) (ca 30 m high), flowing rapidly for the next 70 km, to slow down upon reaching the dendritic swamp-lake Kyoga. Next it turns west to join Lake Albert in the western rift almost exactly at the same point where the Albert Nile leaves that lake to flow north. But first it crosses the Karuma and Murchison (or Kabalega) falls, which are part of a biogeographic barrier that prevents rift biota from migrating up to Lake Victoria. Nile perch occurs naturally in Lake Albert, but was stopped from migrating upstream by these falls (Green, 2009).

The western rift section of the Nile consists of Lakes Edward, Albert, George and a number of smaller lakes and rivers that drain into them. The rivers draining the Rwenzori Mountains, locally rising to above 5,000 m, are short, steep, and fed partly by direct precipitation, partly by glacial melt-water (Eggermont et al., 2009). The Rwenzori, the mountains of the moon, rose as part of the rifting process, around 10 million years ago, in late Miocene–early Pliocene times. Originally, the water that collected on the floor of the rift formed a single water-body, (Palaeo) Lake Obweruka. In the early Pleistocene, this lake, that was rich in endemic biota, broke up in two parts, Lakes Lusso and Kaiso, which were the predecessors of lakes Albert and Edward. Currently, Albert and Edward are separated by a drop in altitude of about 300 m and connected by the Semliki River. A series of rapids constitutes a barrier to faunal exchange between both.

Lake Kivu, or a predecessor of it, originally belonged to the same series. If not part of Lake Obweruka, it was at least connected to it, until it was isolated by the Virunga volcanoes, a series of eight huge volcanoes that rose between 9 and less than 3 million years BP and intermittently remained active to the present time. Evidence for this is found, at the molecular level, in the fact that Kivu cichlids form one superfloc with Lake Albert-Edward-Victoria endemics, not with those of Lake Tanganyika, to which Lake Kivu now evacuates excess water via the Panzi falls and Rusisi River (Verheyen et al., 2003).

Oddly, the Nile leaves Lake Albert near the point where it entered it, a swampy delta. The total drop in altitude between Lakes Victoria and Albert is ca 515 m, and the influence of Victoria water into the (more saline) Lake Albert is hardly felt. The Albert Nile, as it is now called, flows steadily northwards through flat country until it reaches Nimule. It then works its way through a narrow gorge rich in rapids, and is joined by a couple of affluents from the SE, including the Aswa, that drains a zone to the north of Lake Kyoga.

When the Nile emerges from the Nimule rapids, it has left Uganda and has entered the Sudan, where it is known as the Bahr el Jebel (bahr = sea, lake or river; jebel = mountain). It flows across a hilly tract, dropping in level for about 1 m per km across the next 150 km. North of Mongalla, it reaches the great swamps of southern Sudan, known as the Sudd (= blockage). The Sudd is a vast stretch of permanent (ca 7,000 km^2) and seasonally (ca 90,000 km^2) flooded marshland. More than rapids and cataracts, it long constituted a barrier to human penetration from the north. As well the pharaohs as the Romans failed to cross it. The Bahr el Jebel flows in a braided channel, although one river rapidly and permanently separates from it, the Bahr el Zeraf. Numerous lakes are found all along the swamps, with the largest ones (Lake Ambadi, Lake No) situated near the junction of the Bahr el Jebel with a tributary coming from the west, the Bahr el Ghazal (Green & El-Moghraby, 2009). The Bahr el Ghazal becomes a seasonal stream west of the city of Wau. It drains the hills at the confines between the Sudan and the Central African Republic. From the north, it receives a tributary, the Bahr el Arab, that is also partly seasonal, partly permanent and drains the eastern flanks of the Chaine des Bongos in the Central African Republic and the south of Jebel Marra. A number of lakes, such as L. Kundi and L. Keilak are part of its drainage (Green, 2009). At the tripoint Chad-Central African Republic-Sudan, in the area of the town of Birao, the Nile and the upper Logone-Chari are very close. This is one of two corridors across which temporary faunal exchange may have taken place during humid spells of the Pliocene–Pleistocene–Holocene.

Just south of Malakal, the White Nile receives another major tributary from the East, the Sobat, with a basin of 224,000 km^2, including some huge swamps (the Machar marshes). Of its two major branches, the Paro (or Baro) springs in western Ethiopia. The upper reaches of its southern branch, the Pibor, contain the extensive Lotigipi swamps, across which Lake Turkana used to overflow to the Nile until mid-Holocene times (Johnson & Malala, 2009). Lake Turkana (formerly Rudolf) (Kenya) and the Omo catchment (Ethiopia and Kenya) in the Eastern Rift are part of the White Nile sub-basin. Currently, the Turkana basin is closed, but around 7,000 BP, the lake rose by some 80 m and Lakes Abaya and Chamo, as well as the current salt pan – then lake – Chew Bahir (formerly Stephanie) in the Eastern (Gregory) Rift evacuated towards it (Adamson & Williams, 1980; Tudorancea & Taylor, 2002). In spite of a degree of salinisation since the closing of their basins, the fauna of Lakes Turkana, Abaya and Chamo has maintained a strong Nilotic character (e.g. the fish and zooplankton: Witte et al., 2009; Dumont, 2009). The Turkana basin is a relatively recent addition to the Nile basin. Until mid-Pliocene times, the Palaeo-Turkana, then a (mainly) riverine system, emptied in the Indian Ocean (Van Damme & Pickford, 2003). At that time, the marine stingray *Dasyatis* managed to migrate up to the lake (Feibel, 1988; Stewart, 2009).

From Malakal to Khartoum, a stretch of about 730 km, no further tributaries enter the While Nile, but at Khartoum (378 m asl) the Blue Nile (known in Ethiopia as the Abbay) joins from the east, at a place called the Mogran (the "elephant's trump", presumably after the shape of the elongated island present at the junction). The Blue Nile, with a basin area of 325,000 km^2, flows out of Lake Tana (1830 m asl) in the central Ethiopian highlands (Vijverberg et al., 2009). It is itself fed by about 60 short rivers all around it. In contrast to the While Nile the profile of the Blue Nile is very steep once it has left the East African plateau, and its flow is torrential (Morris et al., 1976). After leaving the lake at its southern extremity, and cascading over the Tissisat falls, it forms an elaborate loop, running first south, then west, through a spectacular gorge that is up to 2 km deep, and has eroded away some 100,000 km^3 of material (Talbot & Williams, 2009). When it touches the Sudan plain, after some 900 km, its altitude is 464 m asl (at Roseires). In its remaining course to Khartoum, it only drops for another 75 m, working its way through a fossil floodplain, the Gezira, largely built from sediment extracted from the Abbay gorge.

Between Khartoum and the Mediterranean delta, only one partially active tributary, the Atbara, joins the Nile, some 310 km north of Khartoum. The discharge of the Atbara is seasonal, and after the summer floods the lower course gradually dries up, but during the flood, its contribution to total Nile discharge is sizeable (Sutcliffe, 2009).

Between Khartoum and Aswan in Egypt, the Nile describes a giant "S", meandering around the lava fields of the Bayuda Desert. It follows a well-defined bed, punctuated by rapids or "cataracts". Before man's interference, there were six such cataracts, two of which have now disappeared under Lake Nasser-Nubia. The fourth cataract, near Kerma, will disappear as soon as the Meroe dam, now under construction, will become operational. The cataracts seriously impeded navigation of the Nile south of Aswan, and long hindered travel and economic exchange between "Egypt" and "Nubia".

To the west of the Nile, currently defunct but at times during the Holocene a major stream, is the Wadi Howar or Yellow Nile, that used to empty close to the mouth of that second "desert river", the Wadi el Milk. The bed of the lower Wadi Howar, several kilometers wide, is currently obstructed by sand dunes. Its upper course drains the hills of North Darfur (the Meidob and Tabago hills, the north part of Jebel Marra, and the south flank of the Ennedi). Until ca 7,000–6,000 BP, this hydrologic network was intermittently active. Van Neer (1988, 1989) found not less than 18 species of fossil Nilotic fish in Holocene river deposits here (see also Stewart, 2009). As well, Neolithic man settled the whole area, to retreat to the Nile valley and the hills only as the climate became drier after 6,000 BP (Kuper & Kröpelin, 2006). The zone north of Jebel Marra and as far north as the Mourdi depression is the second one where contact and exchange between Nile and Chad biota may have taken place.

Adamson & Williams (1980) state that the Jebel Marra volcano began to rise in the Miocene, and volcanism continued into the quaternary (which would also be valid for the more northerly situated Meidob hills), thereby deleting some 60,000 km^2 of catchment from the Nile basin. Previously eastward-draining rivers (towards Wadi Howar) were suddenly reversed to the west, and the contact Nile-Chad was rendered more difficult, while the divide between Nile-Congo and Chad-Congo remained unaffected.

Just north of Cairo, the Nile builds a flat, triangular delta of ca 25,000 km^2. Somewhat south of Cairo, a left-bank diverticle leads to the Fayum depression, of Pliocene age, in which Lake (Birket) Qarun and the artificial Wadi El Rayan lakes are situated. The Fayum channel, a natural overflow during exceptionally high floods, was artificially maintained since the Middle Kingdom, and the lake, called Lake Moeris, became the centre of a prosperous agricultural area. Originally a deep lake, with surface situated well above sea level, its level has now fallen to about −40 m, and the water has evolved from fresh to hypersaline in less than two centuries (El-Shabrawy & Dumont, 2009a).

The delta is composed of two branches, Rosetta and Damietta (but many more in the past few millennia) and has traditionally been one of the important agricultural areas of Egypt (currently also a source of natural gas and oil – see further). It did not exist as such until the end of the Flandrian transgression, and started building not more than some 6,500 years ago; however, it rapidly expanded afterwards (Hamza, 2009). Four shallow brackish lakes (Idku, Maryut, Borullus and Manzalla) at its northern extremity slowly individualized from a delta-wide salt marsh during historical times, as sediment was deposited at the head of the delta at a rate of about 1 cm per century. Currently, the sand spit separating the lakes from the sea is being eroded, a complex phenomenon but to which the lack of sedimentation since the Aswan dam stopped the summer floods certainly contributes much (Hamza, 2009; Dumont & El-Shabrawy, 2007).

3 Nile Biogeography and Taxon Richness

Per unit area, the taxon richness of the Nile can only be described as mediocre, and so is the degree of endemism of its biota. This contrasts with the fact that particular lakes in the catchment may be centers of radiation for particular animal groups. Cases in point are the species flocks of haplochromine cichlids in Lake Victoria and cyprinids in Lake Tana, two lakes that are usually considered as “ancient”, yet dried out around the onset of the Holocene. In the case of Lake Victoria, the connotation arose that the several hundreds of endemic haplochromines evolved in less than the last 12,000 years. To many evolutionary biologists, such a “speciation at lightning speed” is inconceivable. Some (Fryer, 2005) therefore maintain that the lake cannot have dried completely, although Slater & Johnson (2008) argue that the evidence is incontrovertible.

The controversy is likely to continue for some time (Nagl et al., 2000), but it is worth noting that many haplochromines may have speciated long before the lake dried out. A dry terminal lake does indeed not mean that the rivers emptying in it are dry too, except perhaps in their lower courses. Some cichlids endemic to Lake Kivu seem to have survived a “boiling” of the lake by lava from the Virunga volcanoes by retreating into rivers as well (Dumont, 1986). In fact, the “Victorian” rivers Kagera and Katonga are rich in lakes and swamps that may have served as refuges (Mwanja et al., 2001). The endemic mollusks of Lake Victoria (Van Damme & Van Bocxlaer, 2009) suggest exactly that scenario, and the similarity between the mollusk fauna of Lake Turkana and Lake Victoria suggests that the “retreat” area may have been the foot of Mount Elgon. It may also be useful to attract attention to the fact that even in the Sahara, in conditions of precipitation of less than 30 mm per annum, permanent water may persist in sheltered localities (Dumont, 1979). Around twenty species of fish, including cichlids and cyprinids, have survived here in rock pools or “gueltas” since the last pluvial (Le Berre, 1989; Lévêque, 1990). Their origin is mixed. Some are of northern (Mediterranean) origin (e.g. *Barbus biscarensis*), others of Afrotropical orgin (e.g. *Barbus anema*), and they meet in the central Saharan mountains of Ahaggar and Tassili-n-Ajjer. In spite of their isolation, which lasted for a minimum of 6,000–12,000 years, they show no sign of speciation.

The Lake Tana endemics (mainly *Barbus* and *Labeobarbus*, and thus Cyprinidae and not Cichlidae as in the lakes on the East African plateau) as well likely speciated in rivers away from the lake, and only colonized the lake when it was flooded after a period of drought (Lamb et al., 2007; Vijverberg et al., 2009): one *Labeobarbus,* morphologically close to the ancestral form of the Tana species flock, still has riverine habits. Endemism on the Ethiopian plateau is significantly higher than elsewhere in the Nile basin, including the East African plateau, and it is again mostly in riverine, not lacustrine animals (e.g. gomphid dragonflies: Dumont, 2009). Furthermore, the ancestry of these endemic species (there is no endemism at higher taxon levels) can be traced to two origins: the so-called Afromontane region (East Africa between Kenya-Uganda and South Africa), and the Palaearctic.

In brief, although the species flocks of endemic fish and to a lesser extent of molluscs and copepods of Lakes Victoria, Edward-Albert, Tana, and even Turkana remain impressive, the available evidence does not provide conclusive proof that all this speciation happened in the last 12,000 years. We may never know how long it really took for these faunas to evolve, but chances are that their cradle was in rivers, and that only the final radiation took place in lakes afterwards.

The Ethiopian plateau is relatively species-poor, yet it is the most important, but not the only, focus of aquatic palaearctic relicts (some still identical to their northern populations, others clearly speciated, suggesting more than one wave of immigration). For these to reach Ethiopia, a significant drop in temperature was perhaps more important than a higher humidity in the now arid to hyperarid deserts north of it. A plausible age for at least some of these relicts is therefore the last glacial maximum. Support for this idea is found in the fact that they do not stop on the Ethiopian plateau, but extend to high mountains further south such as Mount Elgon, Mount Kenya, the Drakensberg, and even the Mediterranean zone of the Cape Province. Conversely, several species with a South African range reach their limit of northern extent either in the great lakes area or on the Ethiopian plateau. Van Damme and Van Bocxlaer (2009) provide examples among the molluscs. One peculiar endemic fish of the Ethiopian plateau is *Nemacheilus abyssinicus*. It mainly lives in rivers although few specimens have been found in Lake Tana

(Dgebuadze et al., 1994; Vijverberg et al., 2009). It belongs to a family with an otherwise exclusive European-Asian range. The nearest site where two congeners can be found is the Levant (in and around Lakes Kinneret and Hula) (Ben Tuvia, 1978; Dimentman et al., 1992).

A second focus of palaearctic species is the Egyptian Nile, although the majority of species living there are Afrotropical elements that use the Nile flow to reach northwards. Spectacular examples are found among the megafauna, often linked to historical anecdotes, such as the hippopotamus that killed pharaoh Menes (see further). Many more examples can be found in various contributions in this book, in aquatic insects and zooplankton (Dumont, 2009), but the fish fauna (Witte et al., 2009), and the molluscs (Van Damme & Van Bocxlaer, 2009) are no doubt the most convincing, since these two groups have a fossil record (for fish, see Stewart, 2009). Palaearctic elements in the lower Nile often have circum-mediterranean ranges, or extend from the (semi)arid belt of Middle Asia to North Africa and sometimes the Iberian Peninsula (Irano-Turanian species). In the case of some dragonflies and fairy shrimp, these species are not found in the Nile valley itself, but west and east of it, often in oases in the western desert (Siwa, Kharga…) and in Sinai, which may reflect the presence of superior competitors in the river itself. In some cases, we know what these superior competitors are: in the freshwater crabs, for example (Cumberlidge, 2009), the tropical family Potamonautidae extends to the Nile delta, with two widespread species *Potamonautes niloticus* and *P. berardi*. East and west of it, but not in the river valley itself, the Eurasiatic family Potamonidae is found, with *Potamon potamobius* in Sinai and the Jordan valley, and *Potamon fluviatile* in the Maghreb. The situation with Nile fish is, of course, similar.

In contrast, African species spilling over from the Nile valley to the Levant via Sinai and from here even further north and west is common. Probably the best known case is that of the Papyrus, *Cyperus papyrus*, which established itself in the valley of the River Jordan (Lake Hula) and even extends to Sicily. Other examples occur among fish, mollusks, annelids (Ghabbour, 2009), crustaceans, and insects. Some that became established in the Jordan-Litani valleys have relict populations in the Sinai desert even today.

In the south, exchange of aquatic biota with Arabia across the street of Bab el Mandeb was possible before the street opened, some 4.5 million years ago, but appears to have been group-selective. There is little evidence that fish made the crossing (no cichlids naturally occur in Arabia although *Tristramella* is endemic of the Levant, see further), and most Arabian cyprinids are related to species of the Levant). In zygopteran dragonflies, the African genus *Pseudagrion* has six known species in south Arabia, of which one is endemic (*P. arabicum*) but related to an African congener (*P. kersteni*) that is also ancestral to the levantine *P. syriacum* (see further). It still occurs rather commonly in Yemen, vertically segregated from *P. arabicum* (Schneider, 1987). The others are wide-ranging African species, except the oriental *P. decorum* that is, however, limited to Oman. Several *Azuragrion* also managed to cross from Africa to Arabia, but the reverse movement seems to have been made by no zygopterans and by only few anisopterans, including the oriental *O. taeniolatum*, that has meanwhile speciated in north-east Africa to *O. kollmanspergeri* (Dumont & Verschuren, 2005). Among African anisopterans, at least five African species of *Trithemis* are found in south Arabia; one endemic aeshnid (*Aeshna yemenensis*) is again a close relative of an African species. In contrast to the Nile valley, where endemism is at the species level at best, there are also two endemic genera of damselfies in South Arabia (*Arabineura* and *Arabicnemis*). They are derived from African ancestors, and are clearly older than the current Nile fauna. Like *Tristramella*, they are unrelated to the Nile fauna and their origin should be sought in the Red Sea rift which, prior to the opening of Bab el Mandeb, was a river valley rather than a sea.

In the north, the Sinai "gate" leads into the Jordan valley, where three *Pseudagrion* are found, of which only one is shared with south Arabia, but as a different subspecies (*P. sublacteum mortoni*), while another species (*P. syriacum*) is endemic to the Jordan-Litani valleys. The third species, *P. torridum*, has relict populations in the Sinai desert, and extends to Lake Hula in the north Jordan valley (presumably as a subspecies). Among African-derived libellulids, three endemic subspecies are found: *Rhyothemis semihyalina syriaca, Urothemis edwardsi hulae*, and *Crocothemis sanguinolenta arabica* (see Kinzelbach et al., 1987, for a distribution map). In fish, the comparison turns out differently in the details, but the major lines are similar: as stated earlier, no cichlids are native to Arabia (although some exist in Iran, so their absence from Arabia might be secondary). However, several are known from the Jordan valley, and, as in the dragonflies, some species are widespread nilotic taxa (*Sarotherodon galilaeus*, *Tilapia zillii*, *Oreochromis niloticus*, *Clarias gariepinus*), while others have speciated. Among cichlids, at least three endemic species occur, *Astatotilapia flavijosephi* and two species of the endemic genus *Tristramella*, *viz. T. sacra* and *T. simonis* (Ben Tuvia, 1978). Like *Arabineura* and *Arabicnemis*, *Tristramella* might be a relict of Miocene age. In addition to these Africa-derived elements, a rather large number of Palaearctic cyprinids, some of which endemic, exist here. It is to be noted that the non-speciated Levantine fish are identical to species currently surviving in the Sahara desert.

Faunal exchange across Sinai may have occurred in several waves in the late Pleistocene–early Holocene. Taxa that have speciated may be considered to belong to older waves than those that did not. However, this might not be as straightforward as it seems since some species, genera or families may take longer than others to evolve. Haplochromine cichlid fish, for example, are currently considered capable of rapid speciation (even if perhaps less rapid than sometimes assumed), while *Sarotherodon* and *Tilapia* are "slower". On the other hand, in libelluline dragonflies, three relict pockets are known where the same two species, *Urothemis edwardsi* and *Rhyothemis semihyalina* co-occur. Only in the Lake Hula refuge do these show signs of (sub)speciation, not in a site (Wadi Darbaat) in Dhofar, South Arabia (Schneider & Dumont, 1997), and not in the wetlands of El Kala, Algeria. Of two models (simultaneous sequestration of the relicts and a different rate of evolution, versus a similar rate of evolution, but a different time of arrival time) it is unclear which one to choose. In conclusion, it seems that progress in this domain must await the discovery of DNA markers suitable for the derivation of a trustworthy molecular clock.

Physically, the basin from which the Nile is currently best isolated is that of the biologically much richer Congo. This separation came in the form of the deletion of the entire lakes plateau area from the Congo basin, near the end of the Miocene (Talbot & Williams, 2009), when the current great lake's area was uplifted and so tilted that it started to drain towards the north instead of the west. Compounded by strong climatic fluctuations, a suite of impressive extinctions of pre-existing faunas (fish: Stewart, 2009; molluscs: Van Damme & Van Bocxlaer, 2009) followed, all along the Pliocene. The result, still tangible today, is an impoverishment of the Nile vis-à-vis the Congo, and a quasi-complete difference between both faunas (Fish: Witte et al., 2009a; Molluscs: Van Damme & Van Bocxlaer, 2009; Crabs: Cumberlidge, 2009; Odonata: Dumont, 2009).

There remains the question of the relatedness of the biota of the Logone-Chari basin, The Niger, and the Nile. When biogeographers use the term "Nilotic", they refer to a fauna and flora that extend from the Senegal and Niger to the Logone-Chari and Nile basins, the connotation being that the origin of this assemblage is situated in the Nile valley. This is almost certainly wrong (Van Damme & Van Bocxlaer, 2009). True, of the ca 115–130 fish species that are found in the main Nile, some 74–80 are shared with Lake Chad and the Logone-Chari (Greenwood, 1976; Lévêque, 1997; see also Witte et al., 2009). Similar figures can be given for molluscs, and, among planktonic crustaceans, the only place where the calanoid copepod *Thermodiaptomus galebi* is found outside the Nile basin is in Lake Chad. These data argue for a recent connection between both basins, even if a double caveat is in order: (1) there definitely exist species that are not shared between both basins, and (2) the Logone-Chari fauna is richer than that of the Nile. Van Damme & Van Bocxlaer (2009) therefore suggest that the refuge zone for this fauna during dry periods of the Pliocene–Pleistocene was not the Nile but the upper Logone-Chari, situated in an equatorial climate and thus relatively well shielded from droughts. A third argument is that, if the connection between the basins had been long-lived, some indication would be found in the geomorphology of the divide. This is not the case.

On the other hand, the altitudinal flora and fauna of Jebel Marra contain numerous relicts of tropical biota that must have required much more precipitation than today to become established there (Wickens, 1976; Dumont, 1988). The age of these relicts is probably early Holocene. The most probable areas of contact between the basins are either the upper Bahr el Arab south of Jebel Marra, the upper reaches of the Wadi Howar and Mourdi depression north of Jebel Marra and the Ennedi plateau.

4 Invasive Species

Currently, an unprecedented wave of animal and plant invasions is creating havoc worldwide in the ecosystems they overwhelm. In contrast to earlier decades, when species introductions were often intentional, many of the present invasions are accidental or follow from an ever-more intense international traffic. In the aquatic realm, aquarium trade and ballast water are two important vectors. Another stimulus is the construction of canals, that link previously unconnected river systems. This has not happened on a large scale in Africa so far, but in Europe and Western Asia it has created a water network that extends from the Volga to the Rhine.

Biological invasions have probably been triggered by man since prehistoric times, and many probably go unnoticed unless they cause major disruptions in the receiving ecosystems. Some well-documented cases go back to the nineteenth century, including a notorious one, involving the Nile hyacinth, *Eichhornia crassipes*. It appears that the neotropical Nile hyacinth has been introduced to the Nile three times independently. In the lower Nile, around Cairo and in the delta, hyacinths were introduced during the last decades of the nineteenth century, as ornamental plants (Zahran, 2009). They escaped and rapidly became a nuisance in thousands of kilometers of irrigation channels. The problem persists to the present, and fears have been voiced that, now that the regulated Nile at times resembles more a lake than a river, *Eichhhornia* may migrate upstream. Zahran (loc. cit.) cites one isolated finding of few plants just below the Aswan dam in 1986, but no further spread has occurred since.

The second focus is the While Nile in southern Sudan. Here, the first plants were seen around the mid-1950s. They rapidly expanded afterwards and currently are found over more than 1000 km of river, from the Sudd to Jebel Aulia dam. Major river blockages have occurred, and at times, Jebel Aulia reservoir is completely covered in hyacinths. The infestation probably came from the Congo, where it had started a few years earlier than in the While Nile.

The third and most recent focus is Lake Victoria, where it was first sighted in 1989. It quickly developed huge floating mats and occasionally clogs the lake outflow and power generating system (Lehman, 2009).

Among fish, the most widespread intentionally introduced species is *Gambusia* sp., intended at combating mosquitoe larvae in the irrigation systems. This is moderately successful, even if the fish also feeds on zooplankton. Yet, no major disturbances seem to have been created by it.

Among the crustaceans of the plankton, some delta lake copepods are suspected to be invaders. This is the case of *Acanthocyclops trajani*, of presumed American origin, and currently the most abundant copepod of the delta (Dumont, 2009). Van Damme & Van Bocxlaer (2009) cite several species of invasive mollusks. Again, none seem to cause much ecological damage, although some may facilitate the transmission of parasitic diseases such as bilharzia (shistosomiasis). Among decapods, two freshwater crayfish species have been intentionally introduced to combat precisely some bilharzia-transmitting snails. Although these species have created additional problems by their burrowing habits and although their diets turned out to be broader than suspected, the balance of their effects is not entirely negative: they have proven comestible to man and are well accepted by the local population (El Shabrawy & Fishar, 2009).

A most surprising finding has been that, of the few species of cnidarians that live in the Nile, more than half are invasive (Dumont, 2009). The medusa-forming hydroid

Moerisia lyonsi, described in 1906 and long considered endemic of Birket Qarun, is really a mesohaline species that cannot have lived in the lake in earlier centuries, because its water was too fresh. In the twentieth century, it disappeared, because the water was becoming too salty. It is a synonym of a Caspian species. Curiously, at about the same time as *Moerisia lyonsi* a second hydroid, *Cordylophora caspia* was also first found in lower Egypt. This is an extremely euryhaline animal, that adapted to the Nile and managed to work its way upstream as far as the sudd, before the major dams were in place (Rzóska, 1949). Both species are of Ponto-Caspian origin, and it is well possible that they were introduced together, but how and when this happened is unknown.

5 The Nile as a Multipurpose Natural Resource

5.1 Hydrology and River Damming

After the confluence of the Blue and White Niles, the river flows for over 3,000 km through a desert landscape, and is only augmented seasonally by the Atbara, 300 km North of Khartoum. From Aswan to Rosetta (Rachid) it crosses 1,200 km with no drop of extra water, but plenty of evaporation and some infiltration. Northern Sudan and Egypt are therefore totally dependent on the Nile for their freshwater needs, and their politics reflect that (Allan, 2009). Sutcliffe (2009) discusses the hydrology of the Nile. It is difficult to decide what to emphasize: the regularity of the "hundred days" of summer flood, bringing an abundance of water and fertile silt, or the uncertainty of the variations of that flood, with occasional failures, or, alternatively, floods so high that they drowned much of the valley. Surely, the predictability of the river rising by about 7 m in the lower Egyptian summer must originally have been interpreted as a divine intervention in human affairs. Consequently, the pharaohs were held accountable for failed floods which, if repeated, could lead to famine and political turmoil.

The mythical pharaoh Menes, founder of the first dynasty around 5,100 BP, who may or may not correspond to a single person and is known under a variety of names, lived at a time of high Nile floods. His life, and the centuries that followed, coincided with high rainfalls in the Sahel, creating prosperity in Egypt (Williams & Talbot, 2009). During his long reign of more than 60 years, the first large-scale cereal agriculture in the valley prospered. Among other things, he is remembered for having been killed by a hippopotamus; but he also founded the city of Memphis, and as part of that effort, dammed part of the Nile to create an artificial lake, the first known act of basin irrigation. Since building was mainly using wood and bricks, nothing of this dam remains. Remarkably, Egyptian engineers and architects did not develop skills in river flow manipulation beyond basin irrigation, but rather focused their talents on building temples, palaces and tombs, culminating with the pyramid of Cheops around 4,550 BP. Thus, when about a thousand years later a severe drought occurred, the Egyptians could not react rationally, and the old kingdom collapsed.

The Egyptians never moved beyond basin irrigation; in contrast, they developed skills in canal building. In the days of pharaoh Menes, Lake Moeris (now Birket Qarun) in the Fayum was fed by a natural overflow of the Nile. Around 4,300 BP, as the Nile levels began to fall, the waterway between Moeris and Nile was not allowed to dry out but was actively maintained, and the pharaohs of the 12th dynasty are known to have used the lake as a regulator of Nile flow, useful to store excess water (El-Shabrawy & Dumont, 2009).

For the idea that variation in discharge of a river can be brought under control by dam building, and extend the irrigation period, we have await the late nineteenth century AD, a period when the full geography of the Nile basin was finally clarified and its climatic forcings adequately understood (Camberlin, 2009). That the entire basin, save Ethiopia, came under British colonial rule, facilitated the deployment of comprehensive management initiatives. But it was under the Mohammed Ali dynasty, which was also the time of the construction of the Suez Canal, that the first barrages were constructed near Cairo, and on the Rosetta and Damietta branches of the delta. The main incentive was that cotton had become the new cash crop, and by elevating the river level, and digging an intricate network of secondary, tertiary, etc. canals, agricultural yields received a first boost (Waterbury, 1979). However, the technical level of river damming did not differ much from what pharaoh Menes had attempted 5,000 years earlier.

After 1882, the situation rapidly changed: strong population growth in Egypt (three doublings between 1820 and 1970, and a fourth one underway) fueled a thirst for water that continues to the present, at first mainly for agriculture, later increasingly for industrial use. As the need for perennial irrigation rapidly consumed the full flow of the Nile during low flow, a real dam was constructed at Aswan, with a storage capacity of 1×10^9 m^3. Its height (and capacity) soon needed to be raised, in 1907–1912 and 1929–1933, but it threatened to overflow in 1946, and plans for a high dam in addition to a series of smaller dams between Aswan and Cairo were worked out in the framework of a management plan that has become known as the Century Storage Scheme (Waterbury, 1979). The foundations for this were laid as early as 1904 by the then British Undersecretary of Public Works in Egypt, and included storage in the equatorial lakes, the building of a canal that would bypass the Sudd swamps, and damming of Lake Tana and the River Atbara.

To the exception of the Jonglei canal, most of these objectives have been achieved. The *raison d'être* of this canal is to cut down the huge loss to evaporation in the Sudd swamps, thereby gaining about 4.7×10^9 m^3 of water for downstream use, as well as to reclaim ca 100,000 ha of agricultural land. Numerous ecological and sociological objections against the canal have been voiced. The digging started in 1980 but was stopped by civil war in Sudan in 1983, after 260 out of 360 km were completed. In 2008, discussions about continuing the work were resumed.

According to a tediously negotiated agreement of 1959 between Egypt and the Sudan, the average yearly Nile discharge of about 85×10^9 m^3 per year is divided as follows: 57 × 10^9 m^3 for Egypt, and 18.5 × 10^9 m^3 for the Sudan; about 10 × 10^9 m^3 are lost to evaporation and infiltration.

British engineers had planned the building of large storage dams on the East African plateau and in Ethiopia, making use of existing lake basins, because evaporation would be lower there. However, once the colonial era had ended, the newly independent Egypt preferred a dam on its own territory, in the desert environment of Aswan. The high dam started to fill in 1964, and with that, full over-year storage was achieved, and the river came under full control. In the words of Hamdan (1970), it was transformed from a destructive force into a giant irrigation canal; in Waterbury's (1979) words: the Nile stops at Aswan! For a discussion of the gains and losses caused by the dam, see El-Shabrawy (2009).

When filled to capacity, the Nasser-Nubia reservoir may hold up to 160 × 10^9 m^3 of water, which amount to about twice the average yearly discharge of the Nile at Aswan (85 × 10^9 m^3). A steady year-round flow has been achieved, replacing the old summer highs and winter lows, and perennial agriculture is now widely applied.

Exceptionally, the dam may close for 2–3 weeks in winter, at which time the water level in the delta lakes may drop to a point where seawater briefly enters the delta lakes (Dumont & El-Shabrawy, 2008). During the high water levels of the late1990s, Egypt implemented the so-called New Valley or Toshka-project: from the days of the earliest conception of the High Dam, the possibility that the reservoir might overflow had been considered. The Toshka valley in the western desert was identified as a sort of "safety valve" through which excess water could be evacuated. Between 1978 and 2005, 50 km of canal and a pumping station were constructed, to yearly pump up to 5 × 10^9 m^3 of water into the Toshka depression, creating four lakes and irrigating some 400,000 ha of new land. However, after the exceptionally high Nile floods of 1998–2001, falling water levels have now caused these lakes to shrink. The westernmost one is rapidly increasing in salinity (El-Shabrawy & Dumont, 2009b). There is a clear danger that what happened to the Fayum will repeat itself here!

A second recent and ambitious water-diversion project is the Sinai peace canal ("El Salaam"), aimed at irrigating some 260,000 ha of land and create an artificial lake of 6,000 km^2. To this end, up to 4.5 × 10^9 m^3 of water is pumped through a series of ducts that pass under the Suez Canal.

Dam building in the Sudan began with the dam at Sennar on the Blue Nile in 1925, aimed at irrigating the Gezira, a large cotton-growing area. Jebel Aulia dam followed in 1937, Roseires dam in 1966, and Khasm el Ghirba dam on the Atbara in 1966 as well. The latter dam was the result of an agreement with Egypt, aimed at resettling the Nubians that had been moved from the flooded Nasser-Nubia reservoir area.

In Ethiopia downstream developments are closely monitored, and occasional tensions arise between the Upper Nile countries that, according to Allan (2009), provide water but lack power, and the Lower Nile countries that are dependent on this water but wield power. In 1992, the Nile Basin Initiative (NBI) was initiated, aimed at improving cooperation between all riparian states, but a deep-rooted suspicion between Egypt and Ethiopia over Nile water usage subsists (Degefu, 2003). Sadly, as the amount of water a per capita basis continues to dwindle, such tensions are likely to exacerbate, not subside.

5.2 Hydropower

Hydropower was never the first priority of dam construction, but it was never neglected either. Thus, the installed capacity of Sudan currently reaches some 240 MW (from Roseires, Sennar, and Khasm el Ghirba combined). To this, Meroe dam will add another 600 MW. The total potential of the Sudan Nile is estimated at 1.4 GW. Only Egypt does better, with the Aswan High Dam alone producing 2.1 GW. This is an impressive figure, since the country as a whole produces “only” 2.8 GW. Of the other riparian countries, only Uganda and Ethiopia currently produce hydro-electricity. Owen Dam in Uganda produces some 180 MW, an amount that might be doubled in the future.

Ethiopia has installed hydropower capacity only recently, at the Lake Tana outlet. This mountainous country has a great potential, estimated at 6 GW, but currently only some 400 MW are developed. Power generation is not likely to create a conflict with Egypt, but irrigation, consuming a part of the Blue Nile outflow, could well raise a *casus belli.*

5.3 Fisheries

Not much needs to be added to the account given by Witte et al. (2009b). Fish is a major source of animal proteins all across the basin. Egypt has the best developed fisheries industry, and in some zones, overexploitation is suspected to occur. Fish landings in the delta lakes, for example, now overshoot the limits of sustainability (Dumont & El-Shabrawy, 2008), but fish farming has begun to play a more and more important role. In Lake Nasser, fish are also exploited, and even the Toskha lakes were fished as soon as they formed (El-Shabrawy & Dumont, 2009). El-Shabrawy (2009) argues that Lake Nasser lacks a true pelagic fish, and proposes to introduce a clupeid to create additional capacity.

In Sudan, fishing is unevenly distributed, especially in the little-inhabited zone north of Khartoum. Much of it is subsistence fishery, including in the Sudd marshes.

At Lake Victoria, after the introduction of *Lates*, the local people needed time to adjust to the newcomer that was at first rejected from the diet. Later, the local population continued to benefit relatively little from the fishery, because *Lates* is a highly prized table fish that is primarily exported to Europe. Overfishing has now become evident, and has led to the partial recovery of the endemic haplochromine flock (Lehman, 2009; Witte et al., 2009b).

5.4 A Non-renewable Resource: Fossil Hydrocarbons

In recent decades, fossil fuel deposits have been discovered in at least three zones of the basin. The Nile delta (both onshore and offshore) is currently Egypt's main source of hydrocarbons and natural gas (Hamza, 2009). Egypt's oil production peaked in 1996 at 1×10^6 barrels per day, and has since fallen back to about 600,000 barrels per day. Although minor new discoveries are announced from time to time, it is unlikely that the delta area will ever become a major international oil supplier.

Sudan has in a short time (first oil was produced in 1999) become an important though not uncontested crude oil producer and has seen its economy revolutionized, even while marred by civil war. A large part of the oil is exported, via a pipeline that connects Central Sudan to the Red Sea port of Bashair. Production amounted to 400,000 barrels per day in 2005, and reached 600,000 barrels in 2006.

Finally, exploitable hydrocarbon deposits were recently discovered in the western rift, Uganda, around and below Lake Albert. Exploitation is expected to start in 2009, at a rate of 10,000 barrels per day. The total reserves are estimated at $100–300 \times 10^6$ barrels, and Uganda hopes to reach a production of 40,000–60,000 barrels per day in few years.

5.5 Water Pollution

As Talling (1976) wrote, the Nile has always been famous because its water was drinkable. Locally, this is doubtlessly still the case, but changes have begun to occur in several places: Lake Victoria, for example, has turned into a eutrophic lake in a matter of few decades (Lipiatou et al., 1996; Lehman, 2009). Lake Tana is bacteriologically and chemically polluted near population centres like the city of Bahir Dar (Vijverberg et al., 2009). The zone around Khartoum and large stretches of the Egyptian Nile, especially at and downstream of Cairo have a chemically and microbiologically degraded water quality (El Sheekh, 2009; Rabeh, 2009). Shipping, mainly concentrated in Egypt, contributes to a decreasing water quality. Egypt is the only country in the basin with a developed industry and with all ecological side-effects thereof. The industrial plants releasing polluted sewage are well known, and water purification facilities get better and better, but a long way remains to be covered. The Nile water behaves like a Malthusian resource: to increase its quantity is a difficult and costly process, and progress is only linear, while demand by agriculture, industry, and households tends to increase exponentially or even hyperbolically. Currently, every drop of Nile water in Egypt is recycled up to three times before it reaches the Mediterranean, yet further efforts in making water use more efficient and safe are needed. According to Allan (2009), Egypt has entered a demographic transition, but for the near future that only means that population increase will slow down, not stop. This may put rather severe constraints on the country's prospects for the twenty-first century and explains the nervousness with which it watches the moves of its upstream neighbours as regards Nile water use.

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The Nile: History of Scientific Research

Jack F. Talling

Abstract The history of Nile science is briefly reviewed, with reference to both environmental and biological aspects. Five chronological phases are distinguished; they have successively involved traveller-observers and collectors, locally based institutions that include universities, and international agencies. Especially for hydrology, chemistry and plankton biology, longitudinal patterns observed along the river have been combined with studies of local time-sequences and other characteristics. Diverse upstream origins in headwaters include some major lakes; downstream, both the quality and quantity of river water have been shown to be influenced by passage through swamps and retention in reservoirs. The reservoirs, together with annual floodwater, have been shown to have important consequences for water quality, plankton biology, fish stocks, and insect emergences. There have been major recent advances in understanding the environmental history of the river system.

1 Introduction

The Nile is a river rich in human history, which includes an ancient civilisation and achievements of geographical exploration. Accounts of these are numerous, but there appears to be no general summary–history of scientific research on the river itself. The following outline has emphasis upon hydrobiology and its physical and chemical background. References are given only as *examples*; naturally they postdate the time that the actual work was done.

Many aspects of the Nile, including its scientific study, have been influenced by its great length combined with a south–north orientation. The latitudinal differentiation that results (examples in Fig. 1) is unmatched in any other large tropical river. Past centres of scientific activity were widely separated; they operated under varied climatic conditions and sources of support. Longitudinal sampling and measurements also depended on feasibilities of transport and navigation.

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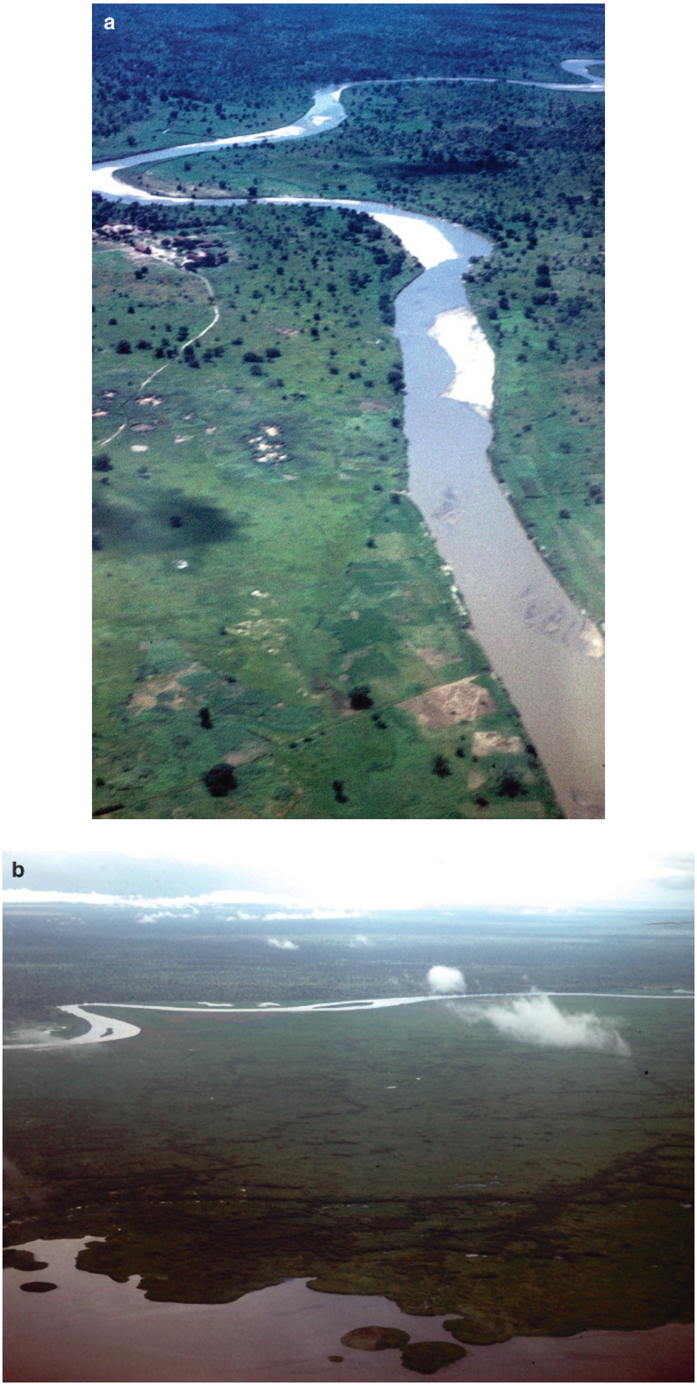

Fig. 1 Dissimilar river sectors down the Nile: (**a**) savanna, southern Sudan; (**b**) floodplain swamps (‘Sudd’)

Fig. 1 (continued) (**c**) desert cataract (from Talling, 2006, with permission of the Freshwater Biological Association, Windermere) (*see Color Plates)*

2 Pre-1900

The ancient Egyptian civilisation left abundant pictorial records (as in tomb paintings) of river and swamp scenes and their larger biological components. Papyrus and lotus were extensively stylised and were symbols of Upper and Lower Egypt. Species of riverine birds can be recognised, as can distinctive nilotic fishes such as the Nile perch, *Lates niloticus*. Hydrology began with maintained records of river level, of which examples after 600 AD have been re-analysed in modern times (Riehl & Meitin, 1979; Hassan, 1981). But the sources of the river, and the origin of its annual flood, were unknown when the Greek traveller and historian Herodotus visited Egypt about 460 BC. More than two thousand years later the Jesuit Father Lobo made the crucial connection (Southwell, 1668) between seasonal rains in Ethiopia and floodwater in Egypt – although possibly some inkling of this had not escaped inhabitants of the old intermediate centres of Meroë and Sennar.

Travellers in the seventeenth to nineteenth centuries brought observations and samples that were recorded in scientific literature, mainly European. Plant and animal specimens were the foundation for later taxonomy, floristics and faunistics. Celebrated field collectors included the German botanist Schweinfurth and the zoologist Stuhlmann who first dipped a plankton net into Lake Victoria (Stuhlmann, 1891).

3 1900–1920

Sampling of aquatic organisms continued, with associated taxonomic work. It extended to upper reaches, especially of the White Nile in Uganda and the Sudan. In the latter there were records of micro-Crustacea by Daday (1910), Gurney (1911) and Chappuis (1922). The major single faunistic work was that of Boulenger (1907) on the fishes of the Nile. This was made possible by collections held in Europe, especially at the British Museum of Natural History in London where he worked.

In this period the foundation was laid for the hydrological study of the entire river system inclusive of headwaters (Garstin, 1904). This was an ecological as well as a hydrological landmark. It required long-term records of water level and related flow-gauging. It had support from advances in regional geography, meteorology and climatology. The main centre, led for many years by Hurst, was at the Physical Department of the Ministry of Public Works in Cairo. Here the economic applications were all-pervasive, and led to the creation of the first Aswan dam with upstream reservoir and seasonal storage.

A beginning was also made on the chemical study of the river water. It was handicapped by the current limitations of water analysis, as evident in the survey relating to the lower Nile by Lucas (1908). This, and later work by Aladjem (1928), showed a seasonal (low water) increase of salinity between Aswan and Cairo. Upstream at Khartoum, and associated with the newly founded Gordon Memorial College, Beam (1906) worked for several years in the Wellcome Laboratories. He demonstrated considerable changes with season in the waters of the Blue and White Niles before their union; also evidence of chemical modification during passage through the Sudd swamp region upstream.

4 1920–1940

The most important contribution was the expansion, by Hurst and his associates, of a network of hydrological stations and flow-gauging. Results, involving topography and ultimately water budgets, were summarised in a series entitled *The Nile Basin*. Example volumes dealt with headwaters of the Lake Plateau (Hurst & Phillips, 1938), the White Nile in the Sudan plain (Hurst & Phillips, 1931), the Blue Nile (Hurst, 1950), and the whole system (Hurst, 1944). The hydrology itself was much altered, with more seasonal storage, by a heightening of the Aswan dam and the creation of new reservoirs above dams at Sennar (1925) on the Blue Nile and Gebel Auliya (1936) on the White Nile. These had considerable biological consequences, as for fishes like the Nile perch (Kenchington, 1939) and enhanced insect emergence from an altered bottom fauna (Lewis, 1956).

Limited but much needed information was obtained from Ethiopian headwaters of the Blue Nile, especially Lake Tana. It included chemical analyses. In part it derived from a small Anglo-Egyptian expedition from Khartoum (Grabham & Black, 1925), and partly from a more extensive Italian survey of the limnology of Lake Tana (Morandini, 1940).

5 1940–1960

In addition to hydrology, government-sponsored science continued to make contributions to the wider ecology of the Nile. Applied aspects included water ‘quality’, aquatic insect pests and fisheries. Thus routine analyses of chemical characteristics were maintained at Cairo (Ramadan, 1972) and Khartoum, and some consequences of reservoir development for fisheries established. Another consequence in the Sudan was the mass emergence (reviewed by Rzóska, 1964) of simuliids and chironomids as adults from an enriched bottom fauna. Severe nuisances from clouds of these ‘nimitti’ resulted at Khartoum and Wadi Halfa. Their occurrence and biology were studied by Lewis (1956, 1957), who also extended earlier taxonomic work by Kieffer in the 1920s, and cooperated with the Khartoum Wellcome Laboratories in an assessment of the chemical quantities involved (Lewis et al., 1954) that constituted a loss from the river.

In 1947 the East African Fisheries Research Organisation was established as a laboratory near the origin of the White Nile from Lake Victoria. Its later work concerned lakes more than rivers, but contributed to some relevant fish biology and chemical water characteristics in the Nile tributary system that included short-term changes (deduced from electrical conductivity) in the West Rift (Beauchamp, 1956).

Within the Sudan, after 1950, the governmental Jonglei Team began a lengthy study of the Sudd swamp region, with reference to consequences of a planned bypassing of this area of net water loss by a major canal (Jonglei Canal). Its scope included physical aspects and impact on a cattle-based local economy.

Universities and their research expanded during the years after 1945. Chief in the Nile system were Cairo University (e.g. Migahid, 1947; Abdin, 1948a,b,c), the University College (later University) of Khartoum, and Makerere College, Kampala (Beadle & Lind, 1960; Lind & Visser, 1963). It was, however, at Khartoum that a university group had the greatest possibilities for sustained work on the river. The location was strategic for exploratory studies on environment and organisms of the White Nile and Blue Nile. In 1953 the University College, with

Fig. 2 Research on the White Nile, Sudan (1953): cabin of the launch *Malakal* with Julian Rzóska (standing) and the author (from Talling, 2006, with permission of the Freshwater Biological Association, Windermere)

backing from the University of London that included the support of F.E. Fritsch, set up a Hydrobiological Research Unit (HRU) equipped with research launch (Fig. 2) and truck. Even before this, from 1947, local collections and expeditions up the White Nile had made contributions that involved water chemistry (Pyle, 1950), algae (Brook, 1954), invertebrates (Rzóska, 1949) and fish (Girgis, 1948; Sandon & El-Tayib, 1953). A longitudinal section of a reservoir region by Brook and Rzóska (1954) inaugurated integrated ecological work, continued by Rzóska et al. (1955) and by others within the HRU – which was led by the émigré Polish hydrobiologist Julian Rzóska. Work on water characteristics and plankton emphasized both longitudinal and seasonal changes in flowing water (Talling, 1957a; Prowse & Talling, 1958; Talling & Rzóska, 1967), and included the first work on photosynthetic production (Talling, 1957b). Invasion of the White Nile by the water hyacinth *Eichhornia crassipes* was detected and studied by Gay (1960). Besides his work on zooplankton, Rzóska (1974) assembled information on the 'landscape ecology' of the Sudd swamp region, and found a unique community of desmids in its Lake Ambadi that others studied taxonomically (Grönblad et al., 1958). Thornton (1957) characterised the isolated arthropod communities within umbels of *Cyperus papyrus* and the rosettes of the floating *Pistia stratiotes*.

Other work on the river was done by visitors from abroad, especially Europe. Probably the most notable was that in Egypt (Delta lakes to Aswan) by two experienced limnologists, Elster and Vollenweider (1961). Their contributions included water chemistry, plankton and its primary production, and fish biology.

In Uganda the construction in the late 1950s of the Owen Falls dam just below the L. Victoria outflow had relatively little effect on the river. It involved, however, the use of the insecticide DDT against an insect vector, *Simulium damnosum*, whose larval stage was present in the bottom fauna.

6 1960–1980

Conditions on the river system were much altered after the creation of the Aswan High Dam (1964) and the Roseires Dam on the Blue Nile (1966). The former introduced a large over-year storage in a man-made lake, L. Nubia-Nasser; both greatly altered within-year seasonality and the water-borne transport of silt. Scientific research in Egypt intensified, involving universities, other national organisations and international agencies. The FAO supported work from Aswan, ranging from water characteristics (Entz, 1976) to fish biology and fisheries (Latif, 1976). Also based here and in Cairo was a team associated with Mancy, with studies on chemical aspects, phytoplankton and (Whittington & Guariso, 1983) hydrological modelling.

In the Sudan, river research continued from the University of Khartoum. There were geomorphological studies on the White Nile by Berry (1976) and further work on the infesting *Eichhornia crassipes* (Obeid, 1975) and its effects (Abu-Gideiri & Yousif, 1974). A Russian expedition contributed information on the little studied zoobenthos (Monakov, 1969). On the Blue Nile there was regular longitudinal and seasonal sampling (Hammerton, 1972) that demonstrated consequences for water characteristics, plankton and bottom fauna of changes introduced by the Roseires reservoir. El-Moghraby (1977) implicated diapause as a significant factor in the seasonal re-appearance of zooplankton. There were further studies on the seasonality of phytoplankton and nutrients in both the Blue and White Niles (Abu-Gideiri, 1969; Sinada & Karim, 1984a, b), with additional work on photosynthetic production and algal floristics; also on swamp vegetation (Denny, 1984), zooplankton (Green, 1967) and bottom fauna (El-Moghraby & Adam, 1984). Much of this and other research was brought together in a volume on hydrobiology in the Sudan (Dumont et al. 1984). On the Upper White Nile work proceeded on excavation of the Jonglei Canal – unfinished for reasons of military unrest – and further associated scientific surveys (Mefit-Babtie, 1983; Howell et al., 1990).

In Egypt there were significant studies of the Delta lakes and Nile branches, in part from the Institute of Oceanography and Fisheries at Alexandria. They included chemical transfers and nutrients (Saad, 1976), plankton communities and bottom fauna (Samaan & Aleem, 1972). Salinity, nutrients and coastal sedimentation showed changes influenced by the Aswan High Dam (Sharaf-el-Din, 1977; Banoub, 1983).

An influential book, edited by Rzóska (1976), set out to describe and integrate the ecology of the entire Nile against the geographical background. Here much historical information was presented. Another book, by Beadle (1974), included a shorter account of the river. General problems, especially relating to conservation, were considered in a 1978 symposium at Cairo (El-Hinnawi, 1980).

7 1980+

Numerous studies of Nile science continued in Egypt, with centres at Alexandria, Cairo, Assiut and Aswan. They included hydrology and chemical characteristics (Saad & Abbas, 1985), plankton (El-Ayouty & Ibrahim, 1980; Habib et al., 1987), and fisheries (Latif, 1984). Many are summarized in the book edited by Bishai et al., 2000), that is centred upon the consequences of the Aswan High Dam and its impoundment, and also gives general accounts of the groups of plants and animals involved.

In Sudan, work at Khartoum University continued on phytoplankton in the Blue and White Niles by Sinada and his students. By this time the former Hydrobiological Research Unit was assimilated within an Institute of Environmental Studies. The discovery and exploitation of oil reserves in the Sudd region involved impacts upon the river and issues of ecological conservation. For the Main Nile within Nubia, above Dongola, plans and associated surveys proceeded after 2000 with the creation of a new reservoir involving seasonal storage.

Two biological invasions had influence in the headwaters at Lake Victoria. The Nile perch, *Lates niloticus*, had risen to abundance after its controversial introduction (Jackson, 2000) in the late 1950s, with adverse effects on the original fish fauna. The water hyacinth *Eichhornia crassipes*, entered the lake, probably from across the Zaïre-Nile watershed, and during the 1990s was an extensive floating pest especially in northern waters. Both these situations led to numerous studies, as from the Fishery Research Institute (formerly EAFFRO) at Jinja (Oguto-Ohwayo, 1988) and other lakeside institutes at Kisumu (Kenya) and Mwanza (Tanzania).

Besides such regional problems, there was renewed interest in the historical evolution of the Nile system as a whole (Adamson et al., 1980).

8 General Remarks

Clearly, hydrological knowledge has been a major and integrative component of Nile science. It has directed attention to the river system as a whole, with longitudinal transmission and local retention also evident and especially studied in works on chemical transfers, silt distribution and plankton development. Here downstream transfer, flow limitation and seasonal cycles have been interrelated. Local differentiation in distinctive river sectors is ensured by the latitudinal and hence climatic span, plus the consequences of an interposed rift valley, a major swamp and a near-rainless desert. In many long sectors the river is a single transmission channel rather than a tributary-rich drainage.

The history of Nile science is probably unequalled amongst that of tropical and sub-tropical rivers for the length and subject-diversity of study. As in Africa more generally (Talling, 2006), successive phases have involved traveller-collectors and observers, locally based institutions, and international agencies.

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Part I

Origin

Cenozoic Evolution of the Nile Basin

Michael R. Talbot and Martin A.J. Williams

Abstract The Cenozoic evolution of the Nile basin reflects a complex interaction between tectonic, volcanic and climatic events. The Ethiopian and Ugandan headwaters of the Nile attain elevations in excess of 2 km, while the watersheds rise to over 5 km. The Ethiopian tributaries of the Nile (notably the Blue Nile/Abbai and the Atbara/Tekezze) provide the bulk of the flood discharge and sediment load, but the Ugandan tributaries, via the White Nile, provide the reliable dry season discharge responsible for maintaining perennial flow in the main Nile. The hydrological differences between the Blue and White Nile rivers reflect their very different geomorphic histories, reflecting the Cenozoic tectonic and volcanic evolution of their respective headwaters.

The volume of rock eroded from the Ethiopian headwaters of the Blue Nile/Abbai and the Atbara/Tekezze river basins since the extrusion of the Oligocene Trap Series basalts 30 Ma ago amounts to 102,000 ± 50 km^3 from a catchment area of 275,000 km^2. The volume of rock eroded from the Ethiopian headwaters region of the Blue Nile and Atbara rivers is comparable to that estimated for the total volume of the Nile delta and submerged Nile cone in the eastern Mediterranean, which amounts to 150,000 ± 50,000 km^3. The concordance between these two independent estimates is consistent with an Ethiopian source for the bulk of the Nile cone sediment since the Pliocene, when there seems to have been an increase in erosion in the Blue Nile headwaters linked to an increase in the rate of tectonic uplift.

The origin of the White Nile as a large, permanent river is intimately connected with the development of the western branch of the East African rift system. Prior to the onset of rifting much of the drainage from central Africa was directed westward, into the Congo basin. Rifting led to the capture of a number of major tributaries of the Congo River and the redirection of river systems, producing south-to-north

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directed axial drainage within the rift and radial drainage into the Victoria basin. Rifting and associated rift-flank uplift was also responsible for the development of the large lake basins (Victoria, Albert, Edward, George and Kyoga), which characterise the upper White Nile catchment. Exactly when drainage from the present headwaters became linked to the White Nile is still unclear, but it seems likely that Lake Victoria, which today provides around 90% of the runoff to the White Nile, may be no more than about 0.5 million years old.

While rift development and ongoing rift-related tectonic activity have controlled the long-term evolution of the White Nile headwaters, it is clear that much of the shorter term variations in discharge are probably related to climate change. There is evidence of a progressive tendency to drier conditions over the past 1.5 Ma, which may have been related to the development of topographic barriers that limited the penetration of humid air masses into the continental interior. Superimposed on this long-term trend are astronomically driven changes and brief, abrupt climatic excursions that were probably driven by events outside tropical Africa.

1 Introduction

The Mesozoic and Cenozoic history of the Nile basin is one of episodic reactivation of geological structures (mylonites, shear zones, fractures) generated before and during the 550 Ma Pan-African orogenic event. These ancient structures account for the complexity and variable alignments of the present Nile and of all the major depocentres within the Nile basin. The focus on this chapter is on the last 30 million years (30 Ma) of Nile basin history – the latter half of the Cenozoic – since the evidence beyond that time is both poorly preserved and inadequately dated. The Cenozoic evolution of the Nile basin reflects a complex interaction between tectonic, volcanic and climatic events. We here discuss the tectonic evolution of the two major tributaries of the main Nile, notably the White and Blue Nile rivers, and conclude with a brief overview of the Cenozoic climatic history of the Nile basin. The present Nile basin drains about one tenth of the African continent and covers an area of 2.96 million km^2. It is about 6,825 km long, making it the longest river in the world. The Ethiopian and Ugandan headwaters of the Nile attain elevations in excess of 2 km, while the watersheds rise to over 5 km. Despite its impressive catchment area, the annual discharge of the Nile is only 84 km^3. The Amazon, in contrast, drains 7,050 km^2 and has an annual discharge of 5,518 km^3. At the present time three major tributaries provide much of the water discharge and sediment load of the Nile, namely, the White Nile, the Blue Nile and the River Atbara. The White Nile derives much of its flow from the lake plateau of Uganda and is vital in maintaining perennial flow to the Nile during times of severe drought in Ethiopia. The Blue Nile rises in the volcanic uplands of Ethiopia, and flows through a deep gorge out across the Gezira alluvial fan to join the White Nile at Khartoum. The headwaters of the Atbara arise close to those of the Blue Nile. The Blue Nile and the Atbara furnish 68% and 22% of the peak flow and 72% and 25% of the annual sediment load of the Nile, respectively. (Williams & Talbot, 2009). The hydrological differences between the Blue and White Nile rivers reflect their different geomorphic histories and are evident also in the ways in which human societies have adapted to these mighty rivers from Neolithic times onwards.

North of Khartoum the main Nile flows through the eastern Sahara desert north into the Mediterranean and receives no further inflow north of the Atbara confluence until it reaches the sea after a waterless journey of 2,689 km. On numerous occasions in the past the climate has been wetter in northern Sudan and Egypt, and now dry tributary valleys provided sediment and water to the Nile. In addition, the Nile has changed course, sometimes radically. It is therefore of interest to explore when, how and why such changes occurred.

2 How Old Is the Nile?

The Nile flows through a narrow gorge across an ancient ring-complex at the sixth cataract and is cut across granites and dolerites at the second cataract, both of which point to drainage superimposition from a cover of Upper Cretaceous Nubian Sandstone, sporadic remnants of which still occur in these localities. Maley (1969, 1970) considered that the ancestral Nile was even older, noting that basal gravels in the Nubian Sandstone near the second cataract occupy a linear depression parallel to the axis of the present Nile valley. It is thus possible that the ancestral Nile may be as old as 100 million years, but since the evidence is limited, it seems wiser to consider the Nile as younger than the Upper Cretaceous Nubian Sandstone into which it is entrenched in northern Sudan and southern Egypt. We will therefore focus our attention primarily on the Cenozoic history of the Nile.

The most striking evidence for an earlier Nile in Egypt is the canyon cut during the Late Miocene Messinian salinity crisis (Hsü et al., 1973) that began ~6.5 Ma ago and lasted until ~5 Ma. During this time the Mediterranean dried out almost completely and refilled again on about a dozen occasions. The drying out on each occasion was probably relatively rapid in geological terms, perhaps no more than a thousand years, leading to repeated substantial drops in base level and vertical incision by the former Nile to perhaps 4 km below present sea-level in the northern reaches of the delta, −2.5 km north of Cairo, −0.8 km at Assiut and −170 m at Aswan (Chumakov, 1967; Said, 1993, p. 38). Said termed this Late Miocene canyon the ‘Eonile’ canyon.

Renewed and permanent flooding of the Mediterranean brought this remarkable episode to a close, and the Pliocene sea drowned the Late Miocene halites and other evaporites beneath several kilometres of seawater. An arm of the Pliocene sea submerged the lower Nile canyon and estuarine sediments accumulated as far upstream as Aswan, where 135 m of montmorillonitic clays interbedded with sands and rich in organic matter, glauconite and zeolites are preserved at elevations of −172 to −35 m (Chumakov, 1967). These sediments were derived in part from the main Nile flowing from the south and in part from active wadis flowing westwards from the Red Sea Hills and eastwards from the present Western Desert region of Egypt. Said termed the river that flowed into and eventually replaced this estuary the ‘Paleonile’ (Said, 1993, p. 39).

Likely canyon dimensions would have been a total length of ~1,200 km, a maximum depth of 4 km at the distal end tapering to 170 m near the proximal end, and corresponding widths of 50 and 1–2 km. Assuming that these figures are broadly correct, the total volume of rock and sediment eroded from the canyon during Messinian time and subsequently replaced by Pliocene estuarine deposits would amount to roughly 80,000 km^3.

The climate in Egypt remained wetter than present throughout much of the Pliocene. The fossil plants and pollen preserved in the late Pliocene Plateau Tufas of Kurkur and Kharga are consistent with an abundance of surface water and a sub-humid to semi-arid climate (Butzer & Hansen, 1968, pp. 355–394 and 515–520), in contrast to the present-day aridity in these latitudes. Said (1993, p. 41) considered that the Egyptian Nile did not become connected to the Ethiopian headwaters until the middle Pleistocene (the 'Prenile'), some 0.8 million years ago, a view supported by the heavy mineral assemblage of Nile alluvium in Egypt (Hassan, 1976). However, Rossignol (1961, 1962) recovered Ethiopian montane forest pollen and spores in early Pleistocene Nile cone sediments, so that the question of when the Ethiopian link to the main Nile was first initiated remains open, which brings us to the issue of the age and origin of the Nile cone.

3 The Nile Cone

The Nile cone has been described as 'one of the great submarine delta fans of the world', and is comparable in scale to the deltas of the Brahmaputra and Ganga rivers in the northern Bay of Bengal. The cone is 320 km wide and extends out to depths of −2,800 m to the west and −1,600 m to the east. Harrison (1955) used gravity anomaly data to infer the thickness and spatial extent of the cone. Assuming no crustal sag would give a total volume of 95,000 km^3 for the Nile cone and delta, but allowing for the Plio-Pleistocene subsidence caused by the weight of overlying water and sediment yields a more realistic estimate of ~220,000 km^3. Emery et al. (1966) used Harrison's contour data to infer a volume of 140,000 km^3, but Wong & Zarudski (1969) carried out new seismic analyses and concluded that the submerged area of the Nile delta-cone complex was greater than previously thought, suggesting that an estimated sediment volume of 100,000 km^3 to 200,000 km^3 is reasonable. Emel'yanov (1972) noted a high proportion of Ethiopian volcanic minerals in early Pleistocene Nile cone sediments, in good accord with the Ethiopian pollen spectra described by Rossignol (1961, 1962), all of which suggest an early Pleistocene minimum age for the Nile cone, with the strong possibility that some of the deeper sediment offshore may be Pliocene sediment reworked by turbidity currents and by the effects of glacio-eustatic sea-level fluctuations.

4 Ugandan Headwaters of the White Nile

Although sometimes referred to as the Albert Nile or the Bahr El Jebel, the White Nile can be regarded as starting at the point where overflow exits Lake Albert (Fig. 1). Thus the state of the White Nile and its contribution to the main Nile is determined by runoff

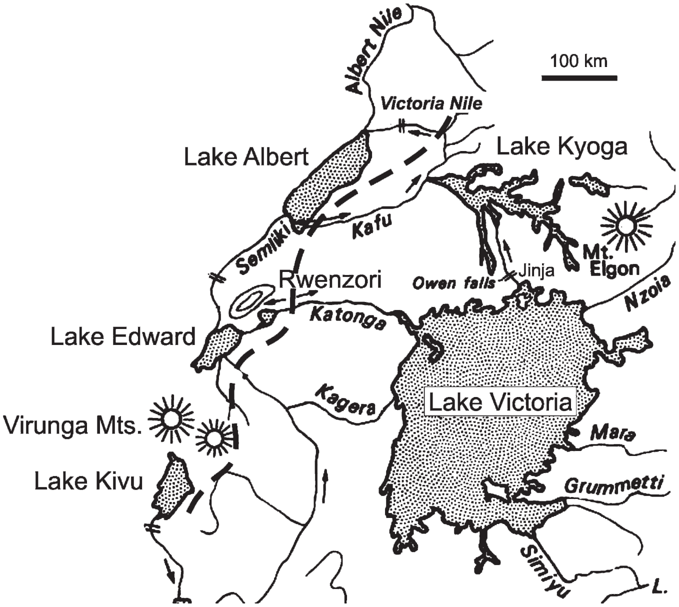


Fig. 1 Headwaters of the White Nile. The heavy dashed line marks the drainage divide due to uplift along the eastern flank of the Western Rift. Uplift caused drainage reversal and ultimately the formation of Lake Victoria (see Fig. 2). Base map drawn by the GMT (http://www.aquarius.geomar.de/make_map.html)

in a catchment that stretches across Lakes Victoria, Albert and Edward, to the peaks of the Virunga volcanoes and the snowfields of Mt. Elgon and the Rwenzori (Fig. 1). Although climate over this large and varied swath of tropical Africa controls discharge conditions on annual to millennial time scales, a proper understanding of the White Nile's long-term history is impossible without also considering the tectonic evolution of its headwaters. Several lines of evidence suggest that these drainage basins are all geologically recent additions to the White Nile catchment. Tectonics have clearly had a decisive influence upon basin configuration and drainage routes, and have probably also had a secondary effect on the White Nile by causing topographic changes which have impacted regional precipitation patterns. In this section we review briefly the tectonic history of the White Nile headwaters and make some suggestions as to when a White Nile drainage system comparable to the one we know today became established. We also present previously unpublished strontium isotope data from some of the catchment lakes, which throw new light on the palaeohydrology of these waterbodies.

4.1 Pre-rift Configuration

The present morphology and drainage patterns of the White Nile headwaters have been primarily shaped by the evolution of the western branch of the East African rift system (WEARS) and its associated volcanic centres. Although unequivocal

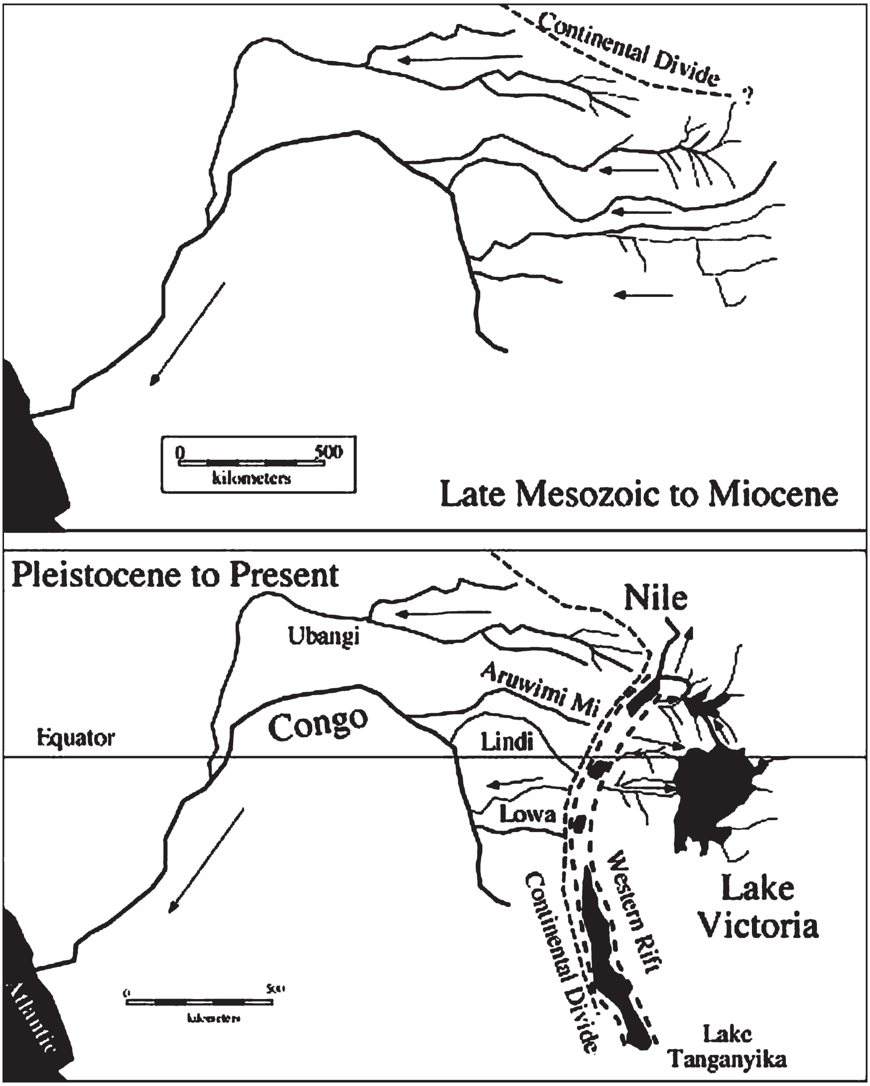


Fig. 2 Truncation and capture of part of the Congo drainage system due to the formation of the Western Rift Valley (from: http://utdallas.edu/geosciences/remsens/Nile/)

data are few, there is general consensus that prior to the onset of rifting, regional drainage was directed mainly into the Congo basin which was separated from the Nile Basin to the north by a roughly NW–SE-oriented topographic high (Fig. 2). Rifting truncated this palaeoriver network, causing a fundamental reorganisation of the drainage pattern, first by the development of a rift basin, and then through rift segmentation and rift-flank uplift (Fig. 2).

4.2 Early Rift Phase (ca 8–2.5 Ma)

Rifting at the northern end of the WEARS seems to have commenced 8–9 Ma ago (Ebinger, 1989; Pickford, 1990) and had the initial effect of creating a NE–SW oriented basin. Capture of a number of major Congo tributaries apparently brought abundant runoff to the basin, and from the widespread distribution of characteristic fossil mollusc assemblages, Van Damme & Pickford (2003) suggest that it was occupied by a single large waterbody, Palaeolake Obweruka, that was comparable in area and longevity (ca five million years) to modern Lake Tanganyika (Fig. 3). Outflow was still to the west, into the Congo basin, and there appears to have been little, if any, significant contribution to the embryonic White Nile. Potential drainage to the south was probably already blocked by the Virunga volcanic centre where lava extrusion commenced around 11 Ma (Kampunzu et al., 1998).

4.3 Rift Segmentation (2.5 Ma–Present)

Segmentation refers to the subdivision of the rift valley into a series of individual, typically asymmetric basins separated by topographically higher areas that are usually related to structural features transverse to the rift trend (*accommodation zones*, e.g. Rosendahl, 1987; Ebinger, 1989; Upcott et al., 1996). Segmentation was a critical development in the evolution of the WEARS, producing the deep, elongate basins we recognise today and opening the way for a reorganisation of the drainage network that ultimately led to much of the region's runoff being directed into the White Nile. Structural-stratigraphic data indicate that basin subsidence accelerated in the Plio-Pleistocene (Ebinger, 1989), thus enhancing rift segmentation. This tendency has been further augmented by rapid uplift of the Rwenzori massif over the last 2.5 million years (MacPhee, 2006), and on a regional scale, uplift of the eastern flank of the rift (Fig. 1). Together these events led to the development of axial drainage systems in the Edward-George, Semliki and Albert rift segments (Fig. 1). A further, important consequence of rift-flank uplift was the well-documented reversal of river systems that had previously drained into the WEARS (Holmes, 1965; Doornkamp & Temple, 1966; Bishop & Trendall, 1967; Ollier, 1990; Fig. 1). Easterly flow, together with westward-directed rivers of similar origin draining the uplifted western flank of the eastern EARS (Shackleton, 1951; Holmes, 1965) brought abundant runoff into the low-relief area between the two arms of the rift, creating Lake Victoria.

Lake Victoria This waterbody today provides around 90% of the flow that ultimately exits Lake Albert into the White Nile and is thus of critical importance in maintaining the base flow of the main Nile (Hurst, 1952; Adamson et al., 1980; Shahin, 1985). The times of formation of Lake Victoria and its subsequent connection to the White Nile are still poorly constrained, but a number of lines of evidence suggest that these must have been relatively recent events. Bishop (1969)

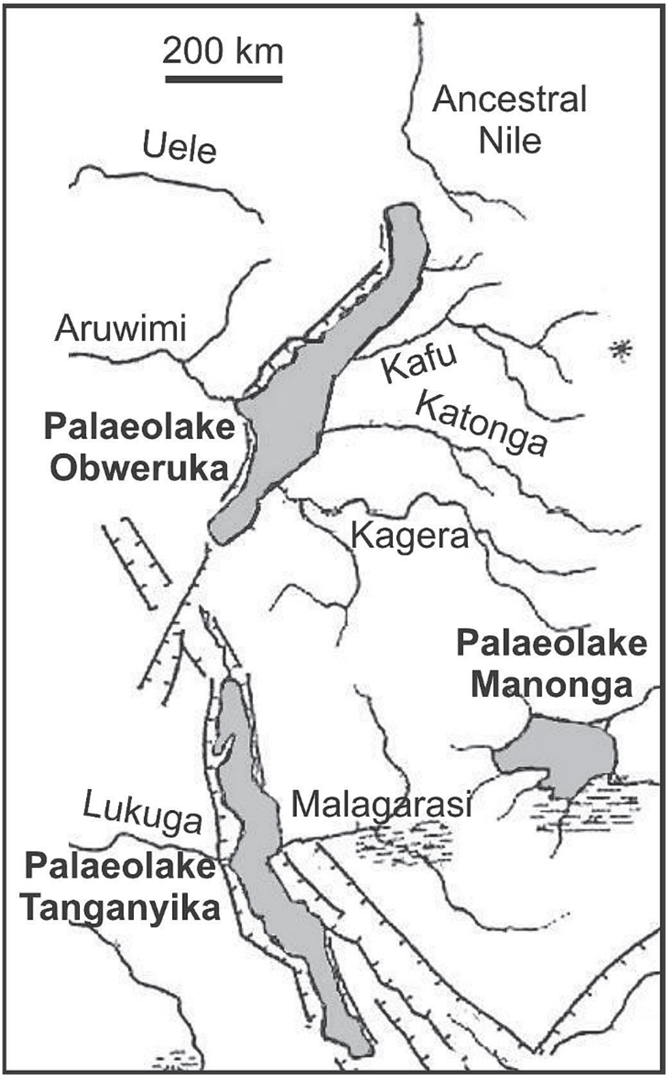


Fig. 3 Palaeolake Obweruka, ancestral waterbody to Lakes Albert and Edward (figure redrawn and modified from Van Damme & Pickford, 2003)

suggests that the lake initially developed by the amalgamation of two smaller waterbodies formed by ponding and flow reversal of the Katonga and Kagera rivers (Fig. 1). Seismic profiles collected during the 1995 and 1996 IDEAL cruises on Lake Victoria reveal a well-bedded lacustrine succession separated from the underlying basement rocks by an irregular surface that presumably represents the pre-lake land surface (Johnson et al., 1996; Scholz et al., 1998; Fig. 4). The lake deposits have yet to be drilled to basement, but their maximum thickness deduced from seismic velocities is ca 60 m (Johnson et al., 1996). Extrapolating from late

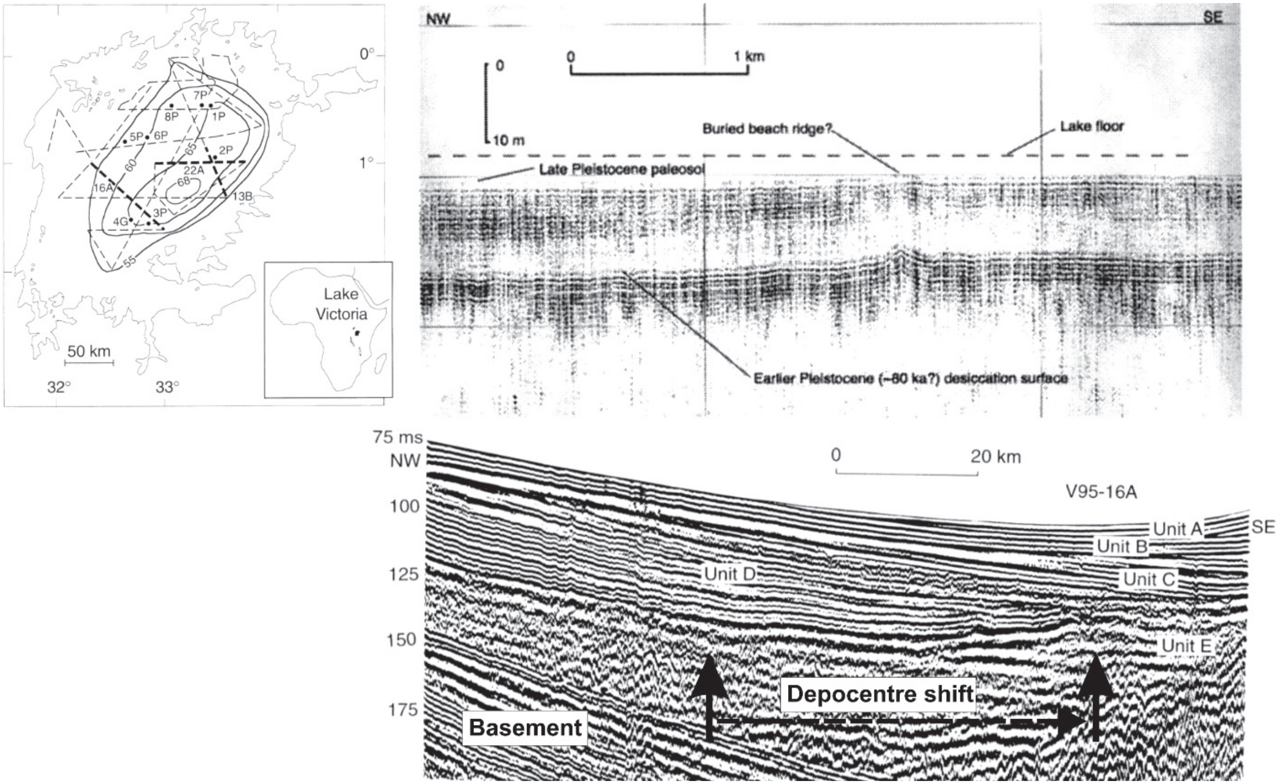


Fig. 4 (B) Shallow (1 kHz Geopulse) and (C) intermediate depth (airgun) seismic profiles from Lake Victoria. In (A) the heavy dashed line is the trackline for the profile in (C) and the diamond marks the position of the shallow seismic profile (B). The latter shows clearly that the Late Pleistocene desiccation surface extended to the deepest part of the lake. A possible earlier desiccation event is also apparent that may correlate with a particularly severe drought ca. 70–80 kyr ago (Scholz et al., 2007). In (C) Lake Victoria's complete sediment fill is imaged, illustrating how the lake's depocentre has migrated eastward as a result of flank uplift along the Western Rift (figures modified and reproduced with permission from Stager & Johnson, 2008 and Johnson et al., 1996.)

Pleistocene–Holocene sedimentation rates suggests that the basal sediments may be no more than ca 0.5 Ma old, although the presence of hiati makes an exact estimate difficult (Johnson et al., 1996; Fig. 4). An age of this order accords well with the presence of exposed mid-Pleistocene lacustrine sediments presumed to have accumulated in palaeolake Victoria (Bishop, 1969; Temple & Doornkamp, 1970). It is also consistent with the 0.4 Ma age estimate for the green laminated lacustrine clay that underlies White Nile alluvium nearly 2,000 km downstream. This lacustrine clay may well reflect initial overflow from Lake Victoria into the southern Sudan (Williams et al., 2003).

Although outside the rift zones, the Lake Victoria basin has been significantly affected by rift-related tectonics, particularly flank uplift along the eastern margin of the WEARS, where local uplift may have been as much as 700 m (Temple & Doornkamp, 1970). East–west seismic profiles clearly show that the basin has been tilted progressively eastwards, moving the depocentre some 50 km in that direction and exposing mid- to late Pleistocene sediments west of the lake (Fig. 4). Episodic tilting continued until at least the late Pleistocene (Bishop, 1969; Temple & Doornkamp, 1970) and in the western half of the modern lake, large areas of the shallow lake floor are swept clean of terminal Pleistocene-Recent lake muds (which are up to 10 m thick in the east) exposing gently tilted late Pleistocene deposits (Fig. 4). The same zone of uplift has probably had a major influence upon the connection between Lake Victoria and the White Nile.

The extensive palaeolake Victoria deposits west of the modern lake represent an under-exploited archive of the basin's mid- to late Pleistocene history. Initial work in the 1950s and 1960s (Bishop & Posnansky, 1960; Bishop, 1969; Temple & Doornkamp, 1970) was hampered by the limitations imposed by the conventional ^{14}C dating technique and poorly constrained lithic artefact-based chronologies. New studies using a modern sedimentological approach in combination with sound chronologies based upon the AMS, OSL and cosmogenic isotope techniques would undoubtedly provide greatly refined insights into the history of the Victoria basin.

The Victoria Nile Little can be said in detail about the age of the Victoria Nile and the history of its role as the link between Lakes Victoria and Albert, but geomorphological indicators all point towards a relatively recent origin. The characteristic "barbed arrow" form of Lake Kyoga, the Victoria Nile channel, with it numerous falls, rapids and deeply incised stretches, are all clearly youthful features. Bishop (1969) has suggested that Lake Kyoga, which formed by flow reversal of the Kafu, was initially a much larger waterbody overflowing into Lake Albert via the Kafu-Nkusi divide (Fig. 1). Continued uplift of the divide, perhaps aided by back-cutting of the ancestral lower Victoria Nile, subsequently captured the Kyoga overflow, causing it to exit the basin at its current, more northerly position (Fig. 1). Lake Victoria itself seems to have become only recently linked to the Kyoga system via the outflow at Jinja (Fig. 1). Prior to capture, overflow of palaeolake Victoria into the Albert rift was probably to the west, via the Katonga divide (Bishop, 1969; Fig. 1), but continued uplift here eventually brought the divide above the level of the Jinja threshold at which time outflow was redirected into Lake Kyoga. Bishop (1969) suggests that closing of the Katonga outlet occurred during the period 25–35 Ka. At present it is not known whether capture of Lake Victoria by the Kyoga system preceded the capture of Kyoga's outflow by the lower Victoria Nile, but in either case it seems likely that much of the discharge from Victoria found its way into Lake Albert.

The Edward-George and Semliki basins Today the Edward-George basin receives significant runoff from the Virungas, Rwenzori and western rift escarpment. The outflow forms the Semliki River which is fed by additional runoff from both rift flanks before entering Lake Albert (Fig. 1). Discharge at the Semliki delta represents ca 10% of the total inflow into Lake Albert (Hurst, 1952; Shahin, 1985) and thus a significant proportion of the lake's hydrological budget. Modelling suggests that under present conditions this would be sufficient to maintain an open basin in Lake Albert, the overflow providing a modest contribution to the White Nile (Talbot et al., 2000).

The Edward-George and Semliki rifts are currently among the most tectonically active segments of the WEARS. Active faults cutting Holocene-Recent sediments are documented from both Lake Edward and the upper Semliki valley (de Heinzelin & Verniers, 1996; Lærdal & Talbot, 2002; McGlue et al., 2006), and asymmetric meander belts (cf. Leeder & Alexander, 1987), visible in satellite images of the lower Semliki, indicate recent tilting of the rift floor. There seems little doubt that tectonics have had a major influence on the connection between Lakes Edward and Albert. The Semliki river does not exit Lake Edward at the modern topographically lowest point in the rift (close to the main border fault) but through an incised valley ca halfway along the hanging wall (Fig. 5). Tributaries entering the upper Semliki from the west are also incised into the hanging wall and flow in the opposite direction to the tectonically controlled slope of this feature, indicating that they and the Semliki outflow must predate rotation of the fault block (Fig. 5). In Lake Edward itself, well-developed fault scarps displacing Holocene-Recent sediments indicate that rotation is probably an ongoing process (Lærdal & Talbot, 2002; McGlue et al., 2006).

De Heinzelin and Verniers (1996) have studied in detail the area around the Semliki outflow, and although they provide no palaeocurrent data nor age determinations, suggest (op. cit., p. 7) that "the present situation, the Upper Semliki flowing north, is conceived as a late event, not older than a few millenia…". They attribute this dramatic change in flow direction to Holocene tilting of the hanging-wall, a reorientation that has presumably accompanied the recent phase of rotation described above. Such a late date for the reversal of the Upper Semliki is not supported by the Sr-isotope stratigraphy of Lake Albert, which indicates that Lake Edward exerted a strong influence on the Sr-isotope signature of this lake during the terminal Pleistocene and early Holocene (Fig. 6).

Separation of the upper and lower Semliki valleys is at a topographic high formed by an accommodation zone crossing the rift in a NW–SE direction (Lærdal & Talbot, 2002) and which is skirted by the modern Semliki in a narrow valley adjacent to the main rift border fault (Fig. 5). High-resolution satellite imagery suggests the former presence of a previously undocumented palaeolake with a

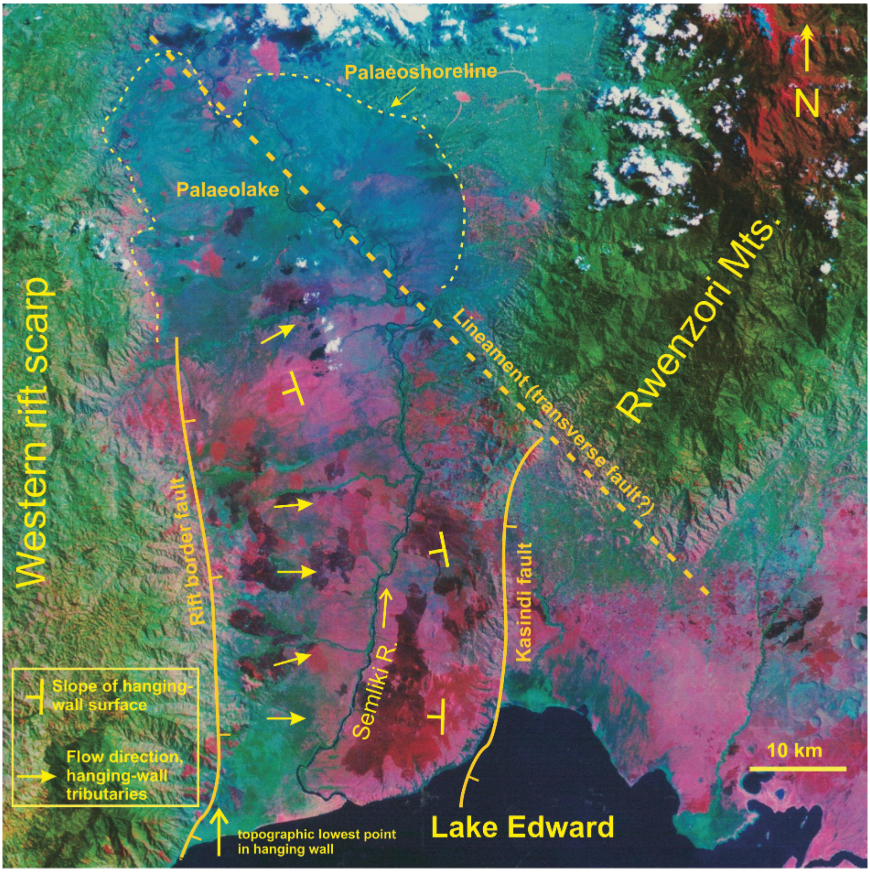
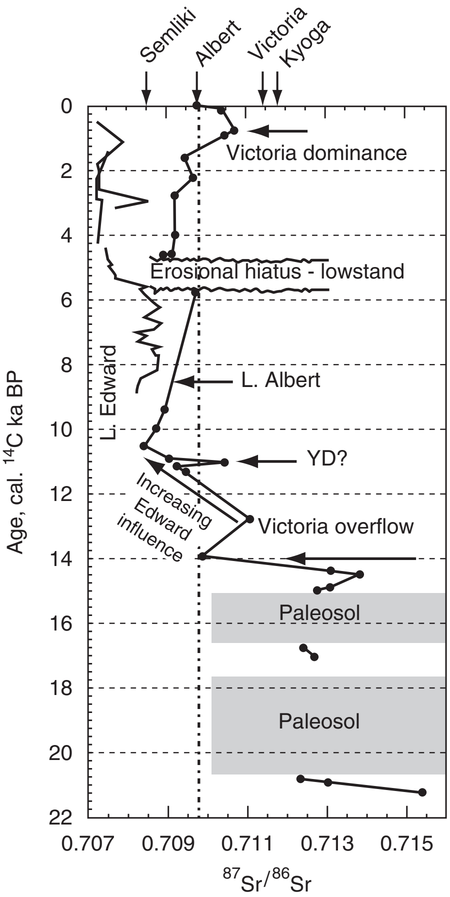


Fig. 5 Satellite image of the northern shore of Lake Edward and the upper Semliki valley. The proximal Semliki is incised into the hanging wall to the main rift-boundary fault. Evidence of recent rotation of the fault block is provided by the incised antecedent drainage from the western rift scarp. Further downstream there is geomorphological evidence of a palaeolake that formed between the northern edge of the hanging-wall fault block and the southern margin of a topographic high related to a rift transfer zone (satellite image courtesy of Amoco Norway) (*see Color Plates*)

well-defined shoreline immediately south of the accommodation zone (Fig. 5). At present nothing is known about the age of this palaeolake, nor its hydrology. Its southern shoreline seems to have been disrupted by recent fault-block rotation (see above) so it is not possible to establish whether the preserved shoreline reflects a high stand of Lake Edward or a separate waterbody. Incision of the accommodation zone by lake overflow, or back-cutting of a former south-draining river could have opened the way for the unification of the southern and northern stretches of the Semliki River, but without further data this must remain pure speculation. The palaeolake is now completely drained and crossed by the modern Semliki River whose course coincides with the tectonic lineament that truncates the southwestern

Fig. 6 Strontium-isotope stratigraphy of Lakes Edward and Albert. Lake Edward data from three cores E96-2p, -5 M and -6 M. Lake Albert data from Williams et al. (2006)



margin of the Rwenzori massif (Lærdal & Talbot, 2002; Fig. 5). It is thus clear that tectonics must have exerted a strong influence on the Edward-Semliki drainage system with a clear possibility of blocked or reversed flow. A blocked or southward-flowing upper Semliki would imply removal of a major water source to Lake Albert and a correspondingly reduced outflow into the Nile system.

Lake Albert Lake Albert is the critical link between the White Nile and its headwaters, with no outflow from the lake the White Nile would be reduced to a seasonal stream and could play no significant role in maintaining the base flow of the main Nile. As we have already shown, there are numerous indications that discharge from headwater lakes and rivers is likely to have been anything but constant over the last ca 2 Ma and this variability will undoubtedly have impacted the hydrology of Lake Albert. In common with the other catchment lakes, little is known in detail about the pre-late Pleistocene history of this lake but based upon a recent geophysical survey, Karp et al. (in press) suggest that the basin contains up to 5 km. of mainly lacustrine sediments. On the basis of seismic attributes and comparison with borehole data, they infer that the lake was relatively deep for much of the late Miocene and Pliocene, but thereafter has fluctuated between generally shallow or desiccated conditions. This deep lake presumably developed as part of the Palaeolake Obweruka phase of rift evolution described above. Of particular interest with respect to the history of Lake Albert's connections with Lakes Victoria and Edward are the seismic records of the Semliki and Victoria Nile deltas. The former are unfortunately poor because of gas blanking, but Karp et al.'s profiles from the north end of the lake indicate that only the youngest part of the sedimentary record shows typical deltaic features, suggesting a relatively recent origin for the Victoria Nile. This would be entirely consistent with the inferred recent origin of the Jinja overflow from Lake Victoria and connection to Lake Albert via the modern Victoria Nile.

5 Ethiopian Headwaters of the Blue Nile

The orientation of now deeply entrenched tributaries in the Blue Nile/Abbai headwaters points to an earlier flow towards the east, before the present-day northwest Ethiopian plateau became uplifted and tilted to the west. Uplift of the Ethiopian plateau took place in several stages, with initial uplift accompanied by extrusion of the Trap Series basalts towards 30 million years ago (Hofmann et al., 1997), followed by several phases of more rapid uplift, culminating in accelerated uplift and concomitant river incision during the last five million years of Pliocene–Pleistocene time.

Age and erosion of the Blue Nile gorge The Blue Nile gorge is located in the Ethiopian highlands between Lake Tana and the present-day Sudan border, and is one of the most spectacular features in the Nile basin. Below Lake Tana, the Blue Nile/Abbai flows for 150 km across mid-Cenozoic basalt lavas of the Trap Series. The Addis Ababa-Debre Markos road crosses the gorge 280 km below the lake at 10° 05′N and 38° 10′E. At this location the river has cut through 250 m of Trap Series basalts and a further 1,150 m of horizontal Mesozoic and Palaeozoic rocks (the Precambrian basement rocks are not exposed until 50 km further downstream). The gorge at this site is 1.4 km deep, 20 km wide and is entrenched into a plateau 2.6 km in elevation. In seeking to establish the age of the gorge, McDougall et al. (1975) dated fresh samples of basalt from the top four flows on the south side of the gorge, and obtained ages ranging from 23.5 to 27.4 Ma. Later workers using improved dating methods have shown that the Ethiopian flood basalts were all erupted within about a million years approximately 30 million years ago (Hofmann et al., 1997). These authors estimated that the volume of rock eroded from the Ethiopian headwaters of the Blue Nile/Abbai and the Atbara/Tekezze river basins since that time amounted to about 100,000 ± 50,000 km^3 from a catchment area of roughly 275,000 km^2, which is roughly equivalent to the volume of the Nile cone. This pioneering work has inspired a number of subsequent investigations into the tectonic history of the Ethiopian uplands, to which we now turn.

Rifting chronology and uplift of the Ethiopian plateau One assumption implicit in the work of McDougall et al. (1975) concerns the long-term geomorphic persistence of the Blue Nile drainage system in the Ethiopian uplands. A good test of this assumption is provided by the work of Pik et al. (2003, 2008) who used a thermo-chronological approach to test models of landscape evolution in this region. Their apatite helium ages indicated partial resetting of pre-existing basement rock ages resulting from burial of the basement rocks beneath a thick mantle of Trap Series flood basalts ~30 Ma ago. They concluded that erosion of the Blue Nile gorge began as early as 25–29 Ma ago, in accord with the earlier results of McDougall et al. (1975), with erosion along the present scarp starting after 11 Ma (Pik et al., 2003). The volcanic and uplift-related tectonic divides date back to 20–30 Ma and predate the rifting and break-up of the original Ethiopian volcanic plateau, which did not begin until after 20 Ma (Pik et al., 2008). In his comprehensive review of the East African rift system, Chorowicz (2005) has argued that a mantle plume form initially around 30 Ma ago in the present Lake Tana region, leading to domed uplift and faulting from three directions, converging at Lake Tana. Rifting began 30–29 Ma ago in the Gulf of Aden and 27.5–23 Ma ago in the southernmost Red Sea. The triple-junction Afar Rift developed later during the Miocene, and is floored by Mio-Pliocene sediments (24–5.5 Ma old) and by Pliocene and Quaternary volcanic rocks. The main Ethiopian rift did not begin to form until after 11 Ma. The orientations of the Red Sea rift, the Gulf of Aden, the Ethiopian rift and the fault-bounded margins of the Afar depression coincide with the orientations of much older lineaments, shear zones and eroded suture zones, extending back in time into the Proterozoic, and exposed since by uplift and erosion (Adamson & Williams, 1980; Williams & Williams, 1980; Adamson & Williams, 1987; Adamson et al., 1993; Chorowicz, 2005). The present Nile is controlled by the re-activation of these same ancient geological structures, and is reflected in the angular bends and linear reaches of the main Nile.

The work of Pik et al. (2003, 2008) indicates that the elevated Ethiopian plateau, which exerts such a strong control over the hydrology of the Abbai/Blue Nile and Tekezze/Atbara river systems, has been in existence since the Oligocene. This important result offers independent confirmation that the bulk of sediment within the Nile delta and its more voluminous submerged cone did indeed derive from the Ethiopian highlands and that the Blue Nile and Atbara have transported sediment onto and across the lowlands of the Sudan at intervals throughout the last 30 million years.

Blue Nile incision, pulsed plateau growth and Pliocene uplift An interesting recent contribution to our understanding of Blue Nile history is that of Gani et al. (2007) who use a digital elevation model to reconstruct initial topography before erosion in the area of the Blue Nile gorge. They compared their results with available potassium-argon ages for the volcanic rocks comprising the present-day remnants of eroded volcanic rocks, and concluded that the Blue Nile and its tributaries had eroded at least 93,200 km^3 of rock from the Ethiopian plateau since 29 Ma during the course of a three-phase uplift (29–10, 10–6 and 6–0 Ma) with long-term erosion rates accelerating at ~10 and ~6 Ma. The inferred rapid increase in erosion at 6 Ma (Gani et al., 2007) is coeval with renewed volcanism in the Afar and renewed movement along the Dead Sea transform fault that Adamson and Williams (1987) suggest may have been triggered by the repeated loading and unloading of the

Mediterranean seabed during the Messinian salinity crisis of 6–5 Ma. If confirmed by subsequent work, the results of Gani et al. (2007) would support earlier notions of episodic uplift and erosion and are consistent with the conclusion that much of the sediment in the Nile cone is of Pliocene age and younger.

Southern Sudan is underlain by a series of Jurassic-Cretaceous rifted sedimentary basins into which sediments rich in quartz and feldspar, indicating erosion of the Basement Complex, accumulated for over 100 and possibly150 Ma (Adamson et al., 1992). These rifts contain fluvio-lacustrine deposits 10–15 km thick and reflect long intervals of mostly internal drainage with restricted outflow across sills alternating with phases of external drainage. Except for the influx of volcanic rocks from Ethiopia via the Sobat and Pibor rivers, the depositional environments were similar to those in the southern Sudan today (Adamson et al., 1992). The river systems that flowed into these basins have modern analogues in the western tributaries of the White Nile but have long seen replaced by rivers flowing north from the uplifted and rifted lake plateau of Uganda and northwest or west from the Ethiopian volcanic plateau.

Enduring claims for alternative courses for the Nile either eastwards across the Red Sea or westwards into the Chad basin lack supporting sedimentary evidence and in our view remain somewhat speculative working hypotheses. Goudie (2005) has provided a useful summary of some of the proposed early courses of the Nile in Egypt, some of which show a complete reversal in the flow direction of the main Nile to the southwest. While we cannot rule out the possibility of such periodic disruptions to the drainage network, we consider that the long-term supply of water and sediment to the main Nile since the Pliocene was primarily from the Ethiopian plateau.

6 Ancient Rivers of the Eastern Sahara

A much-debated question is whether the Nile once flowed to the west or northwest into the Chad basin and Libya. Given the present state of our knowledge relating to the timing of volcanic, tectonic and climatic events in this region, we can only offer some qualified suggestions, and pinpoint some of the present uncertainties.

Much of the Sahara is underlain by Proterozoic and older metamorphic and igneous rocks that were uplifted and eroded during and after the Pan-African orogenic event of 550–500 million years ago. These ‘Basement Complex’ rocks are intruded or overlain by a thick suite of Palaeozoic sedimentary, volcanic and igneous rocks, which are in turn overlain by relatively thin Mesozoic continental and marine sediments (Williams, 1984). Starting in the Albian, warm shallow Cretaceous seas flooded much of the Sahara. This marine transgression was followed by a slight retreat of the sea during the Lower Cenomanian, with the sea subsequently attaining its highest level during the Upper Cenomanian and Lower Turonian, when it reached as far as the edge of the Hoggar and the narrow embayment between Tibesti and the Hoggar. There are sporadic remnants of probable Cretaceous sediments at elevations up to 1,400 m in the Aïr mountains of the south-central Sahara, indicating considerable post-Cretaceous uplift in and around the Aïr. There is also good evidence of Cenozoic updoming of the Hoggar and Tibesti mountains. During the Palaeocene and Eocene prolonged and widespread deep weathering was followed by Miocene uplift and erosion. This was also a time of initial climatic desiccation. Much of the present topography of the central Sahara dates from this time.

Jebel Marra volcano in western Sudan lies astride the present drainage divide between the Nile and Chad basins. It is a Miocene strato-volcano that has remained active well into the Holocene. The volcanic rocks of Jebel Marra in places rest directly upon eroded Basement Complex rocks that attain elevations up to 500 m higher than similar rocks out on the plains a hundred kilometres from the mountain. If the basalt flows that fill old valleys in the basement rocks are indeed of Miocene age, as Andrews (1948) and Lebon and Robertson (1961) have argued, then the present topography may not have altered greatly since that time. However, the age of the flows remains uncertain, so that the most that can safely be concluded is that the Nile-Chad divide in this region may date back to the Miocene (Williams et al., 1980).

A series of large, sinuous, dry river valleys are clearly shown on the Gemini space photographs of Libya and Tibesti (Pesce, 1968) and the later satellite imagery of the eastern Sahara (Griffin, 1999, 2001, 2006). One of these valleys can be traced north from the Chad basin into the hyper-arid desert of southeastern Libya, where it is bounded by Tibesti volcanic massif to the west and a set of recently mapped Nubian sandstone plateaux (Willams & Hall, 1965) to the east. The most comprehensive accounts of the age and climatic significance of these dry valleys are given by Griffin (1999, 2002, 2006) who drew upon an array of sedimentary evidence from marine and terrestrial sites in and around the Mediterranean, the Gulf of Suez and the Red Sea. Rapid deposition of the Messinian Zeit Formation (7.04–5.34 Ma) and its high clastic content (relative to the preceding Tortonian Stage sediments) led him to conclude that the Messinian was a time of high rainfall and high fluvial sediment yield, reaching peak monsoonal activity in the late Messinian, when the Mediterranean was at very low level during the Messinian Salinity Crisis (Griffin, 1999). Griffin gave the name Sahabi rivers to describe this late Neogene river system which continued to cross central North Africa until about 4.6 Ma ago, when the monsoon shifted to the south and the eastern Sahara became drier (Griffin, 2002). The inferred late Miocene and early Pliocene climate in the Chad basin was characterised by repeated fluctuations, favouring the emergence of animals adapted to highly varied ecosystems, including lacustrine, lake margin, riparian, woodland and savanna habitats (Griffin, 2006). It was within this varied set of habitats that the late Miocene Toumaï hominid *Sahelanthropus tchadensis* (TM 266) emerged (Brunet et al., 2005). In the eastern Sahara, McCauley et al. (1982, 1986) and McHugh et al. (1988a, b, 1989) used shuttle imaging radar to identify a series of ancient river valleys, some of them former tributaries of the Nile. These valleys range in age from Oligocene to Quaternary, with the younger channels associated with Acheulian and younger artefact assemblages. Small rivers occupied many of the Tertiary river valleys during wetter intervals in the Quaternary, but they were never as large as the Neogene and older river systems.

Several factors may have been responsible for the progressive desiccation of both northern and eastern Africa, which we discuss in more detail in the next section. Here we note that massive tectonic uplift in East Africa (including Ethiopia) during the past 6–8 Ma led to the creation of a major topographic barrier and an ensuing change in atmospheric circulation (Sepulchre et al., 2006), reducing rainfall in the Chad basin. The change in rainfall regime over East Africa resulted in a change from tropical forest to open grassland and woodland and was associated with the proliferation of the Pliocene hominids unique to Africa (Williams et al., 1998; Sepulchre et al., 2006).

7 Cenozoic Cooling and Desiccation

The climatic history of the Nile basin relates as much to global as to regional influences and is one of progressive cooling and desiccation from 45 Ma onwards, culminating in the Quaternary glacial–interglacial cycles that had such a major impact on the biota. Events in both hemispheres contributed to late Cenozoic desiccation over NE Africa. After separating from Antarctica 45 Ma ago, Australia has moved north into dry subtropical latitudes at a mean rate of 6 cm/year, resulting in the birth of the Southern Ocean between Australia and Antarctica. The Drake Passage between South America and Antarctica opened about 34 Ma ago, leading to the establishment of the circum-Antarctic ocean current driven by the prevailing westerly winds. As a result, Antarctica became thermally isolated from warmer ocean waters to the north, and rapid cooling ensued. In the Southern Ocean, the changing isotopic composition of both planktonic and benthic foraminifera indicates major cooling of deep ocean water as well as surface water (Shackleton & Kennett, 1975; McGowran et al., 2004). Cumulative ice build-up in Antarctica saw the creation of mountain glaciers followed by the growth of a major ice cap, first in East Antarctica 33–34 Ma ago and later in West Antarctica.

Uplift of the Tibetan plateau as a result of the collision of India and Asia ~45 Ma ago caused a major change in the distribution of land and sea and was followed by severe desiccation of the region to the north and east of the plateau. Widespread sedimentation in playa lakes at the north-eastern edge of the Tibetan plateau persisted during the Eocene and ended abruptly at the Eocene–Oligocene transition, coincident with the global cooling 33–34 Ma ago associated with the inception of permanent Antarctic ice sheets at that time (Dupont-Nivet et al., 2007). A major drop in temperature is also evident 33–34 Ma ago in the Great Plains of North America (Zanazzi et al., 2007). We do not yet know when the Northern hemisphere ice caps began to grow. Drop-stones from ice-rafted debris laid down in the Norwegian-Greenland Sea between 38 and 30 Ma ago and apparently derived from East Greenland suggest that northern high latitude ice accumulation may be far older than previously envisaged (Eldrett et al., 2007).

In East Africa, uplift and rifting created the Neogene sedimentary basins with their unrivalled record of Pliocene and Pleistocene hominid evolution. The emergence in this region of the early Pliocene hominids may be linked to the

Messinian salinity crisis of 6–5 Ma ago, during which the Mediterranean Sea dried out, refilled and dried out repeatedly, resulting in the creation of a salt desert and the genetic isolation of Africa from Eurasia (Williams et al., 1998). The late Miocene Nile responded to this change in base level by cutting a gorge over 1,000 km long and up to 2 km deep at its northern end.

It is often hard to separate out the precise causes of environmental change. For example, closure of the Indonesian seaway 3–4 Ma ago as a result of northward displacement of New Guinea in the early Pliocene may have triggered a change in the source of water flowing through Indonesia into the Indian Ocean from previously warm South Pacific water to cooler North Pacific water, leading to reduced rainfall over East Africa (Cane & Molnar, 2001). Just as plausibly, the late Pliocene increase in aridity evident in East Africa and Ethiopia 3–4 Ma ago (Feakins et al., 2005) may have arisen from closure of the Panama Isthmus and northward diversion of the warm equatorial water which until then had flowed westwards from the Atlantic into the Pacific Ocean. The presence of warm moist air over the North Atlantic, allied to changes in solar insolation, resulted in widespread and persistent snow accumulation over North America (Williams et al., 1998). The rapid accumulation of ice over North America at 2.7–2.5 Ma was accompanied by global cooling in high latitudes and intertropical desiccation, revealed in the drying out of the large Late Pliocene tropical lakes of the Sahara and East Africa. The emergence of stone toolmaking at this time in East Africa may have been an adaptation by our ancestors to the increase in seasonality and the need to diversify their sources of food protein. This was also a time of widespread loess accumulation in central China (Heller & Liu, 1982) and of the first appearance of stony desert plains in central Australia (Fujioka et al., 2005). The region around the Mediterranean also developed its now characteristic dry summer, wet winter climatic regime. The net effects of these late Cenozoic environmental changes were an increase in the temperature gradients between high and low latitudes, a more seasonal rainfall regime, a reduction in forest and the replacement of woodlands by deserts in North Africa, Arabia and Australia, and the emergence in Africa some 2.5 Ma ago of upright-walking, stone toolmaking ancestral humans.

8 Quaternary Glacial–Interglacial Cycles

The rapid accumulation of ice over North America at 2.7–2.5 Ma was followed by repeated oscillations from glacial to interglacial conditions. These glacial–interglacial cycles were accompanied by glacio-eustatic sea level oscillations, by alternating morphogenetic systems, and by periodic extinction and speciation events (Hewitt, 2000). Within the tropics, the cold and dry glacial maxima were times of desert expansion and forest retreat. Over the past 0.8 Ma, each cycle lasted 100 ka, reflecting the influence of the 100-ka orbital eccentricity cycle. These rapid climatic fluctuations had a considerable impact on the African biota. The Last Glacial Maximum (LGM), dated to 21,000 ± 2,000 years ago, represents the time of most extreme global climate since the dominantly warm, wet Last Interglacial of 125,000 years ago. During the LGM, the area now covered by humid rain forest in the Congo basin may have been reduced by ~84% as a result of a 30–40% decrease in LGM precipitation accompanied by a temperature drop of 5°C (Anhuf et al., 2006). In the Nile basin, LGM lake levels fell and desert areas expanded while woodland areas contracted.

No continuous, high-resolution, chronologically well-constrained palaeoclimatic records pre-dating the late Pleistocene are available from the White Nile catchment. Compilations of long proxy lake-level records from East Africa (mainly Kenya) suggest a strong precessional control on regional precipitation (Trauth et al., 2003). First results from the recent IDEAL deep-drilling projects in tropical Africa support this observation, and also suggest a change in lake response to climate forcing after about 60 ka BP (Scholz et al., 2007). Prior to this time the amplitude of precession-driven insolation at tropical latitudes was relatively large and seems to have induced both wetter (evidenced by prolonged periods of high lake levels) and drier (indicated by drought conditions) than have occurred since. There seem to have been some particularly intense periods of reduced rainfall that led to continent-wide aridity on a scale far exceeding that experienced around the time of the Last Glacial Maximum (Scholz et al., 2007; see below). Such conditions were almost certainly felt in the White Nile catchment. The change to generally wetter conditions from about 60 Ka may have been an important factor in triggering the expansion of anatomically modern man out of Africa (Cohen et al., 2007).

Underlying the millennial-scale, astronomically driven climatic variations is a longer-term trend to drier conditions. Several East African basins which previously held permanent waterbodies have over the last 1–1.5 Ma become either dry or have contained lakes only episodically (Trauth et al., 2005). The reason for this trend is not known with certainty, but one possible explanation is the impact that the rising rift-flank mountains may have had on the access of moisture-bearing winds to the interior of East Africa (Trauth et al., 2005; Karp et al., in press). Blocking or reduction of the Congo airflow, in particular, could have significantly reduced precipitation over large parts of the region.

9 Conclusion

The Cenozoic evolution of the Nile basin reflects a complex interaction between tectonic, volcanic and climatic events. The present Nile basin drains about one tenth of the African continent and covers an area of 2.96 million km^2. It is 6,825 km long, making it the longest river in the world. The Ethiopian and Ugandan headwaters of the Nile attain elevations in excess of 2 km, while the watersheds rise to over 5 km. The Ethiopian tributaries of the Nile (notably the Blue Nile/Abbai and the Atbara/Tekezze) provide the bulk of the flood discharge and sediment load, but the Ugandan tributaries, via the White Nile, provide the reliable dry season discharge responsible for maintaining perennial flow in the main Nile. The hydrological differences between the Blue and White Nile rivers reflect their different geomorphic histories, reflecting the Cenozoic tectonic and volcanic evolution of their respective headwaters.

Tectonics, volcanism and climate change have all had significant impacts on the discharge history of the White and Blue Niles, and will in all probability continue to do – with potentially dire consequences for human populations from the headwaters to the Nile Delta (see accompanying chapter on human impact on the Nile basin).

The Nile and its tributaries had eroded at least 93,200 km^3 of rock from the Ethiopian plateau since 29 Ma during the course of a three-phase uplift (29–10, 10–6 and 6–0 Ma) with long-term erosion rates accelerating at ~10 Ma and ~6 Ma. The inferred rapid increase in erosion at 6 Ma (Gani et al., 2007) is coeval with renewed volcanism in the Afar and renewed movement along the Dead Sea transform fault that Adamson and Williams (1987) suggest may have been triggered by the repeated loading and unloading of the Mediterranean seabed during the Messinian salinity crisis of 6–5 Ma. If confirmed by subsequent work, the results of Gani et al. (2007) would support earlier notions of episodic uplift and erosion and raise the possibility that much of the sediment in the Nile cone may be of Pliocene age and younger.

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Late Quaternary Environments in the Nile Basin

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Abstract The Late Quaternary history of the Nile has been reconstructed using well-dated sedimentary, stable isotope and fossil records and associated archaeological remains. The White Nile flows over the bed of an ancient lake dating to ~ 400 ka (Marine Isotope Stage 11). High flood levels in the White Nile since that time appear to coincide with times of sapropel accumulation in the eastern Mediterranean. During times of aridity, the most recent phase being roughly coeval with the Last Glacial Maximum, the large lakes in Uganda either dried out or were too low to provide flow into the White Nile, which became a highly seasonal river, as did the main Nile.

The sediments of Lake Albert, from where the White Nile starts its long journey to the Mediterranean, preserve critical evidence on the discharge history of this river. The lake's sedimentary record confirms the coincidence between overflow of Lake Victoria and reestablishment of flow in the White Nile north of Khartoum at ~14.5 ka and also shows a lake low-stand at ~ 4.2 ka that, by cutting off flow to the White Nile, may have contributed to the fall of Egypt's Old Kingdom. The modern hydrological regime in the Nile was thus re-established at ~14.5 ka, with strengthening of the summer monsoon and overflow from Lake Victoria. A modest number of calibrated radiocarbon ages on White Nile gastropod shells indicate that White Nile levels were high around 14.7–13.1 ka, 9.7–9.0, 7.9–7.6, 6.3 and 3.2–2.8 ka. The Blue Nile and main Nile flood records, albeit less complete, accord with those of the White Nile. Preliminary OSL ages obtained by us from the upper 2 m of dunes west of the White Nile and main Nile show discrete phases of Holocene dune activity that seem to correlate with at least three of six significant periods of rapid global climatic change during 9–8, 6–5, 4.2–3.8, 1.2–1.0 and 0.6–0.15 ka, the first five of which coincided with polar cooling and tropical aridity. The intervals in between were wetter in the tropics and, allowing for dating errors, tally reasonably well with the intervals of high White Nile floods identified here.

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1 Introduction

Big rivers provide useful sedimentary records of past environmental changes and the Nile is no exception (Williams et al., 1998). The Nile is the longest river in the world (ca 6,670 km), spans 35 degrees of latitude (3°S to 32°N) and crosses a climatic gradient from equatorial to Mediterranean. It also has the longest historic flood record of any river in the world (Hassan, 1981). The Nile consists of three very distinct hydrological systems: the Ugandan headwaters and White Nile, the Ethiopian headwaters and Blue Nile, and the main or Saharan Nile (Fig. 1a). The Blue Nile rises in the volcanic uplands of Ethiopia (Fig. 1b) and flows through a

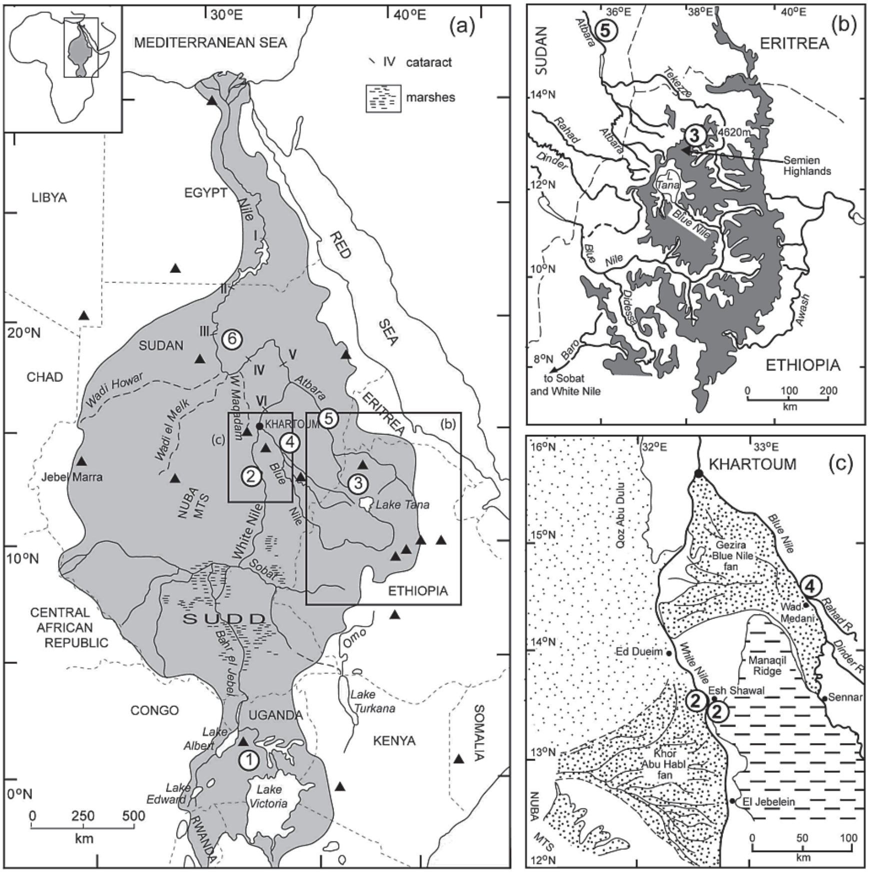

Fig. 1 Location maps. (**a**) Locations 1–6 are discussed in the text (*numerals in white circles*). The dark grey shading shows the extent of the Nile basin. Black triangles show localities already studied by the two authors. (**b**) Detail of the Blue Nile headwaters. The dark shading represents land >2,000 m, dashed lines show international boundaries. (**c**) Detail of lower White and Blue Nile. Light stippling indicates sand sheets and dunefields, heavy stippling alluvial fans, and dashed infill the Manaqil Ridge

gorge nearly 2 km deep and 35 km wide, from which it has eroded some 100,000 km^3 of rock (McDougall et al., 1974; Gani et al., 2007), before it emerges from the highlands onto a vast alluvial fan (Fig. 1c). It then flows across this fan through the semi-arid plains of the central Sudan to join the White Nile at Khartoum. In strong contrast to the highly seasonal Blue Nile, the White Nile emerges from the equatorial lake plateau of Uganda and disappears into the extensive swamps of the southern Sudan whence it emerges as a river of nearly constant flow throughout the year, but with a much diminished sediment load.

The White Nile provides 83% of Nile discharge during the month of lowest flow and is responsible for maintaining perennial flow in the Nile during drought years in Ethiopia (Williams and Adamson, 1982). The two major Ethiopian tributaries of the Nile (the Blue Nile and the Atbara) provide, respectively, 68% and 22% of the peak flow and 61% ($140 \pm 20 \times 10^6$ t a^{-1}) and 25% ($82 \pm 10 \times 10^6$ t a^{-1}) of the sediment load of $230 \pm 20 \times 10^6$ t a^{-1} (Garzanti et al., 2006). North of the confluence of the Blue and White Nile rivers at Khartoum the main Nile flows through the eastern Sahara desert north into the Mediterranean Sea and receives no further inflow below the Atbara confluence until it reaches the sea after a waterless journey of 2,689 km. The inhabitants of northern Sudan and Egypt owe their very existence to the Nile. By the year 2020 over 300 million people will depend upon its waters for their livelihood, so that a clear understanding of the links between present land use, alluvial history and the impacts of climate change on Nile flooding is essential for future planning. This chapter offers a concise summary of our current understanding of Late Quaternary environments in the valleys of the Blue Nile, the White Nile and the Main Nile, while noting gaps in our present knowledge and scope for future research.

2 The Blue Nile

Since its inception some 30 million years ago (McDougall et al., 1974; Pik et al., 2003; Gani et al., 2007), the Blue Nile has incised into its tectonically uplifted volcanic headwaters, depositing part of its load in the form of a large alluvial fan known as the Gezira (Fig. 1c). Gezira is Arabic for island and refers to the land between the Blue and White Nile rivers bounded to the south by the Managil Ridge (Fig. 1c). During earlier soil surveys, Williams (1966) mapped a series of former Blue Nile channels. These Late Pleistocene and Early Holocene channels radiated across the Gezira and carried a bed load of sand and fine gravel from the volcanic uplands of Ethiopia. The heavy mineral suite of the source-bordering dunes and sandy point-bars associated with these channels is virtually identical to the heavy mineral assemblage from channel sands collected from the bottom of the Blue Nile gorge in the highlands of Ethiopia (Williams & Adamson, 1973). Incision by the main channel of the Blue Nile beheaded the distributary channels and deprived them progressively of their flood discharge. The abandoned channels show a fining-upwards sequence from medium and coarse quartz sands and fine quartz and carbonate gravels to sandy clays and clays in the upper 50–150 cm. Clay deposition in the back-swamps and flood plains of these channels dwindled and finally ceased about 5,000 years ago, when the seasonally flooded swampy plains gave way first to acacia-tall grass savanna and finally to semi-desert steppe, changes evident in the fossil vertebrate and mollusc fauna (Williams & Nottage, 2006).

The depositional changes evident in the Late Pleistocene and Holocene alluvial record reflect changes in the load/discharge ratio indicative of hydrological/climatic changes in the headwaters. Such changes in river erosion and sedimentation have occurred repeatedly in the past, and are evident in the fining-upwards sequences revealed in scattered bore-logs from the Gezira Formation (Williams & Adamson, 1982).

Williams & Adamson (1980) and Adamson et al. (1980) have discussed possible reasons for the change in the Blue Nile from a Late Pleistocene bed load channel to a Holocene suspension load channel. Quaternary fluctuations in climate, vegetation, soil cover, and geomorphic processes would have repeatedly altered the hydrology and sediment load in the headwaters of every major Nile tributary but only the more recent record is well preserved.

There are extensive periglacial and more limited glacial deposits in the rugged Semien Highlands of Ethiopia close to the headwaters of both the Blue Nile and the Tekezze/Atbara (Fig. 1b) (Williams et al., 1978; Hurni, 1982). The glacial moraines and periglacial solifluction deposits are well mapped but have never been dated although assumed to be of LGM age (Hurni, 1982). It is entirely likely that there may be more than one phase of Late Pleistocene glacial activity in this region, with concomitant impacts on Blue Nile and Atbara discharge and sediment loads.

A coring programme now in progress at Lake Tana (Lamb et al., 2007) and a recently started project involving archaeological excavations in rock shelter sites in the forested uplands of SW Ethiopia are expected to yield new and well dated information about Late Quaternary vegetation history in this region.

The Atbara originates in Ethiopia and flows parallel to the Blue Nile to join the main Nile 320 km north of Khartoum. As noted earlier, the Atbara provides 22% of the peak flow and 25% of the annual sediment load of the Nile, or $82 \pm 10 \times 10^6$ t a^{-1} (Garzanti et al., 2006). In contrast to the Blue Nile, which carries more K-feldspar and hornblende from amphibolite-facies basement rocks, the Tekezze-Atbara carries more volcanic rock fragments, brown augite and olivine from basaltic rocks (Garzanti et al., 2006). Given its importance as a seasonal contributor of water and sediment to the Main Nile, it is surprising that the Quaternary depositional history of this river is so poorly documented.

The late Quaternary flood record of the Blue Nile record is still very incomplete. Calibrated radiocarbon ages for high Blue Nile flows indicate very high flood levels towards 13.9-13.2 ka, 8.6 ka, 7.7 ka and 6.3 ka (Williams, in press).

3 The White Nile Headwaters

During the last two decades, major piston-coring campaigns with associated high-resolution seismic surveys on Lakes Edward and Victoria, carried out under the auspices of the International Decade for the East African Lakes (IDEAL) project, have provided detailed insights into the terminal Pleistocene – Holocene history of these waterbodies and their proxy palaeoclimatic records. In addition, new analyses and reinterpretation of the 1971 Lake Albert cores (Harvey, 1976) have greatly refined our understanding of the evolution of this lake over the past ca 33 ka (ages in this section are given in calendar years B.P.). All the studies reveal periods both of prolonged lowstand and inferred high lake levels in the three basins, with obvious consequences for the discharge of the White Nile.

Lake Edward. As a partial consequence of active tectonics within the lake itself, and tectonically induced changes in the upper Semliki valley (see accompanying chapter on the Cenozoic evolution of the Nile basin), the sedimentary record from Lake Edward is complex and locally incomplete. ^{14}C-dating problems provide an additional complication. Lake Edward has a significant old carbon effect, on the order of 3000–4000 years, probably due to the addition of magmatic CO_2 to the basin's DIC reservoir (Lærdal et al., 2002; Beuning & Russell, 2004; Russell et al., 2003). Meticulous sample preparation has therefore been necessary to minimise the influence of old carbon on core chronologies, the most reliable dates coming from hand-picked detrital charcoal fragments (Russell et al., 2003).

Pre-Holocene deposits are to date only known from a displaced slump fragment in one core (Russell et al., 2003), but some insights into the late Pleistocene sedimentary history, albeit poorly constrained chronologically, can be gained from seismic reflection images from the eastern half of the lake (Lærdal & Talbot, 2002; McGlue et al., 2006). These are consistent in indicating lowstand conditions during the late Pleistocene, presumably around or just after the Last Glacial Maximum (LGM; see below), when the lake apparently reached a minimum level of about 37 m below present lake level (McGlue et al., 2006).

The in situ record begins at ca 11 ka (Russell et al., 2003). The sedimentary succession from four cores, taken at depths of 12–60 m, are summarised in Figure 2. As is apparent from these logs, none of the cores sampled the sediment/water interface, three of the cores contain at least one significant hiatus, and the deep-water core, although ca 7 m long, sampled only a relatively short period of the later Holocene. Sediment lithology, organic-matter (OM) composition, authigenic carbonate and biogenic silica contents all point to high lake levels and precipitation:evaporation greater than today during the first half of the Holocene, with generally lower lake levels and a long-term drying trend from about 5400 yr BP, culminating in a phase of particularly arid conditions from ca 2050 to 1850 yr. BP at which time Lake Edward was about 15 m lower than today (Lærdal et al., 2002; Russell et al., 2003; Russell & Johnson, 2005). Both events, and the drying trend, are reflected in the Sr-isotope stratigraphy of Lakes Edward and Albert. The Albert record indicates a progressive decline in the influence of Edward-Semliki discharge on the Sr-isotope budget of the lake (Fig. 3), and in Lake Edward the onset of drier conditions at around 5.4 – 5.0 ka is marked by a fall in 87Sr/86Sr implying a relative increase in runoff from the volcanic rocks (low 87Sr/86Sr) that dominate the Sr budget of the southern part of the basin. A corresponding decrease in the supply of radiogenic Sr (high 87Sr/86Sr) from basement rocks suggests drier conditions in the northern half of the basin. The relatively abrupt transition (Fig. 3) is consistent with other proxy records from northern tropical Africa, and is inferred to have been due to a southward shift in the ITCZ (Gasse, 2000; deMenocal et al., 2001; Russell & Johnson, 2005). Given the dating uncertainties in both lakes, the exceptionally dry interval

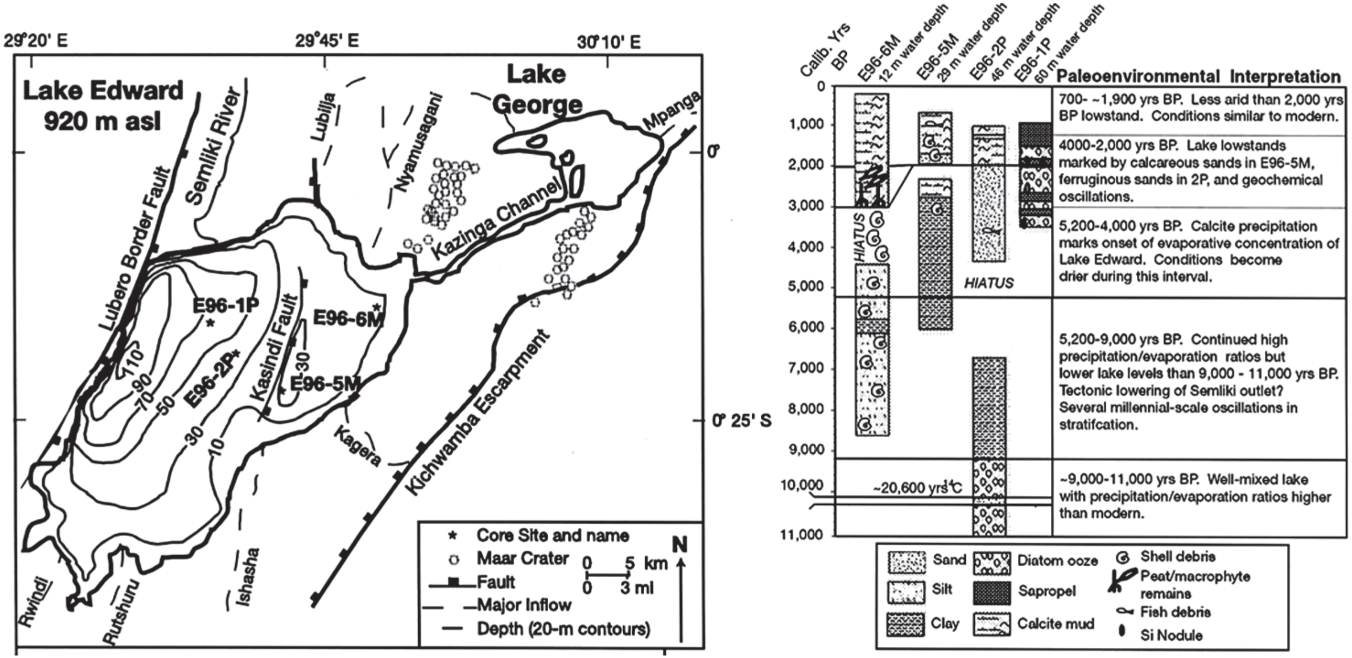

Fig. 2 Lake Edward showing core sites and lithostratigraphy of the IDEAL 1996 cores. Figures reproduced with permission from Russell et al. (2003).

identified in Lake Edward between 2.05 and 1.85 ka is probably represented in the Lake Albert Sr-isotope record by a switch to a Sr-isotope budget dominated by inflow from the Victoria Nile. This drying trend was subsequently reversed, leading to generally wetter conditions over the last 1500 years interrupted by at least two significant drought intervals (Russell & Johnson, 2005). All these droughts are likely to have resulted in greatly reduced or no discharge into the Semliki; Lake Edward's contribution to the flow of the White Nile is thus likely to have been highly variable, especially during the later Holocene.

Lake Victoria. As its principal source of water (ca 90% of the total flow), Lake Victoria is the key to the discharge history of the White Nile. Instrumental records of variations in the level of the lake are cl.

The lower White Nile flows across the floor of an ancient lake that existed ~400,000 years ago (Williams et al., 2003). This may also be the time when Lake Victoria first originated and began to overflow to the north. As a result, the White Nile unregulated flood gradient is a remarkably gentle 1 cm per km during peak flow. Owing to the very gentle slope of the flood plain, the depositional record is unusually well preserved, unlike the main Nile and Blue Nile where phases of erosion have destroyed segments of the sedimentary record. Millennial-scale evidence for at least the past 15,000 years shows that times of high flow in the Blue Nile and main Nile were essentially synchronous with those in the White Nile, so that the use of the White Nile flood record as a general surrogate for the Nile basin seems justified when other evidence is not available (Williams et al., 2006).

Owing to its very gentle flood gradient, the White Nile has been spared from major erosion so that it has a relatively well-preserved record of terminal Pleistocene and Holocene floods. A modest number of calibrated radiocarbon ages on White Nile gastropod shells indicate that White Nile levels were high around 14.7–13.1, 9.7–9.0, 7.9–7.6, 6.3 and 3.2–2.8 ka (Williams, 2008, in press).

The Khor Abu Habl (KAH) mega-fan (Fig. 1c) adjoins the White Nile west bank near the town of Kosti and contains a high-resolution record of depositional events linked to *local* climatic changes. The distributary channels on the fan range from long abandoned to still active but have never been dated. The KAH alluvium interfingers with at least one generation of N-S aligned desert dunes. Preliminary OSL ages obtained by us from the upper 2 m of one such dune reveal discrete phases of dune activity that seem to correlate with three of the six periods of rapid Holocene climate change identified by Mayewski et al. (2004) based on the results from 50 global Holocene records. There were six significant periods of rapid climate change during 9–8, 6–5, 4.2–3.8, 1.2–1.0 and 0.6–0.15 ka, the first five of which coincided with polar cooling and tropical aridity. The intervals in between were wetter in the tropics and, allowing for dating errors, tally reasonably well with the intervals of high White Nile floods identified here.

Small lakes occupied hollows between dunes at En Nahud in Kordofan towards 7.6 ka and in the Wadi Mansurab basin west of Jebel Aulia at intervals between 9.4–7.8 ka (Williams et al., 1974; Ayliffe et al., 1996). These were times of high flow in the White Nile and of stronger summer monsoon. We turn now to the sedimentary record in the main Nile.

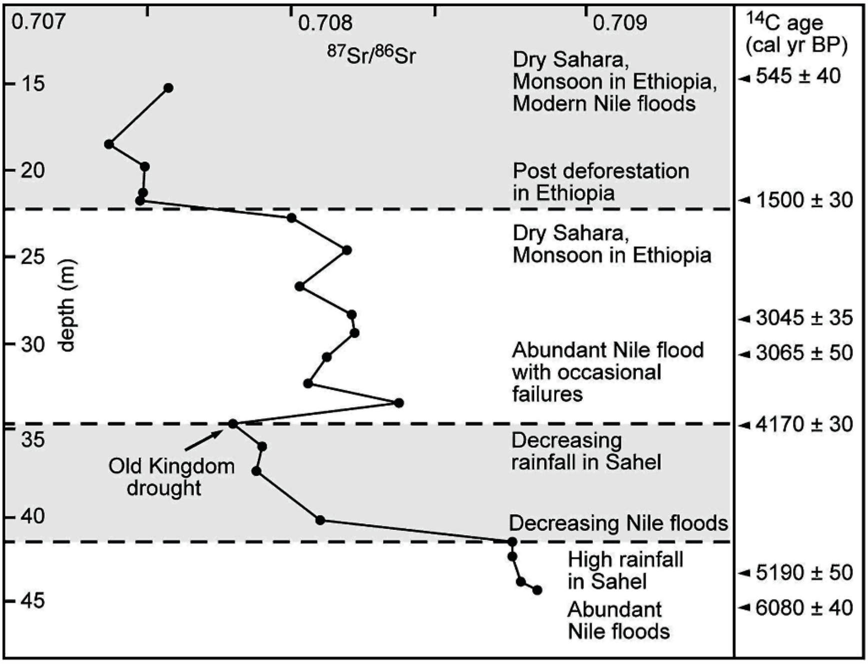

Fig. 3 Depth profile of $^{87}Sr/^{86}Sr$ from core S21 in the Nile Delta (Stanley et al., 2003)

4 Main Nile

Earlier efforts to reconstruct and interpret Late Quaternary Nile flood history using alluvial deposits along the main (or Saharan) Nile failed to take adequate account of the very different hydrological responses to climate change of the major tributaries. Williams and Adamson (1980) and Adamson et al. (1980) confronted this problem and their depositional model has since been widely accepted (Woodward et al., 2007). However, the model they put forward was perforce general and assumed that the Last Glacial Maximum (LGM) was uniformly cold and dry in the Blue and White Nile headwaters, resulting in bare, unstable slopes, highly seasonal Blue Nile flow and a seasonal influx of coarse bed-load sediment. More recent evidence from tropical Africa indicates that the LGM and ensuing postglacial climates were far more variable than previously supposed (Sylvestre et al., 2007) so that in future years we might expect that a more complex alluvial history will be unravelled.

Butzer (1980) has provided a clear overview of the main phases of Nile sedimentation in Egypt indicating very high floods towards 12.0–14.5 ka, with episodes of Nile alluviation between 12.9–13.5 and 8.4–9.0 ka and again towards 8.0 ka, coeval with Sapropel S1 in the eastern Mediterranean (Rossignol-Strick et al., 1982; Freydier et al., 2001). These intervals were times of high flow in the Blue and White Nile rivers, suggesting that the more complete White Nile depositional record can be used as a surrogate for times of high flow in the main Nile when the alluvial record in these rivers is incomplete.

Working under the auspices of the Sudan Archaeological Research Society, a team of archaeologists and geomorphologists affiliated with the British Museum has conducted detailed surveys of archaeological sites and stratigraphic sections east of the Nile in northern Sudan. This team has mapped a large number of archaeological sites and three former Nile palaeochannels and associated floodplains, for which they have obtained ten OSL ages and two radiocarbon ages that range from 7.5 to 0.5 ka (Woodward et al., 2001; Welsby et al., 2002). The sites cluster along certain palaeochannel belts and cover the cultural sequence from Neolithic (7.5–5.7 ka) through Kerma (4.5–3.5 ka), New Kingdom/Kushite (3.1–2.8 ka) to Meroitic and Post-Meroitic (0.5 ka).

Sites belonging to the Kerma Period (4.5–3.5 ka) were concentrated along the margins of the former Nile channel belts, some of them located more then 15 km from the present river. Two major palaeochannels (the Hawawiya and the Alfreda) converge downstream into the present-day Seleim Basin. The Kerma sites on the Hawawiya palaeochannel contain no pottery later than the Classic Kerma Period (1750–1580 BC), interpreted as suggesting that the Hawawiya Nile ceased to flow during or soon after this period (Woodward et al., 2001; Welsby et al., 2002). The youngest OSL ages show that both the Alfreda and the Seleim Nile palaeochannels were active until at least 800 BC and possibly on occasion until about AD 500. This work has once again shown the close relationship between former human settlement and the Nile.

5 The Nile Delta

Nearly 2,000 km downstream, in the Nile delta, Krom et al. (2002) and Stanley et al. (2003) have analysed the strontium isotopic and petrological composition of Nile sediments (Fig. 3). Changes in the strontium isotope ratios at a coastal site in the Nile delta east of the Suez Canal (Fig. 3) have shown a major hydrological change towards 4.2–4.0 ka, when there was a sharp decline in the proportion of sediments derived from the White Nile basin (Stanley et al., 2003). This major reduction in the low season flow of the river Nile might have been in part responsible for the collapse of the Old Kingdom.

6 The Record from the Eastern Mediterranean

Marine sediment cores collected from the floor of the eastern Mediterranean show a repetitive depositional sequence of alternating dark, organic rich sediments (known as sapropels) and calcareous muds with a significant content of Saharan wind-blown dust (Krom et al., 2002). The sapropel units are thought to reflect accumulation in anoxic bottom waters during times of enhanced freshwater flow into the Mediterranean from now inactive Saharan rivers and from the Nile (Rossignol-Strick et al., 1982; Rossignol-Strick, 1985). The influence of the summer monsoon over northern Africa was apparently stronger, and Nile floods more extreme, during intervals of sapropel accumulation (Freydier et al., 2001; Larrasoaňa et al., 2003; Scrivner et al., 2004) and there is some evidence of enhanced winter rainfall over northern Africa at these times. Many of these inferences about former Nile floods are based on indirect and often circumstantial evidence, as are the inferences about variations in winter rainfall and in the summer monsoon regime (Claussen et al., 1998). Future work will need to test the marine depositional models (and derived climate models) against the terrestrial archives provided by the big Nile tributaries upstream in order to provide independent insights into the climatic changes in the northeast quadrant of Africa. The rich archives of fluvial, aeolian and lacustrine sedimentary sequences and landforms preserved in the Nile basin (Williams & Faure, 1980) augur well for this important task.

7 Conclusion

The Greek historian Herodotus (ca 485–425 BC) was puzzled by the hundred days of annual Nile floods during the time of the summer solstice when no rain fell in Egypt, correctly interpreting the cause as heavy precipitation in the Nile headwaters during this time of year. The question then arises as to when the present hydrological regime of the Nile originated. In a successful effort to resolve this same issue, Talbot et al. (2000) analysed the strontium isotope ratios in the shells of freshwater mollusca collected from every major tributary throughout the Nile basin. The strontium isotopic composition of present day lakes and rivers in the Nile basin varies with catchment geology, and is reflected in the composition of the shells of mollusca living in those waters. The results demonstrated that the present flow regime of the Nile was re-established ~15,000 years ago, when the abrupt return of the summer monsoon precipitated the overflow of Lakes Albert and Victoria in the Ugandan headwaters of the White Nile (Fig. 2a). The technique has been used with success in the Nile Delta to define times of much reduced sediment inputs from the White Nile (Fig. 2b).

Calibrated radiocarbon dates obtained on freshwater shells within White Nile flood deposits indicate that White Nile levels were high around 14.7–13.1, 9.7–9.0, 7.9–7.6, 6.3 and 3.2–2.8 ka. The Blue Nile record is more fragmentary and that of the main Nile even more so except for the Holocene Nile delta. Calibrated radiocarbon ages for high Blue Nile flows indicate very high flood levels towards 13.9–13.2, 8.6, 7.7 and 6.3 ka.

Ongoing research in the Nile basin will provide the fine-resolution depositional history needed to test climatic models relating to the waxing and waning of the summer monsoon (Claussen et al., 1998; Chylek et al., 2001; Kuper & Kröpelin, 2006). In particular, it would be useful to build upon the pioneering research of Abell and Hoelzmann (2000) and Rodrigues et al. (2000) into past changes in rainfall seasonality inferred from changes in the stable oxygen isotopic composition in Nile oyster and Nile gastropod shells.

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Part II
Major Nilotic Environments

The Nile Delta

Waleed Hamza

Abstract The Nile Delta, an area of about 22,000 km^2, accounts for two thirds of Egypt's agriculture. In the late Pliocene, the delta started to advance across a marine embayment and developed, especially in the Pleistocene, through major sea-level changes associated with glacial periods. The Nile Delta area is now the major oil and gas-producing area of Egypt. Chemical industry located in the Nile Delta is the main source of hazardous waste. Water pollution in the Nile branches as well as its lakes is caused by agricultural pesticides, raw sewage, and urban and industrial effluents.

The decision of the Egyptian government to reduce the Nile water discharged to the Mediterranean is not only affecting the quantity of discharge, but also its quality. Sewage from coastal lakes and other land run-offs became the substitution source of nutrients of coastal fisheries. The limited Nile nutrient-rich sediments and water reaching the delta negatively affect both the agricultural activities as well as the functioning of the ecosystems in the coastal area facing the delta.

This chapter highlights the main factors characterizing the Nile Delta: the geology, hydrology, and ecology of this delta-estuary-coastal marine system are described and illustrated. It also forecasts future trends in the development of the Nile Delta and uses numerical simulations as a tool to predict future variations within the coastal area of the delta.

Abbreviations AHD: Aswan High Dam; Ma: Million years of age; Mt: Metric tons

1 Geological Development of the Nile Delta

The Nile Delta is part of the Egyptian Mediterranean coast and extends for approximately 240 km from Abu Quir headland at Alexandria in the west, to Port Said in the east (Fig. 1). The most conspicuous features of its margin are the Rosetta

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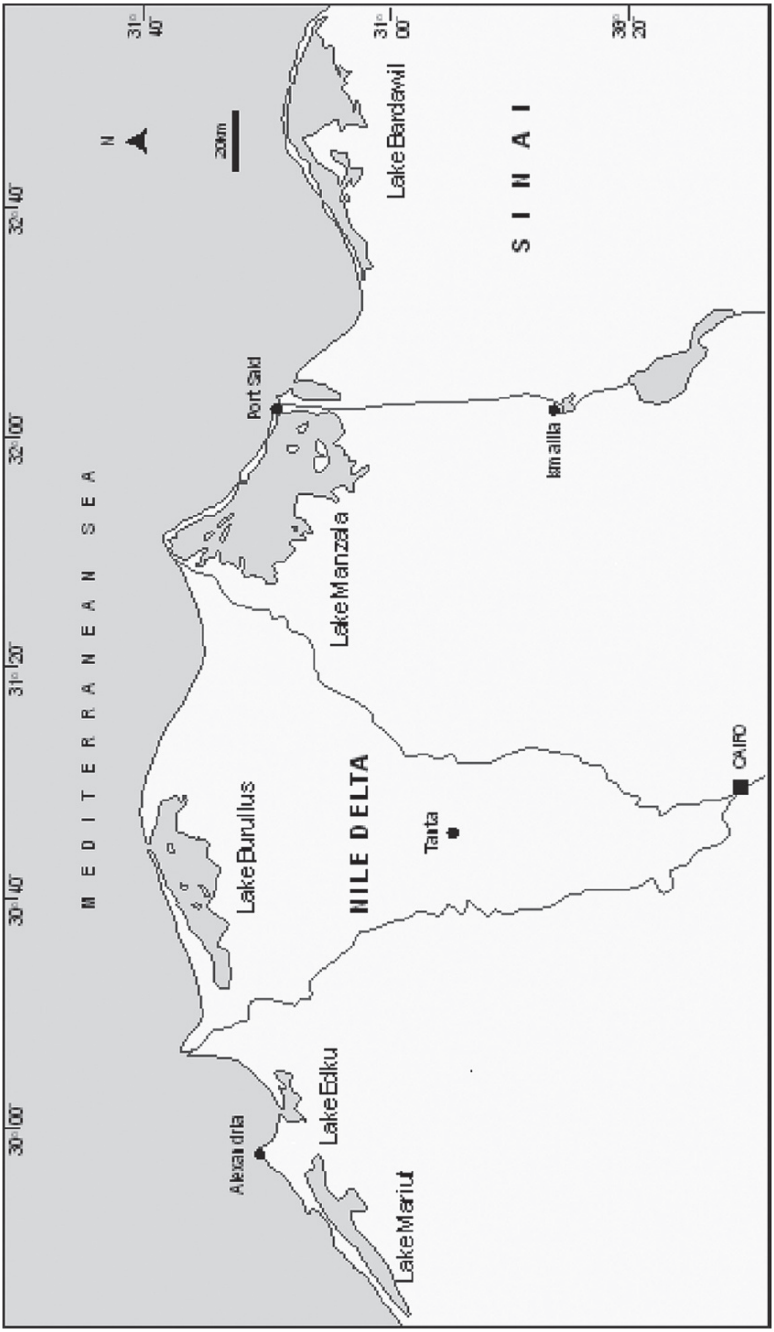

Fig. 1 The Nile Delta and its northern lakes connections with the Mediterranean Sea along the Egyptian coast

and Damietta promontories, which emanate from a point of bifurcation 23 km north of Cairo. Between these promontories lies a broad headland composed of Nile sediments deposited since 6,500 years ago (Stanley & Warne, 1994; Frihy & Dewidar, 2003; Hamza et al., 2003). The recent geological age of the delta has been noted in the literature (Goudie, 2005). The Nile negotiates its way through five regions, each differing in terms of history and structure: the great lake plateau of Central Africa, the Sudd and Central Sudan, the Ethiopian Highlands, the cataract tract from Khartoum to Aswan, and Egypt down to the delta and Mediterranean (Said, 1981). According to Issawi & McCauley (1992), Egypt was drained during the Cenozoic by a succession of three major drainage systems that competed for survival by means of gradient advantage (but see Talbot & Williams, 2009, for an alternative view). This competition took place in response to tectonic uplifts and sea level changes in the interval between the retreat of the Tethys Sea in late Eocene (40 Ma) and the birth of the modern Nile during the late Pleistocene (ca ~25 Ma). In his review, Goudie (2005) presented the three different drainage systems as follows:

1. Oldest: the Gilf system, which consisted of north-flowing consequent streams that followed the retreating Tethys Sea across the newly emerging lands of Egypt, and streams that formed on the flanks of the Red Sea region toward the end of the Eocene (Fig. 2a).
2. Intermediate: the Qena, where a major south-flowing stream developed down the dip slope of a zone of intensified uplift in the Red Sea range during the early Miocene. This stream flowed into the Sudan basin, and was limited in the west by the retreating scarp of the limestone plateau, and in the east by the uplifted Red Sea range (Fig. 2b).
3. Youngest: the Nile system, which came into existence as a result of the drop in the Mediterranean sea-level in the late Miocene. Formerly local drainage eroded headward into the limestone plateau. The Nile captured the Qena system and reversed its flow from south to north (Fig. 2c).

In the late Pliocene, the Nile began to advance across a marine embayment. It developed, especially in the Pleistocene, through major sea-level changes associated with glacial periods. During low sea-level stands, large quantities of sand and mud were dispersed far into the eastern Mediterranean, forming a large submarine fan (Sestini, 1991). Coastal changes can be followed from maps since the early eighteenth century and with more precision from topographic surveys since the early 1800s (UNDP/UNESCO 1978). Throughout the last century there was a steady advance of the Rosetta and Damietta promontories (Fig. 3), averaging 30 and 10 m year^{-1}, respectively, and accretion in all embayments towards the east. Around 1910, reduced monsoonal rainfall over eastern Africa resulted in an overall 25% decrease in Nile discharge that set the theme for present-day coastal instability and headland recession. From 1910 to 1965, the Rosetta promontory receded by 2.5 km and the Damietta promontory by about 2 km (Frihy et al., 1998; Frihy, 2001).

Although the Aswan High Dam (AHD), completed in 1964, was aimed to produce clean energy and to conserve and protect the agriculture in Egypt by

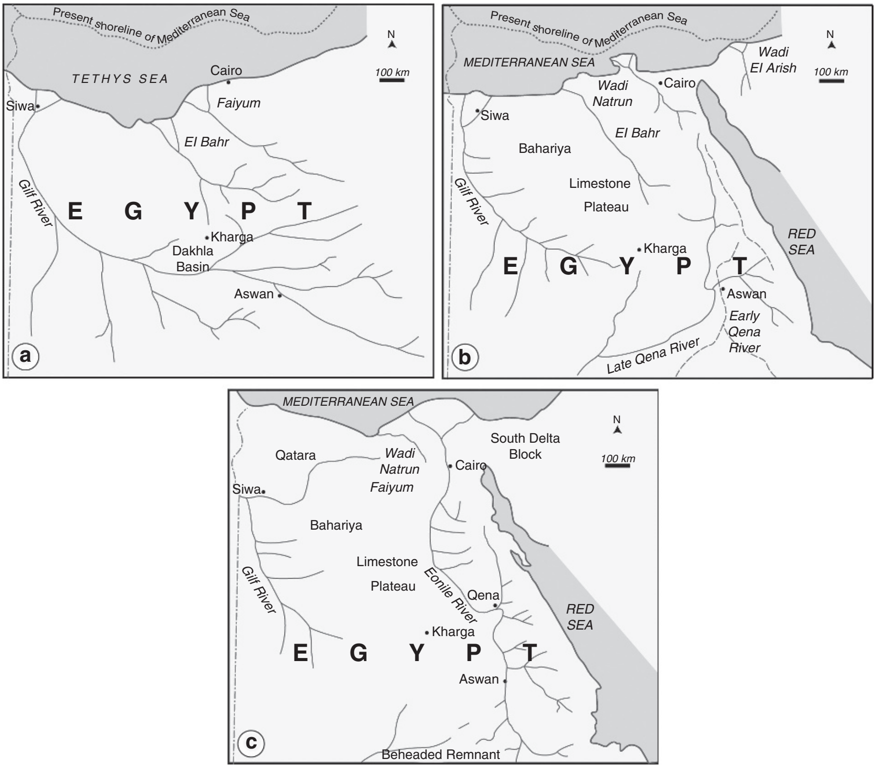

Fig. 2 Sketch showing (**a**) the oldest, (**b**) the intermediate and (**c**) the youngest formation of the Nile Delta (modified from Goudie, 2005 after Issawi & McCauley, 1992)

controlling the Nile flood, it had a dramatic negative effect on the sediment flux to the delta. Since that time the supply of sediment reaching the river mouth at Rosetta and Damietta has no longer been sufficient to stabilize the delta coastline and prevent coastal erosion. Alternatively, Stanley (1996) claims that neither the blockage of the Nile flow at Aswan and other large river control structures, nor additional influence of natural factors including subsidence, sea-level rise, and near shore current processes, fully explain the altered sedimentary regime currently prevailing along the Nile Delta coast. He finds that the trend of land loss along the delta margin is better explained by increased sediment entrapment in the delta proper, between Cairo in the south and the coast in the north. Retention of sediment on the delta plain is directly related to catchments by irrigation waterways, land reclamation structures and wetlands in the delta proper, rather than to blockage of the Nile by dams in upper, middle and lower Egypt (Fig. 4). Stanley (1996) concluded that near-complete entrapment of Nile sediment on the delta plain by canalization, coupled with strong coastal processes, account for the alteration of the delta shoreline.

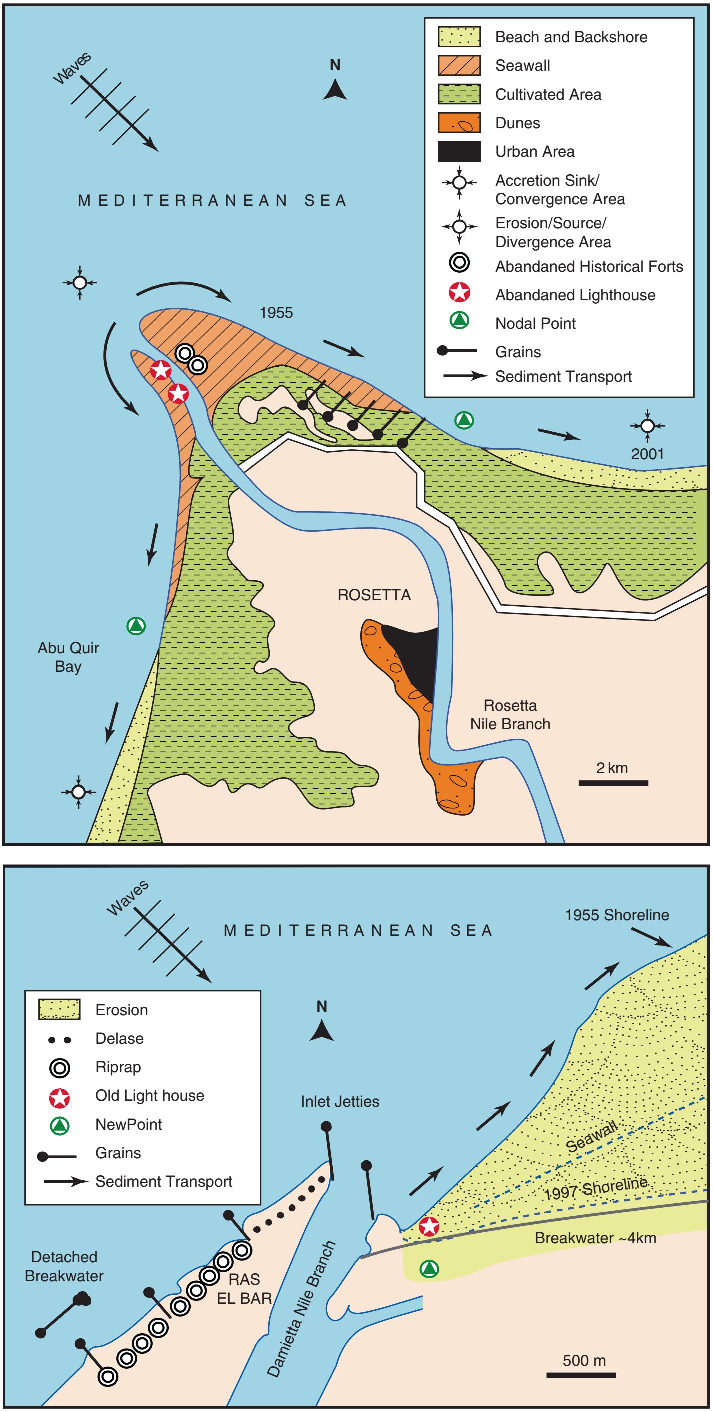

Fig. 3 Erosion and accretion features of the Rosetta (*upper*) and Damietta (*lower*) promontories and the developed protective measures (modified from Frihy et al., 1998 and 2001) (*see Color Plates*)

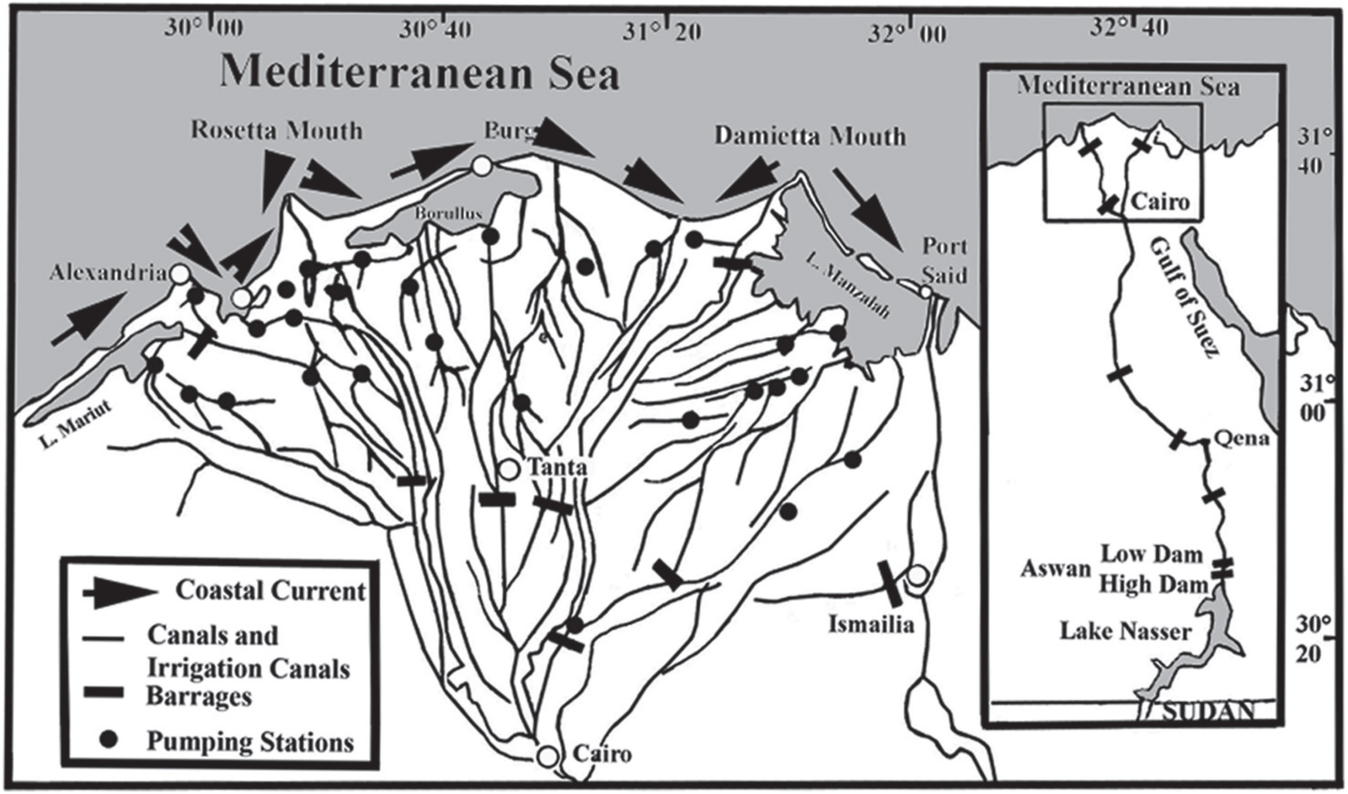

Fig. 4 Ancient and recent irrigation waterways, barrages, canals and wetlands which entrap Nile sediments at the Nile Delta before discharging to the coastal area (modified from Stanley, 1996)

2 Nile Branches Serving the Delta

Both the Rosetta and Damietta branches extend northwards from Cairo to the Mediterranean over distances exceeding 200 km. Along their course, they provide for the needs of agriculture, industrial activities, and they supply drinking water for the most populated area of Egypt. Water flowing through the Damietta and Rosetta branches accounts for less than half of the original total northward flow across the delta plain, that is now captured by artificial waterways comprising >10,000 km of canals, usually only 2–3 km apart. Some canals originally dug in Dynastic times have been expanded and enlarged over the years. The position of major canals and drains, compiled from charts held by the Defense Mapping Agency, is given by Stanley (1996). As shown in Fig. 5, drains and large irrigation and navigation canals flow past major urban centers. Most extend as far as the delta lakes and wetlands, including the southern margin of Manzalah Lake and its large poorly drained southern area to the southeast; the southern margin of Lake Borullus, and its south-eastern marshy area; and Lakes Idku and Mariut. Most numerous are the small to moderate-sized canals that flow through hundreds of delta villages and criss-cross the deltaic plain. These are interconnected with large irrigation canals and drains and flow northwards (Stanley, 1996). They discharge to one of the Nile branches or to the northern delta lakes; some reach the Mediterranean Sea.

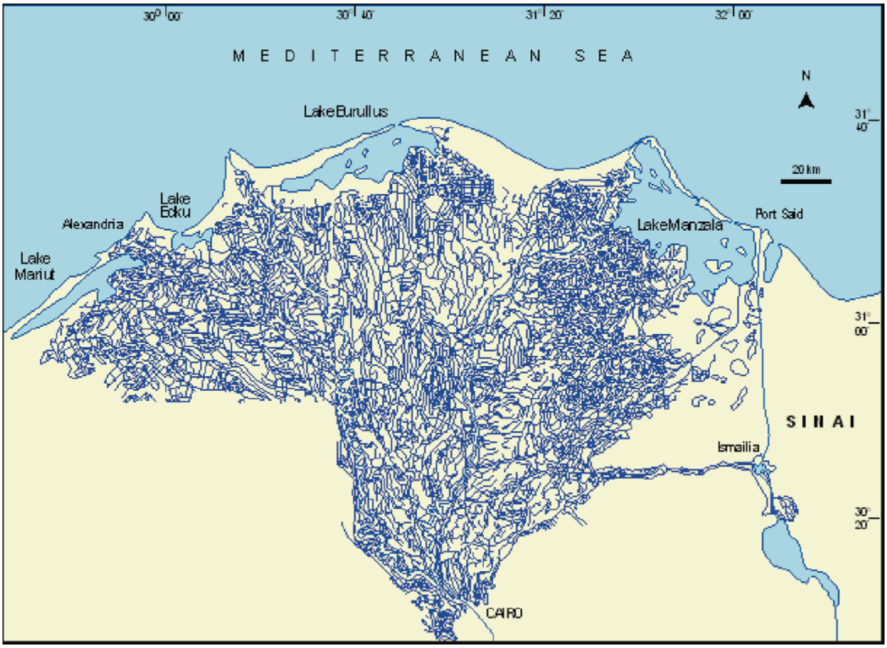

Fig. 5 Map showing >10,000 km of irrigation canals and drains forming the extensive waterway system in the Nile Delta (modified from Stanley, 1996) (*see Color Plates)*

Hamza (2006) stated that approximately 85% of Egyptian water resources (mainly supplied by the Nile) are committed to irrigation of the 3.4 million hectares of cultivated lands. About 65% of these agricultural activities are within the delta area. The dense agriculture in the delta as well as the available infrastructure have enhanced socio-economic growth in this area, with a consequent faster growth in population density in the delta than in other areas of the country. In addition to catering for agricultural needs, the Nile branches also serve industrial activities concentrated around the cities of Cairo and Alexandria. Although the demand for Nile water by the industrial sector is relatively small compared to that for agriculture, the waste discharge from the industrial sector has resulted in degradation of the water quality of the Nile branches. This discharge is supplementary to the domestic sewage making its way into the northern lakes, before it is discharged to the Mediterranean Sea (Hamza et al., 2004; Hamza, 2006).

Since the construction of the AHD in 1964, the Nile discharge to the Mediterranean has been restricted to the Rosetta branch. The Damietta branch is blocked 12 km upstream from its mouth by a dam at the city of Faraskur. The water flowing through the mouth of the Rosetta branch is controlled by the Edfina Barrage located 35 km south of the river mouth. Stringent control of the flow through the Nile branches to the Mediterranean is due to the almost total dependence of Egypt on the Nile (95% dependent) as the main freshwater source to satisfy the fast increase in its population growth. As a result of these controls the quantity of water released to the Mediterranean is no longer determined by Nile flooding, but is composed of wastewater considered unsuitable for recycling. In his review, Hamza (2006) indicated that the actual quantity of Nile surplus reaching the Mediterranean annually amounts to 2.5–4 km^3. Almost all of this water passes through the northern delta lakes and other land effluents connected to the sea, instead of flowing through the main Nile branches. According to El-Arabawy's (2002) water balance strategic model for the year 2017, an estimated 6–7 km^3 of return flow into the Mediterranean and northern lakes is required to mitigate salt-water intrusion and preserve the Nile Delta salt balance.

3 The Nile Delta Lakes

As the final reservoirs of Nile water before it flows into the Mediterranean, lakes Mariut, Edku, Borullus, and Manzalah are the last opportunity for Egyptians to use the Nile water (Fig. 1). The four lakes occupy an area of about 1,100 km^2. They are common shallow (average depth 1.10 m), and their salinity changes from fresh to brackish in seaward direction. They are connected to the Mediterranean Sea either directly or indirectly. The quantity and quality of water discharging to the lakes are determined by up-river activities, not by the requirements for activities within the lakes.

During the last 50 years the surface area of the four lakes has been reduced to ca 50% of their area during the 1950s (Table 1). Lake area was lost to highway construction, reclamation of land for agriculture, and in some cases for residential

Table 1 Gradual changes in the surface areas (km^2), of the northern Delta Lakes during the last 50 years (after Hamza, 1999)

Lake Years	L. Mariut km^2	L. Edku km^2	L. Burullus km^2	L. Mazalah km^2
1950s	136.9	150.1	571.8	1274.2
1970s	68.4	129.2	534.4	997.3
1980s	66.1	115.3	481.6	904.1
1990s	62.3	109.7	350.8	650.3

construction. Such unnatural use has certainly modified the ecosystem as a whole, beginning with hydrological changes and resulting in the reduction of their economical and natural value. Due to their position along the coast, the lakes are surrounded by or included within highly populated coastal cities. This is reflected, especially during the last 20 years, in different forms of human impact on these water bodies, such as industrialization and the construction of new infrastructure, responding to population density increase. Such impacts deteriorated water quality and reduced lake surface area (Hamza, 1999). One negative effect of human impact on the Nile Delta Lakes (NDL) ecosystems is the decline in fish production. Up to 1985, the annual fish production of the lakes accounted for >50% of the total annual yield for the country. Amongst these lakes, Lake Mariut was the most fertile (Aleem & Samaan, 1969). Now, Mariut as well as Manzalah are the least productive ones because of a continuous discharge of sewage and industrial waste into their basin (Siegel, 1995), causing algal blooms in all of the lakes. From their study on changes of zooplankton community structure in the NDL for the last seven decades, Dumont & El-Shabrawy (2008) concluded that the construction of AHD reduced the marine influence in the lakes and an elimination of some large grazers by freshwater fish took place. They also added that major changes to the Lake Borullus faunal community were caused by intensified agriculture at the delta region, especially during 1980s–1990s, responsible for eutrophication, and leading to the elimination of large to medium sized (micro)crustaceans.

The reduction of lake area has forced fishermen to harvest fingerlings and dredge the lake bottom in search for adult fish in their breeding grounds. Dredging the bottom sediments re-suspends particulate organic matter, which consumes oxygen and results in fish kills. Also, turbid water reduces the photosynthetic capacity of algal cells, making re-oxygenation more difficult. The removal of fingerlings alters the ecosystem balance and creates an imbalance between plankton and fish. Over-fishing is common, as is the practice of bottom dredging, despite the passing of laws aimed to protect the lake ecosystems.

As shown in Table 2, all lakes are eutrophic to hypertrophic, reflecting their high organic loads. Although the water residence time in the lakes is small (range 10–42 days), their trophic status is high. This phenomenon is consistent with high organic loads and a high binding capacity of the clayey sediments that have accumulated in the lakes over time. The lakes are fed by Nile water rich in phosphorus compounds, which are easily captured by clay deposits. The shallowness of these lakes

Table 2 Main geographic and hydrographic features of the Nile Delta Lakes (modified after Hamza, 2000)

	Location			
Parameters	L. Mariut	L. Edku	L. Burullus	L. Manzalah
Lon. (E)	29.28	30.20	31.00	31.48
Lat. (N)	31.20	31.33	31.62	31.46
Surface area (km^2)	62.00	109.00	350.00	650.00
Depth range (cm)	50–150	40–220	50–200	50–140
Av. water salinity (‰)	6.3	3.8	2.5	5.9
Annual discharging volume ($\times 10^9$ m^3)	2.37	2.06	3.2	6.7
Discharging rate (m^3 s^{-1})	74.0	60.0	80.0	165.0
Water residence time (days)	10	21	42	32
Trophic status	Hypertrophic	Eutrophic	Eutrophic	Hypertrophic
Water sources	A, I, S, G	A, S	A	A, I, S

A = Agriculture, I = Industrial, S = Sewage, G = Groundwater.

is an important factor in increasing the capacity of clay to bind with phosphorus compounds, because continuous agitation of the short water column by wind helps to keep bottom sediments in an oxic condition. This helps the clay particles to accumulate phosphorus to the limit of their binding capacity (Gachter & Meyer, 1993; Hamza et al., 1995) and explains the high phosphorus loads shown in Table 2.

4 Human Activities and Their Impact on the Nile Delta

The Nile Delta accounts for two thirds of Egypt's agricultural land (Stanley, 1996). Egypt covers an area of about 1 million km^2, but about 99% of the Egyptian population (now approaching 80 million) is concentrated in 5.5% of that territory, mainly located along the Nile valley (area = 2.7%, population = 36%) and delta (area = 2.8%, population 63%). The remaining 94.5% host only 1% of the population (Attia, 2002). Egypt is the most populous country in the Arab world, and the second most populous in Africa. It is a middle-income nation with a diversified economy. Agriculture accounts for about 17% of GDP. The principal export crops are cotton and winter vegetables. Cultivation of basic grains is also extensive. Egypt is a rapidly industrializing country with extensive use of chemicals in a wide spectrum of industrial sectors. The main industrial sectors are raw and fabricated metals, vehicles, pharmaceuticals, textiles, pesticides, fertilizers, petrochemistry, cement, paper and pulp, and food processing. About 50% of all industrial activity is concentrated in Greater Cairo and about 40% in Alexandria. The rest is in delta, upper Egypt, and new cities (Barakat, 2004).

With an arid landscape, little rain and 94.5% desert, Egypt is dependent on the Nile for its existence and faces a host of environmental problems. These are aggravated by a high population density, which places a strain upon resources. Since the Nile Delta is the most populated, cultivated and industrialized part of the Egyptian territory, it receives the highest quantities of contaminants derived from human activities. The sources of these contaminants and their release and ultimate fate may be summarized as follows:

4.1 Chemical Contaminants

The chemical industry located in the delta is the main source of hazardous waste. Frequent problems have been faced by these industries in the disposal of their waste. Water pollution in the Nile branches as well as the northern lakes is caused by agriculture pesticides, raw sewage, and urban and industrial effluents. Barakat (2004) noted that the use of organochlorine insecticides in Egypt began in the 1950s and lasted until 1981, to protect crops from insects, fungi and weeds, to remove undesired vegetation and for domestic household use in the control of insects. The reported total active ingredients include: toxaphene 45,000 Mt (1955–1961), endrin 10,500 Mt (1961–1981), DDT 13,500 Mt (1952–1971) and lindane 21,000 Mt (1952–1978) (El-Sebae et al., 1993). The main purpose of these insecticides is the control of cotton leafworm and bollworms. DDT is still in limited use as a rodenticide and termiticide. These compounds, released into drainage canals, reach the delta branches and lakes, which partially release their waters to the Mediterranean. According to the Ministry of Agriculture, the application of pesticides decreased from 20,500 tons in 1980 to 16,435 tons in 1995. Since chlorinated pesticides have been banned, the pesticides currently used are organophosphorus compounds (Barakat, 2004). Table 3 shows concentrations of PCBs, DDTs, HCB and lindane in waters of the delta region.

Table 3 Concentrations (ng l^{-1}) of HCB, DDTs, PCBs and lindane in freshwaters from different locations of the Nile Delta (modified from Barakat, 2004)

Location	Sampling	HCB	DDTs	PCBs	Γ-HCBs
River Nile					
Cairo	1993	<0.001	0.08–0.12	3–640	0.05–0.07
Rosetta Branch	1998	1–77	0.2–99	5–161	
Damietta Branch	1988	<DL–93	90–102	25–53	<DL–126
				7–21	
Nile Estuaries					
Rosetta	95–97	197–217	83–97	166–181	286–310
				390–430	
Damietta	95–97	195–240	109–128	270–330	312–352
				581–700	
Coastal Lakes					
Lake Manzala	1993	0.03–0.18	0.10–0.56		0.37–1.57
	92–93	0.84–2.28	26–55	18–48	8.6–12.1
			3–26	<DL–20	1–11

<DL: below detection limit.

4.2 Hydrocarbon Contaminants

The Nile Delta area harbors the major producing oil and gas fields in Egypt. Vandre et al. (2007) described how the geological history of northern Egypt generated multiple petroleum sources, reservoir and seal combinations of source rocks in the delta. Between 1966, when drilling for hydrocarbons began, and 2002, over 36 trillion cubic feet of gas have been discovered in northern Egypt (Dolson et al., 2002). Since oil and gas exploration activities are increasing dramatically in the delta area it is imperative to prevent the leakage of hydrocarbon contaminants to the environment, from exploration activities and other activities of the oil and associated petrochemical industries.

4.3 Sewage, Trace Metals and Nutrient Contaminants

Domestic and industrial sewage represent major sources of nutrient enrichment to waters of the Nile Delta. Sewage contributes to the development of eutrophication and the degradation of water quality. Often, municipal and rural domestic wastewater is discharged directly. It contributes pathogens, nutrients, trace metals, suspended solids, salts and oxygen-demanding materials (Hamza & Mason, 2004). Siegel (1995) reported that the nutrient base for aquaculture in Lake Manzalah is sewage carried by drains from as far away as Cairo, 140 km to the south. He added that untreated or poorly treated industrial wastes, heavy metals and other pollutants are released into the Nile Delta drain network and are discharged along with sewage and agriculture wastes into the northern delta lakes and their associated wetlands. In an earlier study Siegel et al. (1994) measured sedimentary deposits in the southeastern sector of Lake Manzalah. They detected Hg (up to 822 ppb), Pb (up to 110 ppm), Zn (up to 635 ppm), Cu (up to 275 ppm), Cr (up to 215 ppm), Sn (up to 14 ppm) and Ag (up to 4.7 ppm). They concluded that high concentrations of heavy metals in lake sediments contaminated fish, especially bottom feeders. This may be the case in the northern lakes, since all of them receive the sewage discharges of major cities. Unfortunately, with the dwindling of the natural nutrient-rich Nile water discharge into the Mediterranean, the sewage discharges from coastal lakes and other land run-offs have become the alternative source of nutrients for coastal fisheries (Hamza, 2006). Satellite images of discharges into the Mediterranean show the impact of the degraded water quality on the coastal lakes, which act as transitional basins for sewage (Fig. 6).

Dissolved humic substances of agricultural or industrial origin have been measured in Lake Edku (El-Sayed et al., 1993). The seasonal variation showed a minimum average of 1.93 mg l^{-1} during winter and a maximum average of 4.33 mg l^{-1} during summer. The total humic substance budget derived from an autochthonous source represented by primary production which contributed about $5{,}150 \times 10^6$ g year^{-1}; allochthonous (drains) sources contributed about 4328×10^6 g year^{-1}. About 65% of dissolved humic substance input is lost (trapped, transformed, or degraded) in the lake before being discharged to the sea.

Fig. 6 Eutrophication of Alexandria coast by sewage discharge from Lake Mariut (after Halim & Abu-Shouk, 2000) (*see Color Plates)*

5 Effects of the Nile Delta Effluents on the Coastal Ecosystem

The capricious Nile floods between the late 1970s and early 1980s, motivated the Egyptian Ministries of Irrigation and Public Works to adopt policies to face any future shortage of Nile water supply. Despite the fixed 55.5 km^3 of Nile water allotted to Egypt yearly, the rapid increase in its population during the last 30 years has resulted in more freshwater needed to satisfy the nation's demands. This circumstance forced policy makers to turn to non-conventional resources such as underground water accessible to drilling, water recycling and, to some extent, desalination. These sources of freshwater are not suitable to satisfy all needs and are always mixed with Nile water. The decision of the Egyptian government to reduce the discharge of Nile water to the Mediterranean not only affects the quantity of the Nile water discharge, but also its quality. That is mainly because the water undergoes a series of recycling before finally reaching the Mediterranean (Hamza, 2006). The discharge points to the sea have been identified by Stanley (1996) as El-Tabya and El-Maadiya (Lake Idku), El-Burg (Lake Burullus), El-Gamil (Lake Manzalah), Shibin drain at Gamasa (west of the Damietta branch), and Kitchener drain (east of lake Burullus). These are in addition to the El-Max pumping station, which pumps sediments and sewage water from Lake Mariut to El-Max Bay along the Alexandrian coast. Recent quantitative data on sediment

Table 4 Location and discharge water characteristics of the main land-runoffs and the winter season discharge percentages (after Hamza et al., 2003)

	Location					Nutrient loads	
	Lon.	Lat.	Discharge	Winter	Salinity	N	P
Sources	deg.	deg.	km^3 year^{-1}	%	S%	T year^{-1}	T year^{-1}
Lake. Mariut	29.82	31.20	2.3	40	6	90.85	11.41
Lake Idku	30.20	31.33	0.4	40	4	16.16	2.03
River Nile	30.37	31.50	3.5	90	2	138.17	17.35
Lake Burullus	31.00	31.62	2.2	40	5	87.14	10.94
Nile Delta drains	31.28	31.55	3.5	40	4	138.17	17.35
Lake Manzalah	31.48	31.46	5.2	40	5	205.44	25.80
Total	–	–		–	–	676.37	84.88

and water discharge from the above-mentioned effluents are lacking. Based on nutrient concentrations in the major effluents during 1986, a total of 676.37 tons of inorganic nitrogen and 84.88 tons of orthophosphate were discharged to the Nile Delta coastal area (Table 4). These quantities were carried in the total discharge, about 18 km^3 of Nile water, to the Mediterranean Sea at that time (Hamza et al., 2003). If the nutrient concentrations in the quantity of water actually discharged (ca 2–4 km^3) remain similar, a simple calculation shows an actual load of 112.73 tons of nitrogen and only 14 tons of orthophosphate released annually through the Nile Delta effluents to the Mediterranean. However, higher concentrations may be found in the coastal area of the Nile Delta, due to highly polluted water after its agricultural use, in addition to poorly treated sewage. Dumont & El-Shabrawy (2007) reported concentrations of dissolved nutrient salts measured in the water column of Lake Burullus during 2004. They found that the average concentrations of nitrogen ions NO_2, NO_3 and NH_3 were up to 147, 613, and 1120 μg l^{-1}, respectively. Concentrations of PO_4 ranged between 100–1647 μg l^{-1}. These high concentrations could be measured at all the NDL, since their sources of water supply and its water quality are almost similar.

On the other hand organochlorine pesticide concentrations along the Nile estuary are high (Table 5), with some dilution due to mixing with marine coastal water. As shown in Table 4, about 40% of the discharge to the Mediterranean through the Nile Delta effluents and about 90% of the discharge through the Nile branches occurs during winter. This is due to the relatively high precipitation (200 mm cm^{-2}) over the delta during winter, and to the opening of the Nile branch barrages during this season. The release during one season of such a large portion of the total flow is the main cause of an algal bloom along the Egyptian coast in front of the Nile Delta (Dowidar, 1984, 1988; Hamza et al., 1998). This bloom is anomalous, considering the oligotrophic state of the Mediterranean in general and the Levantine basin in particular. Tselepides & Lampadariou (2004) stated that the eastern Mediterranean has one of the lowest meiofaunal standing stocks, reflecting the low productivity of this area. But they also concluded that the highest meiofaunal densities occur over the shallow continental shelf of the Nile Delta (340 ind cm^{-2}). This phenomenon is explained by the fact that the Mediterranean occasionally undergoes periods of

Table 5 Concentrations (ng l^{-1}) of HCB, DDTs, PCBs and lindane in seawater from different locations in Egypt (modified from Barakat, 2004)

Location	Sampling	HCB	DDTs	PCBs	Γ-HCBs
Mediterranean Sea					
Alexandria Coast		5–19	12–20	37–131	1–9
Abu Quir Bay		2–52		20–844	<0.1–60
			17–166	31–872	
El-Max Bay		6–32	16–88	40–153	9–39
			16–48	26–191	
Wastewater discharge (av. conc.)					
Edku Lake output	97–98	30	78	310	310
				410	
El-Max pump station	97–98	85	72	620	420
				810	
El-Amia Drain	97–98	37	61	420	410
				520	

increased nutrient availability, such as the effect of the Nile Delta effluents on productivity along the Egyptian Mediterranean coast.

6 Prediction of Future Variations in the Nile Delta

The Nile Delta is a complex environment, combining the effects of both natural and human factors. The reduction of Nile water flow through the delta branches, in addition to recent intensification of agricultural activities (Hamza & Mason, 2004), limit the ability of the nutrient-rich sediments to reach the delta agricultural lands. North of Cairo there have been marked increases in population and agriculture and industrial activities. These human activities and the shortage of freshwater resources have led to water recycling becoming a common practice before its release as waste and sewage to the northern lakes, and then into the Mediterranean as a polluted but complex nutritive discharge. Along the northern coastal area, the arrival of diminished quantities of Nile sediment have not been sufficient to combat coastal erosion due to long-shore coastal currents (Stanley, 1996; Frihy & Dewidar, 2003; Conway, 2005). There are also erosive effects from strong coastal wave action along the Nile Delta headland (El-Asmar & White, 2002).

To predict changes within the Nile Delta area and its coastal environment, it is necessary to assess the effects of various combinations of the above-mentioned parameters. Neither monitoring nor simple statistical analysis will reveal future characteristics of the Nile and its coastal ecosystem if these parameters remain unquantified. In an attempt to provide a quantitative tool, a 3D numerical model has been established to simulate, analyze and predict quantitative variations in the Egyptian-Mediterranean coastal area (Hamza et al., 1998). This model takes into account meteorological variations and their effects on the coastal area. For example, El-Asmar & White (2002) found that wave action along the Nile Delta coast is seasonal with high storm waves approaching from the NW-NNW during winter. These generate eastward long-shore currents with velocities up to 0.9 m s^{-1}. The 3D numerical model couples hydrodynamics and biological components in its calculations based on data collected along the Egyptian Mediterranean coastal area during the period 1982–1986. The model also considers nutrient inputs, and the full range of topographic features along the coast (Hamza et al., 2004). Based on the FinEst model of Tamsalu & Ennet (1995), the basic equations are as follows:

$$\partial \mathbf{c}/\partial \mathbf{t} + \mathbf{Lc} = \mathbf{F} \tag{1}$$

where

$$\mathbf{c} = \left| \begin{array}{lllll} \mathbf{u} & & & & \\ & \mathbf{v} & & & \\ & & \mathbf{T} & & \\ & & & \mathbf{S} & \\ & & & & \mathbf{C} \end{array} \right| \begin{array}{l} \\ \text{hydrodynamic parameters} \\ \\ \\ \text{ecosystem parameters} \end{array}$$

$$\mathbf{F} = \left| \begin{array}{llll} \mathbf{-1/r0\partial p/\partial x + fu} & & & \\ & \mathbf{-1/r0\partial p/\partial y - fv} & & \\ & & \mathbf{1/(cp\ r0)\partial I/\partial z} & \\ & & \mathbf{0} & \\ & & & \mathbf{G} \end{array} \right| \begin{array}{l} \text{pressure + Coriolis} \\ \text{pressure + Coriolis} \\ \text{solar radiation} \\ \\ \text{biochemical reactions} \end{array}$$

$$\mathbf{Lc} = \mathrm{div}\mathbf{h}\ [\mathbf{Uc} + \langle \mathbf{U'c'} \rangle] + \partial/\partial\mathbf{z}[(\mathbf{w} + \mathbf{w})\mathbf{c} + \langle \mathbf{w'c'} \rangle]$$

Here, U is the horizontal velocity vector with components u and v; U′ = fluctuation of the horizontal velocity vector with components u′ and v′; w = vertical velocity; w′ = fluctuation of the vertical velocity; T = temperature; S = salinity; p = pressure; ρ = density; ρ0 = mean density; b = buoyancy; g = acceleration due the gravity; f = Coriolis parameter; C = ecosystem parameter; c′ = fluctuation of parameter C; G = biochemical reactions; F = linked reaction results of the model; Lc = spatial variations of the model parameter.

For calculations, the continuity equation is required:

$$\mathrm{div}\mathbf{h}\ \mathbf{U} + \partial \mathbf{w}/\partial \mathbf{z} = \mathbf{0} \tag{2}$$

The hydrostatic equation is:

$$\mathbf{1/r0\partial p/\partial z = g(r = r0)r0 = b} \tag{3}$$

The components of the plankton community are autotrophs (photosynthetic plant organisms), heterotrophs (non-photosynthetic organisms), and detritus. Five categories of autotrophs (**Ai**) and heterotrophs (**Hi**) are classified:

Their evolution is governed as follows:

$$\partial \mathbf{A}_i /\partial \mathbf{t} + \mathbf{LA}_i = \mathbf{Ga1}_i - \mathbf{Ga2}_i - \mathbf{Ga3}_i - \mathbf{Gh5}_i \tag{4}$$

i = 1,…,4

$$\mathbf{\partial A_5 / \partial t + LA_5 = Ga1_5 - Ga2_5 - Ga3_5} \tag{5}$$

$$\mathbf{\partial H_i / \partial t + LH_i = -Gh2_i - Gh4_i + b(Gh5_i + Gh6_i) - Gh6_{i-1}} \tag{6}$$

$i = 1,\ldots,4$

$$\partial D/\partial t + LD = \sum_{i=1}^{5} (Ga2_i + Gb2_i) - Gd3 \tag{7}$$

Here: $Gd3$ = detritus decay; $Ga1_i$ = autotrophs growth; $Ga2_i$ = autotrophs mortality; $Ga3_i$ = autotrophs respiration; $Gh1_5$ = bacterioplankton growth; $Gh2_i$ = heterotrophs mortality; $Gh3$ = - heterotrophs respiration, $Gh4_i$ = heterotrophs excretion; $Gh5_i$ = heterotrophs grazing; Gh2i = heterotrophs predation; b = efficiency coefficient.

All biochemical reactions are parameterized for autotrophs as follows:

$$\mathbf{Gaj_i = ca\ Ma_i^{-1/4}\ cta_i\ fj_i\ A_i \quad i = 1,\ldots,5;\ j = 1,\ldots,3} \tag{8}$$

The biochemical reactions for heterotrophs may be written as follows:

$$\mathbf{Ghj_i = ch\ Mh_i^{-1/4}\ cth_i\ fj_i\ H_i \quad i = 1,\ldots,5;\ j = 1,\ldots,6} \tag{9}$$

The model has four phosphate compounds and five nitrogen compounds. Although the hydrodynamic part of the model is established, the ecosystem equations are still in a developmental stage. Certain processes of the food-web interactions, such as fish competition and predation, can be included following the same mass dependent bases. Further details regarding the model and coefficients used are found in Hamza et al. (2003).

The results of simulations for the winter season demonstrate an effect of wind direction and intensity on the delta coastal area (Fig. 7). Biological simulations show that the effect of wind along the coastal area is variable. In certain areas near the

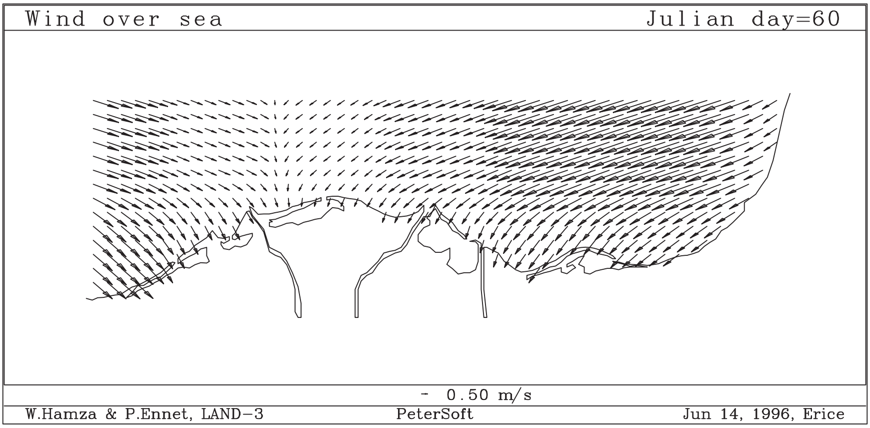

Fig. 7 Finest model simulation of wind components data obtained from Mars Archives over the Egyptian coast during the 60 Julian days (after Hamza et al., 2004)

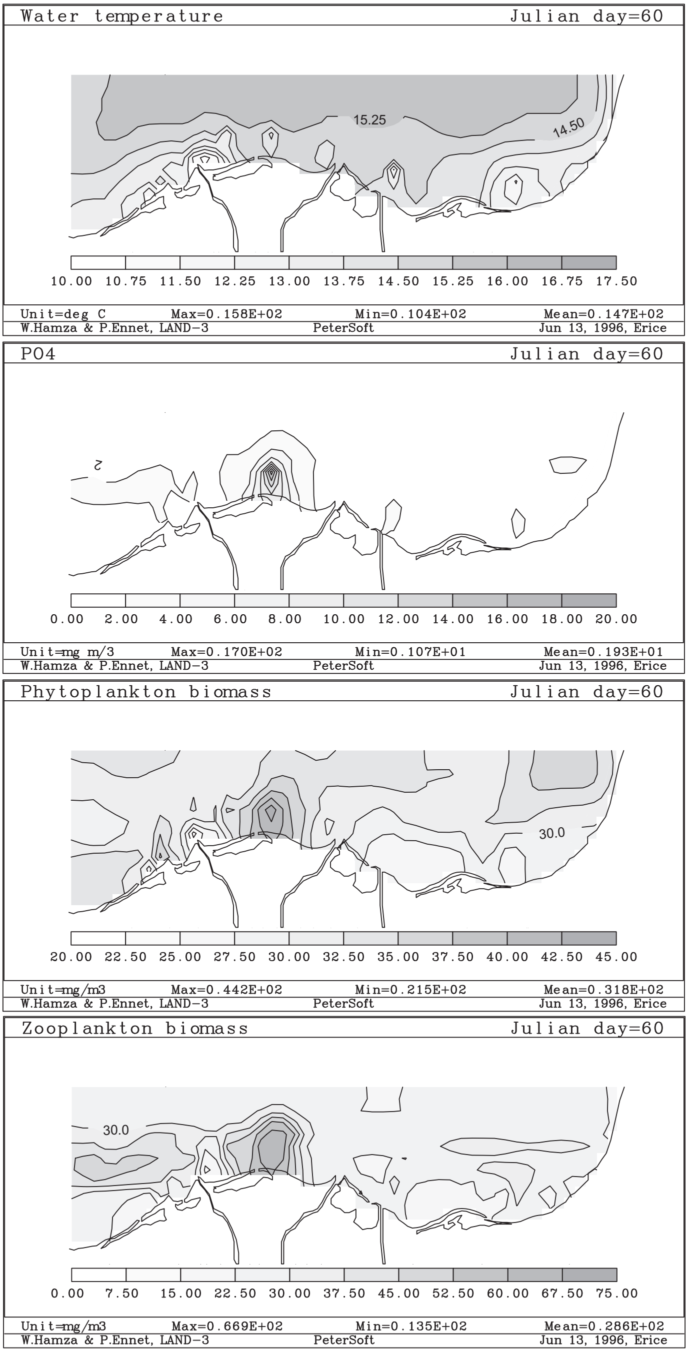

Fig. 8 Calculated water temperature, PO4-P, phytoplankton and zooplankton biomasses along the Egyptian Mediterranean coastal area (after Hamza et al., 2004)

Rosetta mouth, a calm condition develops during winter, when the Rosetta branch is discharging up to 90% of its annual load to the Mediterranean. Such circumstances may promote the development of a winter algal bloom that thrives on the nutrients in the delta effluent (Hamza et al., 2003). A summary of the environmental parameters along the Egyptian Mediterranean coast during winter is shown in Fig. 8.

In conclusion, it is evident that the accentuated erosion of significant stretches of Nile Delta shoreline results from the inferior supply of sediments presently reaching the sea, compared to the sediment removed by currents from the coast. The Nile Delta is an extreme example of human interference in the stability of a depocenter, which is no longer prograding. Maintaining a healthy Nile Delta region, capable of sustaining a dense population, requires reconciling support to agricultural intensification with the need to release sediments to the coast. Careful monitoring based on quantitative analysis is of extreme importance in future planning for sustainable development of the Nile Delta – a region vital to the national food supply of Egypt.

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The Fayum Depression and Its Lakes

Gamal M. El-Shabrawy and Henri J. Dumont

Abstract The Fayum is a depression below sea level, formed by wind erosion 1.8 million years ago, covering ca 12,000 km^2. It consists of two lacustrine complexes, Birket Qarun and the two artificial Wadi el-Rayan lakes. Lake Qarun is a saline remnant of the historical freshwater Lake Moeris. It used to be supplied by Nile water between its formation (about 1980 BC) and the Ptolemaic period (323–246 BC). The lake is no longer connected to the Nile and needs to be supplied with pumped water that evaporates in its basin. Consequently, the lake showed a strong increase in salinity, especially during the twentieth century. It evolved from a brackish to a hypersaline state, with incisive repercussions on all biota. In Wadi el-Rayan area, two successive lakes, separated by a waterfall, were created as a reservoir for drainage wastewater. These lakes currently exceed the capacity of Lake Qarun. The physical and chemical variables, phytoplankton, zooplankton, macrobenthos and fish of the two lake complexes are discussed. Among other things, it is argued that the rapid change in salinity of Lake Qarun excludes the presence of endemic species in its fauna.

1 Introduction

The Fayum (also written as Faiyum), a natural depression extending over 12,000 km^2, was formed by wind erosion ca 1.8 million year ago (Ball, 1939). It is situated ca 100 km southwest of Cairo, and separated from the Nile by a 25 km strip of desert. It is bounded by sandy hills, broken in the south, where a carrier canal (Bahr Yousef) enters the depression. This is its only source of water. The systems of irrigation and drainage are different from those of the Nile Valley. Terraced lands

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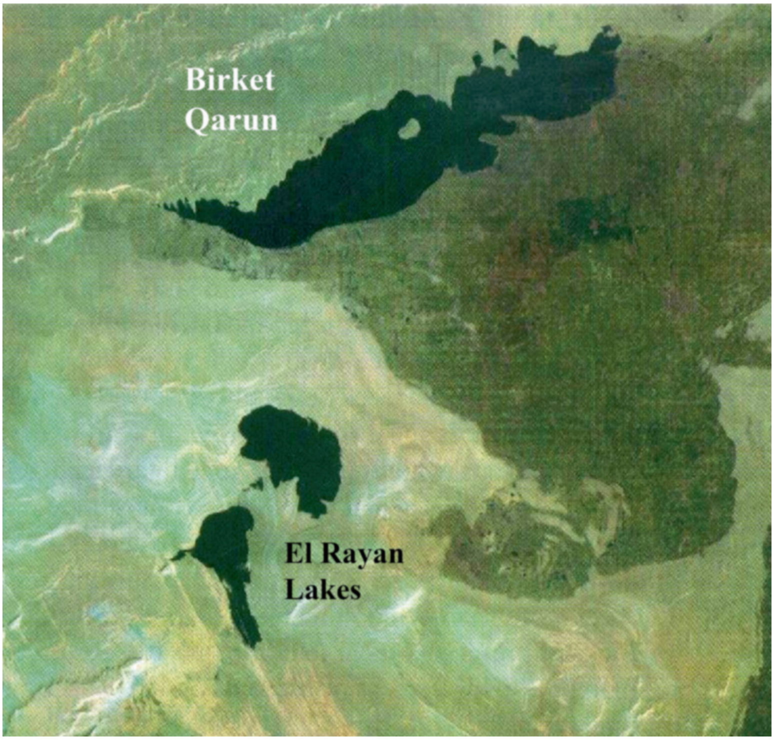

Fig. 1 Map of the Fayum province with its two lakes (Qarun and Wadi El Rayan). Source: (http://www.freesearch.co.uk/out?t=i&dest=http%3A%2F%2Fwww.utlcairo.org%2Fturismo%2Fturismo_fayoum.htm)

allow the use of masonry weirs for the distribution of irrigation water, instead of the regulators and pipe intakes of the Nile valley. One standard Fayum type of weir is used and Lake Qarun collects agricultural drainage water through two drains. Since 1973, about 30% of this water has been diverted to a second depression, Wadi El Rayan, south-west of the Fayum (Figs 1 and 2).

2 Lake (Birket) Qarun

Lake Qarun (29.48° N, 30.29° E) is located ca 43 m below sea level, in the northern Fayum (Figs 1 and 2). Documentary records for this lake began when Herodotos visited Egypt around 450 BC (Brown, 1892). He saw a large water expanse, Lake Moeris, assumed artificial, 50 fathoms deep, and maintained by a seasonal supply of Nile water. In the late nineteenth and early twentieth centuries (Ball, 1939), archaeologists showed that the modern lake is the shrunken remnant of this Lake Moeris. Lake Qarun is currently saline (see below), turbid (Secchi disc transparency <40 cm), and without surface outflow. It covers an area of 235 km^2, has an

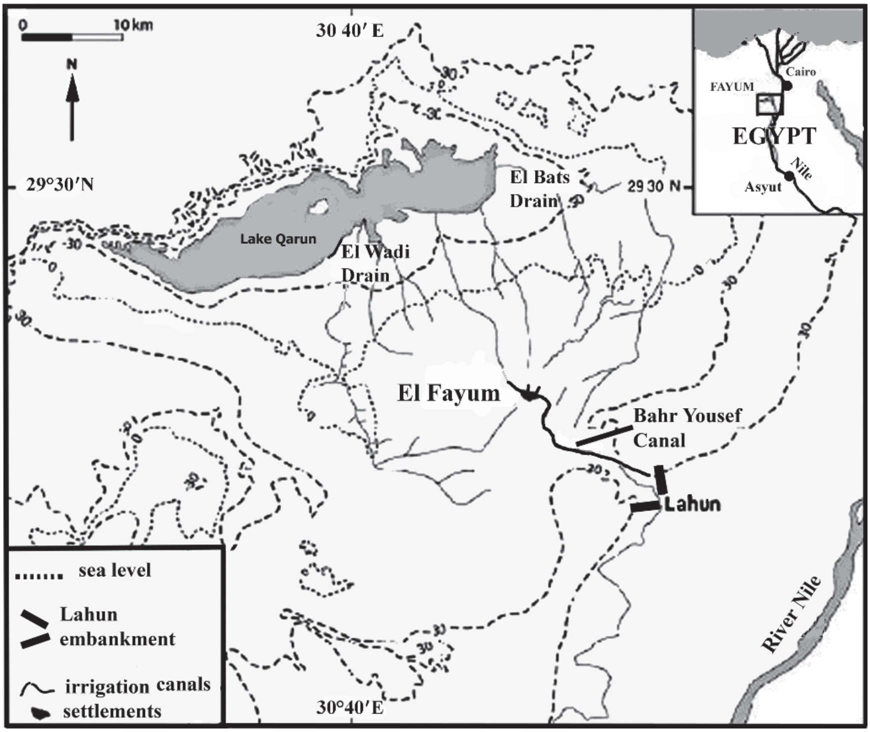

Fig. 2 Map of the Fayum Depression showing the surface hydrology including Bahr Yusef, irrigation canals, drains, and Lake Qarun (after Flower et al., 2006, with permission from Springer)

elongated rectangular shape, and stretches for 40 km from east to west. Average depth is 4 m, with the main western basin deeper than the eastern (maximum 8.8 m) (El-Wakeel, 1963). The lake is one of Egypt's prime sites for migratory and waterbirds. Kittlitz's plover, Kentish Plover, Collared Pratincole and Little Tern breed and Great Crested Grebes and Black-necked Grebes spend winter here. Fayum City, the principal town in the region, is a distribution centre from which a network of canals and pumping stations deliver water to the agricultural regions around it (Brown, 1892; Hewison, 2001). Agricultural returns and excess water are passed to Lake Qarun by two principal 'drains': the El Bats Drain, flowing into the lake's east end and the El Wadi Drain entering the western basin (Fig. 1). The water in these drains is fresh (El-Sayed & Guindy, 1999) but contaminated by agro-chemicals. About 360×10^6 m^3 of water annually enter the lake, carrying an average of 430,000 t of salts (Meshal, 1973). There is less incoming drainage than loss by evaporation. Consequently, salinity increases with time, reaching 45.31‰ in 1996 (Anonymous, 1997). Water level typically varies by less than 1 m annually and temperature changes seasonally between about 33°C and 15°C (Ball, 1939; El-Sayed & Guindy, 1999). Physical and chemical variables have been documented by Lucas (1906), Abu-Samra (1934), Ball (1939), Naguib (1958), Meshal (1973), Ishak & Abdel-Malek (1980), Abd Ellah (1999), Elewa et al. (2001), Mansour et al. (2001) & Ali (2002). Bacteria were studied by Sabae (1993, 1996), Sabae & Rabeh (2000), Sabae & Ali (2004). Wimpenny & Titterington (1936), Girgis (1959), Bolous (1960), Khalil (1978), Shaaban et al. (1985), Abdel-Malek & Ishak (1980), Abdel-Moniem (1991), Gad (1992), Ahmed (1994), Abdel-Moniem (2001a, b). El-Shabrawy (2001a), Mansour & Sidky (2003), El-Shabrawy & Belmonte (2004), Fathi & Flower (2005) & Mageed (2005) investigated the plankton. Abdel-Malek & Ishak (1980) & Fishar (1993, 2000), El-Shabrawy (2001b), & Flower et al. (2006) studied the benthic fauna. Lake fisheries were addressed by Wimpenny & Faouzi (1935), Faouzi (1936), Wimpenny (1936), El-Zarka (1963), El-Zarka & El-Sedafy (1967), Bolous & Ashour (1973), Boraey (1974), Kirollus (1977), Abdel-Malek (1980, 1982), Ishak et al. (1982), Swielum (1989), Mosaad (1990), Shafik (1991), Yacoub (1994), Gabr (1998) & El-Shabrawy & Fishar (1999).

2.1 The Egyptian Company for Salts and Minerals (EMISAL)

The Egyptian Company for Salts and Minerals (EMISAL) operates on the south coast of the lake. Here, a zone known as Batnat Abu Ksah has been cut off from the lake and divided into a series of evaporation ponds, to concentrate lake water to at least 10 times its original salinity. The main product of the EMISAL is sodium sulphate. The amount of water pumped from the lake to the ponds of plant has increased from about 7.5×10^6 m^3 in 1986 to 20×10^6 m^3 in 1997 (Abd Ellah, 1999).

2.2 Historical Review

The Fayum depression was artificially connected with the Nile under the reign of pharaoh Amenehat I (1980–1970 BC). The digging of the Hawara canal, now Bahr Yousef, was one of the great Nile projects of the ancient Egyptians (Fig. 1). In the flooded valley, Lake Moeris formed, with an area of about 724 km^2 and a mean depth of 80 m (Ball, 1939). The Lahun Embankment, constructed during the reign of Ptolemy I and II (323–246 BC), diverted the annual influx of Nile water. Lake Qarun thereby dropped to 5 m below sea level and the newly exposed land was colonized by Macedonian soldiers (Ball, 1939; Shafei, 1940). The lake continued to shrink during the Roman period (35 BC–AD 385), and declined from −7 m in the second century AD to −17 m or lower in the third century AD (Ball, 1939). Under Mohamed Ali (1805–1848), it dropped to −40 m (Shafei, 1940). The lowest level, −46 m, was recorded in 1932–1933 (Shafei, 1940). While climate was undoubtedly a factor regulating lake volume and water quality in the past, human interventions now determine its hydrology. Since the engineering feats of the ancient Egyptians, hydrologic modifications have continued (see Rivlin, 1961; Shahin, 1985) but after the completion of the Aswan High Dam in the mid-1960s, Nile floods ceased to affect the Fayum. Sediment records confirm these environmental changes. The high levels of the mid-Holocene lake are reflected in freshwater diatom deposits immediately north-east of the modern lake (Aleem, 1958; Przybylowska-Lange, 1976; Zalat, 1991). Diatom analysis of two shallow-water (3–4 m depth) cores indicate that salinity also fluctuated in the past (Müeller-Wilmes, 1988). The vegetational history of the Fayum is not well known, although classical accounts attest to the fertility of the region; 2,000 years ago, Strabo (in Hewison, 2001) listed a variety of fruit and vegetable crops available in the area. Now, much agriculture is given over to cotton, wheat, sugarcane and fodder crops. Earlier pollen analysis of near-shore cores from the east basin revealed a low plant diversity (Mehringer et al., 1979). These pollen diagrams span approximately the last 325 years (dates inferred from exotic pollens and pollen influx calculations) and show a vegetation dominated by ruderals (mainly chenopods). Cereals increase towards the core top, and twentieth century introductions of *Eucalyptus* and *Casuarina* are clearly recorded. Marine dinoflagellate cysts in the core are attributed to a reworking of marine sediments of Eocene age.

2.3 Some Physical Characteristics (Table 1)

The annual average radiation in 1996, ca 148 W m^{-2}, fluctuated from 242 W m^{-2} in summer to 53 W m^{-2} in winter (Anonymous, 1997). Ball (1939) first measured evaporation directly and found an annual average of 177 cm. Gorgy (1959) arrived at an annual average of 185 cm, using the energy budget method. Meshal & Morcos (1981) recorded 190 cm, and Abd Ellah (1999) 174 cm. Relative humidity in the lake area is directly proportional to air pressure and inversely proportional to wind speed. It fluctuates between 40% in May and 59% in December, with annual average 49% (Abd Ellah, 1999). Wind speed is low during winter (2.5 m s^{-1}), and maximum in summer (5.5 m s^{-1}). The dominant direction is north-west; in winter, it changes to north-east.

2.3.1 Water Budget

Meshal and Morcos (1981) calculated the water budget of Lake Qarun from:

$$(I + R + G) - (E + Q) = S \tag{1}$$

Where the terms are the time average of I = inflow of drainage water, R = rainfall, G = seepage, E = evaporation, O = outflow and S = salinity.

Since the lake has no outflow, Eq. 1 reduces to $(I + R + G) - E = S$ (2)

Table 1 Components in (10^6 m^3) of the water budget and factors (10^6 kg) affecting the salt budget of Lake Qarun (Abd Ellah, 1999)

Months 1996	Water inflow	Water loss	Water pumped to EMISAL	Salt gain through drains	Salt extracted by EMISAL
Jan	8.54	9.173	0.313	30.982	11.714
Feb	27.66	17.395	0.387	58.315	14.356
Mar	30.39	20.067	0.904	55.707	32.981
Apr	34.18	31.427	1.192	57.65	43.017
May	20.86	52.372	2.106	44.801	76.448
Jun	17.48	57.756	2.581	45.645	98.082
Jul	15.34	52.9	3.033	38.262	120.41
Aug	19.56	57.744	2.727	53.066	111.262
Sep	37.28	46.943	2.329	58.936	93.168
Oct	39.72	36.651	2.250	74.036	89.775
Nov	43.71	25.038	0.806	66.714	31.53
Dec	43.38	7.869	0.468	106.783	17.784
Total	338.1	415.335	19.096	690.89	740.527

The monthly net gain or loss shows that there is seepage from the lake during July, August and November and seepage to the lake during the rest of the year. The annual gain through seepage is 65 × 10^6 m^3. Water level usually rises in spring and drops in late summer and early autumn. The minimum (–44.1 m) is in September, the maximum (–43.4 m) in May. The lake gains water (338 × 10^6 m^3 y^{-1}) from El-Bats and El-Wadi Drains; losses (415 × 10^6 m^3 y^{-1}) are by evaporation and by pumping to EMISAL (19 × 10^6 m^3 y^{-1}). The water budget is negative during 7 months (January–July), and positive during the rest of the year. The net budget is negative by about 96 × 10^6 m^3 y^{-1} (Table 1).

2.3.2 Salinity and Salt Budget (Table 1)

The agricultural drainage water that reaches the lake has a salinity fluctuating between 1.32–3.46‰ and 1.26–4.14‰. As Lake Qarun is closed, it receives dissolved salts through the drains (690 × 10^6 kg y^{-1}), but looses some of them to the EMISAL plant (740 × 10^6 kg y^{-1}). This budget appears negative but the loss of salt is compensated by seepage from cultivated land around the lake (Abd Ellah, op. cit.).

The salinity of the lake has strongly increased in the course of the twentieth century (Fig. 3). In 1906, it was 10.5 g l^{-1}, but already reached 18 g l^{-1} in 1919–1925 (Coastguards Administration). Naguib (1958) mentioned 17.8–25.5 g l^{-1} in 1953–1955. Salinity increased further, to 30.9‰, 38.7‰ and 42.8‰ in the 1971, 1995 and 1999–2000, respectively (Mashal, 1973; Anonymous, 1997; Ali, 2003). This rapid evolution has important consequences for the biota of the lake which, for obvious reasons, cannot contain endemics. Soliman (1989) predicted a further increase in salinity in the twenty-first century, eventually leading to a biologically "dead waterbody". A (temporary?) decrease to 32.4‰ was, however, recorded in 2003 (Sabae & Ali, 2004).

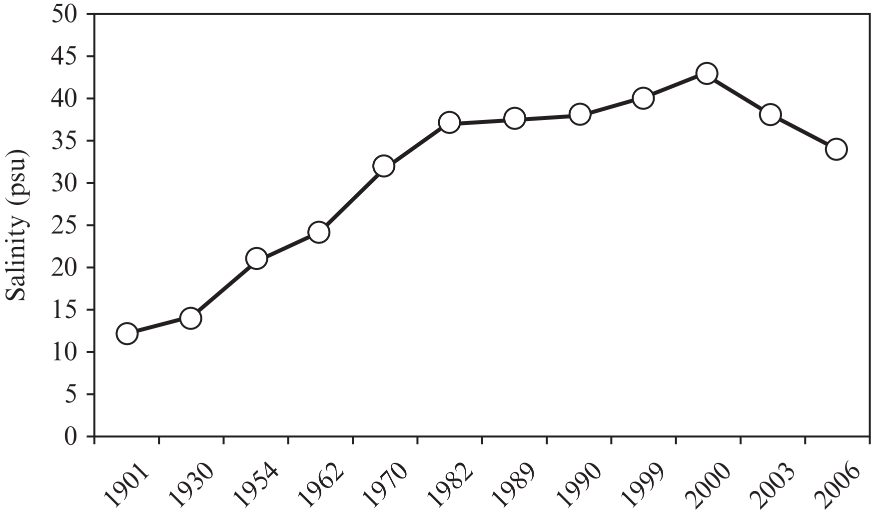

Fig. 3 Average salinity fluctuation in Lake Qarun from 1901 to 2006 (original)

2.3.3 Temperature

Surface water temperature is minimum (15°C) in winter (December and January), while a maximum of 33°C occurs in summer (July and August).

2.3.4 pH and Nutrients (Table 2)

pH fluctuated around 8 during 1974–77, slightly increased in 1994–95 and reached 8.8 in 1999–2000. Table 2 shows some of the nutrient chemistry of the lake. There was an increase in Nitrate and Nitrite from 35 and 0.16 $\mu g\ l^{-1}$ in 1953–1955, to 94 and 14 $\mu g\ l^{-1}$ in 2003. Orthophosphate increased from 0.4 $\mu g\ l^{-1}$ in 1953–1955 to 60 $\mu g\ l^{-1}$ in 2003.

2.4 Bacterial Indices of Sewage Pollution

The distribution of coliform Bacteria shows that the eastern region is more polluted than the west. The highest bacterial counts occur in the drains (Sabae, 1993; Sabae & Rabeh, 2000).

2.5 Phytoplankton

Bacillariophyceae, Dinophyceae, Cyanophyceae, Chlorophyceae, Euglenophyceae and Cryptophyceae occur. Phytoplankton seasonality varies between years. In 1989,

Table 2 Physical and chemical Features of Lake Qarun in different periods

Variables		1953–1955	1995	1999–2000	2003
Water temperature	°C	25.15 (16.4–32)	24.9 (17.7–31)	23.26 (14.4–32.6)	22.9 (13.2–31.4)
Secchi-depth	Cm	*	54 (44.3–94)	59.86 (25–110)	55 (35–80)
Salinity	‰	21.94 (17.9–25.4)	38.7 (36.5–42.7)	42.86 (38.38–49.07)	32.4 (29.7–37.2)
Dissolved Oxygen	mg l^{-1}	*	6.89 (4.25–11.1)	7.99 (4.8–12)	7.9 (4–14)
Chemical Oxygen Demand	mg l^{-1}	*	14.9 (6.2–21.1)	28.1 (13–43.2)	20.9 (12.8–24.58)
Biological Oxygen Demand	mg l^{-1}	*	4.7 (1.9–10.43)	6.9 (1.47–11.4)	5.9 (2.7–13.9)
pH		8.12 (7.98–8.25)	8.4 (8–8.71)	8.2 (7.3–8.8)	8.4 (7.7–8.9)
Carbonate	mg l^{-1}	34.89 (22.4–60.5)	89.6 (65.7–118.7)	65.38 (6.6–125.4)	27.8 (5–75)
Bicarbonate	mg l^{-1}	164.36 (142.3–186.8)	191.2 (129.4–284)	330.2 (198.8–391.6)	190.84 (100–268)
Sodium	mg l^{-1}	*	3880	9880 (8130–13700)	9064 (7357–10511)
Potassium	mg l^{-1}	*	440	460 (381–606)	363 (280–486)
Calcium	mg l^{-1}	*	2331 (1619–3669)	595.9 (432–810)	611 (360–882)
Magnesium	mg l^{-1}	*	5505 (4718–5983)	1589 (1211–1982)	1886 (1348–2340)
Nitrite	µg l^{-1}	0.16 (0.04–0.31)	4.46 (2.61–13.2)	8.15 (1.1–43.1)	13.7 (1.2–51.8)
Nitrate	µg l^{-1}	34.84 (36.83–55.92)	61.2 (27.4–222.7)	66.1 (20.2–664.5)	93.9 (59–776)
Ammonia	mg l^{-1}	*	0 .05 (0.02–0.25)	0.36 (0.08–1.1)	0.15 (0.03–0.68)
Total nitrogen	mg l^{-1}	*	7.5 (2.38–14.28)	*	*
Orthophosphate	µg l^{-1}	0.38 (0–0.8)	25.6 (12.3–63.6)	55.23 (37.8–83.5)	59.5 (21–152)
Total phosphorus	µg l^{-1}	*	120 (84.1–25)	181.9 (122.4–291.5)	367.7 (175–775)
Silica	mg l^{-1}	*	6.7 (3.35–10.7)		6.16 (1.3–11.8)

* Not available.

1953–1955 after Nagiub (1958); 1995 after Anonymous (1997); 1999–2000 after Ali (2002); 2003 after Sabae and Ali (2004).

algae peaked in summer (1,100 × 10^3 cells l^{-1}), dropping to a minimum in spring (200 × 10^3 cells l^{-1}) (Abdel-Moniem, 1991). During 1993–1996, peaks were in spring (1994 and 1996) and in summer (1993–1995) (Anonymous, 1997). Diatoms were dominant, followed by dinoflagellates and blue–green algae. A major peak in August 2001 was attributed to the genus *Cyclotella* (Fathy & Flower, 2005). The species in Lake Qarun are partly freshwater and partly of saline and brackish-water. Although the lake is now strongly saline, many species are still of freshwater (e.g. blue-greens, *Scenedesmus, Ankistrodesmus*). Some enter the lake with drainage water (e.g. *Aulacoseira granulata*) (Abdel-Moniem, 2001), some indicate brackish conditions (e.g. *Cyclotella caspia*), and some are marine (El-Wakeel & Dowidar, 1969), introduced with mullet fry. The diversity dropped from 119 and 101 species in 1989 and 1996 (Abdel-Moniem, 1991; Anonymous, 1997) to 50 and 49 species in 1999 and 2001 (Fathy & Flower, 2005; Abdel-Moniem, 2001b).

Abdel-Moniem (2001a) measured ^{14}C uptake in relation with physical and chemical variates. Primary productivity was highest during the hot period and the eastern part of the lake was more productive than the western one.

2.6 Zooplankton (Table 3)

In 1931, Wimpenney & Titterington (1936) recorded a brackish-water assemblage, dominated by *Arctodiaptomus salinus* (Copepoda) and *Moina salina* (Cladocera). The later increase in salinity eradicated these species. Grigis (1959) and Naguib (1961) noticed their demise, the marine neritic copepod *Paracartia latisetosa* replacing them. El-Maghraby and Dowidar (1969), Khalil (1978), Abdel Malek and Ishak (1980) and Ahmed (1994) observed how after 1928 the lake gradually became monopolized by marine zooplankters, imported with marine fish fry. The standing crop reached an annual average of 30,000 ind m^{-3} in 1974–1977 with Copepoda dominant, followed by meroplankton larvae and by Rotifera. It increased to 1,600 × 10^4 ind m^{-3} in 1989, mainly due to Protozoa but Rotifera and Copepoda also increased, to 247,000 and 109,000 ind m^{-3}. Winter was the peak period; lowest density occurred in summer (1989). The standing crop of total zooplankton decreased in 1994–1995 (average 356,000 ind m^{-3}) with Rotifera now contributing more than 70% to the total and summer the most productive season. Seven species were identified, but the saline-water *Brachionus* cf. *rotundiformis* monopolized the community (more than 90% of the total, up to half a million individuals per cubic meter). *Synchaeta* spp. were second in rank, with 6–8% of the stock (El-Shabrawy, 2001a). *Paracartia latisetosa* was the only calanoid and the dominant species of the mesozooplankton. Other copepods were *Canuella* sp. (a harpacticoid), and *Apocyclops panamensis* (a cyclopoid). Copepod nauplii were the most abundant items, contributing up to 80% of total Copepoda (El-Shabrawy & Belmonte, 2004).

In spite of the rising salinity, zooplankton species richness increased from 20 species in 1974–1977 to ca 30 in 1999–2000 and 2003 (Table 3). El-Shabrawy & Taha (1999) found that zooplankton grazing regulated phytoplankton biomass in

Table 3 List of Zooplankton species recorded from Lake Qarun

Species	1974/1977	1989	1994/1995	1999/2000	2003
Protista					
Xystonellopsis sp.	–	–	–	*	–
Tintinnopsis strigosa Meunier	*	*	*	*	*
Tintinnopsis amphora Kofoid & Camp.	*	*	*	*	–
Tintinnopsis campanula Ehr.	*	*	–	–	–
Tintinnopsis cylindrica (Daday)	*	*	*	–	–
Tintinnopsis lobiancoi (Daday)	*	*	–	–	–
Favella azorica Cleve	–	*	*	*	*
Favella ehrenbergi Clap & Lach.	*	*	*	*	*
Favella helgolandica (Brandt)	–	*	*	*	–
Favella panamensis Kof. & Camp.	–	–	*	*	*
Favella infundibulum Kof. & Camp.	–	*	*	–	–
Helicostamella subulata Ehr.	–	*	*	*	*
Leprotintinnicus botincus Nord.	–	*	*	*	*
Globigerina inflata d'Orbigny	*	*	*	*	*
Textularia sp.	*	*	*	*	*
Unidentified ciliophore	–	*	*	*	*
Euplotes vannus Müller	–	–	–	*	*
Rotifera					
Brachionus plicatilis Müller	*	*	–	–	–
Brachionus cf. *rotundiformis* Tschugunoff	–	–	*	*	–
Synchaeta sp.	*	*	*	*	*
Synchaeta cf *kitina*	–	*	*	*	*
Colurella adriatica Hauer	–	*	*	*	*
Notholca salina Focke	–	*	*	*	*
Lecane closterocerca (Schmarda)	*	*	*	*	*
Lecane bulla Gosse	–	*	*	*	*
Keratella tropica Apstein	*	*	*	–	*
Copepoda					
Nauplius larvae	*	*	*	*	*
Calanoid copepodids	*	*	*	*	*
Cyclopoid copepodids	*	*	*	*	*
Paracartia latisetosa Kiritchag.	*	*	*	*	*
Apocyclops panamensis (Marsh)	–		*	*	*
Mesochra heldti Monard	*	*	–	–	*
Canuella sp.		–	*	*	–
Meroplankton					
Cirriped larvae	*	*	*	*	*
Polychaete larvae	*	*	*	*	*
Mollusc larvae	*	*	*	*	*

1974–1977 after Abdel Malek and Ishak (1980); 1989 after Ahmed (1994); 1994–1995 and 1999–2000 after El-Shabrawy (2001a) and 2003 after Mageed (2005).

summer, when *Brachionus* cf *rotundiformis* was predominant, but not in winter and spring, when nauplii (Copepoda) and *Tintinnopsis* spp. (Protozoa) were abundant.

2.7 Benthos (Table 4)

The benthos transforms organic sediment to biomass and contributes to the nutrition of fish. According to Naguib (1961), three molluscan species (*Cardium* sp., *Mactra* sp. and *Pirenella* sp.) originally dominated the bottom fauna, but later, Fishar (1993) found Crustacea had become the dominant group. Specific macrobenthic species were studied by Khalil, 1978; El-Gaid, 1980; Hussien and Salem, 1981; Holdish and Tolba, 1983 and Tolba and Hijji, 1994. Regarding long-term changes in macrobenthos community structure, Abdel Malek & Ishak (1980) recorded 12 macrobenthic species in 1974–1975. Mollusca were the major component (93%) of biomass, *Cerastoderma glaucum* alone contributing ca 70%. Around 1989, a collapse occurred, with depletion in standing crop and biomass, from 425 g dry wt m^{-2} to 80 g fresh wt m^{-2}. The sea anemone *Apitasiogeton pellucidus* first appeared, at a density of 95 ind m^{-2} and Arthropoda and Annelida were represented by 6 and 2 species, respectively. The benthos had a density of 13,400 ind m^{-2}, weighed 104 g fresh wt m^{-2} in 1994–1995 but sharply decreased to 7,300 m^{-2}, weighing 84 g fresh wt m^{-2} in 1999–2000 (Table 4). *Polydora hoplura*, *Ficopomatus enigmaticus* (Polychaeta), and *Bulla ampulla* (Mollusca) were newly recorded. The macrobenthos continued to show a decrease in standing crop (6,000 ind m^{-2}), and only 40 g fresh wt m^{-2} in 2006 (El-Shabrawy & Kalifa 2007).

2.8 Status of the Fishery

Since the lake was originally of freshwater, its fisheries were Nilotic. In the first decades of twentieth century it was famous for the large quantities of *Lates niloticus* and *Oreochromis niloticus* produced (Faouzi, 1936). The salinity increase that followed gradually eliminated all species except *Tilapia* and *Anguilla*. Faouzi (1938) mentioned that *Tilapia zillii* was the only species that had not suffered, while El-Zarka (1961) stated that *Tilapia nilotica* could still be found in small numbers in the 1950s.

Because of this disappearance of its original fish fauna, the commercial catch dropped from 4,000 t in 1920 to 1–2,000 t in subsequent years, affecting the livelihood of the fishing community around the lake. Accordingly, the necessity arose to stock the lake with species tolerant of high salinity. Fish and crustaceans of marine origin i.e. Mullet (*Mugil cephalus*, *Liza ramada, L. saliens, L. aurata*), *Atherina mochon*, *Anguilla vulgaris*, *Solea aegyptiaca* and prawn were chosen. Some of the introduced species such as *L. saliens*, *S. aegyptiaca* and prawn succeeded in spawning, but others (*M. cephalus, L. ramada* and *L. aurata*) were unable to do so

Table 4 Macrobenthos abundance (ind m^{-2}) and biomass (g fresh wt m^{-2}) in Birket Qarun

	1974–1977		1989		1993		1994		1995		1999–2000		2006	
Years	**no#**	**wt**	**no**	**wt**	**no**	**wt**	**no**	**wt**	**no**	**wt**	**no**	**wt**	**no**	**wt**
Coelenterata														
Apitasiogeton pellucidus Holl.			93	1.02	356	2.22	388	2.44	229	1.68	159	1.6	100	1.23
Obelia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subtotal			**93**	**1.02**	**356**	**2.22**	**388**	**2.44**	**229**	**1.68**	**159**	**1.6**	**100**	**1.23**
Arthropoda														
Corophium sp.		0	952	1.43	982	0.86	956	0.75	944	0.67	279	0.07	182	0.29
Cyprideis torosa Jones		19.65	0	0	67	0.03	13,200	1.67	9,087	1.19	6,192	0.82	5,382	0.63
Balanus pallidus Darwin		0	213	24.2	120	24.02	206	31.97	208	44.11	17	6.62	34	3.15
Brachynotus sexdentatus Risso		0	1	2.65	2	0.61	2	2.1	7	2.01	21	14.44	2	0.53
Sphaeroma pulchellum (Colosi)		0	*	*	0	0	0	0	0	0	0	0	0	0
Sphaeroma serratum Fabricius		0	3	0.03	27	0.19	6	0.32	12	0.16	3	0.32	12	0.46
Orchestia platensis Kroyer		*	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus aequicauda Mart.		2.82	2	0.02	5	0.02	3	0.01	5	0.02	2	0.05	5	0.03
Chironomid larvae			0	0	9	0.19	0	0	1	0	4	0.02	13	0.14
Subtotal		**22.47**	**1171**	**28.33**	**1,212**	**25.92**	**14,373**	**36.82**	**10,264**	**48.16**	**6,518**	**22.34**	**5,629**	**5.2**
Annelida														
Nereis succinea (Frey & Leuck.)		4.25	202	8.69	216	11.98	185	8.22	121	4.07	37	4.03	88	1.62
Polydora ligni Webster		0	114	0.63	165	0.18	181	0.26	339	0.44	0	0	0	0
Polydora hoplura Clapar.		0	0	0	0	0	0	0	0	0	237	0.59	108	0.13
Ficopomatus enigmaticus Fauv.		0	0	0	0	0	0	0	0	0	136	2.65	61	0.99
Tubificidae		0	0	0	0	0	53	0.03	110	0.19	76	0.5	38	0.03
Subtotal		**4.25**	**316**	**9.32**	**381**	**12.16**	**419**	**8.51**	**570**	**4.7**	**486**	**7.77**	**296**	**2.76**
Mollusca														
Cerastoderma glaucum Poiret		288.5	41	24.86	42	34.22	36	15.96	62	47.07	31	26.24	77	16.95
Venerupsis aurea Gmelin		33	49	14.96	6	1.37	12	7.28	51	31.22	29	23.13	53	11.6
Pirenilla conica Blainville		43.25	3	0.09	1	0.11	3	0.5	12	2.45	8	1.19	7	0.42

Nassarius sp			0	3	2.44	1	0.68	0	0	0	0	0	0	5	0.39
Semisalsa sp			21.63	0	0	0	0	298	1.07	112	0.34	49	0.24	15	0.05
Bula ampula Linnaeus			0	0	0	0	0	0	0	0	0	2	1.35	18	2.24
Melanoides tuberculata Müller			*	0	0	0	0	0	0	0	0	0	0	0	0
Physa acuta Draparnaud			*	0	0	0	0	0	0	0	0	0	0	0	0
Cleopatra bulimoides Olivier			*	0	0	0	0	0	0	0	0	0	0	0	0
	Subtotal		**386.38**	**96**	**42.35**	**50**	**36.38**	**349**	**24.81**	**237**	**81.08**	**119**	**52.15**	**175**	**31.64**
	Total	**1989**	**413.1**	**1,676**	**81.02**	**1,999**	**76.68**	**15,529**	**72.58**	**11300**	**135.62**	**7,282**	**83.86**	**6,199**	**40.83**

#: recorded as total only. *: recorded qualitatively. 1974–1977, after (Abdel Malek & Ishak, 1980); 1993, after (Fishar, 1993); 1993 after (Anonymous, 1997); 1994–1995–1999–2000 (El-Shabrawy, 2001b) and 2006 (El-Shabrawy unpublished).

and have been continuously transplanted since 1928. About two million fry were annually released during 1928–1964 (El-Zarka & Kamel, 1965). These numbers reached 55 million between 1971 and 1978 and more than 100 million fry in recent years (Anonymous, 1997). Mullet first appeared in the commercial catch in 1929 and 1930; after 1934, they started to play a major part in the fisheries. During 1961/1962, when mullet landings were first compiled separately for the different species, it was found that *M. saliens* constituted about 13% of total production, and *M. capito* and *M. cephalus* 5% (El-Zarka, 1963b). To date, the issue of mullet spawning in the lake has remained disputed.

Soles were first introduced in 1938, and again in 1943, 1945 and 1948. A total of 1,603 specimens ranging in length from 7 to 10 cm, collected from the Maadia district of the Mediterranean Sea, were released to the lake. The first record of soles, 38 kg, in the commercial catch was in 1938. In 1943, sole catch rose to 1.5 t and soles successfully spawned in the lake (El-Zarka, 1963a). During subsequent years, the increase of the annual catch was partly due to in-lake production but also to improved skills of fishermen in catching them. From 1961 to 1966, sole fisheries constituted about 33% of total yield (El-Zarka, 1968). During the 1970s, and until 1978, their production ranked at the top, contributing half of lake fisheries (Bishai & Kirollus, 1989).

From 1977 to 1979, about two million sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*) fry, and about three million shrimp seed were released to the lake. Shrimp taxa included *Panaeus japonicus*, *P. semisulcatus*, *P. latisulcatus*, *Metapenaeus stebbingi* and *Metapenaeopsis philipii*. In subsequent years, they successfully acclimated to the lake. In 1987/1988, shrimp production reached ca 500 t, 45% of total lake yield. Unfortunately, shrimp fishing had a destructive effect on fish stocks because shrimp nets catch also fish fry and fingerlings.

Fishing in Lake Qarun involves 550 wooden boats and about 4,000 fishermen. Fish is landed in 11 sites along the southern coast. Fishing is closed in June and July each year, as a regulatory measure to maintain tilapias. The main fishing gear used is trammel gill nets. Their height and construction depends upon the target species. Beach seines are used for catching shrimp. The net is 5.4 m in depth and about 25 m long. Traps and hooks are used for catching *Tilapia zillii*.

2.9 Fish Landings

Total annual fish catch is shown in Fig. 4. There was a drop from ca 2,000 t in 1970–1972 to 600 t in 1993–1998. Sole contributed half of the total during 1970–1973, with annual yield ca 1,000 t. This decreased to a minimum of 11.4 t in 1989/1990. The contribution of tilapias evolved from 20% in 1970–1973 to a maximum of 73% in 1980–1981. Their annual catch represented ca 50% of the total in 1994–1998, with yield around 300 t. Mullet dropped from 580 t in 1970–1972 to 157 t in 1997–1998. The maximal catch of prawn was in 1982–1983 and 1988–1989 with 334 and 326 t, respectively. In recent years, only 3 and 23 t were caught

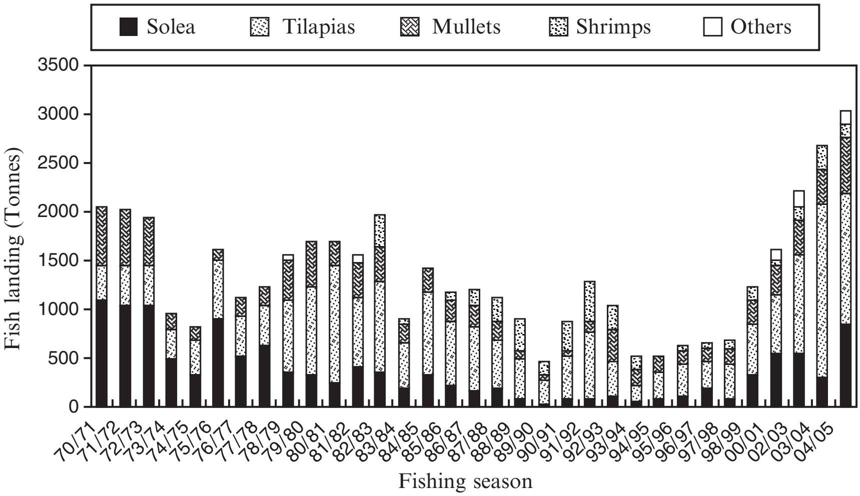

Fig. 4 Evolution of fish landings and percentage composition of the commercial catches in Lake Qarun (original)

during 1994/1995 and 1996/1997, respectively. To compensate this severe drop in lake fisheries, marine fish should be introduced that exploit benthic fauna such as *Balanus*, sea anemones, crabs and mollusks. In the long run, as salinity reaches 60‰, *Artemia salina* will take over, and its cysts may become harvestable.

Fishing in Lake Qarun contributes only 1% to inland fisheries of Egypt, but it is the most important source of fish (65%) in Fayum province. Besides, its luxury fishes (mullet, sea bream and sea bass) are sought-after dishes in the surrounding resorts. Thus, the community around the lake is depending strongly on its fisheries.

3 Wadi El Rayan

Wadi El Rayan (703 km^2, 28° 15′–29° 17′ N) is an uninhabited depression in Egypt's Western Desert, situated southwest of Cairo, at 60 m below sea level. Unlike most desert regions, it has a high biological diversity. The major habitat-types in the depression are sabkhas, sand flats, sand dunes, wetlands (man-made lakes), springs (three natural El Rayan springs, located below Minqar El Rayan at a site known as Oyun El Rayan or spring area, with water believed to flow from Nubian sandstone strata) (Serag et al., 2003).

3.1 Wadi El Rayan Lakes

Wadi El Rayan holds two lakes, connected by a channel (Fig. 1). The upper lake has an area of 50.9 km^2 and the lower of 62.0 km^2. They lie between 30° 20′–30°

25′ E and 29° 05′–29° 20′ N. The connecting area holds permanent shallow water with emergent aquatic macrophytes, forming a swamp. The upper lake is surrounded by dense vegetation and has a maximum depth of 25 m (Saleh, 1984). The lower lake is changing all the time, newly flooded areas continuously being added in the southwest. Its maximum depth is 33 m. The Wadi El Rayan lakes receive water through the El-Wadi Drain, with discharges 11 × 10^6 m^3 in January and 24 ×10^6 m^3 in November, totaling 220 ×10^6 m^3 y^{-1} (Abd Ellah, 1999). Inflow to the second lake varies from 3.6 × 10^6 m^3 in July to 17 × 10^6 m^3 in March, with a total of 127 × 10^6 m^3 y^{-1}. The lakes vary in physical and chemical characters. The upper one is less saline (1.4–1.5 g l^{-1}) than the second (4.5–6.1 g l^{-1}) and its salinity increases from north to south. Nutrients are higher in the upper than in the lower lake (Aboul-ela & Khalil, 1988; Saleh et al., 1988; Anonymous, 1998; Konsowa & Abd Ellah, 2002a, b). The formation and evolution of the lakes since 1973 is illustrated in Fig. 5.

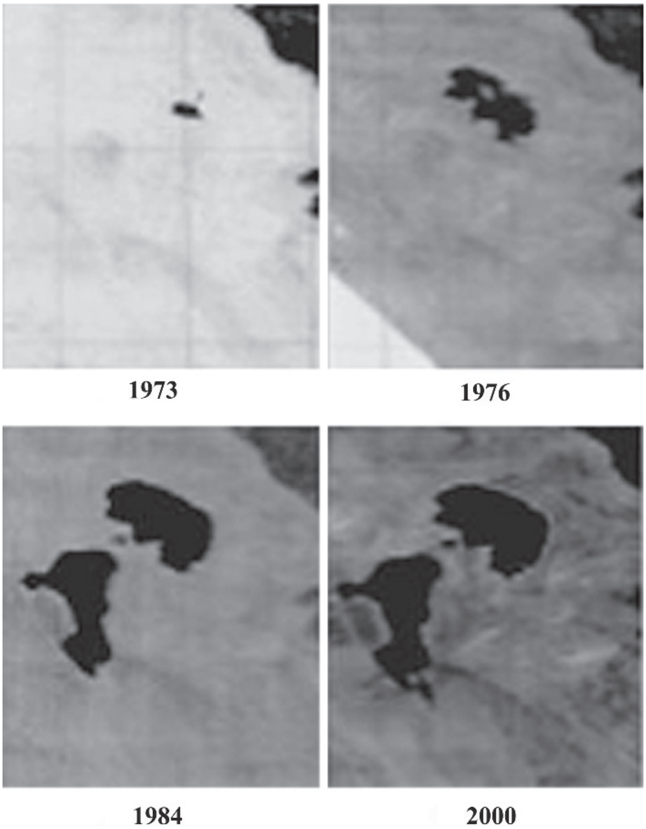

Fig. 5 Progressive formation of Wadi El Rayan lakes (from IUCN, 2001, with permission of Biodiversity Unit, EEAA, Egypt)

3.2 Climate

The climate of Wadi El Rayan is typically Saharan, hot and dry with scanty winter rain and abundant sunshine throughout the year (Smith, 1984).

Absolute maximum and minimum air temperatures, 48.5°C and 1.2°C, were recorded in June and January, respectively. The mean amplitude of diurnal fluctuations is 14.2°C in winter and 17°C in summer. Mean water temperature is minimum (16.5°C) in winter and maximum (31.1°C) in summer.

The minimum evaporation rate (3.18 cm month^{-1}) was measured in autumn, the maximum (25.67 cm month^{-1}) in summer (Maiyza et al., 1999). Overall, the aridity index (P/E + P), where P is annual rainfall (Precipitation) and E is annual evaporation, lies between 0.03 and 0.02 mm, characteristic of a hyper-arid region.

The incident light showed a visible maximum during spring (649 W m^{-2}) began to decrease gradually until reached a minimum value of 241 watt m^{-2} at the end of autumn.

Light winds blow most of the year from the North (north-west to north-east). Wind speed maxima and minima of 5.3 and 2.5 m s^{-1} occur in summer and winter.

Relative humidity is directly proportional with air pressure and inversely proportional with wind speed at Wadi El Rayan. It varies from 37% and 58% in June and November.

3.3 Water Budget of the Lakes

Between the beginning of the water storage project and the present, there have been no systematic measurements of the fluctuation of the water level in the lakes or of their volume and surface area. Therefore the assumption of a constancy of the water volumes (570×10^6 m^3 for the upper lake; 615×10^6 m^3 for the lower lake: Abd Ellah, 1999) is not based on actual values. Recently, millions of cubic meters of waters were forced from the southern basin of the upper lake to reclaim huge areas southwest of the lower lake. This land reclamation resulted in a reduction in volume and surface area, especially of the lower lake. The total inflow of El-Wadi drain to the upper lake is 220×10^6 m^3 y^{-1}, while annual discharge to the second lake is 127×10^6 m^3 y^{-1}. The net water budget for the upper lake used to have a positive value of 13×10^6 m^3 y^{-1}, for the lower lake 39×10^6 m^3 y^{-1}. These values recently became negative.

3.4 Salinity

The salinity of the upper lake (less than 2 psu) increases southward, due to the diluting effect of drainage water in the north (Abd Ellah, 1999). The continuous inflow of brackish water (gain of salt) from El-Wadi Drain and outflow through the connecting channel (loss of salt) keeps salinity constant or at least slows down salinisation (Table 5). Salinity is obviously higher in the lower than in the upper

Table 5 Physical and chemical characteristics of Wadi el-Rayan lakes at different times

	1989		1996		2001		2003
	Upper lake	Lower lake	Upper lake	Lower lake	Upper lake	Lower lake	Upper lake
Water temperature °C	14.9: 31.5	13: 30.5	12.4: 29.1	12.7: 28.7	14: 31	13.4: 31.6	14.6: 31.4
Secchi-depth cm	80: 220	130: 210	150: 190	230: 400	40: 220	200: 500	80: 200
Salinity ‰	0.7: 2.9	2.1: 3.1	08: 02.8	3.7: 5.1	1.1: 1.6	3.4: 6.2	1.1: 1.7
Dissolved Oxygen mg l^{-1}	7.46: 10.3	7.2: 9.13	9.1: 12.4	8.3: 11.1	*	*	7.7: 14.2
Chemical Oxygen Demand mg l^{-1}	1.5: 7.7	1.6: 5.5	*	*	*	*	12.3: 17.6
Biological Oxygen Demand mg l^{-1}	*	*	*	*	*	*	1.6: 5.8
pH	7.4: 9.8	8.2: 9.3	8.1: 8.5	8.2: 8.4	*	*	7.9: 8.9
Carbonate mg l^{-1}	20: 50.3	26.4: 35.5	37.3: 47.8	43.8: 60.5	15: 47	29.7: 52.9	7.6: 12.1
Bicarbonate mg l^{-1}	110: 208	127: 150	159: 176	163: 174	176: 240	145: 169	168: 240
Sodium mg l^{-1}	*	*	*	*	225: 417	1314: 1641	122: 386
Potassium mg l^{-1}	*	*	*	*	*	*	2.9: 15
Calcium mg l^{-1}	*	*	*	*	*	*	40: 68
Magnesium mg l^{-1}	*	*	*	*	*	*	51: 117
Nitrite µg l^{-1}	0.0: 101	0.0: 31	1.1: 11.7	0.6: 1.2	14: 48	2.8:26	3.7: 80
Nitrate µg l^{-1}	24: 418	29: 268	26.7: 124.9	30.1: 42.9	138: 420	193: 386	28.3: 750
Ammonia µg l^{-1}	53: 1378	50: 78	35.3: 140	34.5: 94.9	32: 219	21.7: 112.3	117: 645
Orthophosphate µg l^{-1}	16.2: 130	4.1: 87.2	1.8: 30.6	5.2: 18.6	4.2: 35.3	8.4: 30.6	22.1: 200
Total phosphorus µg l^{-1}	*	*	*	*	*	*	126: 440
Silica mg l^{-1}	8.4: 29.6	7.9: 21.8	*	*	*	*	1.4: 10.5

*Not available.

1989: after Konsowa (1991); 1996: after Taha and Abdel-Moniem (1999); 2001 after Konsowa and Abd Ellah (2003a, b) and 2003 after Soliman (2006).

lake. Since they are closed basins, salinity undergoes an increase in space and time toward the south, reaching more than 10 psu in the lower lake in 2006. The rate of increase reflects discharge from the upper lake, and evaporation. Because discharge has decreased during recent years, the rise of salinity has become faster.

3.5 Transparency

Transparency is always lower in the upper than the lower lake. The vegetation in the connecting channel reduces the suspended material and consequently increases transparency in the lower lake.

3.6 Chemistry

Bicarbonate exceeds carbonate (Table 6), and Sodium is higher than Potassium but all gradually increase southwards in both lakes. The lakes can be classified as hard water (total alkalinity > 250 mg l^{-1}) and is highly productive (Konsowa & Abd Ellah, 2002a). Nutrient concentrations are considerably higher in the upper than in the lower lake.

The springs are below detectable limits for heavy metals and arsenic (Table 6) but are higher in Calcium and Magnesium than the lakes. Nickel, Arsenic, Zinc, Chromium, Barium, Manganese, and Iron were detected in all samples from the lakes; Selenium, Cadmium, and Molybdenum only in few. Generally, concentrations increased from the drain to the southern part of the upper lake and in the lower lake. Relatively high concentrations of chloride and bromide occur in spring water. They also increase from the upper to the lower lake, due to evaporative concentration. The amounts of phosphate and nitrate, 1.3 and 6.9 mg l^{-1}, are surprisingly low, compared to a maximum of 987 mg l^{-1} for sulphate (Saleh et al., 2000).

3.7 Phytoplankton

Konsowa (1996) found 96 taxa of phytoplankton. Cyanobacteria, represented by 21 species, were dominant. They showed a gradual decrease in density southwards in the lower lake. Konsowa and Abd Ellah (2003a) mentioned four classes, Cyanobacteria (16 species), Chlorophyceae (25 species), Bacillariophyceae (21 species) and Dinophyceae (3 species) in the upper lake. Cyanobacteria abound (70%), with the colonial *Microcystis aeruginosa* and *Microcystis flos-aquae* or the filamentous *Planktolyngbya limnetica* dominant. The colonial form blooms in mid-winter (January); the filamentous type in August. *Oocystis parva*, *Scenedesmus quadricauda* are the abundant Chlorophyceae, while *Cyclotella glomerata*, *Cyclotella*

Table 6 Concentration of Elements and Inorganic Anions in Wadi el-Rayan Lakes and Springs

Location		El-Wadi Drain	Upper Lake	Lower Lake	First spring	Second spring	Third spring
Cobalt	mg l^{-1}	1.24 ± 0.02	1.27 ± 0.03	1.25 ± 0.02	nd	nd	nd
Lead	µg l^{-1}	12 ± 0.05	6.2 ± 0.01	4.2 ± 0.02	nd	nd	nd
Sulfur	mg l^{-1}	75.0 ± 3	143 ± 9	412 ± 29	183 ± 6	163 ± 4	126 ± 2
Chromium	µg l^{-1}	122 ± 1	123 ± 1	90 ± 3	nd	nd	nd
Selenium	µg l^{-1}	62 ± 1	80 ± 2	72 ± 3	nd	nd	nd
Cadmium	µg l^{-1}	nd	nd	61 ± 2	nd	nd	nd
Arsenic	µg l^{-1}	144 ± 6	164 ± 4	23 ± 1	nd	nd	nd
Molybdenum	µg l^{-1}	nd	nd	12 ± 0.2	nd	nd	nd
Sodium	mg l^{-1}	210 ± 3.5	420 ± 8.9	1410 ± 89	1060 ± 29	1240 ± 88	920 ± 23
Potassium	mg l^{-1}	1.3 ± 0.1	9.9 ± 0.1	48.9 ± 5.3	21.7 ± 3.2	29.2 ± 3.8	19.1 ± 1.3
Calcium	mg l^{-1}	53.8 ± 1.5	46.9 ± 0.9	96.2 ± 3.1	136 ± 8.2	158 ± 9.2	119 ± 2.3
Zinc	mg l^{-1}	6.9 ± 0.2	12.6 ± 0.4	29.2 ± 1.3	26.5 ± 1.1	27.2 ± 0.8	21.5 ± 0.6
Barium	µg l^{-1}	nd	nd	122 ± 0.05	22 ± 0.02	41 ± 0.03	54 ± 0.02
Magnesium	mg l^{-1}	99.0 ± 2.2	56.4 ± 2.3	153 ± 12	139 ± 19	124 ± 22	103 ± 16
Iron	mg l^{-1}	1.29 ± 0.1	1.34 ± 0.1	1.31 ± 0.4	1.24 ± 0.3	1.31 ± 0.2	1.30 ± 0.1
Nickel	mg l^{-1}	1.15 ± 0.10	0.41 ± 0.06	0.48 ± 0.5	nd	nd	nd
Chloride	mg l^{-1}	144 ± 3.9	362 ± 5.3	1730 ± 25	1860 ± 41	2120 ± 77	1400 ± 18
Bromide	mg l^{-1}	nd	nd	12.9 ± 2.8	140 ± 27	23.2 ± 6.7	20.5 ± 5.2
Nitrite	mg l^{-1}	6.74 ± 0.94	2.62 ± 0.18	0.82 ± 0.08	0.79 ± 0.07	6.92 ± 1.2	nd
Phosphate	mg l^{-1}	nd	nd	nd	0.65 ± 0.04	1.33 ± 0.08	nd
Sulfate	mg l^{-1}	162 ± 4.9	334 ± 1.1	970 ± 10	425 ± 12	428 ± 15	303 ± 2.5

After Saleh et al. (2000); Konsowa (1991); nd = no data.

meneghiniana and *Nitzschia amphibiana* are the leading diatoms. According to Konsowa and Abd Ellah (2003b) phytoplankton standing crop in the lower lake (avr. 1,450 × 10^4 l^{-1}) is much lower than in the upper lake (ca 8,580 × 10^4 l^{-1}). Cyanophyceae, mainly represented by *Planktolyngbya limnetica*, *Merismopedia tenuissima* and *Gomphosphaeria aponiana* are prevalent (70%), abundant during late spring (May), but disappearing in November. The green algae rank second (26%), dominated by *Planktonema spp., Crucigenia quadrata* and *Oocystis parva* in January-March. Bacillariophyceae constituted 9%, with *Melosira granulata, Nitzchia* spp. and *Cyclotella glomerata* the leader species.

3.8 Primary Productivity

The upper lake is more productive than the lower (588 vs. 391 mg C^{-2} h^{-1}). In the upper lake, a positive relation between temperature and primary productivity (r = .89) has been attributed to the stimulatory effect of temperature on photosynthesis. In the lower lake, a positive relation has been observed between primary productivity and PO_4-P concentration such that nutrient availability seems more important than temperature (Taha & Abdel-Moniem, 1999).

3.9 Zooplankton

A total of 46 zooplankton species have been reported from the upper lake. Autumn is their season of highest abundance, spring of the poorest. Rotifera dominate (60% of total density), mainly with the genera *Keratella* and *Trichocerca*. Six species of Copepoda reach a maximum in autumn. *Thermocyclops neglectus*, *Thermodiaptomus galebi* and *Megacyclops viridis* abound. Among 11 species of Cladocera, *Diaphanosoma mongolianum*, *Bosmina longirostris* and *Daphnia longispina* are common; the others are sporadic (El-Shabrawy, 1993). El-Shabrawy (1996) listed 30 zooplankton species in the lower lake; Rotifera were abundant (65% of total zooplankton). *Hexarthra* and *Brachionus* appear in high density in spring and summer, gradually increasing southward. Copepoda contribute about 25%, but gradually decrease in density southward. *Thermodiaptomus galebi* is abundant; while *Mesocyclops ogunnus*, *Nitokra lacustris* and *Onychocamptus mohamed* are sporadic. *Diaphanosoma mongolianum* monopolizes the cladoceran fraction in spring. Rotifers respond more quickly to environmental changes than crustaceans and are sensitive indicators of changes in water quality (Pejler, 1983). In Wadi EI-Rayan area, temperature, turbidity, water flow and salinity control the rotifer community. Carlin (1943) showed a correlation between the occurrence of various rotifer species and temperature. In Wadi EI-Rayan some species indeed prefer warm water, others do not (El-Shabrawy, 1999). For example, *Brachionus plicatilis* is rare during winter but peaks in summer in the lower lake; *Hexarthra* *oxyuris* blooms in the lower and upper lakes in summer; *Keratella quadrata* and *Brachionus calyciflorus*, finally, become abundant during winter. Chlorosity boosts the abundance of some species and the decline of others. *Brachionus quadridentatus*, *Lecane leontina* and *Keratella cochlearis* were recorded in EI-Wadi drain, at low chlorosity. *Brachionus* cf *plicatilis* and *Hexarthra oxyuris,* in contrast, abound in the tail of the second lake, where chlorosity is high (El-Shabrawy op. cit.). It is worth mentioning that marine species such as *Podon polyphemoides* and polychaete larvae started to appear in the lower lake in 2006, concurrent with a rise in salinity to 12‰.

The average zooplankton in the upper lake is more than four times that of the lower one (106,700 and 22,900 ind m^{-3}, biomass 1,625 and 290 mg m^{-3}). Zooplankton therefore adds 60 and 10 mg C m^{-3} to the organic carbon pool of the upper and lower lakes (Mageed, 2004). The food selectivity of *Oreochromis niloticus, O. aureus* and *Sarotherodon galilaeus* for zooplankton was towards cladocerans. That of *T. zillii* was towards *Keratella quadrata* (SI = + 0.81). The dominant items in the guts of *Mugil cephalus, Liza ramada* and *Lates niloticus* were crustaceans, particularly *Thermodiaptomus galebi* (SI = + 0.73, + 0.89 and + 0.95).

3.10 Macrobenthos

The first survey of Wadi El Rayan macrobenthos was conducted by Khalil (1984). He mentioned 10 species, with *Physa acuta*, *Melanoides tuberculata* and *Gammarus* sp. dominant. Fouda and Saleh (1988) found that the coarse sand bottom of Wadi El Rayan supports a poor fauna in terms of number of species and individuals. Mollusca (six gastropod and two bivalve species) were most abundant. El-Shabrawy (1993) mentioned 14 species, with *Echinogammarus veneris*, *Palaemon elegans*, *Chironomus* larvae, *Melanoides tuberculata*, *Theodoxus niloticus, Semisalsa* sp. and tubificidae abundant. El-Shabrawy (1996) recorded 11 macrobenthic species from the lower lake, while El-Shabrawy (2007) lifted the total to 23 species in three phyla: six species of Arthropoda, eight Annelida and nine Mollusca. The density of macrobenthos was higher in the upper (960 ind m^{-2}, or 26 g fresh wt m^{-2}) than in the lower lake (350 ind m^{-2}, 7 g fresh wt m^{-2}).

3.10.1 Long-Term Changes of the Macrobenthos

The total macrobenthos in the upper lake decreased from 2690 ind m^{-2} in 1989 to 1820 and 960 ind m^{-2} in 1993 and 2006. The lower lake first increased slightly, from 1500 ind m^{-2} in 1989 to 1890 ind m^{-2} in 1993, but a sharp decrease occurred in 2006 (Fig. 6). Arthropoda followed the trend of total macrobenthos. The upper lake annelids dropped from 950 ind m^{-2} in 1989 to 100 ind m^{-2} in 1993; a slight recovery occurred in 2006 (310 ind m^{-2}). Mollusca in the upper and lower lakes

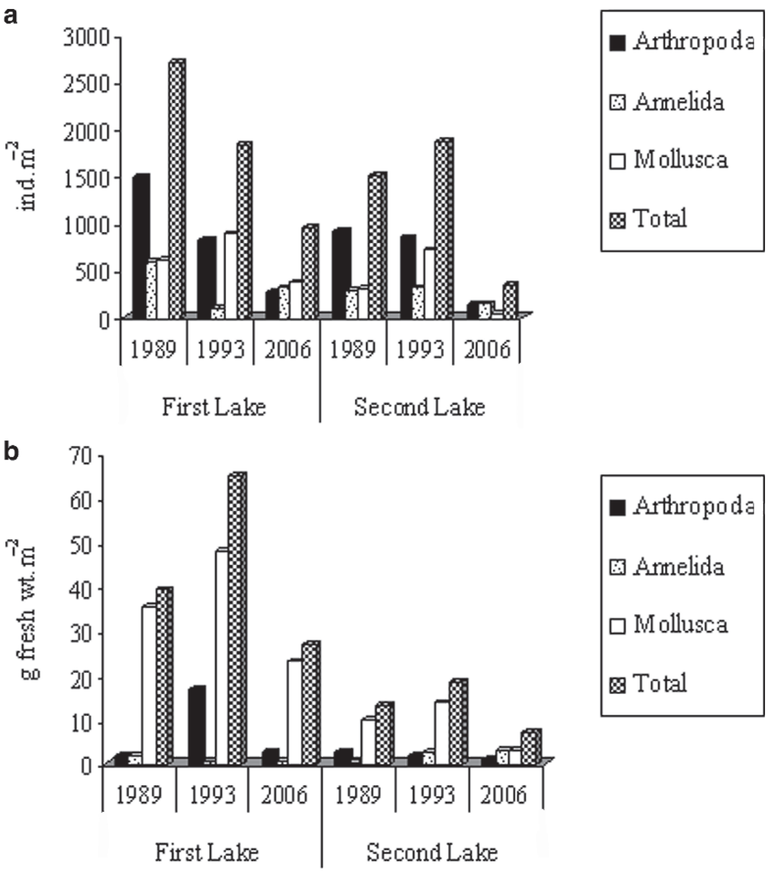

Fig. 6 Changes in macrobenthos community structure in Wadi El Rayan lakes from 1989 to 2006 (original)

increased from 610 and 300 ind m^{-2} in 1989 to 890 and 700 ind m^{-2} in 1993, but collapsed in 2006. Biomass showed a similar trend, except in 1993 when relatively low numbers but with heavy biomass occurred (Fig. 6). Benthic abundance and diversity typically correlate with salinity, dissolved oxygen, depth and sediment type. Seasonal changes are mainly determined by freshwater input (Chainho et al., 2006). An increase in diversity of oceanic species with higher salinity (Lui et al., 2002) and with higher dissolved oxygen have been recorded (Jensen et al., 1985; Dauer et al., 1992; Yap & Nacorda, 1993). In Wadi El Rayan, marine species such as *Hediste diversicolor*, *Nereis succinea* and *Cerastoderma glaucum* populate only the lower lake. The highest standing crop, richness and diversity occur at sites high in oxygen and with plenty of macrophytes (El Shabrawy, in press). Chironomids and *Limnodrilus* spp. are the only macrobenthic species, at deep stations.

3.11 Fisheries in Wadi El Rayan

In the beginning, drainage water carried a freshwater ichthyofauna to the newly formed lake, and some species survived and adapted. They include *Oreochromis niloticus*, *Labeo niloticus*, *Barbus bynni* and *Alestes nurse*. Other species such as *Tilapia zillii*, *Bagrus bayad*, *Bagrus docmak*, *Hydrocyonus forskalii*, *Lates niloticus*, *Schilbe mystus* and *Clarias gariepinus* were present in small numbers (Soliman, 1981). Tilapias, nile perch and *Bagrus spp*. are among the species that became well established. Besides naturally transferred fishes, some euryhaline species (*Mugil cephalus* and *Liza ramada*) were later introduced. Fish fry transplantation started at the beginning of 1978 (Ahmed, 2000).

Fishing activities were first organized in 1980. Between 1976 and 1980, experimental fishing was carried out by fishermen from Lake Qarun. The catch started with 213.5 t in 1976, rising to 295 t in 1979. *Oreochromis niloticus* represented ca 75% of the total (Soliman, 1981). From 1980 to 1982, fishing was managed by a private company. In 1983, the General Authority for Development of Fish Resources (GADFR) took over, with an aim at increasing production. Its policy included fish fry transplantation, limiting fishing season to 7 months, controlling fishing gear, number of boats and fishermen, and establishing a cooperative for each lake.

Fry of *Mugil cephalus* and *Liza ramada* have been introduced to the lake since 1980. The annual number of fry reached 10 millions during 1985. Additionally, 4.5 million of fry of Common carp was introduced in 1984, beside one million of grass carp fry in 1985. Tilapia is represented in the landings by *Oreochromis niloticus*, *Sarotherodon galilaeus*, *Oreochromis aureus* and *Tilapia zillii*. Mullet ranks second to them with about a quarter of the total catch of both lakes combined. *L. ramada* is the most common species now. Nile Perch is worth ca 13% and 5% of the catch of the upper and lower lakes. Carp and Bayad (*Bagrus* spp.) are below 5% (Anonymous, 2003).

The growth of *Oreochromis niloticus* and *Sarotherodon galilaeus* in the upper lake is better than in the lower one; with *Tilapia zillii*, the situation is inverse, while *Oreochromis aureus* and *Liza ramada* grow equally well in both lakes. The exploitation of *Oreochromis niloticus* and *Sarotherodon galilaeus* in the upper lake is higher than in the lower lake. That of *Liza ramada* in the lower lake is higher than in the upper one, and that of *Oreochromis aureus* and *Tilapia zillii* is the same in both lakes. The length at first capture for all species in the upper lake is higher than in the lower lake (Anonymous, op. cit.).

3.11.1 Catch Statistics

Figures 4 and 5 show the annual catch of both lakes by groups of species and the percentage composition of the different groups from 1987/1988 to 2004/2005. Analysis of the catch data shows that the upper lake contributes ca 75%. Catch per unit effort in the upper lake is higher that in the lower lake. The fish stocks in both lakes are overexploited. Application of the Schaefer (1954) model using total catch and fishing effort reveals that the present fishing effort in the upper lake overshoots maximum sustainable yield by 35%. Approximately the same result applies to the lower lake, where fishing effort must be reduced by 26% to achieve sustainable yield.

3.12 Aquaculture

Aquaculture is confined to two large fish farms, covering 10,500 hectares, and 200 fish cages. The first farm of 420 hectares includes 50 concrete ponds (400 m^2 each) and a full complement of feeding ponds, water distribution channels and support infrastructure. Construction work on the second farm started in 1998, and it should enter production soon. In both farms, water is supplied by gravity directly from the waterway between the two lakes, and is returned to it downstream.

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Lake Nasser–Nubia

Gamal M. El-Shabrawy

Abstract The construction of the Aswan High Dam created one of the largest man-made lakes in Africa, extending for 500 km south of the dam. The major portion lies in Egypt (Lake Nasser); the Sudanese part is known as Lake Nubia. Accumulation of water, primarily aimed at generating hydroelectric power and irrigation, started in 1964. The average annual discharge of the Nile is ca 84×10^9 m^3. With its storage capacity of ca 160×10^9 m^3 the reservoir is therefore worth almost 2 years of river discharge. Of this, by an agreement dating to 1959, the annual share of Egypt at a water level of 180 m asl is 55×10^9 m^3, that of Sudan 18×10^9 m^3. More than 70% of the sediment of the River Nile is deposited near Wadi Halfa. Fluctuations of physical and chemical variables, phytoplankton, macro-phytes, zooplankton, macrobenthos and fish are discussed. To fill the hitherto empty pelagic niche and exploit this area of the lake efficiently, the introduction of a pelagic planktivore fish could be considered. A brief overview is provided of the positive and negative consequences of the dam's construction, at a local and at a planetary scale.

1 Introduction

The Aswan High Dam started impounding in 1964 and was officially inaugurated in 1970 (Ahmed, 1999). Its construction resulted in the creation of the longest man-made lake in the world, extending in Egypt for about 300 km as Lake Nasser and for 180 km further south in Sudan as Lake Nubia (Fig. 1). The southern two thirds of Lake Nubia are narrow, due to the presence of a gorge region, about 135 km in length. The remaining part, from Amka to the High Dam, is much wider. The lake is divided into three sections (Latif, 1984): a riverine section, with all-year riverine characteristics, comprised of the southern part of Lake Nubia from the southern

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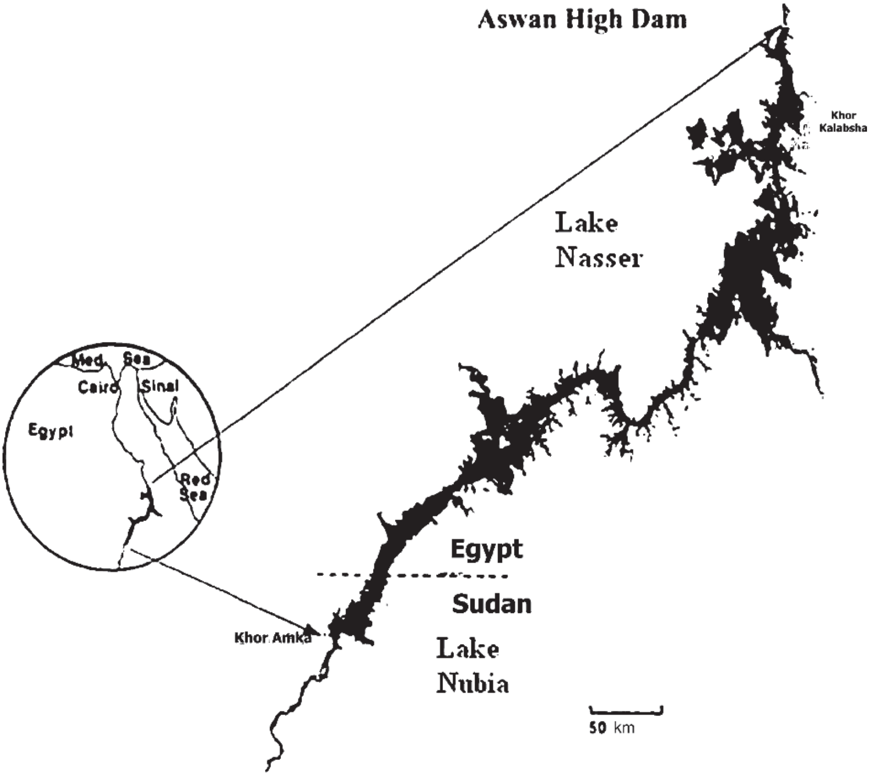

Fig. 1 Map of the High Dam Lake: Lake Nasser–Nubia (after Smith, 1990, with permission from Springer)

end to Daweishat. The semi-riverine section, with riverine characteristics during the flood season and lacustrine conditions during the rest of the year, comprises the north part of Lake Nubia and the south part of Lake Nasser. It extends from Daweishat to Amada/Toshka. The lacustrine section extends from Amada–Toshka to the dam.

2 Lake Morphology (Table 1a)

Lake Nasser (22° 31′–23° 45′ N and 31°30′–33°15′ E) reached its operating level of 175 m asl in 1975, with a total amount of 121×10^9 m^3 of stored water. Of this, 31.6×10^9 m^3 are dead storage (water below the level of the sluices). The deepest zone is situated between 85 and 150 m asl. The central part is a river-lake: the current at the southern end of the Nubian region reaches 100–150 cm s^{-1}. This speed gradually drops to 10–20 cm s^{-1}, and in Lake Nasser it is 0–3 cm s^{-1}. The mean depth of the central part gradually increases from 10 m at the southern end to 70 m in the north.

Table 1a Morphometric features of Lakes Nasser and Nubia at the 160 m and 180 m levels

		Lake Nasser		Lake Nubia	
Parameter		160 m	180 m	160 m	180 m
Length	(km)	292	292	128	190
Shoreline length	(km)	5400	7800	647	1406
Surface area	(km^2)	2585	5238	472	978
Volume	(km^3)	55.6	132.5	10.3	24.4
Mean width	(km)	8.9	18	3.7	5.2
Mean depth	(m)	21	25	20	26
Maximum depth	(m)	110	130	110	130

The bulk of the water masses coming from the south flows through the central part, which holds about half the volume of the lake (Entz, 1976).

Lake Nasser has a number of side extensions known as khors. Their mean length increases from south to north owing to the northwardly declining ancient riverbed (Entz, 1973). All khors have a "U" shape in cross section, with a flat sandy central belt. There are 100 important khors in Lakes Nasser and Nubia combined. Their total length when the lake is full is nearly 3,000 km and their total surface area is 4,900 km^2 (79% of total lake surface). In volume, they contain 86.4 km^3 water (55% of total lake volume). Some khors represent auxiliary, semi-isolated lakes. Khors Allaqi, Kalabsha and Toshka are the largest (for more information about the so-called Toshka lakes, see El-Shabrawy & Dumont, 2009). They have a sandy bottom, while others like Korosko and El-Sadake are steep, relatively narrow and have a rocky bottom (Latif, 1984). The Lake Nubia region (20° 27′–22° 00′ N and 30° 35′–31° 14′ E) is situated in the contact zone of two geological formations. The Nile Valley north of the Second Cataract belongs to the Mesozoic Nubia Sandstone while south of the Second Cataract it is part of the ancient Basement Complex (Barbour, 1961). Alluvial silty loam or clay terraces form a strip along the lakeshore, varying from a few metres to about 2 km in width. Siltation has been confined to Lake Nubia, and particularly heavy siltation occurs in the area between 360 and 430 km south of the dam (Abu Zaid, 1987).

3 Water Levels

The operation policy of the reservoir is based on dividing Lake Nasser storage into six zones, illustrated in Fig. 2. The dead storage zone, that receives sediments during the flood period, has a top elevation of 147 m with total volume of about 31 × 10^9 m^3. This zone releases no flow, regardless of the downstream requirements. The live storage zone, which amounts to 90 × 10^9 m^3 includes the buffer zone and the conservation zone. The buffer zone lies between elevation 147 and

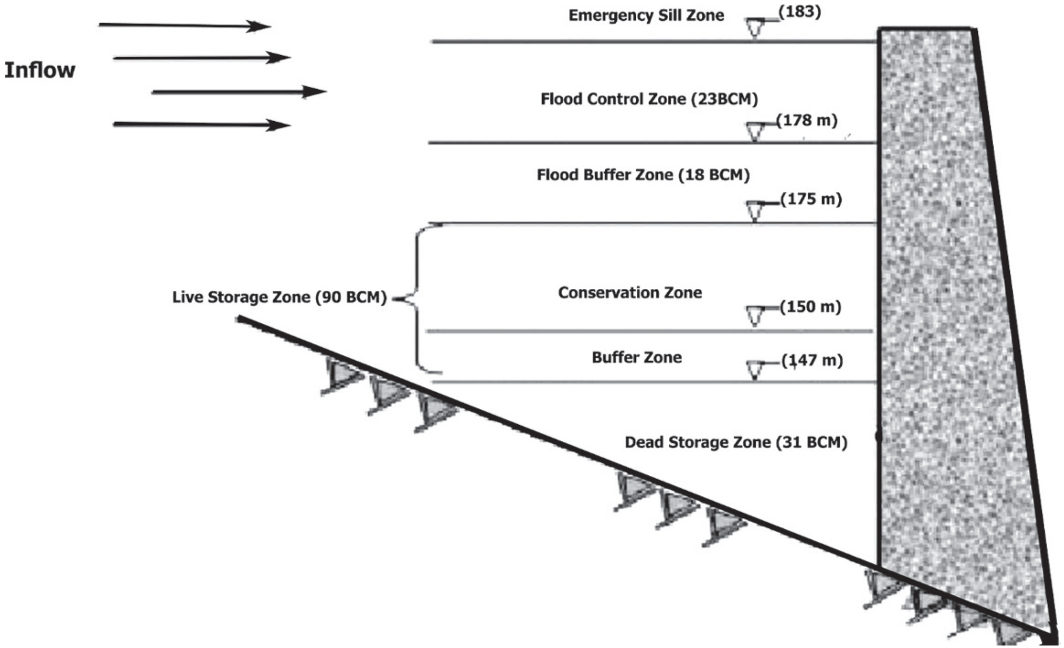

Fig. 2 Inflow as the main component for different operation zones of AHD reservoir (after El-Shafie, 2007, with permission from Springer)

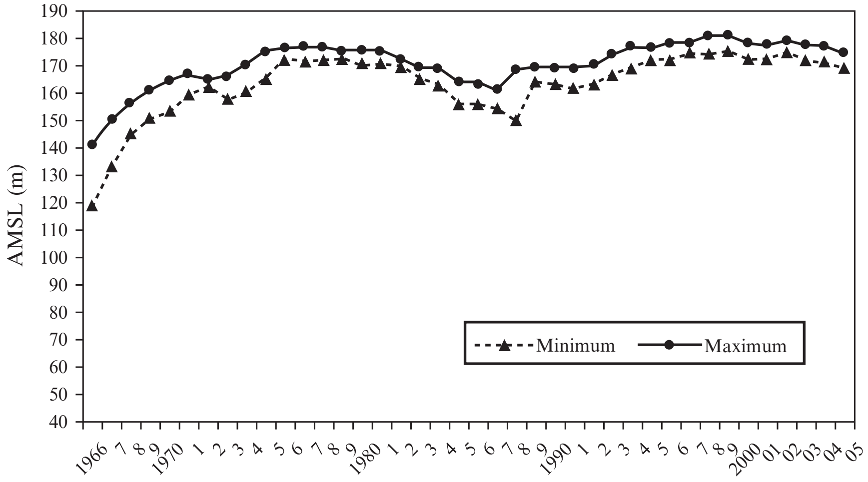

Fig. 3 Yearly amplitude of water level fluctuation in the period from 1966 to 2005 (original data from Nile Research Institute, reproduced with permission)

150 m while the conservation zone lies between 150 and 175 m. An additional storage volume of 40 × 10^9 m^3 is available for high flood waters. It is between elevation of 175 and 182 m, and brings the total lake volume up to 160 × 10^9 m^3. Within the live storage zone, the dam operators make their releases meet downstream requirements, although the total annual release should not normally exceed Egypt's agreed quota (55.5 × 10^9 m^3). The remaining storage is divided into a flood buffer and a flood control zone. Although the emergency spill zone is designed to have a crest level of 178 m, reservoir releases are such that the water elevation does not exceed 175 m at the end of a hydrologic year (31 July). As shown in Fig. 1, the level of 178 m is separating the flood buffer zone from the flood control zone at which any accumulated volume has to be spilled (Abu Zeid & Abdel Daym, 1990; Sadek et al., 1997; Fahmy, 2001). The water level of the lake changes between months and years, depending on the rates of inflow and outflow. The highest levels reached were in November 1996 and December 1997 at 179 m asl, and the lowest occurred in 1988 at 151 m. Figure 3 shows the water levels of the High Dam from 1966 to 2001.

4 Transparency

Transparency is affected by the turbidity caused by silt and clay (allochtonous inorganic materials) of riverine origin. It is particularly strong in the flood season. Secchi disc transparency reveals differences in turbidity between the three sections (Fig. 4). During floods (August–October), inorganic turbidity is high in the riverine

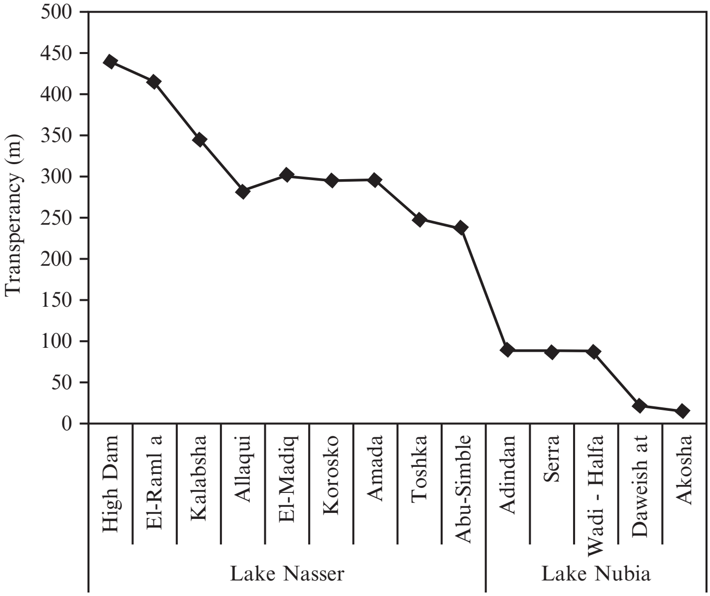

Fig. 4 Secchi disk transparency (cm) at some stations on Lakes Nasser and Nubia (orig.)

and semi-riverine sections. Transparency drops to 15–8 cm at Melik El-Nasser and to 7 cm at Daweishat and Akasha. At the southern end of Lake Nasser, transparency varies between 50 and 100 cm. In the northern part, it is usually higher because of the absence of silt and may reach 300–400 cm. Seasonal fluctuations in turbidity are also observed. Near the High Dam, autochthonous organic turbidity caused by phytoplankton blooms (mainly blue-green algae) reduces Secchi disc transparency to less than 50–100 cm in spring and early summer. In autumn and winter, phytoplankton density diminishes and transparency increases. The transparency in the khors is normally slightly lower than in adjacent open water areas due to suspended organic material. The khors of the southern section, especially those with a wide entrance, are highly affected by turbid floodwater.

5 Water Temperature (Table 1b)

Lake Nasser, situated on the eastern side of the Sahara, has a hot climate with water temperature higher at the southern than at the northern end during all seasons. The highest water temperature, 34.1°C, was recorded at Abou Simbel in summer; the lowest, 16.2°C, at the High Dam in winter. This amplitude of variation is close to that of the Sahelian Lake Chad (18–32°C) (Umeham, 1989). Abd Ellah et al. (2000) mentioned that, due to mixing, the vertical water temperature gradient in

Table 1b Physical–chemical characteristics of Lake Nubia (summarized from Abu Gideiri & Ali, 1980)

Characteristics	1971/1972 Oct.–Sept.	1973/1974 Oct.–June	1975/1976 Oct.–Sept.	1979 May–Dec.
Air temperature, range (°C)[a]	15.8–31.5	13.7–34.7	15.1–32–9	18.3–34.3
Water temperature, range (°C)	15.3–27.7	15.7–30.3	16.3–29.9	20.8–28.8
Secchi (cm)	25.5–226.7	32.3–166.3	29–271.5	60–120
Diss. oxygen (mg l^{-1})	8–9.7	6.3–10	7–9	7.5–9.2
Free CO_2 (mg l^{-1})	1–2	–	0–1.2	–
pH	8.4–8.9	8.45–9.0	6.8–8.3	8.6–8.8
Total alkalinity (mg l^{-1})	86.7–123.3	90–130	76.7–110.8	58.8–124.2
Nitrate (mg l^{-1})	0.02–3.7	–	0.85–2.11	–
Nitrite (mg l^{-1})	–	–	0.01–1.01	–
Orthophosphate (mg l^{-1})	0.02–0.6	0.12–1.2	0.11–0.69	0.04–0.47
Sulphate (mg l^{-1})	3–15	–	4.5–17.8	8–13.3
Chloride (mg l^{-1})	–	12.5–20	–	–

[a] At sampling time.

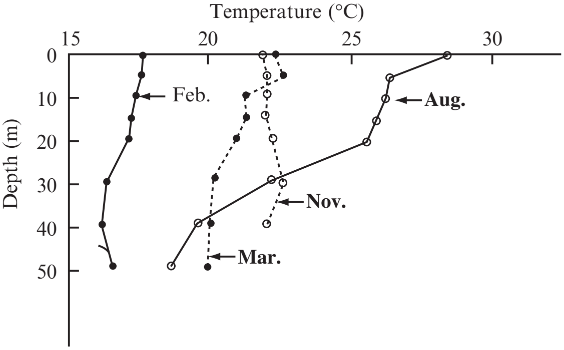

Fig. 5 Vertical (m) variation in water temperature (°C) along the main channel during winter, spring, summer, and autumn (after Goma & Abdel-Rahman, 1992) (reproduced with permission of EEAA Biodiversity Unit, Egypt)

winter 1993 was weak. Surface water temperature ranged from 17°C in the south to 19°C in the middle (Fig. 3). In spring, surface warming caused the development of a negative water temperature gradient, with indications of a thermocline developing: water temperature was 20°C at the surface, decreasing to 16°C near the bottom. In summer, thermal stratification was at a maximum. Surface water temperature reached 28°C, decreasing to <18°C near the bottom. In autumn, surface cooling and vertical convection created a surface isothermal layer (20 m) with a temperature of about 27°C, overlying a stratified layer similar to that in summer. During the next winter 1994, water temperature was similar at all depths (20–21°C) (Fig. 5). In general, vertical temperature gradient was dependent on season, time of day, climatic condition, and inflow from the south. The middle part of the lake usually had a higher water temperature throughout the year, due to a slower flow of water.

For some stations of Lake Nubia, water temperatures in the uppermost 15 m in August 1976 are given in Table 1b. In the riverine section of Lake Nubia, stratified conditions did not occur due to mixing (Ali, 1984).

6 Dissolved Oxygen

The lake water is well oxygenated during winter and spring (average 11.1 and 13.5 mg l^{-1}, respectively), while in summer and autumn lower average values, around 7 mg l^{-1}, occur. Elewa (1978), Latif (1984) and Abdel Moniem (1995) pointed out that thermal stratification coincides with the formation of an oxygenated epilimnion and oxygen-free hypolimnion. The oxygenated epilimnion becomes deeper southwards. The depth of the oxygenated layer was only 8–10 m in the north compared with 20 m at Adindan (Latif, 1984) (Fig. 6).

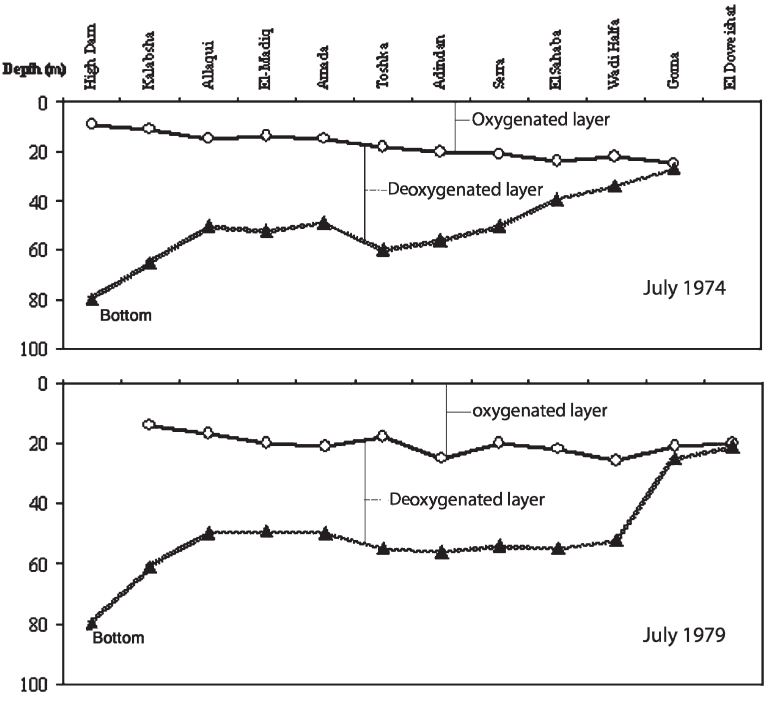

Fig. 6 Depth of oxygenated and non-oxygenated layers along the main channel of Lakes Nasser and Nubia in July 1974 and 1979 (Elewa, 1980) (reproduced with permission of EEAA Biodiversity Unit, Egypt)

7 Hydrogen Ion Concentration

pH is neutral to alkaline (7.2 and 9.5), and decreases with depth, except at Akasha in Lake Nubia, where it slightly increases (Abdel-Moniem, 1995; Rashid, 1995; Yousry, 2003). It ranges between 6.8 and 8.9 in lake Nubia (Abu-Gideiri & Ali, 1975).

8 Major Ions

Sulphate ranges from 5 to 15 mg l^{-1} and remained relatively constant before 1972 and 1975–1976 (Latif, 1984). Shoreit et al. (1992) pointed out that sulphate decreases with depth and fluctuates between 12 mg l^{-1} at the surface and 3.0 mg l^{-1} at the bottom. Abdel-Moniem (1995) recorded values ranging from 0.90 to 9.86 mg l^{-1} with an average 1.63 mg l^{-1} near the bottom during summer. Yousry (2003) recorded a range of 3.83–7.59 mg l^{-1}. Low sulphate at the bottom was attributed to low oxygen content leading to sulphate-reducing bacterial activity.

The concentration of Ca^{2+} and Mg^{2+} was 25–26 and 10–11 mg l^{-1}, respectively (Entz, 1972). Ca^{2+} increases from north to south, similar to the trend in CO_3^{2-}, indicating that it mainly occurs as carbonate. A seasonal variation was observed, with a minimum of 18.3 mg l^{-1} in spring and a maximum of 23.9 mg l^{-1} in autumn, while Mg^{2+} ranged between 7.73 and 10.3 mg l^{-1} (Yousry, 2003). Latif and Elewa (1980) pointed out concentrations of Na^+ and K^+ of 6.2–27.8 and 1.9–8.0 mg l^{-1}, during 1974–1976. Much lower concentrations of Na^+ were recorded in 1993 (Abdel-Moniem, 1995) in the main channel of the lake, 0.89–3.15 mg l^{-1}, with annual average 1.62 mg l^{-1}, while K^+ varied between 2.13 and 5.08 mg l^{-1}, with annual average 4.03 mg l^{-1}.

9 Nutrients

9.1 Nitrite–Nitrogen (NO_2–N)

Latif and Elewa (1980), Rabeh et al. (1999) and Goma (2000) recorded the range of nitrite–nitrogen as 5–180, 0.0–7.1 and 3.0–68.4 µg l^{-1}. Abu-Gideiri and Ali (1975) mentioned nitrite concentrations from 10–101 µg l^{-1} in Lake Nubia.

9.2 Nitrate–Nitrogen (NO_3–N)

Latif and Elewa (1980) found that nitrate–nitrogen fluctuated between 0.5 and 3.0 mgl^{-1}. Recent studies show NO_3–N concentrations between 0.1 and 6 mg l^{-1} (Goma, 2000), 4.6–742.2 (Toulibah et al., 2000) and 250–1900 µg l^{-1} (Yousry, 2003) in Lake Nasser and 20–2110 µg l^{-1} in Lake Nubia (Abu-Gideiri & Ali, 1975).

9.3 Orthophosphate (PO_4)

Orthophosphate ranges between 70 and 460 µg l^{-1} and is higher at the bottom than at the surface (Latif & Elewa, 1977). In early years, higher phosphate values were recorded (20–2000 µg l^{-1}) (Entz, 1972). In recent years, the range fluctuated from 5.5 to 27.7 µg l^{-1} (Toulibah et al., 2000), 40–90 (Yousry, 2003) and 50–530 (Soltan et al., 2005). Abu-Gideiri and Ali (1975) mentioned organic-phosphate concentrations of 20–690 µg l^{-1} in Lake Nubia.

10 Heavy Metals

The ranges of Fe, Mn, Zn and Cu in lake sediment were 236–259, 95–138, 1.5–2.1 and 6.5–12.0 mg kg^{-1}, respectively, with order Fe > Mn > Zn > Cu in 1977 (Elewa, 1980), while the ranges in 1988 were 4.02–8.71%, 485–1,305, 77–432 and 56–81 ppm for Fe, Mn, Zn and Cu, respectively (Elewa et al., 1990). Soltan et al. (2005) mentioned that a relatively high Fe concentration (0.20–0.24 mg l^{-1}) at the north end of the lake might originate from surrounding rocks. Concentrations of Pb and Cd in lake water (range 0.0003–0.0100; 0.0005–0.0040 mg l^{-1}, respectively), may be derived from the use of phosphate fertilizer in shore cultivation and gasoline leaks from fishery boats. Relatively high Zn and Cu concentrations suggest that these contaminants are generated from fishing boats, discharges of ships, and erosion of igneous rocks. However, the concentration of all metals is below the maximum permissible value set by the Environmental Protection Agency and Egyptian Chemical Standards.

11 Bacteria

Total bacteria in the main channel of Lake Nasser peaked at 731 × 10^5 ind ml^{-1} in spring. High temperature helps proliferation of bacteria and phytoplankton, which produce dissolved organic matter, used in bacterial reproduction (Rabeh et al., 1999; Rabeh, 2009). The standing crop of total bacteria in the largest khors varied from 0.12 × 10^5 cells ml^{-1} at Khor Korosko in autumn to 933 × 10^5 cells ml^{-1} at Khor Allaqi in spring. Comparing the results obtained by Elewa and Azazy (1986) in 1974–1984 with those recorded in 1996 (Rabeh et al., 1999), a more than 100 fold increase in total bacterial counts was observed at all sites.

12 Phytoplankton

The phytoplankton community increases southwards from 3.4 × 10^6 algal units l^{-1} at El-Birba to 15.3 × 10^6 algal units l^{-1} at Adindan (Bishai et al., 2000). Diversity increases from 27 (Samaan, 1971) to 84 species (Abdel Moniem, 1995). Chlorophyceae, Cyanophyceae, Bacillariophyceae, Dinophyceae and Euglenophyceae are represented. Numerically, Bacillariophyceae, (about half of the total) and Cyanophyceae are the main component, with Dinophyceae, Chlorophyceae and Euglenophyceae frequent or rare (Zaghloul, 1985; Mohammed et al., 1989; Abdel Moniem, 1995; Habib, 2000). *Melosira* sp. (contributing up to 99%), besides *Synedra* and *Nitzschia* spp. are abundant (Zaghloul, 1985; Habib, 2000). Abdel Moniem (1995) pointed out that diatoms in the main channel are mainly represented by *Aulacoseira granulata*, *Melosira nyassensis* and *Cyclotella ocellata*. Cyanophyceae contributed 47% to total phytoplankton numbers, with *Microcystis aeruginosa*, *Planktolyngbya limnetica* and *Oscillatoria limnetica* dominant.

Khors have a higher population density ($3.62–5.23 \times 10^6$ units l^{-1}) than the main channel ($0.93–1.03 \times 10^6$ units l^{-1}), and southern khors are more productive than northern ones (Gaber, 1982). The phytoplankton shows a vertical distribution with highest density at 2–5 m (Gaber, 1982; Toulibah et al., 2000). In 1987–1992, water blooms of *Microcystis aeruginosa* occurred occasionally in the southern region of Lake Nasser. Currently, blooms occur around the year and throughout the lake. The largest bloom was recorded in December 1989, when patches of 125 km in length occurred from El-Sebra to Abou Simbel (Mohamed & Loriya, 2000).

13 Chlorophyll-*a*

The amount of chlorophyll-*a* provides an index of phytoplankton productivity. The southern region of lake shows higher mean annual values (12 mg m^{-3}) than the northern region (8 mg m^{-3}) (Fead, 1980). The vertical distribution of Chl-*a* is maximum at 2–6 m depth (Habib et al., 1996), reaching its highest value (15.1 mg m^{-3}) in spring and lowest in winter (8.85 mg m^{-3}) (Abdel Moniem, 1995). In contrast, Yoursy (2003) recorded a highest value of Chl-*a* (11.07 mg m^{-3}) in winter, and lowest (2.3 mg m^{-3}) in summer. Nanoplankton represents a considerable fraction (53.4–74.4%) (Abdel Moniem, 1995).

14 Primary Productivity

The primary productivity in Lake Nasser shows high epilimnetic values, usually between 15 mg C m^{-3} h^{-1} in winter and 68 mg C m^{-3} h^{-1} in spring (Abdel Moniem, 1995). In1997/98 it reached a maximum of 239 mg C m^{-3} h^{-1} (Toulibah et al., 2000). Habib (2000) mentioned that primary production varied between 0.7 and 23.8 g C m^{-2} day^{-1} with mean around 4 g C m^{-2} day^{-1}. Seasonal variation depended on transparency and chlorophyll-*a* (Habib, 2000). Yoursy (2003) recorded the highest values of net production and photosynthetic activity (7.08 g C m^{-2} $day^{-1}$and 18.9 g O_2 m^{-2} day^{-1}) in summer and the lowest (0.12 g C m^{-2} day^{-1} and 0.33 g O_2 m^{-2} day^{-1}) in autumn.

15 Macrophytes (Table 2)

Rorslett (1989) summarized the changes in vegetation following impoundment as (a) a decline in species richness; (b) a gradual disappearance of the shallow water and mid-depth communities; (c) a conspicuous absence of submerged vascular macrophytes if lake level varies >7 m annually; and (d) an increase in species with strategies of the rudera1 (R) type.

In 1963–1964, Boulos (1966) recorded *Alisma gramineum*, *Damasonium alisma* Mill var. *compactum* Michell, *Potamogeton crispus*, *Potamogeton pectinatus*, *Zannichellia palustris* and *Potamogeton perfoliatus*. In 1972, *Potamogeton pectinatus* (Entz, 1976), and in 1973–1974 *Najas marina* subsp. *armata*, *N. horrida*, *Z. palustris* and *Potamogeton pectinatus* were found (El-Hadidi, 1976; Entz, 1980). In 1981–1982 Springuel (1985) listed *Najas marina* subsp. *armata*, *Najas horrida*, *Potamogeton trichoides*, *P. crispus*, *Zannichellia palustris*, *Vallisneria spiralis* and *Potamogeton lucens* (identified as *P. nodosus*). After the construction of the Aswan High Dam, two euhydrophyte species (*A. gramineum* and *D. alisma*) were lost, but the other four species colonized the lake with varying degrees of success. In 1967, *Vallisneria spiralis* L. was recorded for the first time in Egypt (El-Hadidi, 1968; El-Hadidi & Ghabbour, 1968). In 1978–1986, of eight species recorded (Ali 1987; Springuel & Murphy, 1991), five (*Potamogeton schweinfurthii*, *Najas horrida*,

Table 2 Freshwater macrophyte species recorded in Nasser–Nubia lakes before and after formation of the Aswan High Dam

Species	1963–1964a	1963–1964b	1972–1974	1980–1986	1984–1986	1989–1990	1993–1994
Alisma gramineum	*	*	–	–	–	–	–
Damasonium alisma	*	*	–	–	–	–	–
Potamogeton crispus	*	*	–	*	*	*	*
Potamogeton pectinatus	*	*	*	*	*	–	–
Potamogeton perfoliatus	*	*	–	–	–	–	–
Potamogeton trichoides	–	–	–	*	*	–	–
Potamogeton lucens	–	–	–	–	–	*	*
Potamogeton nodosus	–	–	–	*	–	–	–
Zannichellia palustris	*	*	–	*	*	*	*
Vallisneria spiralis	–	*	*	*	*	*	*
Najas minor	–	–	–	*	–	–	–
Najas horrida	–	–	–	*	*	*	*
Najas marina	–	*	*	*	*	*	*
Nitella hyalina (macroalga)	–	–	–	–	–	*	*
Ceratophyllum demersum	–	–	–	–	–	–	*
Myriophyllum spicatum	–	–	–	–	–	–	*

(*): present; (–): absent. 1963/1964a: after Boulos (1966), 1963/1964b after El-Hadidi (1976), 1972/1974 after Entz (1976), 1980/1986 after Springuel and Murphy (1991), 1984/1986 after Ali (1987), 1989/1991 after Ali (1992), 1993/1994 after Ali (2000).

N. marina subsp. *armata* and *Nitella hyalina*) were new to the area. Ali (2000) recorded a dense cover of two "nuisance species" *Myriophyllum spicatum* L. in Abu Hor and *Ceratophyllum demersum* L. at Aswan port, in addition to *N horrida*, *N. marina intermedia* from the High Dam to Allaqi and *P. schweinfurthii* at Kalabsha (Table 2).

Ali (2006) recorded 61 species along the Lake Nubia shores. Species with high abundance (C) and frequency (F) were *Tamarix nilotica* (Ehrenb.) Bunge (C 5–100%, F 32.5%), *Persicaria lanigera* (R. Br.) Sojak (C 5–100%, F 19.3%), *Persicaria senegalensis* (Mein.) Sojak (C 5–100%, F 10.8%), *Crypsis schoenoides* (L.) Lam. (C 1–90%, F 16.9%), *Eragrostis aegyptiaca* (Willd.) Delile (C 1–90%, F 15.7%), *Glinus lotoides* L. (C 1–80%, F 43.4%), *Portulaca oleracea* L. (C 1–80%, F 12.0%), *Phragmites australis* (Cav.) Trin. Ex Steud. (C 1–70%, F 19.3%), *Hyoscyamus muticus* L. (C 1–60%, F 39.8%), *Crypsis aculeata* (L.) Aiton (C 1–60%, F 13.3%), *Heliotropium supinum* L. (C 1–50%, F 27%), *Cyperus michelianus* (L.) Delile (C 1–40%, F 34%), *Cyperus alopecuroides* Rottb. (C 5–40%, F 12.0%) and *Fimbristylis bisumbellata* (Forssk.) Bubani (C 1–30%, F 25%). *Tamarix nilotica* and *G. lotoides* dominated the Lake Nubia shores from Debeira (338 km south of Aswan High Dam–AHD) to El-Daka (487 km south of AHD). *H. muticus* extended from Debeira (338 km south of AHD) to El-Dewishat (431 km south of AHD). *P. lanigera* was mainly present in the southern section of the lake, from Semna (404 km south of AHD) to Okma (466 km south of AHD).

16 Zooplankton

16.1 Distribution, Seasonal Variation and Standing Crop

Many investigators have studied the distribution and seasonal variation of zooplankton in the lake and its main khors since its early filling (Samaan, 1971; Samaan & Gaber, 1976; Latif, 1984; Zaghloul, 1985; Mageed, 1992, 1995; Iskaros, 1993; Shehata et al., 1998; El-Shabrawy, 2000; El-Shabrawy & Dumont, 2003; Mageed & Heikal, 2006).

Lake Nasser's zooplankton is rich. In 1971 the annual average in the main channel was 21,000 ind m^{-3}, but the khors were nearly twice as rich (46,000 ind m^{-3}) (Samaan, 1971). The standing crop oscillated from 29,000 to 60,000 ind m^{-3} in 1984. A recent study by El-Shabrawy (2000) showed that density in the main channel varied from 25,000 to 120,000 ind m^{-3} and was highest in the upper 10 m (euphotic zone). Peaks occurred between Korosko and Amada (southern area). Time-wise, zooplankton peaked (88,000 ind m^{-3}) in spring, and dropped (32,000 ind m^{-3}) in winter. The population density in khors was higher than in the main channel and the southern khors (Korosko and Toshka) were richer than the northern ones (El-Shabrawy & Dumont, 2003).

16.2 Zooplankton Composition

The assemblage consists of Copepoda, Cladocera, and Rotifera, besides Protozoa and meroplankton (Table 3). Copepoda dominate, forming more than 65% by numbers (Fig. 2). They are represented by two carnivorous cyclopoida (*Thermocyclops neglectus* and *Mesocyclops ogunnus*) and one herbivorous Calanoid (*Thermodiaptomus galebi*). Cladocera come next in abundance, with a percentage around 20% and 10 species, while rotifera are less abundant, but show the highest diversity (16 species). *Thermocyclops neglectus* and *Mesocyclops ogunnus* constitute around 18% by numbers; *Tropodiaptomus processifer*, *T. kraepelini*, *T. asimi*, *Thermodiaptomus galebi*, and *T. syngenes* 16%; *Moina dubia* 15%; *Daphnia barbata*, *D. lumholtzi*, *Ceriodaphnia cornuta* 13%; *Bosmina longirostris* 8%, Nauplius larvae and crustacean eggs 7%, 5.5% and 4.4%, respectively. *Brachionus calyciflorus*, *B. angularis* and *B. caudatus* form 4%; Chironomids 3.6%; *Keratella tropica* and *K. cochlearis* 2.9%; other occasional organisms, finally, 2.7% (Abu Gideiri & Ali, 1975).

Table 3 Zooplankton species recorded from Lake Nasser at different time periods

	1981	1989–1990	1993–1994	1996–1998	2003
Protozoa					
Arcella discoides (Ehrb.)	–	–	*	*	–
Centropyxis aculeata (Ehrb.)	–	–	*	*	–
Epistylis bimarginata (Nenninger)	–	–	*	–	–
Euplotes patella (Müller)	–	–	*	–	–
Rotifera					
Anuraeopsis fissa (Gosse)	–	–	*	*	–
Ascomorpha ecaudis (Perty)	–	–	*	–	–
Asplanchna girodi (de Guerne)	–	–	–	*	–
Brachionus angularis (Gosse)	*	*	*	*	–
Brachionus calyciflorus (Pallas)	*	*	*	*	*
Brachionus caudatus (Barrois & Daday)	*	*	*	–	–
Brachionus falcatus (Zacharias)	–	*	*	*	*
Brachionus patulus (Müller)	–	–	*	*	*
Brachionus plicatilis (Müller)	–	*	*	–	–
Conochilus hippocrepis (Schank)	–	–	*	–	–
Conochillus unicornis (Rousslet)	–	–	*	–	*
Euchlanis dilatata (Ehrb.)	–	*	*	*	–
Filinia opoliensis (Zacharias)	–	*	*	*	*
Filinia longiseta (Ehrb.)	*	*	*	*	–
Hexarthra mira (Hudson)	–	*	*	*	–
Keratella cochlearis (Gosse)	*	*	*	*	*
Keratella quadrata(Müller)	–	–	*	–	*
Keratella tropica (Apstein)	*	*	*	*	*
Lecane arcula (Harring)	–	–	–	*	–

(continued)

Table 3 (continued)

	1981	1989–1990	1993–1994	1996–1998	2003
Lecane bulla (Gosse)	*	*	*	*	–
Lecane closterocerca (Schmarda)	–	–	–	*	–
Lecane luna (Müller)	*	*	*	*	–
Lecane lunaris (Ehrb.)	–	*	*	*	–
Polyarthra vulgaris (Carlin)	–	*	–	*	*
Pompholyx complanata (Gosse)	–	–	*	–	–
Proalides sp.	–	–	–	*	–
Scaridium longicaudum (Müller)	–	*	–	–	–
Trichocerca similis (Wierzejski)	–	*	*	*	*
Trichocerca porcellus (Gosse)	–	–	*	–	–
Trichocerca pusilla (Lauterborn)	–	–	*	*	–
Trichocerca longiseta (Schrank)	*	–	–	*	*
Testudinella patina (Hermann)	–	–	*	–	–
Copepoda					
Thermodiaptomus galebi (Barrois)	*	*	*	*	*
Thermocyclops neglectus (Sars)	*	*	*	*	*
Mesocyclops ogunnus (Onabamiro)	*	*	*	*	*
Ergasilus sieboldi (Nordmann)	*	–	–	–	–
Halicyclops magniceps (Lilljeborg)	*	–	–	–	–
Cladocera					
Alona rectangula (Sars)	–	–	–	*	*
Alona intermedia (Sars)	–	*	–	–	–
Alona affinis (Leydig)	*		–	–	–
Macrothrix laticornis (Jurine)	–	*	–	*	–
Bosmina longirostris (Müller)	–	–	–	*	*
Chydorus sphaericus (Müller)	–	–	*	*	*
Ceriodaphnia quadrangula (Müller)	–	*	–	*	–
Ceriodaphnia dubia (Richard)	–	–	–	*	*
Ceriodaphnia cornuta (Sars)	*	*	*	–	*
Daphnia barbata (Weltner)	*	*	–	*	*
Daphnia longispina (Müller)	–	–	*	*	*
Diaphanosoma excisum (Sars)	*	*	*	*	*
Diaphanosoma mongolianum (Ueno)	–	–	–	*	–
Simocephalus vetulus (Müller)	–	–	–	*	*

1981: after Zaghloul, 1985, 1998–1990: after Abdel-Mageed, 1992, 1993–1994: after Abdel-Mageed, 1995, 1996–1998: after El-Shabrawy, 2000 and El-Shabrawy and Dumont, 2003, 2003: after Mageed and Hekal, 2006.

16.3 Zooplankton Biomass

In the coastal area of the main channel and main khors, copepoda constituted 53% of zooplankton biomass (280–1,050 mg g^{-1}). Cladocera occupied the second position (27–46%). Regarding seasonal variation of biomass, spring had the highest value (690 mg m^{-3}), and winter the lowest (360 mg m^{-3}).

16.4 Vertical Distribution

In the main channel, *Keratella cochlearis*, *Proalides* sp. (Rotifera), *Bosmina longirostris*, *Ceriodaphnia dubia* (Cladocera) and all Copepoda except *Mesocyclops ogunnus* migrate over ca 20 m. The highest density occurs between 10 and 15 m, and almost all Cladocera disappear below 15–20 m in summer, due to a lack of oxygen.

16.5 Zooplankton Production

No work has been done on zooplankton production in Lake Nasser, except for the study of El-Shabrawy & Dumont (2003), which estimated production (P) from biomass (B), using the IBP regression equation for mixed crustacean lake zooplankton ($P = 9.097\ B^{1.237}$), after Morgan (1980). Such an estimation is rough, but detailed measurements of the production of most cladoceran and copepods species that live in Lake Nasser have been carried out in Lake Chad (Lévêque & Saint-Jean, 1983). They were strongly temperature-dependent. Daily P/B values varied by factors 2.5–7 across species, seasons and lake temperature. Taking average zooplankton dry weight across the top 10 m of Lake Nasser at 5 g m^{-2} yr^{-1}, a yearly usable production of the order 50 t km^{-2} yr^{-1} is found. This is remarkably close to the production of Lake Chad, estimated at 43 t km^{-2} yr^{-1} by Lévêque & Saint-Jean (1983). Extrapolating, total annual production for the whole lake will be around 25×10^4 t. Assuming an efficiency of 10% (Lauzanne, 1983), zooplankton converted to fish biomass should suffice to produce 25,000 t of fish.

17 Macrobenthos (Table 4)

The importance of benthos lies in its position as secondary producer. Fish biomass and yield strongly correlate with macroinvertebrate biomass or production. Lentic fish obtain most of their energy from the benthos (Wissmar & Wetzel, 1987). Entz (1978) stated that before construction of the high dam, mollusca (bivalve) were ubiquitous but died out during stagnation owing to depletion of oxygen. *Tubifex* sp. was abundant, while chironomids were rare in the old river bed of the lake. Other investigations were carried out later (Anon, 1979; Iskaros 1988–1993; Fishar, 1995). El-Shabrawy & Abd El-Regal (1999) mentioned that the main channel harbored little diversity; only nine species of Arthropoda, Annelida and Mollusca were recorded. The southern part showed the highest density, with a peak of 2,920 org m^{-2} at Toshka in winter, mainly *Limnodrilus hoffmeisteri and L. udekemianus*. Kalabsha had the lowest density (150 org m^{-2}) in summer. Annelids therefore contributed ca 80% to total numbers and biomass. The highest density occurred in the south (Toshka & Abu Simbel), with a peak of 1,800 org m^{-2} in winter, while Kalabsha was the poorest site. *Branchiura sowerbyi* was rare and absent from several stations along the main

Table 4 Macrobenthos species recorded in Lake Nasser by different authors

Taxa and species	Entz, 1976	Entz, 1978	Latif, 1984	Elewa, 1987	Lskaros, 1988, 1993	Fishar, 1995	El-Shabrawy and Abd El-Regal, 1999
Cnidaria							
Hydra vulgaris Pallas						*	*
Aquatic insects							
Chironomus larvae	*	*	*	*	*	*	*
Nymphs of Odonata					*	*	*
Nymphs of Ephemeroptera						*	*
Nymphs of Trichoptera				*		*	
Nymphs of Hemiptera			*			*	*
Nymphs of Coleoptera						*	*
Crustacea							
Caridina nilotica (P. Roux)		*	*		*		
Potamonautes niloticus (Edwards)			*				*
Stenocypris malcolmsoni (Baird)						*	*
Annelida							
Branchiura sowerbyi (Beddard)				*	*		
Limnodrilus hoffmeisteri (Claparéde)				*	*		
Limnodrilus udekemianus (Claparéde)				*	*		
Tubifex sp.	*	*					
Helobdella conifera (Moore)					*	*	*
Mollusca							
Bellamya unicolor (Olivier)					*	*	*
Biomphalaria alexandrina (Ehrb.)					*		
Bulinus truncatus (Audouin)				*	*	*	*
Bulinus forskalii (Ehrb.)					*		
Cleopatra bulimoides (Olivier)				*	*	*	*
Gabbiella senariensis (Kuster)					*		
Helisoma duryi (Wetherbg)					*		
Lanistes carinatus (Olivier)					*	*	*
Lymnaea natalensis (Krauss)					*		
Melanoides tuberculata (Müller)				*	*	*	*
Physa acuta (Draparnaud)				*	*	*	*
Pila ovata (Olivier)					*		
Theodoxus niloticus (Reeve)					*	*	*
Valvata nilotica (Jickeli)				*	*	*	*
Gyraulus ehrenbergi (Beck)					*	*	*
Corbicula consobrina (Cailliaud)			*	*	*	*	*
Pisidium pirothi (Jickeli)				*	*	*	*

channel. Arthropods, represented by *Chironomus* larvae, formed about 10% of total benthos numbers and biomass. They were totally absent during summer and autumn and reached a standing crop of up to 300 org m^{-2} during spring and winter. Compared with the main channel, the macrobenthos in the littoral was highly diverse: 21 species were recorded. Arthropods were numerically dominant, constituting about half of the numbers, followed by Annelida and Mollusca (41% and 12%). The total biomass of these groups was the reverse of its numbers: Mollusca contributed the major part of biomass (54%), followed by Annelida and Arthropoda (25% and 21% respectively). *Chironomus* larvae and *Caridina nilotica* were the dominant arthropods at the majority of stations, while other arthropods were scarce (Fishar, 2000) (Table 4).

18 Long-Term Changes

The low standing crop of benthos at the beginning of impoundment (Latif et al., 1979), increased gradually with the rise in water level. The standing crop dropped to a minimum in 1988, and increased again during the following years, due to a drop in lake level resulting from a major drought lasting until 1988. According to the classification of MacLachlan (1974), three stages can be differentiated in the formation of the macrobenthos of Lake Nasser. The first stage (filling phase) covered the early years of impoundment (1966–1978) and was characterized by a mass development of chironomids and oligochaetes (*Tubifex* spp.) able to utilize organic matter and live under anoxic conditions. Some workers (Entz, 1978; Latif, 1984) found the freshwater crab, *Potamonautes niloticus*, the prawn *Caridina nilotica*, and some snails (including *Bulinus truncatus*) in the littoral zone. These species are riverine and most of them died at the end of this stage. The second stage (post-filling phase) covered the next 10 years (1979–1989) and was characterized by an increase in standing crop and in species diversity owing to an increase in organic matter, dissolved oxygen (DO) and surface area of the lake. The standing stock of benthic animals was reduced at the end of this stage due to a decrease in water level resulting from the African drought (Elewa, 1987; Iskaros, 1988). The third stage (equilibrium phase) from about 1990 until the present has been characterized by a further increase in diversity of species, and fluctuations in the number of individuals. The community of the benthos in Lake Nasser is now beginning to stabilize (Table 4).

19 Fish

19.1 Fish Diversity

The 57 species recorded since 1964 (Table 5) belong to 16 families (Latif, 1974). Some, like *Protopterus aethiopicus* and *Polypterus bichir*, are extremely rare. In the course of impoundment, some species became less and others more common. For example,

Table 5 Fishes recorded in Lake Nasser (after Latif, 1974)

Species	Local Name	Species	Local Name
Protopterus aethiopicus	Dabib El-Hout	*Clarias anguillaris*	Hout, Karmout
Polypterus bichir	Abu-Bichir	*Clarias gariepinus*	Hout, Karmout
Mormyrops anguilloides	Gamhour	*Heterobranchus longifilis*	Hout, Karmout
Petrocephalus bane	Gelmaya, Arminya	*Heterobranchus bidorsalis*	Hout, Karmout
Pollimyrus isidori	Anooma	*Schilbe* (Eutropius) *niloticus*	Schilba
Gnathonemus cyprinoides	Um-Shafika	*Schilbe* (Schilbe) *mystus*	Schilba
Mormyrus kannume	Um-Bowez	*Schilbe* (Schilbe) *uranoscopus*	Schilba-Arabi
Mormyrus caschive	Boweza	*Siluranodon auritus*	Schilba
Hyperopisus bebe	Kalamya-Babeh	*Bagrus bajad*	Bayad
Gymnarchus niloticus	Rayah Niliah	*Bagrus docmak*	Docmack
Hydrocynus forskalii	Kalb El-Samak	*Chrysichthys auratus*	Gurgar
Hydrocynus vittatus	Kalb El-Samak	*Chrysichthys rueppelli*	Gurgar Schami
Hydrocynus brevis	Kalb El-Samak	*Clarotes laticeps*	Abu-Meseka
Alestes dentex	Rayah	*Auchenoglanis biscutatus*	Halouf
Alestes baremoze	Rayah	*Auchenoglanis occidentalis*	Halouf
Brycinus nurse	Sardina	*Synodontis schall*	Schall
Distichodus niloticus	Lessan El-Bagar	*Synodontis serratus*	Schall
Citharinus citharus	Kamara	*Synodontis clarias*	Schall
Citharinus latus	Kamara	*Mochocus niloticus*	Mekawkas Nili
Chelaethiops bibie	Bebe	*Chiloglanis niloticus*	Kiloglans
Labeo victorianus	Lebeis Hagari	*Malapterurus electricus*	Rahaad
Labeo niloticus	Lebeis Nili (abyad)	*Sarotherodon galilaeus*	Bolti Galili
Labeo coubie	Lebeis Aswad	*Oreochromis niloticus*	Bolti Nili
Labeo horie	Lebeis Aswad	*Oreochromis aureus**	Bolti Azrak
Garra dembeensis	Abu-Kors	*Tilapia zillii*	Bolti Akhadar
Barbus bynni	Benni	*Lates niloticus*	Samous, Ishr-ayad
Barbus werneri	Benni	*Tetraodon lineatus*	Fahaka
Barbus anema	Benni		
Barbus perince	Benni		
Barbus neglectus	Benni		
Raiamas loati	Morgan loti		
Leptocypris niloticus	Bebee–Margan Nili		

Chelaethiops bibie and *Leptocypris* (*Barilius*) *niloticus* were common in the southern region in 1970, but at present are infrequent. Latif (1974) found that *Eutropius niloticus*, *Schilbe uranoscopus*, *S. mystes*, *Alestes dentex*, *A. baremoze*, *Mormyrus*, *Labeo* spp. and *Barbus* spp. were more frequent in Lake Nubia than in Lake Nasser. The reverse is true for *Sarotherodon galilaeus*, *Oreochromis niloticus*, *Hydrocynus forskalii*, *Brycinus nurse* and *Bagrus* spp. Again *Schilbe* spp. are more frequent in the southern part of Lake

Nubia except during the flood, when they become common in flooded areas. *Alestes baremoze* and *A. dentex* are repelled by these waters and become common in the south, ahead of the flood. However, *A. baremoze* migrates upstream for spawning in Lake Nubia (Rashid, 1977). Similar migration from natural lakes to connecting rivers for spawning has been observed elsewhere (Durand & Loubens, 1971; Hopson, 1972).

Today, *Sarotherodon galilaeus* and *Oreochromis niloticus* represent 90–95% of total fish catch in lake Nasser. The remainder are *Hydrocynus* spp., *Synodontis* spp., *Bagrus* spp., *Lates niloticus* and *Brycinus nurse*. Thus, the species diversity has declined and some species are now restricted to the southern region of the Lake, while others have vanished completely (Khalifa et al., 2000) (Fig. 7).

There are 43 fish species in Lake Nubia (Table 6). The most abundant are the Characidae, Cyprinidae, and Schilbeidae followed by Mochokidae and Centropomidae. In commercial landings, Cichlidae (tilapias) are, again, dominant, but Lates *niloticus* is gaining in importance. *Distichodus*, *Citharinus* and *Bagrus*, which used to form a major part of the commercial fish catches during 1967–1968, almost disappeared. Fish abundance varies temporarily and spatially. For example, the western and southern regions have higher catches than other parts of the lake (Abu Gideiri & Ali, 1975). *Bagrus* and *Synodontis* are abundant during March–May. *Lates* and the *Labeo*'s increase in abundance with the flood during August and September. *Barbus bynni* shows highest catches during January, and in May–June (Fig. 8). In 1985, 26 species belonging to ten families were recorded. Compared with previous studies some species that were commercially important during the early years of the lake are now negligible (*Distichodus*, *Citharinus*, *Bagrus*). The species widely distributed in the lake are *Labeo niloticus*, *Lates niloticus*, *Sarotherodon niloticus*, *Hydrocynus forskallii*, *Alestes baremose* and *Eutropius niloticus*. Their highest production occurs during February–May and July–September.

19.2 Fish Production

Since the early days of impoundment, fish landings from the lake have contributed significantly to total annual fish production of Egypt. They have fluctuated between 34,000 t during 1982, and 13,900 t in 1999 (Fig. 7).

19.3 Fishing Gear

Three main kinds of fishing gear are used: the sinking gill net (kobak), the floating gill net (sakorata) and the trammel net (duk). Longlines (sharak) and cast nets (toraha) are used less frequently. Sinking gill nets and trammel nets are used along the shore at depths of up to 10–15 m. The former are usually operated overnight. When the weather and water conditions are favorable, sinking gill nets are used in the open waters of the Khors and to some extent in the main channel. The predominant fish

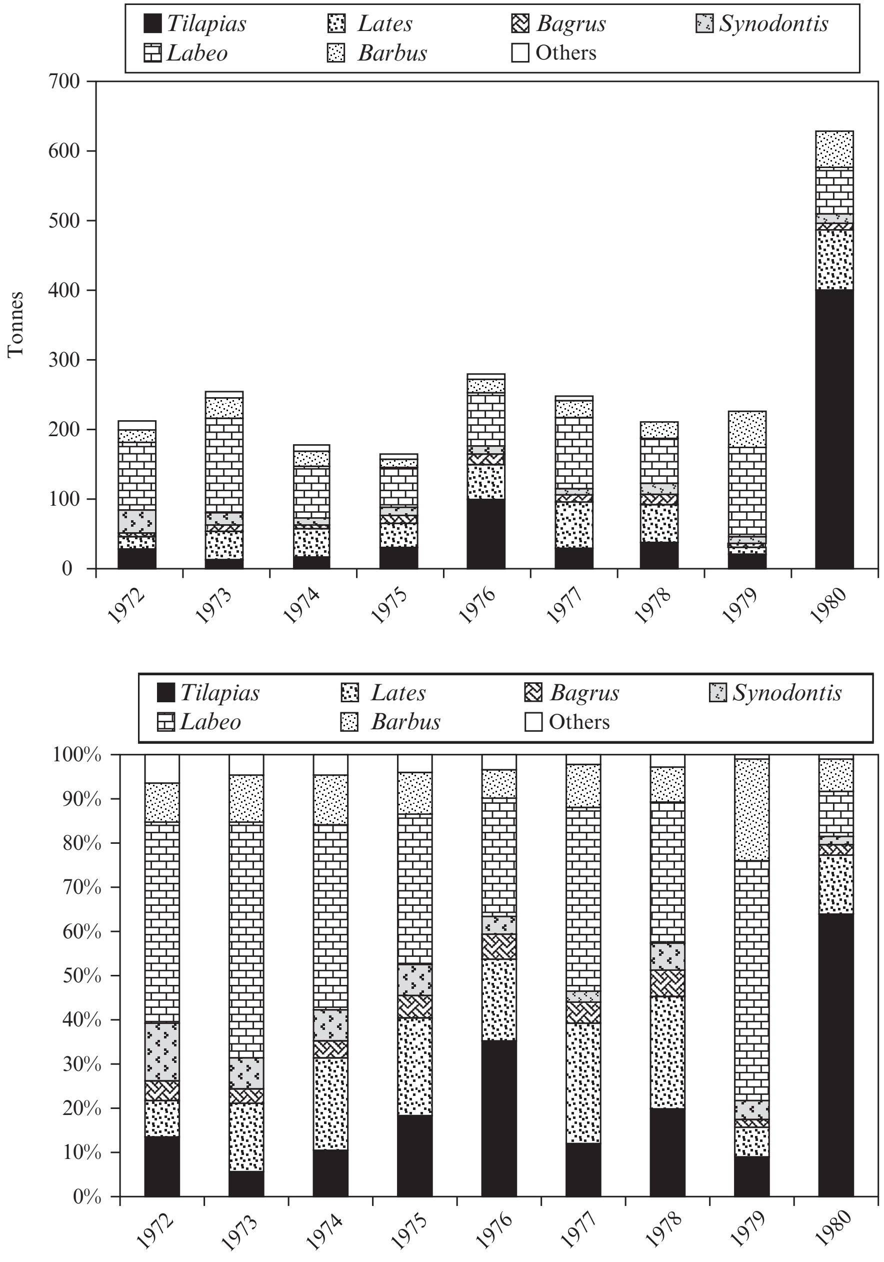

Fig. 7 Evolution of fish landings and percentage composition of the commercial catches in Lake Nasser (orig.)

Table 6 Fish species found in Lake Nubia from 1967 to 1979

Fish species	1967–1968	1971–1972	1973–1974	1975–1976	1979
Protopterus aethiopicus	*				
Heterotis niloticus	*				
Polypterus spp.	*				
Hyperopisus bebe	*	*		*	*
Mormyrus kannume	*	*	*	*	
M. cashive		*			
Mormyrops anguloides	*	*	*	*	
Petrocephalus bane	*	*			
Marcucenius spp.	*				
Gnathonemus cyprinoides	*	*			
Hydrocynus forskalii	*	*	*	*	*
*Alestes dente**	*	*	*	*	*
A. baremose	*	*	*	*	*
A. nurse	*	*	*	*	*
Distichodus niloticus	*	*	*	*	*
D. rostratus	*				
D. engycephalus	*				
Citharinus citharus	*	*		*	
Labeo coubie	*	*	*	*	*
L. niloticus	*	*	*	*	*
L. horie	*			*	*
Barbus bynnie	*	*	*	*	*
Bagrus bayad	*	*	*	*	*
B. docmak	*	*	*	*	*
Clarotes laticeps	*			*	
Auchenoglanis occidentalis	*				
Auchenoglanis spp.	*				
Chrysichthys auratus	*			*	
Clarias lazera	*	*			
C. angularis		*			
Heterobranchus bidorsalis	*				
Synodontis schall	*	*	*	*	*
S. serratus	*	*	*	*	*
S. batensoda	*	*	*		*
S. khartoumensis	*				
Sarotherodon galilaeus					*
Oreochromis niloticus	*		*	*	*
Malapterurus electricus	*				
Lates niloticus	*	*	*	*	*
Eutropius niloticus	*	*		*	*
Schilbe uranoscopus	*	*		*	*
S. mystus	*	*			
Tetraodon fahaka	*	*	*		

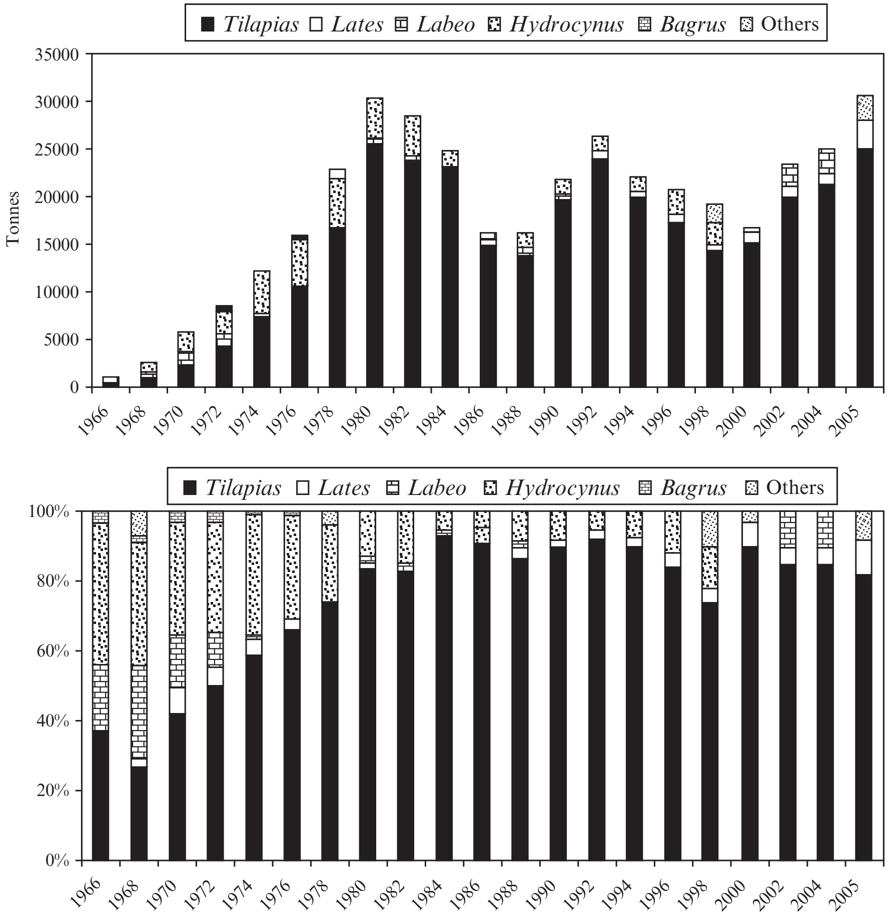

Fig. 8 Evolution of fish landings and percentage composition of the commercial catches in Lake Nubia (modified from Ali, 1984, reproduced with permission of the FAO)

caught in gill nets are *Alestes* spp. and *Hydrocynus* spp. The catch is usually gutted, salted and preserved in tins. Fish species caught in trammel nets are *Oreochromis niloticus*, *Sarotherodon galilaeus*, *Lates niloticus*, *Bagrus bayad*, *B. docmak*, *Mormyrus* spp., *Synodontis* spp. and *Barbus* spp. Tilapias and Nile perch form the bulk of the trammel net catch. The catch is collected by carrier boat. There are about 100 carrier boats each collecting from an assigned area. All of the collected fish, fresh and salted, are landed at the Aswan Fishing Harbour. The landings are sorted. In the case of fresh fish, tilapias and Nile perch are recorded separately (as bolti and samoos, respectively) because they are not difficult to identify, large quantities are landed, and they have a relatively high market value. Minor species, of about the same market value, tend to be combined under one name. Accordingly, the nominal catch statistics do not give an accurate figure of the composition of the landings.

19.4 Introduction of Alien Fish

The fish diversity of Lake Nasser has declined over time, and lacks a true pelagic planktivore. The lake seems to have a vacant ecological niche (pelagic area) that could be exploited by the introduction a pelagic planktivore (clupeid or cyprinid). Such species exist in the River Niger, in Lake Chad and in the large, ancient lakes of east Africa. The Lake Tanganyika clupeid, *Limnothrissa miodon* has been successfully introduced into Lake Kariba, on the border between Zambia and Zimbabwe, to fill the empty pelagic niche (Begg, 1976). A commercial fishery with 26,000 t yr^{-1} developed (Sanyanga et al., 1992) and employs about 3,000 people. The stomach content of *Limnothrissa miodon* (locally known as Kapenta) contains crustacean zooplankton, rotifers and phytoplankton. Cladocera and copepods are its main food items.

Other pelagic cyprinids, like *Engraulicypris sardella*, support productive fisheries in Lake Victoria and Malawi, and are equally good candidates for an introduction. The primary and zooplankton production of Lake Nasser indicates that the predicted yield of its fish landings is about 89,000 yr^{-1}, while recorded landings from Lake Nasser have never exceeded 34,000. The introduction of either of both pelagic planktivorous species could therefore more than double the lake's production (Fig. 7)

20 Impacts of the AHD

The Aswan High Dam has had a tremendous impact on Egyptian life, agriculture, and environment. However, the real question is not whether the Egyptians should have built the AHD or not – for Egypt realistically had no choice – but what steps could have been taken to reduce the adverse environmental impacts to a minimum. Here follows a brief overview of the major effects, positive and negative, of the high dam.

20.1 Positive Impacts

The dam has supported a high population growth rate in Egypt, because it prompted an expansion to agriculture, energy production, and manufacturing. One of the positive effects was that it allowed agriculture to move from basin irrigation to year-round irrigation, so crops could now be produced also during the dry months. And since the fear of flooding no longer existed, farmers were able to work in the fields year-round. The High Dam created a 30% increase in cultivable land in Egypt, and raised the water table in the Sahara. AHD also benefited industry by providing cheap electric power and it supplied even the most remote Nilotic villages with electricity. Lake Nasser became an important fishing site, supplying food and livelihood for the population around it.

Over the last 100 years the average discharge at Aswan has fluctuated around 90 km^3 yr^{-1}, while discharge to the Mediterranean fell from ca 32 km^3 yr^{-1} (before construction of the Aswan High Dam; Osman, 1999) to only ca 4.5 km^3 yr^{-1} (Kempe, 1989). The agricultural sector is the largest user and consumer of water in Egypt, its share being 82% of the gross demand for water. The total volume diverted to agriculture, including conveyance, distribution and application losses, is estimated at ca 55.2 km^3 yr^{-1}. The municipal water demand is currently in the order of 4.5 km^3 yr^{-1}, and is expected to increase significantly due to population growth. Industrial water demand is estimated at 7.6 km^3 yr^{-1}, of which only 0.79 km^3 yr^{-1} is lost to evaporation during industrial processes, while the rest returns to the system in a polluted form (EEAA, 2005).

Until the 1980's, the Aswan High Dam provided half of Egypt's Electricity. The power generating capacity of the Dam is 2.1 gigawatt (GW), produced by 12 Hydro-Generators, each rated at 175 MW. Egypt currently has a total installed generating capacity of 16.6 gigawatt (GW) compared to 3.8 GW in 1976, thus the percentage contribution by the dam has decreased from ca 50% to less than 13%. This percentage will continue to decrease as more thermal power plants are added. Total capacity is expected to be 26 GW by 2010 (http://www.mbarron.net/Nile/envir_nf.html).

In 1946, before the construction of AHD (Aswan High Dam), the yearly flood damaged about 70,000 feddan (ca 30,000 ha) while after its construction it protected about 100,000 feddan from such damages. It also provided protection from damage by high floods in 1975, 1988 and it saved Egypt from drought in 1972/1973, 1979/1980, 1987/1988 (Afifi, 1993).

The HAD also achieved the planned expansions of the agricultural domain, as shown in Fig. 9.

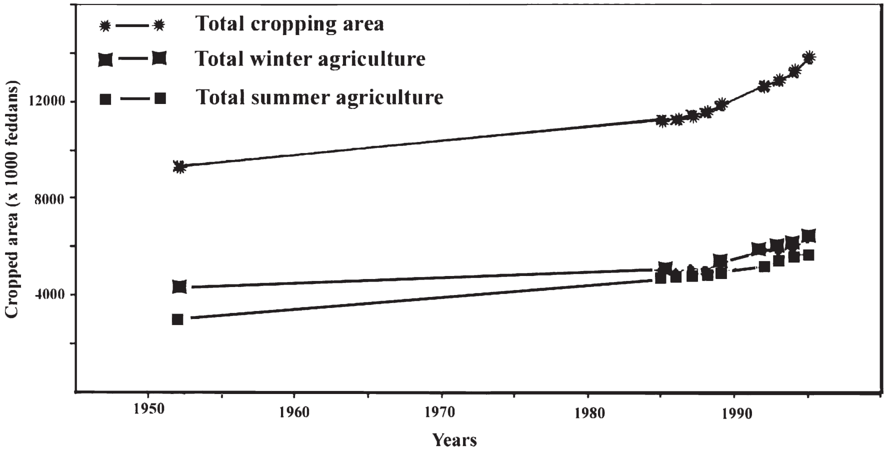

Fig. 9 Development of agriculture in Egypt from 1952 to 1995 (after Moussa et al., 2001, modified)

20.2 Negative Impacts

In the 1970s, the Aswan High Dam became a global symbol of environmental and social problems caused by large-scale development projects. The AHD impacts touch upon a wide spectrum of life aspects, including a change in water quality, as the maximum water release through the AHD is about a quarter of the former flood and is practically silt-free. Bed and bank erosion occurred in the downstream reaches of the Nile, caused by a change in river water levels and flow velocities, and the promontories of the delta started to erode instead of progressing into the sea (see Hamza, 2009).

Siltation of Lake Nasser There was a huge loss of fertility as a result of the creation of Lake Nasser. Fertile silt, henceforth captured by the dam, impacted the quality of soil downstream. This silt, enriched with organic material picked up *en route* used to sediment on the banks of the Nile and in the delta, creating excellent topsoil. As a result of the silt being captured, farmers now have to use about 10^6 t of artificial fertilizer as a substitute for the nutrients which no longer reach the floodplain.

Salinity and water-logging problems have developed due to the over-irrigation of lands, increases in cropping intensities and expansion of rice and sugar cane cultivation. The horizontal agricultural expansion in sandy or light soils that lie at higher elevation have increased seepage, thus contributing to salinity hazards.

Schistosomiasis and the Northward Migration of Malaria Vectors from Sudan Schistosomiasis, also known has bilharzia, is caused by the *Schistosoma* fluke-worm and is transmitted to humans via snails. Urinary schistosomiasis is caused by *S. haematobium*, and intestinal schistosomiasis by *S. mansoni*. Infected snails release the parasites as cercariae larvae, which enter humans spending much time in stagnant water, penetrating through the skin. The creation of the AHD combined with the change of the downstream irrigation from a seasonal to a perennial system has indeed increased the incidence of schistosomiasis (El-Hinnawi, 1980). Intermediate hosts of bilharzia snails (mainly mollusks of the genus *Bulinus*) appeared in the shallow littoral zones of AHD reservoir in great numbers at the end of 1974 (Entz, 1980). The threat was present, but the use of a wide range of control measures since the 1980s (use of molluscicides, introduction of biological control agents…) have prevented the prevalence of both urinary and intestinal bilharzia from reaching epidemic proportions (Jobin, 1999).

Negative effects occurred on the fisheries in the Nile and its coastal lakes, as the migration of certain types of fish were dependent on the arrival of turbid floodwater. As a result, sardines formerly breeding in the Nile estuary have almost disappeared and marine fish that used to seasonally migrate into the delta lakes have been virtually eliminated. Their place has, however, been taken by freshwater fish.

A rise in groundwater levels happened that required a new philosophy of land drainage. With the cessation of the cyclic behavior of groundwater before the AHD (levels rose after a flood wave and gradually sunk afterwards) and the increase in cropping intensities and perennial irrigation, more water seepage occurs that eventually feeds the water table. This has been exacerbated by a lack of effective drainage in some areas of the Nile valley and delta.

A growth of weeds at an epidemic scale in irrigation channels has resulted from the inflow of silt-free water and use of fertilizers in agriculture. This endangered the safety and effectiveness of irrigation and drainage, a significant amount of water was wasted, and water flow through many channels became interrupted.

The clearest losers resulting from the AHD construction have been the 100,000 or more Nubians, half-Egyptian and half-Sudanese, who had to be evacuated from their homes in the valley and were transferred to government-built villages far from the river. The Egyptians settled in eight villages on newly irrigated lands in the Kom Ombo area, 20 km to the north of Aswan. The Sudanese were moved and resettled in the area of Khashm el Girba, in the Upper Atbara valley (Mohieddin, 2000).

Finally, Simpson et al. (1990) state that there is a significant correlation between reservoir water levels and earthquake occurrences. The sheer weight of the water may seismically destabilize the area around it, raising the possibility that the reservoir weight could make underlying faults slip and cause the dam to falter. NASA geophysicists found evidence that large dams cause changes to the earth's rotation, because of the shift of water weight from oceans to reservoirs. Because of the number of dams which have been built, the Earth's daily rotation has apparently sped up by eight-millionths of a second since the 1950s (http://www.arch.mcgill.ca/prof/sijpkes/arch374/winter2001/dbiggs/enviro.html). This is the first time human activity has been shown to have a measurable effect on the Earth's motion.

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The Toshka Lakes

Gamal M. El-Shabrawy and Henri J. Dumont

Abstract As Lake Nasser–Nubia became filled to capacity in the 1990s, a side valley (the "New Valley") to the west of the main lake at Khor Toshka was flooded. Around 2002, this had created four additional lakes, with a maximum surface area of ca 1,500 km^2, holding about 5×10^9 m^3 of water. Part of this evaporates, and part recharges the underlying aquifer. Around 2006, however, with a dwindling water supply, the lakes had started shrinking, and lake 3 even dried out. At the beginning of the flooding, a more or less truncated Nile fauna and flora invaded the Toshka valley, and soon up to 7,000 t of fish (mainly *Tilapia* and *Lates*) was harvested from the lakes, but currently the westernmost lake shows a rapidly increasing salinity. The zooplankton, for example, reacts by a striking impoverishment.

1 Introduction

The Aswan High Dam in Upper Egypt, constructed in 1964–1968, created the world's second largest artificial lake, Lake Nasser–Nubia. The region of the dam has a negligible rainfall (ca 1 mm y^{-1}), wind speed, 3–5 km h^{-1}, and relative humidity ranges from 19% in summer to 45% in winter. From the earliest conception of a high dam, going back to British colonial times, the necessity of providing a "safety valve", to be activated in case of overfilling of the reservoir, was taken seriously. The 1970s and 1980s were times of mediocre to low floods, and it took well over 20 years for the reservoir to fill to capacity. But as soon as it approached maximum storage capacity in the wet 1990s, Egypt decided to divert water to one of the side valleys, known as khors. The dry Khor or Wadi Toshka (also written as Tushkha) on the west

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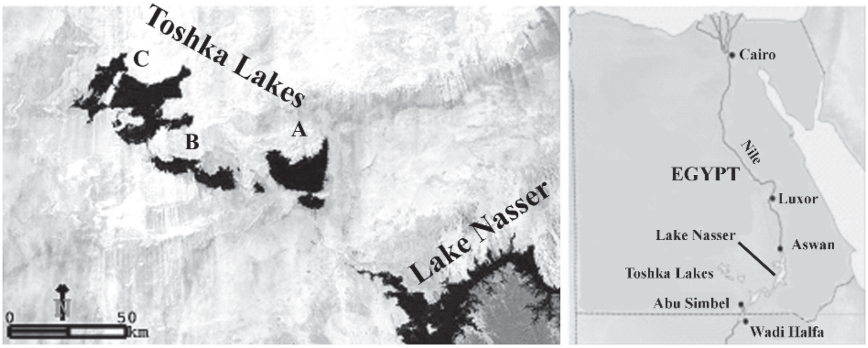

Fig. 1 A space view of the Toshka lakes (*right*) relative to Aswan and Wadi Halfa-Abu Simbel, and maximum extent of the different lakes (A–C) around 2002–2004 (*left*) (reprinted from http://na.unep.net/AfricaLakes/posters.htmlna.unep.net/AfricaLakes/posters, with permission from UNEP)

bank of the reservoir, 220 km upstream of the High Dam and 50 km north of Abu-Simbel, had been selected for the new undertaking; preliminary work had in fact started since 1978. The "New Valley" project, as it became known was, however, not designed as a mere safety valve to the reservoir, but as a grand development scheme that should, ultimately and ideally, link Khor Toshka to the oases of El Kharga and Baris (Paris). The project necessitated the digging of a 51.5 km long canal (known as the Sheikh Zayed Canal) (Fig. 1) and the construction of a powerful pumping facility, the Mubarak station, capable of supplying up to 300 $m^3\ s^{-1}$ of water. The canal was constructed between 1997 and 2002. It allows the diversion of up to $5 \times 10^9\ m^3\ y^{-1}$ of water, enough to convert 250,000 ha of desert to agricultural land. However, in such a dry climate, water requirements for agriculture are high, and were estimated at 20,000 $m^3\ ha^{-1}\ y^{-1}$, including infiltration and losses to evaporation (on average 3.7 mm day^{-1} and possibly up to twice that amount) (Yakoub et al., 2002).

2 The Four Lakes

The easternmost lake was flooded in November 1998. By late 1999, three additional lakes had formed, further and further westward. On average, the lakes cover a surface area of ca 1,300 km^2. The westernmost one started filling between September 2000 and March 2001 (Fig. 2).

In 2002, the estimated total surface area of the Toshka lakes was 1,540 km^2, distributed over lakes 1, 2, 3 and 4 as follows: 449, 265, 20 and 807 km^2. But in 2006, lake surface area had dropped to 937 km^2, significantly below that of 2001. Lake 3 vanished, and the surface areas of lakes 1, 2 and 4 had become 286, 101 and 550 km^2, respectively. Areas of swamp and sand dunes had started forming between the former and present shorelines. The calculated stored water volumes in Toshka lakes 1, 2, 3, and 4 for the year 2002 were 6.78, 2.21, 0.044 and $16.23 \times 10^9\ m^3$; by the year 2006 these had declined to 3.45, 0.44, 0 and $8.78 \times 10^9\ m^3$ (El Bastawesy et al., 2007).

Fig. 2 Development of the Toshka lakes. Situation before the flooding of the new valley (*Left*), with only Khor Toshka (*below left*) naturally flooded; early flooding phase (*middle*); full flooding (*right*) (reprinted from http://na.unep.net/AfricaLakes/posters.html.na.unep.net/AfricaLakes/posters, with permission from UNEP)

3 Physical and Chemical Properties of the Lakes

Some of the physical and chemical variables, including heavy metal concentrations of the Toshka lakes compared to Khor Toshka and the main channel area of Lake Nasser are shown in Table 1. Heavy metals (chromium and copper), as well as iron were low and showed no trends. Dissolved oxygen values were excellent. pH was slightly alkaline, and all nutrients were present in rather low quantities. Only sulphate, used here as an indicator of other macro-ions, gives reason for concern: there is a strong increase from the east to the west. This increase, as could be expected, is paralleled by conductivity, which in lake 4 is almost ten times that of Lake Nasser. This strongly suggests that the huge evaporation rate of $2.5\,\mathrm{m}\ \mathrm{y}^{-1}$ is concentrating the dissolved salts in the Nile water at an alarming rate, and the history of the Toshka lakes might repeat what happened to Birket Qarun in the twentieth century.

4 Biota

Total fecal coliforms were highest in lake 1 in January, at values that are not alarming, while Chl-*a* concentration was highest in lake 1 in May (Table 2) (Anonymous, 2005). The standing crop of total phytoplankton was 37×10^3 cells l^{-1} in lakes 1 and 2, and sharply decreased to 1.6×10^3 cells l^{-1} in lake 4. *Phormidium* sp., *Ceratium* sp., *Peridinium* sp. and *Cymbella* sp. were the only species recorded in the fourth lake. *Najas minor*, *Myriophyllum spicatum* and *Potamogeton lucens* were the main submerged macrophytes that occurred. The second and fourth lakes were poor in zooplankton (average standing crop 5–11 ind m^{-3}), compared with the first lake (average standing crop 16–71 ind m^{-3}). Rotifera was the dominant group, with *Brachionus calyciflorus* and *Keratella cochlearis* abundant. Crustaceans were uncommon, with unidentified cyclopoids present (presumably a *Thermocyclops* species) and Cladocera represented by *Bosmina longirostris* (Anonymous, op. cit.).

Table 1 Some physical and chemical variables of the Toshka lakes (Anonymous, 2005)

		Lake Nasser		Khor Touhka		First Touska lake		Second Touska lake		Fourth Toshka lake	
Abiotic variables		May 2004	Jan. 2005	May 2004	Jan. 2005	May 2004	Jan. 2005	May 2004	Jan. 2005	May 2004	Jan. 2005
Turbidity	(FTUs)	12	2	4	70	13	30	9	36	4	12
Dissolved oxygen	(mg l^{-1})	10.4	12.5	7	12.3	6	7.32	5.4	9.6	6.7	9.7
pH		7.8	7.8	8.2	8.8	8.7	7.9	8.2	7.8	8.3	7.9
Conductivity	µS cm^{-1}	272	189	279	236	344	385	320	604	1,385	1,765
Sulphate	mg l^{-1}	9	11	9	18	42	148	104	142	480	700
Orthophosphate	mg l^{-1}	0.05	0.09	0.01	0.09	0.08	0.02	0.04	1.08	0.09	0.03
Nitrite	mg l^{-1}	0.038	0.01	0.031	0.002	0.05	0.056	0.019	0.005	0.02	0.231
Nitrate	mg l^{-1}	2.4	1.32	4.9	0.7	0.08	0.22	0.01	0.4	1.2	0.44
Ammonia	mg l^{-1}	0.25	0.05	0.23	0.2	0.15	0.31	0.21	0.18	0.19	0.39
Iron	mg l^{-1}	0.19	0.01	0.13	0.03	0.08	0.56	0.14	0.3	0.08	0.02
Chromium	mg l^{-1}	0.05	0.01	0.02	0.03	0.02	0.03	0.01	0.02	0.02	0.02
Copper	mg l^{-1}	0.07	0.18	0.13	0.2	0.05	0.24	0.05	0.22	0.06	0.17

Table 2 Some biotic variables of the Toshka lakes (Anonymous, 2005)

		Lake Nasser		Khor Toshka		First Toshka lake		Second Toshka lake		Fourth Toshka lake	
Abiotic variables		May 2004	Jan. 2005	May 2004	Jan. 2005	May 2004	Jan. 2005	May 2004	Jan. 2005	May 2004	Jan. 2005
Total bacteria	Cells per 100 ml	1,900	3,000	1,600	5,000	3,000	2,900	2,900	1,800	2,900	1,100
Total coliforms	Cells per 100 ml	6,000	2,500	4,800	2,000	1,450	30,000	1,600	18,000	1,750	8,000
Fecal Coliforms	Cells per 100 ml	40	30	30	50	60	2,000	10	900	30	200
Chlorophyll-*a*	µg l^{-1}	2.59	1.5	2.26	3	7.07	4.1	2.44	1.2	1.9	0.4
Zooplankton density	ind l^{-1}	46	12	135	27	71	16	11	5	11	8

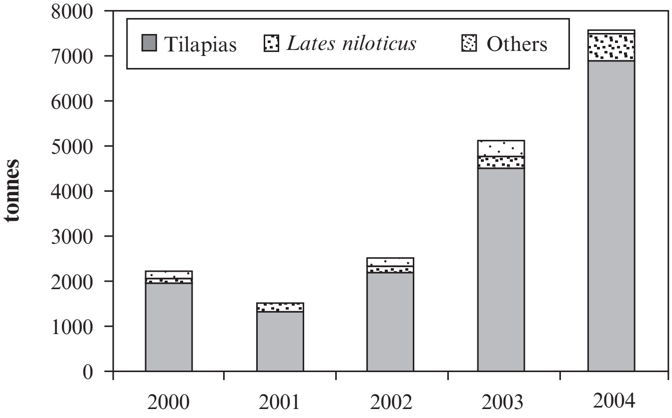

Fig. 3 Fish landings from the Toshka lakes, culminating in 2004. Tilapias and Nile Perch dominate the catch which is expected to have dropped since 2005 (original)

In the beginning, the Nile water carried a freshwater ichthyofauna to the newly formed lakes, and some species tolerant of strong environmental fluctuations survived and adapted. They include *Oreochromis niloticus*, *Lates niloticus*, *Hydrocynus forskalii*, *Sarotherodon galilaeus* and *Alestes nurse*. Beside "wild fish", tilapia fry was released to the first lake, such that *O. niloticus* and *S. galilaeus* formed 60% of the total catch. The Nile Perch *Lates niloticus* contributed another 25%. There are 4, 8 and 40–75 boats that are operational in the first, second and fourth lake, respectively. The fish landings from 2000 to 2004 are shown in Fig. 3. They show a steady increase from 2001 onwards; in 2004, more than 7,000 t of fish was produced. However, it is unlikely that it will be possible to maintain this figure, because of the rapid increase in salinity of the lakes.

Kim & Sultan (2002) and Eugene et al. (2003) estimate that the recharge from these lakes to the Nubian aquifer has been rising over the years (10^5 m^3 y^{-1} in 1998 to 10^6 m^3 y^{-1} in 2002), such that currently the recharge from the Toshka lakes should almost be at par with recharge from Lake Nasser. Therefore, the danger of salination has to be evaluated against the improved recharging of fossil water to the Nubian aquifer, previously being replenished only by Lake Nasser. Bayoumi and Abu-Zeid (2001) summarize the positive impacts of the Toshka lakes as a bonus to the total cultivated area of Egypt, encouraging emigration from over-populated old land to a new agricultural and agro-industrial community. Another benefit is the original aim of reducing the risk of flood impacts in the event of unusually high Nile floods. The main negative aspects are that the lakes evaporate much water and may eventually turn into brines. In the event of repeated below-average Nile flows, keeping the Toshka area flooded would certainly not be a priority, and this would aggravate the salinity situation in the lakes. And, finally, the 1959 agreement about the partition of the Nile water may sooner or later come up for review, in which case the pressure on Egypt can only increase (see Allan, 2009).

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Lake Tana: Source of the Blue Nile

Jacobus Vijverberg, Ferdinand A. Sibbing, and Eshete Dejen

Abstract At 1,830 m altitude, Lake Tana is situated on the basaltic Plateau of the north-western highlands of Ethiopia covering an area of ca 3,050 km^2. It is poor in nutrients and the source of the Blue Nile River (Great Abbay), with a catchment area of ca 16,500 km^2. The Lake has been formed by volcanic activity, blocking the course of inflowing rivers in the early Pleistocene times ca 5 million years ago. The lava also separated the Lake and its headwaters from the lower Blue Nile basin by 40 m high falls at Tissisat, 30 km downstream from the Blue Nile outflow. Terraces suggest that the Lake was originally much larger than it is today. Seven large permanent rivers feed the lake as well as ca 40 small seasonal rivers. The main tributaries to the lake are Gilgel Abbay (Little Nile River), Megech River, Gumara River and the Rib River. Together they contribute more than 95% of the total annual inflow. The Blue Nile is the only outflowing river. The shallow lake (average depth 8 m, max. depth 14 m) is Ethiopia's largest lake, containing half the country's freshwater resources, and the third largest in the Nile Basin. In the main rainy season (July–August) the inflowing rivers carry heavy load of suspended silt into the lake, thereby increasing the turbidity of the lake water. The suspended sediments reduce the under water light intensity and as such the primary production, the basis of the food web. The fish community of the Lake is dominated by cyprinid fishes, 20 of the 27 fish species (e.g. *Labeobarbus* spp., *Barbus* spp., *Garra* spp.) are endemics

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to the Lake catchment. This speciation was possible because the incipient Lake offered new habitats for adaptive radiation and maintained its isolation for millions of years from the lower Blue Nile. Wetlands are located all around the lake, with the exception of the Northeast. Together they are the largest in the country and integral parts of the complex Tana-ecosystem. They consist of permanent swamps, seasonal swamps, and areas subjected to regular inundation. During the raining period these wetlands are connected with the lake. They act as nurseries for most of the fish populations in the lake, and serve as breeding ground for water fowl and mammals. Around the lake and its catchment, including the town of Bahir Dar, live about 2 million people. This lake and adjacent wetlands provide directly and indirectly a livelihood for more than 500,000 people. The Blue Nile drains the NE Ethiopian Plateau (total catchment: 324,000 km^2). Already in ancient Egypt civilization this river was of key importance to early agriculture and today the river is still of critical importance for the economies of Sudan and Egypt.

1 The Lake

At 12°N, 37°15′E, and 1,830 m altitude, Lake Tana is situated on the basaltic plateau of the north-western highlands of Ethiopia covering an area of ca 3,050 km^2. It is the source of the Blue Nile River (Great Abbay), with a catchment area of ca 16,500 km^2 (Fig. 1). Compared to other lakes in the region, the lake has a small catchment to lake area ratio. Seven permanent rivers feed the lake as well as ca 40 small seasonal rivers. The main tributaries to the lake are Gilgel Abbay (Little Nile River), Megech River, Gumara River and the Rib River (Fig. 2). Together they contribute more than 95% of the total annual inflow (Lamb et al., 2007). The Blue Nile is the only outflowing river. The shallow lake (average depth 8 m, max. depth 14 m) is Ethiopia's largest lake, containing half the country's freshwater resources, and the third largest in the Nile Basin.

Based on chemistry, Lake Tana is mesotrophic (Teshale et al., 2001), but based on chlorophyll content and primary production it is oligotrophic (Wondie et al., 2007). Its bottom substrate is volcanic basalt mostly covered with a muddy substratum with only little organic matter (Howell & Allan, 1994). Most of the 37 islands in Lake Tana are small. Two larger islands used to be the seat of Ethiopian Emperors in the distant past. Almost all islands harbour ancient Ethiopian Orthodox Christian churches and monasteries, generally originating from 12–14th century. Daily ferry services transport goods and link major towns around the lake. Tourist traffic is increasing over the last decade offering boat tours for bird watching and visiting monasteries.

Bahir Dar (also written as Bahar Dar), located on the southern border of the lake, is a Regional capital with ca 180,000 inhabitants. Around the lake and its catchment, including the town of Bahir Dar, live about 2 million people. The area around

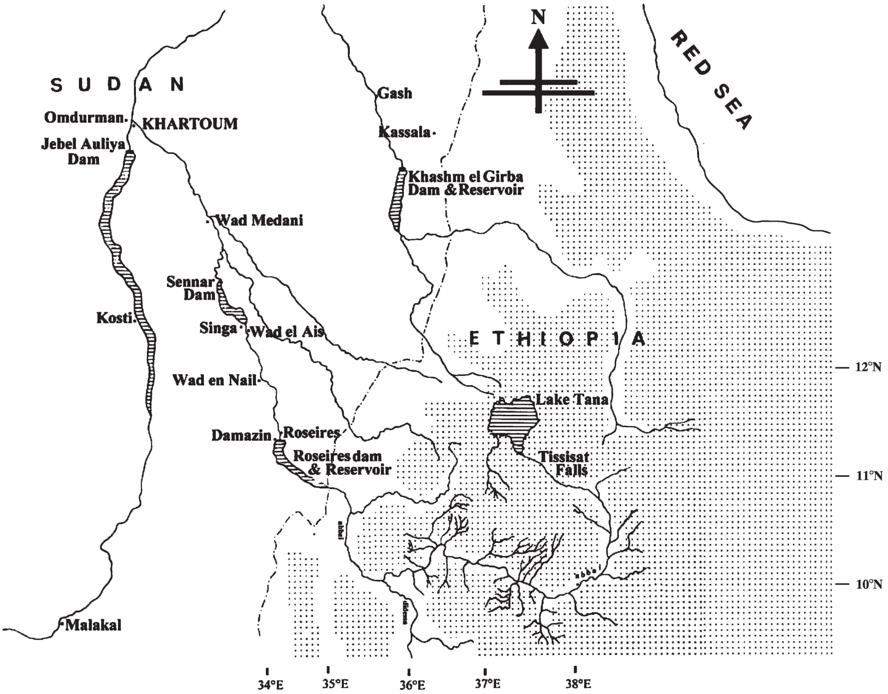

Fig. 1 Map of the Blue Nile system and the location of four large reservoirs in the Sudan of which two, Roseires and Sennar reservoirs, are in the Blue Nile River. Note Lake Tana, the source of the Blue Nile, the Tissisat Falls, 30 km south of L. Tana and the numerous tributaries in the semi circular sweep of the Blue Nile Gorge on its way to the Sudan–Ethiopian border. Dotted areas are over 1,500 m asl (modified after Rzóska, 1976b)

the lake has been cultivated for centuries. This lake and adjacent wetlands provide directly and indirectly a livelihood for more than 500,000 people.

2 Wetlands

The lake is bordered by low plains in the north (Dembea), east (Fogera) and south-west (Kunzila) that are often flooded in the rainy season and by steep rocks in the west and north-west. Wetlands are located all around the lake, with the exception of the Northeast. Together they are the largest in the country and integral parts of the complex Tana-ecosystem. They consist of permanent swamps, seasonal swamps, and areas subjected to regular inundation (Kindie, 2001). During the raining period these wetlands are connected with the lake. They act as nurseries for most of the fish populations in the lake, and serve as breeding ground for water fowl and mammals. Most probably, about half of the *Labeobarbus*

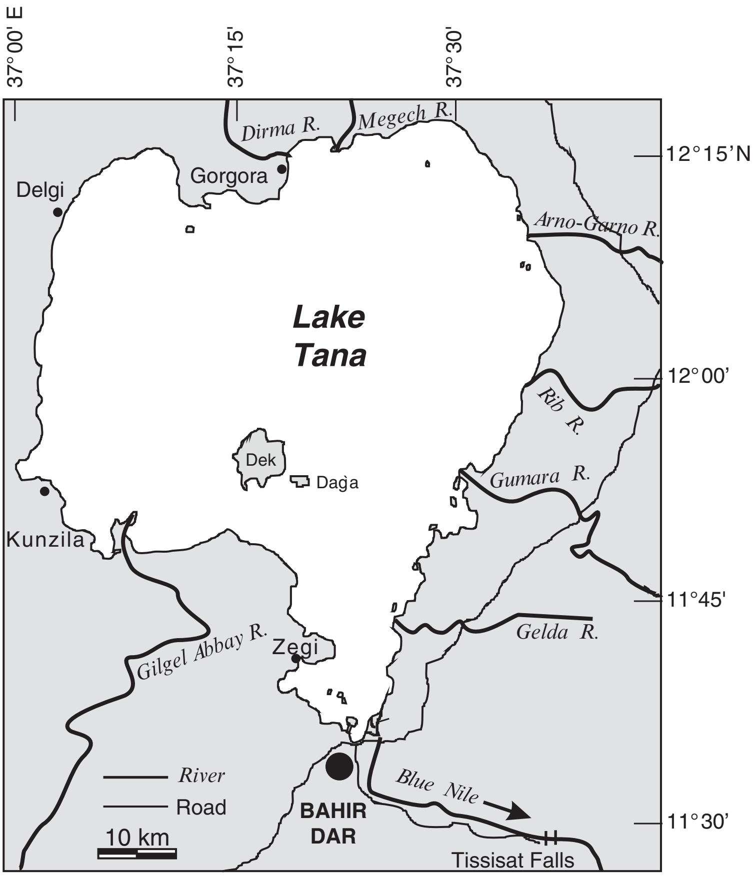

Fig. 2 Map of Lake Tana showing the Gulf of Bahir Dar, where most studies were carried out, the major tributaries and the only outflowing river: the Blue Nile (Abbay) and its falls at Tissisat (modified after Palstra et al., 2004)

species and certainly three other commercially important fish species, Nile tilapia (*Oreochromis niloticus*), African catfish (*Clarias gariepinus*) and Beso (*Varicorhinus beso*) spawn here and their juveniles feed and grow here during the first years of their life.

The littoral region of the eastern and southern part of the lake is dominated by papyrus reed (*Cyperus papyrus*), common cattail (*Typha latifolia*) and common reed (*Phragmites karka*), whereas *Persicaria senegalensis*, hippo grass (*Vossia* spp.), bullrush (*Scirpus* spp.) and *Nymphaea lotus* are common (Muluneh, 2005). Common submersed macrophytes are *Ceratophyllum demersum* and *Vallisneria spiralis*. These wetlands are important resources that supply essential raw materials as fire wood, common reeds (*Typha*, *Phragmites*) and papyrus. When the lake level drops during the dry season hundreds of km^2 of dry lake area become available for agriculture and are used by the farmers to grow crops. The wetlands around the southern Bay of Bahir Dar alone cover ca 1,170 km^2. These wetlands have water for ca 4 months and it is the country's largest rice production area. The livelihoods of ca 3,000 Negada people are totally dependent on the wetland products.

3 Origin and Geology

Lake Tana has been formed by volcanic activity, blocking the course of a number of rivers in early Pleistocene times, ca 5 million years ago (Mohr, 1962). The lava also most likely created the waterfalls at Tissisat (Figs 1 and 2), separating the Lake Tana headwaters from the lower Blue Nile basin. Terraces suggest that the Lake was originally much larger than it is today (Rzóska, 1976a).

Recently collected geophysical and core data show nearly 100 m of accumulated sediments in the lake's bottom substrates (Lamb et al., 2007). In these sediments desiccation layers indicate that the lake dried out at apparent regular intervals during the later stages of the last Ice Age 10,000–25,000 years ago. The data indicate that Lake Tana dried completely out between 18,700 and 16,700 calibrated age (cal) BP, when stiff sediments at the base of the core were deposited. Periphytic diatoms and peat at the base of a core from the deepest part of the lake overlie compacted sediments, indicating that desiccation was followed by development of shallow-water environments and papyrus swamp in the central basin between 16,700 and 15,100 cal BP. As the lake level rose, surface water evaporation from the closed lake caused it to become slightly saline, as indicated by halophytic diatoms. An abrupt return to freshwater conditions occurred at 14,750 cal BP, when the lake overflowed into the Blue Nile (Lamb et al., 2007). Since the lake dried up between 18,700 and 16,700 cal BP, the evolution of the *Labeobarbus*, *Barbus* and *Garra* species, probably took 15,000 years or less. Interestingly, the same happened around the same time in Lake Victoria, where a species flock of *Haplochromis* species evolved in a similarly short time (Johnson et al., 1996).

4 Climate and Water Levels

The climate is typical of semi-arid regions close to the Equator, with a high diurnal temperature variation between day time extremes of 30°C to night lows of 6°C. For a tropical lake, L. Tana has relatively low water temperatures (Dejen et al., 2004), varying only within small limits (range: 20.2–26.9°C) (Table 1). Rainfall may reach up to 2,000 mm per year falling in one rainy season from May to October with one peak during July–August (Fig. 3). The total annual inflow of water to the lake is 10.3×10^9 m^3 yr^{-1} and the outflow as Blue Nile River is ca 36% of this, i.e. 3.7×10^9 m^3 yr^{-1}. The water residence time is ca 3 years (Teshale, 2003). This large difference between inflow and outflow is caused by the high evaporation losses. During October to June evaporation exceeds input via rainfall and during this time many of the inflowing streams dry up completely (Molla & Menelik, 2004). Besides rainfall, two water resources developments have been recently constructed.

Table 1 Environmental characteristics at Southern Gulf of L. Tana from March 2000 to February 2002, annual means ±1 SD, range and the month of minimum and maximum values. Data from Dejen et al. (2004)

Variable	Mean ± SD	Range	Month Minimum	Month Maximum
Temperature (°C)	23.2 ± 1.5	20.2–26.9	January	May
Conductivity (µS cm^{-1})	132.8 ± 11.2	115–147.9	October	February
Chlorophyll-a (µg l^{-1})	6.4 ± 1.1	3.4–12.9	March	January
Oxygen (mg l^{-1})	6.7 ± 0.5	5.9–7.3	December	April
pH	7.7 ± 0.6	6.8–8.3	August	January

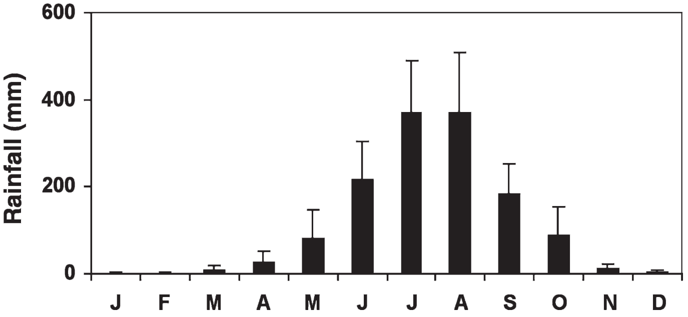

Fig. 3 Mean rainfall for the 10-year period 1992–2002. Error bars represent 1 SD (modified after Wondie et al., 2007)

Around 1995 at the mouth of the Blue Nile a water level regulation weir has been constructed and 30 km downstream of the Blue Nile outflow the Tissisat hydropower plant was build. The construction of the weir serves to increase the water supply for the hydropower plant during the dry season, which is continuously using water from the lake. The 78 MW power plant is connected to the national electricity net and provides electricity for a large part of the country. Water use for the hydroelectric power plant is especially high during the dry season (February–May) because during this time of draught this is often one of the few hydropower plants still operating in the country.

The complex pattern of water losses and inputs can cause large daily and seasonal water level fluctuations. Water levels are highest at the end of the main-rainy season and during the post-rainy period, slowly decreasing to a minimum around the end of the dry season (Fig. 4). The difference between the minimum water level in May–June and the maximum in September–October is generally 2.0–2.5 m. There is a clear trend of decreasing water levels over recent years.

Predominantly southerly winds prevail from January to July, but northerly from August until November (Gasse, 1987). The lake is well exposed to the winds since it is shallow and not protected by vegetation, except on the south-west side which is forested (Zegi Peninsula). Wind speeds show a pronounced diurnal pattern, during the night and morning wind speed is generally below 1.5 m s^{-1}, but in the afternoon starting at noon and going on until the evening (7 pm) wind speeds are generally between 3.0 and 4.8 m s^{-1}. Although a stable thermocline is lacking (Dejen et al.,

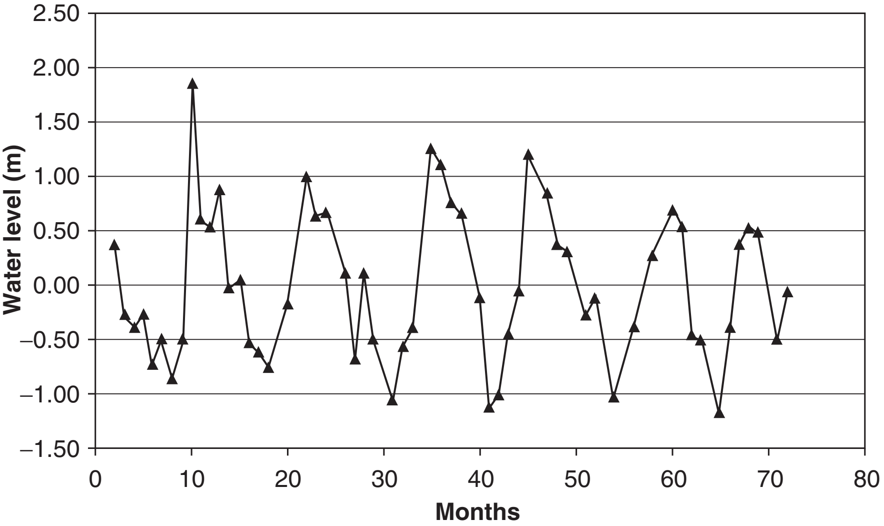

Fig. 4 Temporal variation of relative water level (meters) of Lake Tana's surface during 1996–2002 (source: European Space Agency)

2004), a thermal stratification of short duration (i.e. several hours) may occur especially during the dry season in the morning.

5 Erosion and Silt Load

During the last 15 years deforestation became common practise in the Lake Tana catchment, facilitating conditions for soil erosion. The catchment area of the Lake (ca 16,500 km^2) has a dendritic type of drainage network. Due to this type of drainage, scanty vegetation and high rainfall during short periods in the main rainy season, the soil loss rate from areas around the lake is high (31–50 tons ha^{-1} yr^{-1}) and showed a substantial increase during recent years. Soil loss rates are especially high in the eastern part of the lake, i.e. 5–250 tons ha^{-1} yr^{-1}, and lowest on the western side of the lake (Teshale et al., 2001; Teshale, 2003).

In the main rainy season (July–August) the four major inflowing rivers carry heavy load of suspended silt into the lake, thereby increasing the turbidity of the lake water (Fig. 5) (Wondie et al., 2007). The suspended sediments reduce the under water light intensity and as such the primary production, the basis of the food web.

6 Nutrients, Water Mixing and Primary Production

The lake is characterised by low nutrient concentrations, and a low water transparency due to high silt load of the inflowing rivers during the rainy seasons (May–October) and daily resuspension of sediments in the inshore zone (Table 1, Fig. 5).

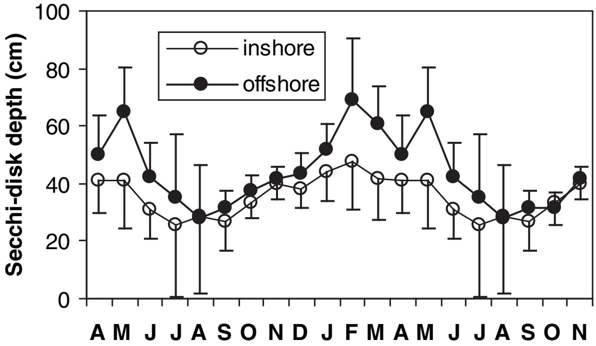

Fig. 5 Seasonal variations in water transparency at inshore (open symbols) and offshore stations (closed symbols) of Lake Tana measured as Secchi-disk depth (cm) for the period April 2003 to November 2004. Error bars represent +1 SD for the offshore and −1 SD for the inshore zone. Sampling at six sites all around the lake (with the exception of the western part), each with one sampling station inshore (ca 250 m from the shore at depth <3.5 m), and one station offshore (ca 1,500 m from the shore at depth >4 m). Six observations per sampling date for inshore and offshore zone, respectively. Note that the transparency is lowest inshore in the rainy season (modified after Wondie et al., 2007)

The phytoplankton was dominated by Cyanobacteria and Bacillariophyceae; Chlorophyta were less abundant (Wondie et al., 2007). Cyanobacteria were dominant in the post-rainy season (October–November), whereas diatoms were dominant during the dry (December–April) and the pre-rainy season (May–June). Cyanobacteria were dominated by two *Microcystis* species of which *M. flos-aquae* was the most abundant and *Anabaena flos-aquae*, *Planktolyngbya limnetica* were co-dominant. Diatoms are dominated by *Melosira varians* and five species of *Aulacoseira* (formerly named *Melosira*) *A. assizi, A. ambigua, A. granulata, A. muzzanensis* and *A. distans*, of which *A. granulata* is the most dominant (>50% of *Aulacoseira* spp. combined). *Staurastrum triangularis* dominated the Chlorophyta. The mean chlorophyll-a concentrations varied seasonally and ranged from 2.6–8.5 mg m^{-3} (mean: 4.5 mg m^{-3}) in the offshore zone (Wondie et al., 2007). Gross primary production in the offshore zone averaged 2.43 g O_2 m^{-2} d^{-1} and ranged between 0.03 and 10.2 g O_2 m^{-2} d^{-1}; production was significantly higher inshore. The highest production rates were observed in the post-rainy season (October–November) which coincided with a bloom of *Microcystis* and higher chlorophyll levels. This seasonal high production is probably caused by a relatively high nutrient availability in combination with favourable light conditions.

The gross primary production rates of L. Tana are among the lowest, compared with other tropical lakes (Wondie et al., 2007). This is primarily the result of the oligotrophic nature of the lake in combination with its relatively low water transparency. The gross primary production per unit chlorophyll in the offshore zone was in the same range as in 30 other tropical lakes and reservoirs. A large proportion of the annual primary production is realised in one of the four seasons only. This productive post-rainy season is relatively short (2 months) and therefore efficiency of transfer of matter between the first and second trophic level of the Lake ecosystem will be poor.

7 Benthic Invertebrates

Macrobenthic invertebrates such as oligochaetes, *Chaoborus* spp. and chironomids, show low densities both inshore and offshore (Vijverberg, unpublished; Tewabe et al., 2005). Chironomid larvae showed also low densities in the zone with submersed macrophytes (*Ceratophyllum demersum*) near the shore, but because of their relative large individual size macrobenthic biomass per m^2 was highest in this area. However, this area is very small (<1%) compared to the surface area of the lake. In contrast the microbenthic ostracods show relatively high densities in the inshore zone (4,000–60,000 ind m^{-2}), but were lacking in the offshore area of the lake. The low densities of benthic invertebrates may be caused by the low content of organic matter in the bottom substrates, which consists of volcanic basalts usually covered with a muddy substratum, transported by the inflowing rivers, which contains only little organic matter. The organic matter content in the offshore substrates is only ca 1.2%, but slightly higher values of ca 3.8% are found near to the shore at a depth of ca 0.25 m (Tewabe et al., 2005).

8 Macrofauna Associated with Macrophytes

The macrofauna associated with macrophytes of the submersed vegetation (*Ceratophyllum demersum*), the low emergent vegetation (dominated by *Persicaria senegalensis*) with submersed vegetation present, and the 100–200 cm high emergent vegetation dominated by reeds (*Phragmites karka*) and bulrush (*Typha latifolia*) with submersed vegetation present were studied by Vijverberg (unpublished) and Tewabe et al. (2005). Densities and biomass of macrofauna taxa in the macrophyte beds – sampled with a sweep net – are relatively high. Especially Ephemeroptera (mayfly larvae) and Odonata (dragonfly larvae) showed relatively high densities, whereas densities of Acari (water mites), chironomids, gastropods and Hemiptera (water bugs) were relatively low. In terms of biomass Odonata dominate the weed beds, due to their large individual weight, but Ephemeroptera showed the highest densities. Dumont (1983) reported 14 species of adult dragonflies along the shores of L. Tana at Bahir Dar (see also Dumont, 2009). Tewabe et al. (2005) observed the highest densities (1,000–1,600 ind m^{-2}) of Ephemeroptera larvae in December–February, intermediate densities (200–500 ind m^{-2}) in March and October–November and very low densities (0–100 ind m^{-2}) in April–September. Gastropods include the endemic subspecies *Bellamaya unicolor abyssinica* and *Bulinus* spp., host to *Schistosoma haematobium*, the trematode causing bilharzia (Bacci 1951/52). Of the 15 species observed 4 are of palearctic origin, i.e. *Theodoxus africanus* (Reeve), *Radix pereger* (Müll), *Unio elongatulus dembeae* (Slowerby) and *Unio abyssinicus* Martens.

9 Crustaceans and Zooplankton

The largest crustaceans are freshwater crabs of the genus *Potamonautes*, but they are fairly rare (Nagelkerke, 1997; see also Cumberlidge, 2009). Since these species are generally associated with flowing water higher densities are expected to be present in the inflowing rivers and the Blue Nile. There have been few previous studies on zooplankton in Lake Tana. The first general account of the aquatic fauna and flora of the lake was documented by Brunelli and Cannicci (1940) and Rzóska (1976a). The freshwater medusa *Limnocnida indica* has been cited regularly during the last 30 years (Thiel, 1973; pers. obs.), but the species living in Lake Tana may really be *L. tanganjikae* (see Dumont, 2009). The densities of littoral Cladocera are relatively low (Brunelli & Cannicci, 1940; Dumont, 1986a).

Zooplankton dynamics were recently studied by Dejen et al. (2004). Of the limnetic species, four copepods and nine cladocerans were identified, 11 of these together contributed more than 99% of all individuals collected (Table 2). Approximately half of the numbers encountered were copepods and the other half cladocerans. The calanoid copepod *Thermodiaptomus galebi lacustris*, dominated the zooplankton community, and is endemic for L. Tana. Of the three cyclopoid copepod species, *Thermocyclops ethiopiensis* was the most abundant. *Bosmina longirostris*, *Daphnia hyalina*, *Daphnia lumholtzi* and *Diaphanosoma sarsi* were the most abundant cladoceran species. Of the two rarely encountered species, *Microcyclops varicans* and *Chydorus sphaericus*, the latter species is probably predominantly littoral and associated with macrophytes. We observed it offshore in low densities, but we found high abundances in the gut

Table 2 Microcrustacean zooplankton species found in Lake Tana with their mean relative abundance (n, %). Data from Dejen et al. (2004)

Species	Relative Abundance (%)
Copepoda	
Mesocyclops aequatorialis similis♦ Van de Velde, 1984	4.2
Microcyclops varicans (G.O. Sars, 1863)	<0.1
Thermocyclops ethiopiensis Defaye, 1988	15.2
Thermodiaptomus galebi♦ *lacustris* Defaye, 1988	31.2
Cladocera	
Bosmina longirostris♦ (O. F. Müller, 1776)	13.9
Ceriodaphnia cornuta♦ Sars, 1885	0.3
Ceriodaphnia dubia♦ Richard, 1894	1.4
Chydorus sphaericus♦ (Müller, 1785)	<0.1
Daphnia hyalina♦? Leydig, 1860	9.1
Daphnia lumholtzi♦ Sars, 1885	8.1
Diaphanosoma excisum♦ Sars, 1885	3.3
Diaphanosoma sarsi♦ Richard, 1894	10.8
Moina micrura♦ Kurz, 1874	2.5

♦ = also present in the Blue Nile River (Dumont, 1986a).

contents of littoral feeding fish. *Daphnia hyalina* was identified following Flössner (2000) and confirmed by using mitochondrial DNA sequences from the small subunit ribosomal RNA (Schwenk et al., 2000). This species was not reported before in Lake Tana, but was probably previously wrongly identified as the closely related *D. longispina* (see Dumont, 1986a).

Annual production of the calanoid *T. galebi* and total cyclopoid copepods was similar, ca 380 and 310 mg dwt m^{-3} respectively, which is low when compared to other tropical lakes (Wondie & Mengistu, 2006). The zooplankton community structure of L. Tana is unusual for tropical lakes because of its relatively high proportion of temperate species, i.e. *Daphnia hyalina*, and *Ceriodaphnia dubia*. Most probably this effect is due to its high altitude resulting in relatively low water temperatures in the lake. The addition of temperate species to its zooplankton community resulted in a relatively high biodiversity of limnetic microcrustacean zooplankton in this lake. Significant temporal differences in copepod and cladoceran abundance were observed, with highest densities during the dry season. Zooplankton abundance was negatively affected by turbidity, but not all species were affected to the same degree. *Daphnia* spp. were most strongly affected and *Diaphanosoma* spp. to the least extent. Cladocerans showed significant higher densities in the sublittoral zone, but copepods showed similar densities in littoral, sublittoral and offshore.

10 Fish Species

Twenty of the 27 fish species of Lake Tana are endemics to the Lake Tana catchment (Table 3). This speciation was possible because the incipient Lake offered new habitats for adaptive radiation and maintained its isolation since ca 5 million years from the lower Blue Nile basin by 40 m high falls (Fig. 6), 30 km downstream from the Blue Nile outflow (Fig. 2) (Sibbing et al., 1998). In case of the *Labeobarbus* species (15 endemic species out of 16), their niche divergence was responded by a divergence in their immune system, since molecules involved in recognizing different antigens differentiated accordingly during evolution (Dixon et al., 1996; Kruiswijk et al., 2005).

There is only one cichlid, *Oreochromis niloticus* (Nile tilapia), which is the most widespread tilapia species in Africa. This species is predominantly a herbivore, feeding on macrophytes, algae and detritus (Table 3). The catfish family (Clariidae) is also presented by a single species, *Clarias gariepinus* (African catfish), the most common member of its genus. This species is a facultative piscivore, feeding occasionally besides fish also on zooplankton, benthic invertebrates and algae. The obscure loach, *Nemacheilus abyssinicus* (Balitoridae), was only once found in the Lake itself (Nagelkerke, 1997), and was also found in small streams of the Lake Tana catchment and in large parts of the Ethiopian high plateau (Dgebuadze et al., 1994). Interestingly, this loach is the only species from this Palaearctic family known from Africa.

The most species-rich fish family in the lake are the cyprinids, represented by four genera: *Varicorhinus*, *Garra*, *Labeobarbus* and *Barbus*. *Varicorhinus* is represented

Table 3 The fish species of Lake Tana, their taxonomic group, maximum length (Fork Length, cm), relative abundance, food and habitat

Family	Species	Maximum Length (FL, cm)	Abundance	Food	Habitat
Balitoridae	_Nemacheilus abyssinicus_	3.6	Rare	Algae	Benthic
Cichlidae	_Oreochromis niloticus_♦	40	Common	Macrophytes, algae-detritus	Pelagic, littoral, sublittoral
Clariidae	_Clarias gariepinus_♦	70	Common	Fish, zooplankton, benthic invertebrates, algae	Pelagic, littoral, sublittoral
Cyprinidae	_Barbus tanapelagius_*	8.9	Common	Zooplankton	Pelagic, sublittoral, offshore
	B. humilis	9.6	Common	Zooplankton, benthic invertebrates	Benthic, littoral, sublittoral
	_B. pleurogramma_*	4.0	Common	Benthic invertebrates	Benthic, wetlands, flood planes
	Garra dembecha	17.0	Common	Algae	Benthic
	Garra dembeensis♦	12.0	Rare?	Algae	Benthic
	_G. regressus_*	13.5	Common	Algae	Benthic
	_G. tana_*	12.0	Common	Algae	Benthic
	_Labeobarbus acutirostris_*	41	Common	Fish	Benthic, inshore
	_L. brevicephalus_*	32	Common	Zooplankton, adult insects	Pelagic, sublittoral, offshore
	_L. crassibarbus_*	51	Common	Detritus, benthic invertebrates	Benthic, sublittoral, offshore
	_L. dainellii_*	49	Occasional	Fish	Littoral
	_L. gorgorensis_*	62	Occasional	Benthic invertebrates, bivalves	Pelagic, littoral, sublittoral, offshore

*L. gorguari**	53	Occasional	Fish	Littoral
L. intermedius♦	49	Common	Benthic invertebrates, gastropods, macrophytes	Benthic, littoral
*L. longissimus**	61	Occasional	Fish	Pelagic, littoral, sublittoral
*L. macrophtalmus**	43	Common	Fish, benthic invertebrates, detritus	Pelagic, sublittoral, offshore
*L. megastoma**	82	Common	Fish	Pelagic, littoral, sublittoral, offshore
*L. nedgia**	71	Common	Insect larvae, benthic invertebrates	Benthic, littoral
*L. osseensis**	29	Rare	Adult insects, macrophytes	Littoral
*L. platydorsus**	64	Common	Fish, insect larvae, molluscs, detritus	Benthic, sublittoral, offshore
*L. surkis**	43	Occasional	Macrophytes, algae, benthic invertebrates	Pelagic, sublittoral
*L. truttiformis**	44	Occasional	Fish	Pelagic, sublittoral, offshore
*L. tsanensis**	39	Common	Insect larvae, gastropods, benthic invertebrates	Benthic, sublittoral, offshore
Varicorhinus beso♦	36	Common	Benthic algae	Benthic, littoral

* = endemic to Lake Tana catchment. Data from Nagelkerke and Sibbing (2000), De Graaf et al. (2006), Dejen et al. (2006a) and Vijverberg (unpublished). ♦ = also present in the Blue Nile River (Abu Gideiri, 1967; Banister, 1973). Habitats refer to: benthic = predominantly present near the bottom in the lower part of the water column, pelagic = predominantly present in upper part of the water column, littoral = inshore with or without macrophytes (0–4 m deep), sublittoral = inshore without macrophytes (4–8 m deep), offshore = openwater (8–14 m deep).

Fig. 6 The high (40 m) Tissisat Falls ('The smoking waters falls'), 30 km downstream from the Blue Nile outflow. The falls effectively isolate the lake's fish community from the lower Nile basin. During the rainy season the waterfall is 400 m wide and is the second largest of Africa (photo by F.A. Sibbing) (*see Color Plates)*

by a single species *V. beso* Rüppell which scrapes algae from substrates, and a common species in the rivers and lakes of the Ethiopian Highlands. The genus *Garra* is represented by four species in Lake Tana, *G. dembecha* Boulenger which is common and generally distributed in the Ethiopian Highlands, *G. dembeensis* Rüppell which is widely distributed all over Africa and although common in Ethiopia rare in Lake Tana, and two endemic species, *G. regressus* and *G. tana*, recently described by Stiassny and Getahun (2007). All four species are algivorous.

Fifteen large (max. 82 cm fork length, FL) hexaploid labeobarbs (*Labeobarbus* spp.) (Fig. 7, Table 3) belong to a unique species flock of endemic cyprinids as was supported by mtDNA markers (de Graaf et al., 2003c). Surprisingly eight of these are piscivores (de Graaf et al., 2003a, 2008). Many of the labeobarb species predominantly inhabit the large offshore zone as adults, whereas the juveniles probably occupy the inshore zone among macrophytes and/or in the adjacent wetlands. The only non-endemic labeobarb species present, the polymorph shore complex of *L. intermedius*, is probably most ancestral to this labeobarb species flock and a riverine generalist who feeds mainly on macrofauna associated with macrophytes and benthic invertebrates. *Labeobarbus intermedius* can be found all over Ethiopia in lakes and rivers (Banister, 1973). The fish community contains, furthermore, three diploid species of small (<11 cm FL) barbs: *Barbus humilis* Boulenger, *B. pleurogramma* Boulenger and the recently discovered *B. tanapelagius* (de Graaf et al., 2000). The latter two species are endemic to the

Fig. 7 A large *Labeobarbus megastoma* caught by commercial fishermen (photo by F.A. Sibbing) (*see Color Plates)*

L. Tana catchment, *Barbus pleurogramma* is mainly present in the wetlands around the lake, whereas *B. tanapelagius* is common in the large pelagic zone of the lake. *B. humilis* was assumed to be endemic to Lake Tana too, but was recently collected from the Beshilo River in the Ethiopian Plateau (Amhara Region, Wollo province). The last two named species have a long breeding period (from March to September) and the distinct bimodal size frequency distribution of eggs suggest multiple spawning for both species. The range of fecundity in both species (172–339 eggs per gram) was low compared with small lacustrine cypinids and clupeids from other African lakes (Dejen et al., 2003).

11 Evolution of *Barbus* and *Labeobarbus* Species

Barbus humilis is a riverine species, distributed in the littoral and sublittoral of the Lake and its inflowing rivers. Most likely *B. tanapelagius* evolved out of a *B. humilis* like ancestor following the rise of large pelagic zooplankton resources after the lake filled again with water approximately 15,000 years BP. Investigations on the phylogenetic relationships of the two barbs using the mtDNA cytochrome b gene showed that the genetic divergence between the two species is very low (de Graaf et al., 2007).

The 15 large labeobarb species (*Labeobarbus*) compose a world unique concentration of endemic cyprinid fish (Nagelkerke & Sibbing, 2000). The species occupy different habitats as characterised by water depths and substratum types (Nagelkerke et al., 1994). Seven of these species do not spawn in the lake itself, but in the permanent rivers (de Graaf et al., 2005). These seven species do not show spatial segregation among inflowing rivers but significant temporal segregation occurs in aggregating in the river mouths and in migrating towards the upstream spawning areas during the breeding season (June–October). Among the eight other species, peak gonad development occurs generally in the same period as in the riverine spawners, but they do not aggregate in the river mouths during the breeding period and are absent from the upstream spawning areas (Palstra et al., 2004). Most probably, they spawn in the wetlands where also their juveniles feed and grow, possibly extending their spawning season beyond the two rainy months.

Evolution most likely went according to the following scenario (Nagelkerke & Sibbing, 1996). After Lake Tana was formed, through volcanic blocking of the Blue Nile River, a population of riverine labeobarbs was present. This was probably a species resembling the riverine *L. intermedius*, which to day is still found all over Ethiopia both in rivers and in lakes. The *L. intermedius* populations are known to be highly variable in morphology (Mina et al., 1996). After Lake Tana was formed, an extensive new lake area, providing new lacustrine habitats with their specific resources, became available. Around this time a wave of habitat radiation probably occurred, followed by a trophic radiation (de Graaf et al., 2008). The incipient morphotypes might have radiated into different niches driven by competition for space and trophic resources. This sequential adaptive radiation probably started from the inshore areas which, because of the presence of macrophyte vegetation, look more like a riverine habitat than the offshore zone of the lake. Genetically based morphological differentiation resulting from disruptive selection became fixed by assortative mating. In the riverine spawning species this occurred by temporal segregation during the aggregating phase in the river mouths and during the migration phase towards the upstream spawning areas. How segregation occurred among the species presumably spawning in wetland areas is not known.

12 Fish Community Structure and Food Utilisation

The *Barbus* and *Labeobarbus* species dominate the fish community in terms of biomass and production (Fig. 8). The total annual *Labeobarbus* production was ca 32 kg ha^{-1} yr^{-1}, of which the piscivorous *Labeobarbus* species account for 12% (3.8 kg ha^{-1} yr^{-1}) (Wudneh, 1998). Annual production of *B. humilis* was ca 3.7 kg ha^{-1} yr^{-1}, based on a P/B ratio of 3.94. For *B. tanapelagius* this amounts to 23.6 kg ha^{-1} yr^{-1}, given a P/B ratio of 3.88. Total annual production of both small barb species in Lake Tana is estimated at 27.3 kg ha^{-1} yr^{-1} (Dejen et al., submitted).

Zooplankton is highly utilised by the fish community (Dejen et al., 2006a). The three *Barbus* spp., the juveniles of all 15 *Labeobarbus* spp. and the adults of *L. brevicephalus* feed all on zooplankton. *Barbus tanapelagius* is, however, the only obligate zooplanktivore since the other species utilise also other animal food items. *Barbus pleurogramma* maintains the most benthivorous diet, whereas *B. humilis,* juvenile labeobarbs and *L. brevicephalus* feed for ca half (by biovolume) their

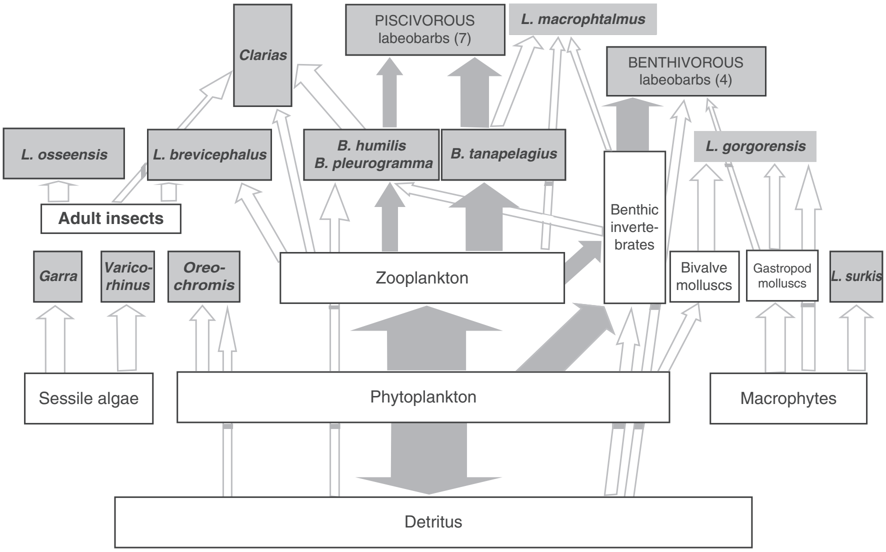

Fig. 8 Food web of L. Tana with emphasis on the fish community. Grey blocks represent fish species, white blocks food resources. Grey arrows indicate the systems main streams through zooplankton and benthos. Width of arrows reflects the contribution of a food type in the diet of a species. For benthivorous and piscivorous labeobarbs, number of species between brackets (*see Color Plates)*

diet on zooplankton and for the other half on adult floating insects, insect larvae and benthic invertebrates. *Barbus tanapelagius* and the adults of *L. brevicephalus* occupy the same habitat, the large pelagic. They differ, however, in feeding modes and utilization of zooplankton (Dejen et al., 2006a). Both species positively select *Daphnia* as prey item. Especially *B. tanapelagius* was infected (10%) by the cestode *Ligula intestinalis* after feeding on infected cyclopoid copepods (Dejen et al., 2006b).

Eight species of the fifteen endemic *Labeobarbus* species (more than 65% of all labeobarbs) are piscivorous, four are obligate piscivorous (>80% fish in *L. acutirostris*, *L. truttiformis, L. longissimus* and *L. megastoma*) and four others are facultative piscivores (>60% fish in *L. dainellii*, *L. gorguari*, *L. macrophtalmus*, *L. platydorsus*) (Sibbing & Nagelkerke, 2001). Experiments showed, however, that these piscivores are clumsy predators (de Graaf et al., 2003b) not being able to feed on fish larger than 15% of their fork length, most probably because they have a narrow pharyngeal slit and lack teeth on their oral jaws (Fig. 9). These species may only survive because specialised and more efficient non-cyprinid piscivores are lacking, whereas the abundant small barbs exactly match their potential prey size (6 cm FL barbs for a 40 cm FL labeobarb). Lake Tana is an evolutionary laboratory showing in an experiment by nature how among labeobarbs the potentials for piscivory are developed to the fullest. The piscivorous niche of these co-occurring species is segregated by habitat, diet composition and prey size (de Graaf et al., 2008). The main prey items eaten and matching their optimal prey size were *B. humilis*

Fig. 9 The 'clumsy' piscivorous labeobarbs of Lake Tana, showing lack of teeth on oral jaws and a narrow pharyngeal slit (*Labeobarbus megastoma*, photo by F.A. Sibbing) (*see Color Plates)*

(40% of the gut contents), *B. tanapelagius* (32%) and *Garra* species (21%). Therefore, the two small barbs form the main link between the zooplankton and the piscivorous fish in the food web of the Lake.

Besides piscivores, there are five other trophic groups of labeobarbs (Table 3, Fig. 8). One species feeds mainly on macrophytes (*L. surkis*), one upon macrophytes and molluscs (*L. gorgorensis*), one species on macrophytes and adults insects (*L. osseensis*), one species predominantly on zooplankton (*L. brevicephalus*) and four species are benthivorous feeding mainly on chironomid larvae and on macrofauna associated with macrophytes (*L. crassibarbus*, *L. intermedius*, *L. nedgia*, *L. tsanensis*).

13 Birds, Reptiles and Mammals

Lake Tana and its wetlands are rich in bird life, in total ca 215 bird species were observed of which ca 83 typical wetland species (van Perlo, 1995; Frances & Aynalem, 2007; see also Green, 2009). Piscivorous species include residents such as African spoonbill (*Platalea alba*), yellow-billed stork (*Mycteria ibis*), pied kingfisher (*Ceryle rudis*), giant kingfisher (*Megaceryle maxima*), little grebe (*Tachybaptus ruficollis*), great white pelican (*Pelecanus onocrotalus*), great and long-tailed cormorants (*Phalacrocorax carbo*, and *P. africanus*), African darter (*Anhinga rufa*), many species of herons (*Ardeola* spp., *Egretta* spp., and *Ardea* spp.), and African fish eagle (*Haliaeetus vocifer*). The density of fish eating birds is invariably higher in the shallow inshore zones of the lake and its wetlands than in the offshore region of the lake. Grey crowned crane (*Balearica regulorum*), common crane (*Grus grus*), greater flamingo (*Phoenicopterus ruber*), African open-billed stork (*Anastomus lamelligerus*), woolly-necked stork (*Ciconia episcopus*), sacred ibis (*Threskiornis aethiopica*), glossy ibes (*Plegadis falcinellus*), Hadada ibis (*Bostrychia rara*), hamerkop (*Scopus umbretta*), Egyptian goose (*Alopochen aegypticus*), spur-winged goose (*Plectropterus gambensis*) and the African pygmy goose (*Nettapus auritus*) are the most conspicuous non-piscivorous aquatic birds. Palaearctic migrants include osprey (*Pandion haliaetus*), great black-headed, lesser black-backed and herring gulls (*Larus ichthyaetus*, *L. fuscus*, and *L. argentatus*), and whiskered and white-winged black terns (*Chlidonias hybridus* and *C. leucopterus*) (Nagelkerke, 1997).

The largest reptiles are the Nile monitor (*Varanus niloticus*) and a python (*Python sebae*) of which the latter is rare. There are few aquatic mammals. The Hippopotami are mainly restricted to the river mouth of the Blue Nile. Otters are caught sometimes in the nets of the fishermen. Amphibians, especially Anurans are mainly present in the marshy shore-areas.

14 Fisheries

The maximum sustainable yield for Lake Tana fishery is only ca 4 kg ha^{-1} (10,000–15,000 tons for the whole lake), which is low compared with the Ethiopian Rift valley Lakes (ca 10 kg ha^{-1}) and other tropical African lakes physically similar to Lake Tana (10–100 kg ha^{-1}) (Pitcher, 1995). There are fish processing and marketing enterprises in Bahir Dar. Traditionally, Lake Tana fisheries consisted of mainly artisanal predominantly subsistence fishery conducted from papyrus reed boats (tankwa's, Fig. 10), which resemble those of ancient Egypt. The fishermen, who are using mainly fish traps and small gill nets, are almost exclusively members of the Negede Woito tribe.

Fig. 10 A traditional fisherman of L. Tana using a papyrus reed boat (tankwa) and a fish trap made from reeds (photo by F.A. Sibbing) (*see Color Plates)*

Since 1986 a motorized commercial gillnet fishery was developed by the Ethiopian Orthodox Church in cooperation with an interchurch NGO and fishermen from Urk (Netherlands). Commercial catches of large barbs in Lake Tana initially (1987–1997) increased six fold (Wudneh, 1998). However, over the last decade they have sharply decreased, due to overfishing during fish migration to their spawning rivers (de Graaf et al., 2004; see also Chapter on Fisheries by Witte et al., 2009).

The three main species groups targeted by this fishery are a species flock of endemic, large *Labeobarbus* spp., African catfish (*Clarias gariepinus*) and Nile tilapia (*Oreochromis niloticus*) (Table 4). The commercial gillnet fisheries was monitored during 1991–1993 and in 2001 in conjunction with an experimental trawling program (de Graaf et al., 2006). In the experimental fishery large specimens of African catfish (>50 cm) and Nile tilapia (>20 cm) decreased significantly over ca 10 years time, but recruitment of young fish to the adult populations was not negatively affected. During the same period the commercial catch of riverine spawning *Labeobarbus* spp. declined with 75%. In the experimental fishery a similar decrease was observed and the populations of juvenile labeobarbs in the littoral (length range: 5–18 cm) decreased even by more than 85% (de Graaf et al., 2006). The major reason for the collapse of these fish species is due to destructive fishing during their spawning season. These species form aggregations in the river mouths in August–September, during which period they are targeted by the commercial gillnet fishery. Overfishing of labeobarbs near and in rivermouths and upstream in the rivers on and near the spawning grounds by traditional fishermen and opportunistic farmers reduced their densities to a very low level. Additionally destruction

Table 4 Lake Tana: Fish ecology and susceptibility to fisheries. Based on information from de Graaf et al. (2006)

	Labeobarbs	African Catfish	Nile Tilapia
Reproductive Biology			
Spawning period	2 months August–September	4 months June–September	All year
Spawning aggregations	River mouths	None	None
Spawning areas	Floodplains, upstream rivers	Floodplains	Floodplains
Ecology			
Diet	Specialists	Generalist with broad diet spectrum	Generalist feeding mainly on algae and detritus
Habitat	Specialists	Bottom-dwelling All over the lake	Water column Inshore zone
Growth			
Age at maturity	3–5 years	2–3 years	1–2 years Highly flexible
Susceptibility to Fisheries	High Vulnerable	Moderate Resilient	Low Most resilient

of spawning grounds by farmers who build small scale irrigation channels for their agricultural lands contributes to the reduced recruitment. It is clear that in case of the migrating labeobarbs recruitment-overfishing is taking place and that the seven species of this unique species flock are in danger of becoming extinct.

Fisheries on the small barbs is no common practise in Lake Tana, although small fish are caught and dryed especially on the island Dek. *Barbus tanapelagius* would be the most safe target for fisheries since it is spatially segregated from the juvenile large barbs (Dejen et al., 2006a). However, night fishing using strong lights, as applied in Lake Victoria for catching *Rastrineobola*, only yields small catches in Lake Tana, probably because of its lower fish densities and its high turbidity (Eshete Dejen, pers. comm.).

15 Blue Nile

Lake Tana is the source of the Blue Nile (Great Abbay), and not as most Ethiopians believe the Little Nile (Gilgel Abbay, Fig. 2) which is the most important tributary. It springs lie ca 100 km south of the lake. The Blue Nile drains the NE Ethiopian Plateau (total catchment: 324,000 km^2) (Fig. 1). The name 'Blue Nile' is misleading and an incorrect translation of the Arabic name 'Al Bahr al Azraq' meaning 'dark' Nile. The latter name is very appropriate because in the rainy season when the river flow rate is highest, the water has a dark reddish-brown muddy colour because of all the sediments it contains. Already in ancient Egypt civilization this river was of key importance to early agriculture and today the river is still of critical importance for the economies of Sudan and Egypt. Since L. Tana was dry between 18,700 and 16,700 cal BP and did not reach overflow until 14,750 cal BP, when base flow was re-established, the Blue Nile must have been reduced to an intermittent seasonal flow during 18,700–14,750 cal BP. During that period without base flow, it must have been totally dependent on intermittent inflows from tributary streams in a rainfall regime that was significant drier than that of today (Lamb et al., 2007).

The source of the Blue Nile was first discovered by a Portuguese Jesuit, Fr. Pedro Paez, in 1613. The Blue Nile descends from the Ethiopian high plateau (Fig. 11). The mean annual outflow is about 3.7 km^3 per year, which is only ca 8% of the total flow of the Blue Nile (Teshale et al., 2001). It receives a great number of tributaries in its upper course in the Ethiopian Highlands and two more tributaries in its lower course in Sudan. Although the Blue Nile flows for fewer miles than its sister the White Nile and has a relative small drainage area, it carries 60–69% of the total discharge and a vastly greater proportion of its transported sediment (Dumont, 1986b). Most of the water flows during the rainy season from May to October each year. Annual river flow is on average ca 46 km^3, but there are strong annual variations associated with variations in rainfall (Conway, 2000).

After leaving the lake the Blue Nile flows to the south-east before descending over the high (ca 40 m) Tissisat Falls ('Smoking waters' falls), 30 km downstream from its outflow (Figs 1 and 2). The falls effectively isolate the lake's fish community

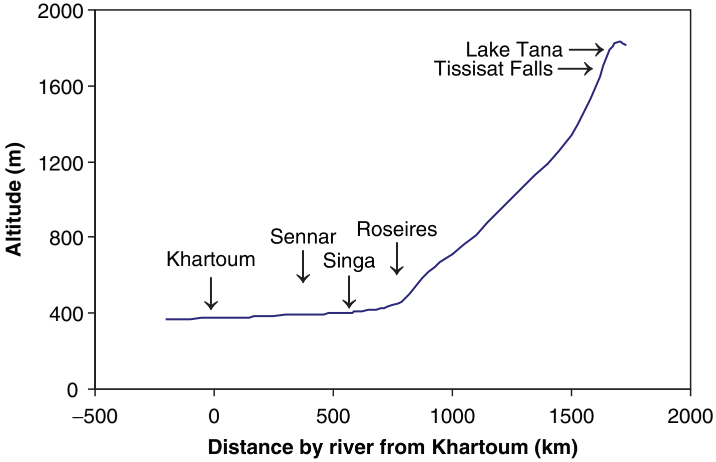

Fig. 11 Longitudinal altitude-profile of the Blue Nile. Note the location of Lake Tana and the Tissisat Falls in the right hand upper corner (modified after Rzóska, 1976b)

from the lower Nile basin. During the rainy season the waterfall is 400 m wide and is the second largest of Africa (Fig. 6).

From Lake Tana to the Sudan border at Roseires the river drops ca 1,300 m in about 860 km (Figs 1 and 11). The river cuts deep through the Ethiopian Highlands and flows only a short distance through the arid lowlands of Eastern Ethiopia, before it reaches the Sudan. The Blue Nile Gorge stretch is ca 500 km long, this region has provided the sediment which has built up the Gezira in Sudan, the alluvial Nile valley and the Delta. Most of the Gorge has very steep slopes which rise immediately from the river banks. Not much is known about the hydrobiology of the Gorge region. Most information comes from the Great Abbay Expedition (August–September 1968) (Morris et al., 1976). The Gorge is sometimes several kilometres wide, the sides descending in steps. At the bottom of this chasm the river flows for a considerable distance in a narrow 'inner Gorge'. Sand banks and a narrow fringe of forest or dense undergrowth occur at the river's edges. In relative few places the river is calm enough to allow growth of aquatic vegetation. The Gorge generates its own climate. Large quantities of bare rock store up heat during the day so that the Gorge is warmer at night than the plateau 1,000 m or more above it. This special area supports its own fauna, quite separate and distinct from that of the adjacent plateau. Through the Nile and its Gorge, many riverine animals have penetrated from lower, warmer areas of the Sudan, eastwards deep into Central Ethiopia from whose high grounds they are otherwise absent. Most obvious examples are the hippopotamus (*H. amphibius*), Nile monitor (*Varanus niloticus*), Nile crocodile (*Crocodylus niloticus*), leathery turtle (*Trionyx triunguis*) and the side necked terrapin (*Pelomedusa subrufa*), but it also applies to the fish species.

During the main rainy season (July–August) the river is very turbulent and often broad (sometimes >100 m) and full of suspended mud, but during the dry season the river almost ceases to flow and meanders between broad banks. In the wet season the river constitutes an inhospitable environment for aquatic life. This is no doubt the reason of the scarcity of fish, zooplankton and phytoplankton in the Gorge (Morris et al., 1976; Talling, 1976). A large majority of the fishes in the river in the Gorge are not visual predators. Catfish (*Bagrus docmak*, *Synodontis schall*, *Heterobranchus*) predominate whereas electric fishes (*Malapterurus electricus*, *Mormyrops anguilloides*) are also found. Four other species, *Garra blanfordii, Garra dembeensis*, *Labeobarbus intermedius* and *Varicorhinus beso* are restricted to the Blue Nile River in the Ethiopian Plateau (Banister, 1973; Berie, 2007; Stiassny & Getahun, 2007). The three last named species also occur in Lake Tana. *Oreochromis niloticus* (Nile tilapia) has also recently been found in the upper reaches of the Blue Nile below the falls (Dr Abebe Getahun pers. comm.). Furthermore, *Clarias gariepinus* (African catfish) and *Labeobarbus nedgia*, both also present in Lake Tana, have been also reported from tributaries of the Blue Nile in Ethiopia that join it downstream of the Tissisat Falls and hence their presence in the Blue Nile proper is likely (Anonymous, 2003; Berie, 2007). Therefore, most likely L. Tana and the Ethiopian part of the Blue Nile below the Tissisat Falls share only 6 fish species (Table 3). This large difference in species composition is no doubt the result of the 40 m high falls in the Blue Nile, only 30 km downstream of the river mouth in Lake Tana.

From the Sudan–Ethiopian border the Blue-Nile flows north under humid to increasingly arid conditions, and there is usually little additional runoff north of Roseires. The exceptions are two tributaries, the Dinder and the Rahad. They join the main flow downstream of the Sennar Dam and have their headwaters in the Ethiopian Highlands. By Roseires the slope has nearly levelled out and the river begins to meander through the Sudan plains, an Acacia-grass savannah, and finally merges with the White Nile at Khartoum (Figs 1 and 11). This section has undergone great changes in water regime and its biology due to the construction of two reservoirs, at Sennar in 1925 and at Roseires in 1966 (Rzóska, 1976b). Besides supplying water for irrigation and hydroelectric power these reservoirs support important fisheries.

Phytoplankton and zooplankton densities were closely linked to water flow rates (Talling & Rzóska, 1967). The low densities observed during the flood increased rapidly after the flood period ended and reached two maxima one in January–February and one in May. In May the White Nile at Khartoum slows down the weak discharge of the Blue Nile. This creates almost lake-like conditions, with almost stagnant water and high temperatures which together favour plankton increases in the Blue Nile in its final stretch (Hammerton, 1972). Generally cladocerans dominated over copepods (Talling & Rzóska, 1967). After the Roseires Reservoir has been completed phytoplankton composition in the Blue Nile was similar to that of Lake Tana with the diatom *Aulacoseira* (formerly named *Melosira*) *granulata* dominating immediately after the flood and blue green algae (mainly *Microcystis flos-aqual*) dominating in February–May.

Primary production was measured at four stations from the Ethiopian border to Khartoum during May 1968 (Hammerton, 1976). In the river, gross primary production was much lower at Diem (1 g C m^{-2} d^{-1}) than at the final stretch at Khartoum (6 g C m^{-2} d^{-1}), whereas both reservoirs also showed a high productivity (5.5–6.6 g C m^{-2} d^{-1}) and much higher densities of zooplankton. The depth of the photosynthetic zone increased from 2.5 m at Diem to 4.0 m at the Blue Nile near Khartoum; the photosynthetic depth was much deeper in the two reservoirs (6–7.6 m).

The cladoceran species composition showed a high similarity with that of Lake Tana (Table 2). Of the 9 cladoceran species reported for Lake Tana, 8 species were also reported for the Blue Nile (Dumont, 1986a). It is likely that the only cladoceran species present in the Lake and so far not reported for the Blue Nile, *Daphnia hyalina,* is also present in this river. This species is easily mistaken for the closely related *D. longispina* reported earlier from Lake Tana and the Blue Nile (see Dumont, 1986a). Of all cladoceran species reported for the Blue Nile, only *D. longispina*, *D. barbata* and *Ceriodaphnia reticulata* were not observed in Lake Tana. *Daphnia hyalina* and *D. longispina* belong to the *D. longispina* temperate species complex, common in Europe and Central Asia and favoured by low temperatures. In contrast, *D. barbata* and *D. lumholtzi* are tropical-subtropical species favoured by high temperatures. The copepod species composition showed less similarity: of the 4 species observed in Lake Tana only 2 species are in common, viz. *Mesocyclops aequatorialis* and *Thermodiaptomus galebi* (Dumont, 1986a). Furthermore, 4 cyclopoid and 3 calanoid species reported for the Blue Nile are lacking in Lake Tana.

Information about the benthic fauna is scarce; no systematic quantitative studies were carried out. The inshore benthic fauna is poor, probably because of drastic changes of water level (Rzóska, 1976c). Hammerton (1976) reported the presence of large numbers of the giant bivalve mussel *Etheria elliptica* attached to rock outcrops in the river between Diem and Roseires.

To date the fish fauna between Roseires and Khartoum contains 50 species belonging to 14 families (Abu Gideiri, 1967; Mishrigi, 1970). Most species were found downstream of Roseires, probably because these reaches were more intensively sampled than the upper reaches. There are large differences between the fish fauna of the Blue Nile and Lake Tana (Table 3). Of the 50 species reported between Roseires and Khartoum only two species, *Oreochromis niloticus* (Nile tilapia) and *Clarias gariepinus* (African catfish), are also occurring in Lake Tana.

16 Major Threats and Conservation Measures Needed

This account is largely based on the recommendations from the workshop ‘Management and Conservation of Lake Tana’ (Dejen et al., 2006c).

1. Despite the limited direct human influences on Lake Tana, both wetlands and surrounding catchment area have already been seriously damaged by man and most of the original forest has disappeared. A number of factors are responsible for the degradation of the catchment, of which population pressure and associated deforestation, cultivation of marginal lands and soil erosion by heavy rains

are the most important. The indiscriminate forest clearing, complete removal of crop residue, overgrazing, poor soil management and land use practices further aggravate the situation. Overgrazing of grasslands by livestock and continuing deforestation are on the moment the most important direct causes for the further degradation of the catchment area. Several soil conservation and reforestation programs are currently carried out by the Government.

2. The littoral region and wetlands of the lake are currently under severe degradation by the local inhabitants. Especially the area covered by papyrus has been decreasing recently (Teshale et al., 2001) by the ever growing human population in the wetlands around the lake and the need to increase the food and firewood production for their livelihoods. The local community is harvesting papyrus reed roots during low water level to use it as fuel wood. Farmers are cultivating the wetlands when the water is residing.
3. In the outflow of the Blue Nile from the lake, a large dam has been constructed, resulting in increased silt load and turbidity of lake water and reduced water levels (Fig. 4) Local fishermen in the Gulf of Bahir Dar observed that since the dam was constructed more sediment has accumulated on the lake bottom. The withdrawal of lake water for generating hydroelectric power in combination with the predicted increased variations and progressive decrease of rainfall over the years (Global Change) is expected to cause severe water level fluctuations and reduced water levels in the coming decade. Both will have a negative effect on the wetland functions such as, duration of the inundation period, sediment transport and biological production. Furthermore, the construction of five more major dams for irrigation, and power generation by diverting water from Lake Tana through a canal in the western part around Kunzila (Fig. 2) and connected to Beles river are foreseen for the near future (Tana-Beles Hydro-power Project for the Electric Power Corporation).
4. The increasing silt inflow and, due to the dam, its sedimentation in Lake Tana will raise the floor of this basin and eventually flood adjacent areas, even threatening the city of Bahir Dar.
5. The abundance of endemic *Labeobarbus* species in Lake Tana decreased dramatically with ca 75% in 10 years time (1991–2001). The destructive fishing operations during the spawning season (August–September) in rivermouths and upstream on the spawning grounds in combination with alteration and destruction of spawning habitats may lead to extinction of 7 of the 15 endemic labeobarbs. Recently the Amhara Regional State approved regional fisheries legislation, which is the first positive development for the proper utilization of the fish resource which was recognized as an important commodity by the government.
6. Introduction of specialized piscivorous fish (e.g. Nile perch) from other waterbodies in Ethiopia or from outside the country would certainly lead to the extinction of at least the 8 piscivorous *Labeobarbus* species. They are clumsy predators, being cyprinids, and will be out competed by more specialist piscivores from other fish taxa.
7. Bahir Dar is a rapidly growing town, a six times population increase up to 1,800,000 inhabitants is expected in the next 50 years (Teshale, 2003).

The current practice of discharging untreated industrial and domestic waste into the lake will have adverse effects on the quality of the lake water. Therefore, the construction of sewerage with waste water treatment plant is urgently needed. Furthermore, pollution from agricultural sources as fertilizers, insecticides and herbicides are recently increasing.

8. The Lake catchment lacks a proper institutional arrangement for the wise use of the resource. The lake resource use is not regulated and there is open access for any body who want to use it. There is no responsible organization which monitors, controls and plans integrated utilization of the resource.

17 The Call for an Integrated Water Management

As we have shown, Lake Tana is a multipurpose lake which has become a source of conflict for the different stakeholders such as: farmers, fishermen, local inhabitants, authorities, community based organizations and NGO's. Currently, there is no platform that brings those different stakeholders together. All the development activities are not integrated. Therefore, there is a strong need to establish a Lake Tana Basin Authority that will bring the different stakeholders together, to enhance a more harmonious development and a sustainable utilization of the resources and protecting the people around the lake area from human caused flooding.

18 Conflicts over Water Use

Ethiopia, Sudan and Egypt, the three countries depending on the water of the Blue Nile, traditionally depend on rain-fed agriculture for their food supply. Because of their fast growing population, water demands are expected to increase in the coming years in order to meet the food requirements of these additional people. Egypt and Sudan have little water supply of their own and are strongly dependent on water from Ethiopia. A large potential for conflict over water use is therefore evident, which is why achieving an integrated regional development of water resources on a sustainable basis is critical to the socioeconomic development of the Nile countries. Currently, efforts are under way to promote a water agreement between all Nile Basin countries through the Nile Basin Initiative (see also Allan, 2009).

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Swamps of the Upper White Nile

Jim Green and Asim I. El-Moghraby

Abstract The Sudd swamps developed from a large lake which extended north to Khartoum during the Pleistocene. The main channels are stable over decades, but the bends show upstream migrations of about 20 m in 3 years. In permanent swamps the channels often have a band of *Vossia*, backed by papyrus, which in turn is backed by an extensive area of *Typha domingensis*. Before 1950 the Nile Cabbage, *Pistia stratiotes*, was an important part of the floating vegetation in permanent swamps, but in recent years it has been largely replaced by *Eichhornia crassipes*.

Seasonal flooding enables the growth of grasses such as *Echinochloa* spp. and *Oryza longistaminata*. Further from the channels, where rain is the main source of water, *Hyparrhenia rufa* is the main grass. The grasslands grade into open woodland with *Acacia seyal* and *Balanites aegyptiacus*.

A rich fauna was associated with *Pistia*, and a similarly rich fauna has developed around the invasive *Eichhornia*. The marginal vegetation shelters an association of microcrustacea, with a biomass 100 times that in the open water. Macroinvertebrates are also abundant and diverse; for instance there are at least 70 species of aquatic Coleoptera, 60 species of mosquitoes, and a special fauna of terrestrial forms occurs in the umbels of papyrus. About 68 species of fish occur, and they occupy a wide range of niches, from mud feeders to carnivores.

Mammalian swamp dwellers include *Hippopotamus*, and several antelopes such as the Sitatunga and Nile Lechwe, while the White-eared Kob makes large migrations in the seasonal grasslands.

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1 Introduction

The swamps of southern Sudan are centred on the triangle formed by the Bahr el Ghazal, flowing west to east, the Bahr el Zeraf, and the Bahr el Jebel (or Gebel), flowing from the south to north. The junction of the last two rivers is via the man-made Zeraf cuts. The swamps extend southwards along the braided Bahr el Jebel, reaching just beyond Bor. The Bahr el Ghazal is fed by numerous tributaries, mostly arising on the Congo-Sudan divide. Many of these tributaries are seasonal, but the Sue, which flows into the Jur, reputedly flows throughout the year. A good account of the early exploration of the waterways in this area is given by Christie (1923). On the eastern side the Nile is joined by the Sobat, which receives tributaries from highlands on the borders of Ethiopia. The enormous extent of this area is indicated by the width of Fig. 1 representing approximately 1,300 km, which is about the distance from London to Vienna.

These swamps are known as the Sudd, a name derived from the Arabic for a blockage, and originally applied to the barriers formed by floating papyrus, but the term Sudd is now more widely used in other parts of Africa to include any type of mat-forming floating vegetation (Thompson, 1985).

A vast amount of information on topography, climate, hydrology, vegetation and human geography is contained in the four volumes of the report of the Jonglei Investigation Team (JIT, 1954). In addition, the four volumes produced by Mefit-Babtie (1983) take into account the changes in hydrology since the exceptional rains of 1961–1962. Much of this information was gathered in relation to the proposed construction of the Jonglei Canal, which has been discussed in detail in the book edited by Howell et al. (1988). The present chapter will not consider the Jonglei Canal

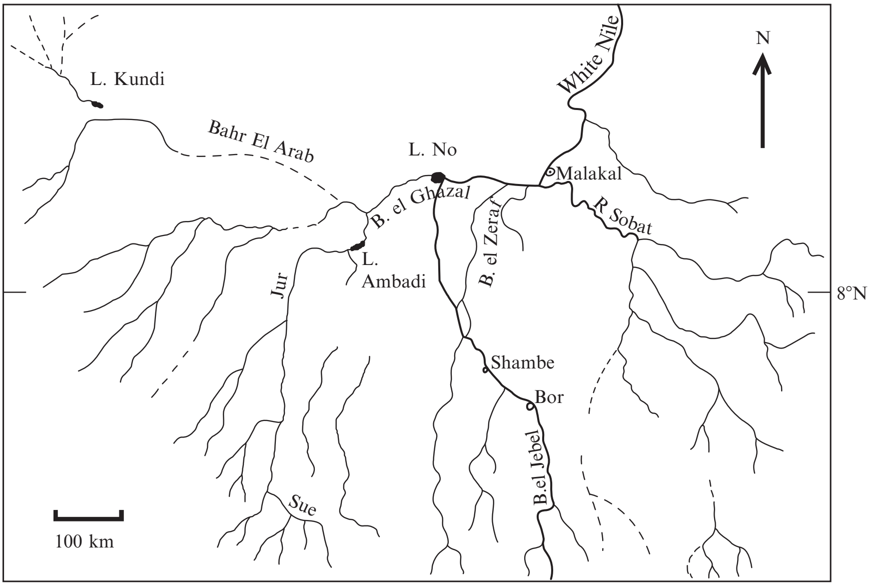

Fig. 1 Map of the upper White Nile showing the main localities mentioned in the text. Note the scale

(construction of which is at present incomplete), but instead will concentrate on the biological communities in the swamps, and the conditions under which they survive.

Talling (1957) made a major study of the succession of water characteristic along the White Nile. Two surveys were made: one in June 1954, the second in December 1954. In both there were decreases in dissolved oxygen and pH as the water entered the Sudd, with a gradual recovery after leaving the swamp. Differences in inorganic phosphate were found between the surveys, with roughly twice as much present in June. Ammonia and nitrate were also more abundant in June. Data for sulphate were available only for December, but showed the most clear-cut effect of passage through the swamp, with a marked decrease that was not followed by any significant recovery. This result was attributed to the activities of sulphate reducing bacteria in low oxygen concentrations.

2 Origin and History

The Lake Sudd hypothesis envisaged a huge lake, extending from Juba to Khartoum (Lombardini, 1865; Lawson, 1927; Ball, 1939), but Whiteman (1971) reviewed evidence for a much smaller lake, extending southwards from Khartoum. He obtained radiocarbon dates of 11,300 and 8,730 BP from shell bearing deposits, which indicated that during that period the water level near Khartoum was up to 10 m above the present flood level. The present Sudd swamps are a relict of a Pleistocene lake that covered a larger area, and extended further north than at present. The change from lake to swamp started with the onset of drier conditions about 4,000 BP. There are still numerous areas of open water: and some, such as Lake Shambe, have areas up to 30 km^2.

3 Vegetation

The distribution of swamp vegetation varies over time. Lock and Sutcliffe (1988) give three maps for the years 1930, 1952 and 1983 showing how the permanent swamp expanded from 6,700 km^2 in 1952 to 19,200 km^2 in 1983. This expansion was linked to the exceptional rains of the early 1960s and the raised discharge from Lakes Victoria and Albert. Apart from this general expansion there are detailed local changes in the channels and smaller lakes. Petersen et al. (2007) examined satellite pictures taken in 1973, 1979, 1987 and 2002 of the region between Bor and Shambe. They found that the main channel system was fairly stable, but the bends showed upstream movements of about 200 m over the 30 year period. The lakes were stable in location, but some showed significant reductions in area. Between 1973 and 2002 the surface area of Lake Shambe decreased from 30 to 27 km^2. Over a different timescale, between 1930 and 1981, in the southern part of the swamp, a new lake system appeared at Wutchung (Lock & Sutcliffe, 1988).

In spite of such physical changes there remains a fairly consistent pattern in the vegetation. Along the main channels there is often a *Vossia* swamp, forming floating mats. Before the 1950s the Nile Cabbage, *Pistia stratiotes*, was associated with this region, but it has since been replaced by *Eichhornia crassipes*, which can form a broad band in the more sheltered regions. Behind the *Vossia* there is an extensive area of *Cyperus papyrus*, usually forming a floating mat, often strong enough for a man to walk on. The tall plants form a framework for climbers, such as *Luffa cylindrica* and *Vigna luteola*, while the umbels provide shelter and food for a range of terrestrial insects and arachnids. In some areas the papyrus is replaced by the tall reed *Phragmites karka*, which does not form a floating platform. Further away from the main channels there are swamps dominated by *Typha domingensis*, which occupy three times the area covered by papyrus. These *Typha* swamps are difficult of access and little studied.

During the wet season, water spills out from the permanent swamps and floods nearby grasslands. Where the water is deeper the wild rice-grass, *Oryza longistaminata*, is dominant. Its success depends on the duration of flooding, as it requires several months of surface water in order to flower. Where the floodwater is shallower the dominant grass is *Echinochloa pyramidalis*, which may be accompanied by *Sporobolus pyramidalis*, *Digitaria debilis*, and legumes like *Desmodium hirtum*.

In the area of seasonal flooding from the river there are slightly deeper areas, which persist as pools as the water recedes. These pools can develop their own separate vegetation, consisting of the grass *Echinochloa stagnina*, small herbs, such as *Glinus lotoides*, and sometimes woody species like *Sesbania rostrata* and *Aeschynomene indica*.

Beyond the flooding by the river there is an area seasonally flooded by rainfall. *Hyparrhenia rufa* covers most of this area, although *Sporobolus pyramidalis* can also dominate in some areas, and where the soil is better drained, *Echinochloa haploclada* becomes important. There is of course no sharp distinction between river flooding and rain flooding, so areas inundated by the river can receive additional water from rainfall, and this is important in maintaining the seasonal pools.

The grasslands merge into open woodland, characterised by the red barked *Acacia seyal* and the larger, grey-brown barked *Balanites aegyptiaca*. These trees can be killed off if they are flooded for a long time, and the maps given by Lock and Sutcliffe show that woodlands disappeared from some areas between 1952 and 1983, when the permanent swamps expanded. Regeneration of woodland occurs after several years without flooding, and may have unwelcome consequences for the local tribes. Ashford and Thomson (1991) regard the regeneration of *Acacia*/*Balanites* woodland as the key event in an epidemic of visceral leishmaniasis, because the young woodland provided a suitable habitat for the sandfly vector *Phlebotomus orientalis*.

4 Fauna Associated with Floating Macrophytes

Perhaps the most striking change that has taken place between the survey by Migahid (1948) and the later surveys by Denny (1984) and Lock (1988) is the replacement of *Pistia stratiotes* by *Eichhornia crassipes*. *Pistia* provided a floating rosette with a mass of roots extending down into the water. In 1954, Ian Thornton made a study of the animals associated with *Pistia*, and his results were presented by

Rzóska (1974). The complex fauna included Diptera, Ephemeroptera, Hemiptera, Odonata, Trichoptera, Coleoptera, Hymenoptera (mainly ants on the aerial rosette), Araneida, Acarina, Crustacea, Gastropoda, Hirudinea and Oligochaeta. One individual plant could harbour up to 300 animals, particularly on the fringe of a patch where oxygen was available. Coleoptera were particularly abundant, and included over 40 aquatic species. The Crustacea included a small decapod, *Caridina nilotica*, and the conchostracan *Cyclestheria hislopi*.

A parallel study of the fauna of *Eichhornia* in the Sudd has been made by Bailey and Litterick (1993). They found that *Eichhornia* effectively provides the same niches as those provided by *Pistia*. Coleoptera were again the most abundant group, with about 30 aquatic species, but rather surprisingly only about five species were the same as those found on *Pistia*. This implies a pool of at least 70 species of aquatic Coleoptera in the Sudd. The crustaceans *Caridina* and *Cyclestheria* apparently transferred to the shelter provided by *Eichhornia* and became important members of the community associated with that plant.

Numerous small crustaceans are associated with the marginal vegetation. Rzóska (1974) found 34 species of Cladocera, and Monakov (1969) gives biomass figures for microcrustacea in fringing vegetation up to 100 times higher than in the open water. Among the copepods Rzoska lists *Mesocyclops leuckarti*, but this was before the revision of the African species of *Mesocyclops* by Van de Velde (1984). More recent surveys (Mefit-Babtie, 1983) show *Mesocyclops ogunnus* in the lake at Wutchung, *M. rarus* in the River Atem, and *M. salinus* in seasonal pools. *Thermocyclops neglectus* appears to be the most widespread of the cyclopoids in the swamps.

5 Zooplankton

Away from the marginal vegetation the crustacean zooplankton becomes sparse and poor in species. Table 1 shows the species present in Lake No in January 1949 and April 1978. The overall composition of these samples forms a contrast to those from Lakes Albert, Edward and Victoria, where the percentage of cyclopoid copepods is very much higher.

Table 1 Percentage composition of crustacean zooplankton in Lake No

	January 1949[a]	April 1978[b]
Diaphanosoma excisum	2	10
Daphnia barbata	0	1
Ceriodaphnia dubia	0	1
Moina micrura	54	8
Bosmina longirostris	0	2
Thermodiaptomus galebi	21	62
Cyclopoida	12	15
Others	11	1

[a] Data from Rzóska (1974).

[b] Data from Green (1984).

Information on the Rotifera present in the Sudd has been provided by De Ridder (1984), based on samples collected by A. I. El-Moghraby, and by Green (1984), plus identifications in Mefit-Babtie (1983). Combining these three sources gives a total of 86 species found in the area shown in Fig. 1. More species will certainly be found. For the whole of Sudan, De Ridder (1984) lists 145 species, most of which are likely to occur in the Sudd. The commonest species in the open water are *Brachionus calyciflorus*, *B. caudatus*, *B. falcatus* and *Keratella tropica*, while *Lecane bulla* is the most frequent of the 26 species of *Lecane* recorded from the Sudd. The small pools that develop in the flooded grassland during the wet season have a rich association of rotifers, with about 30, mostly periphytic, species. They include the rarely recorded *Pseudoploesoma greeni*, which is not listed by De Ridder, but also occurs in Lake Ambadi. The peculiar nature of the rotifer association in Lake Ambadi has been discussed by Green (1984). Although rotifers are sparse in the lake their index of diversity (α) is much higher than elsewhere in the Sudd. A similar high diversity is found among the desmids in Lake Ambadi (Grönblad et al., 1958), and this was thought to be unique, but the pools in the grasslands also develop a rich association of desmids. Although a detailed comparison has not been made, the desmids in the pools appear to be dominated by species of *Closterium* and *Cosmarium* (Mefit-Babtie, 1983).

6 Macroinvertebrates

The macroinvertebrates in the Sudd near Bor have been listed in Vol. 3 of the Mefit-Babtie Report. Five species of Ephemeroptera, including the tunnelling larva of *Povilla adusta* were found, but only two species of Trichoptera are listed. The Odonata were much more abundant, with 24 species, and there were 30 species of Coleoptera. Sixteen species of aquatic Hemiptera are listed, but this is probably an underestimate, since Linnavuori (1971) listed 38 species from the province of Bahr el Ghazal, and some additional species from Equatoria. There are only eight species common to both lists, so there must be over 45 species of aquatic Hemiptera in the Sudd.

About 180 species of mosquitos are known from the Sudan, and at least 60 of these occur in the Sudd, including five species of *Taeniorhynchus*, the larvae of which become closely connected to vegetation by piercing plant tissues with saw-like siphons to gain access to air spaces. This enables the larvae to remain permanently underwater when there is little dissolved oxygen.

The Mefit-Babtie Report lists 14 species of gastropods, although Brown et al. (1984), working in the same area found 23 species, including the transmitters of schistosomiasis, fascioliasis and amphistomiasis. The large snails of the genera *Pila* and *Lanistes* are often found in the seasonal pools in the flooded grasslands, where they survive the dry season by aestivating. They form a large part of the diet of *Anastomus lamelligerus*, the Open-bill Stork.

An unexpected inhabitant of the Sudd is the hydroid *Cordylophora*, which is widespread in brackish water through out the world, but is also known from freshwater, though rarely so deep into a continent (Rzóska, 1949).

7 Upland Tributaries of the Bahr el Ghazal

As one travels upstream on the tributaries of the Bahr el Ghazal towards the Congo/Sudan divide the slopes become steeper, and the riverbeds rockier, eventually they become bare of vegetation, apart from an occasional species of Podostemaceae (Schweinfurth, 1873). This is reminiscent of the streams on Mount Elgon, and it is probable that the tributaries of the Bahr el Ghazal have a similar invertebrate fauna, although it has not been studied to the same extent. One group, the blackflies (Simuliidae), because of their importance as transmitters of disease, has been studied in detail (Lewis, 1948, 1952, 1953). Of the 22 species Lewis records from the Sudan, nine also occur on Mount Elgon. Some of these species are widespread in the Nile, but others are restricted to the upper reaches of the Ghazal tributaries. An extreme example is *S. lepidum* which is abundant only at the base of the Aga Falls at 1,100 m asl. *Simulium damnosum* is well known as a transmitter of the nematode *Onchocerca volvulus*, which causes river blindness, and the main area of transmission in the Sudan occurs along the Rivers Jur, Sue and nearby tributaries.

8 Fauna of Papyrus Umbels

The umbels of papyrus open well above water level, so one would expect the animals living there to be predominantly terrestrial. Thornton (1957) found a rich fauna of arachnids and insects in the swamps of the upper White Nile. He also studied the succession of the fauna as the umbels developed. From closed bud to fully opened umbel, with rays up to 55 cm, took about 40 days. Many of the insects and spiders occurred as solitary individuals, probably using the umbels merely as a substratum to move about on above the water, but there were some species that occurred regularly in considerable numbers.

The sap-sucking Thysanoptera and Homoptera were among the earliest colonisers of the umbels. Figure 2 shows the occurrence of two species of thrips as the umbels age and eventually shrivel. *Catina papyri* was described from Thornton's material, but *Haplothrips avenae* is more widespread; originally found on oats in Malawi. Some species of *Haplothrips* are known to be predators, so it is possible that the later occurrence of *H. avenae* was related to its invasion of the umbels after the development of suitable populations of smaller prey species.

The Homoptera were also early invaders, and the most abundant species was *Schizaphis cyperi*. Among the Heteroptera *Agramma lineatum* was the most frequent, but invaded the umbels somewhat later than the thrips and aphids. Spiders were the latest invaders, reaching their peak as the umbels matured. The Salticidae and Thomisidae were the most frequent, but most of the specimens were immature, making specific identification difficult. These young spiders represent opportunistic invaders from grasslands behind the swamps, moving in to exploit prey populations that had been developing on the papyrus for several weeks. The papyrus umbels provide a constantly changing habitat, with a diverse arthropod community that changes as prey and predator interact.

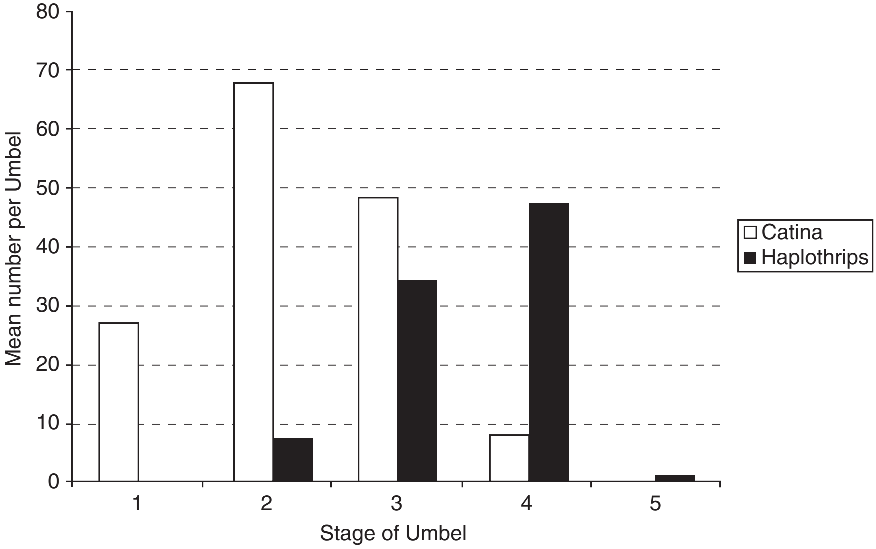

Fig. 2 Succession of two species of thysanopterans on umbels of papyrus; by stage 5, the umbels are dry and shrivelled (based on data given by Thornton, 1957)

9 Fishes

The fishes in the swamps are most diverse and abundant where there are areas of open water. Bailey (1988) has summarised the work of Hickley and Bailey (1986, 1987a, b). In a survey that included a large number of samples from river channels, lakes, shaded swamps and river floodplains they found a total of 68 species, of which 61 were found in the lakes. Each of the other habitats had between 16 and 24 fish species, which were essentially sub-sets of the species found in the lakes. The exception was the killifish *Nothobranchius virgatus*, which was found only in seasonal water bodies at the edges of river flooded grassland, where it fed on microcrustaceans and insects. *Nothobranchius* has the ability to produce drought resistant eggs, enabling it to survive through the dry season. The lungfish *Protopterus* also occurs in these marginal habitats, but is by no means restricted to them, as it is also found in the permanent shaded swamps. The lungfish can aestivate underground in grassland inside a mucous cocoon, and its lung serves a dual purpose, enabling it to breath in water of low oxygen content, and to survive out of water.

Hickley and Bailey (1987b) divide the fishes of the swamps into five major feeding groups:

1. Mud feeders, such as *Heterotis niloticus* and *Labeo niloticus*. It is probable that *Heterotis* sorts the mud to some extent, so that the ingested material contains a high proportion of ostracods and other benthic microinvertebrates.
2. Microherbivores, such as *Oreochromis niloticus* and *Sarotherodon galilaeus*.

3. Macroherbivores, such as *Distichodus rostrata* and *Alestes macrolepidotus*.
4. Omnivores, eating both plants and animals. The animals may be planktonic, as in the diet of *Alestes dentex*, or benthic as taken by *Synodontis frontosus*.
5. Carnivores. More species fall into this category than any other, and the group can be subdivided in:

    (a) Surface feeders: the best example is the little cyprinid *Chelaethiops bibae*, which feeds entirely on terrestrial insects.
    (b) Zooplanktivores: many juvenile fishes fall into this category, and some adults, such as *Alestes nurse*, take a high proportion of zooplankton, but also include some plant material so that they become omnivores.
    (c) Benthic feeders, such as *Synodontis schall*, taking a high proportion of molluscs, and *Mormyrus cashive* feeding mainly on chironomid larvae.
    (d) Browsers among vegetation, such as *Polypterus senegalensis* and *Micralestes acutidens*, with insects forming a large part of the diet.
    (e) Macropredators such as *Hydrocynus forskalii*, which was found to have eaten 13 species of fish, and *Clarias gariepinus*, which had eaten 12 fish species. Seven other species were macropredators, including *Lates niloticus*, which is the top predatory fish, reaching the largest size and liable only to predation by crocodiles and man.

10 Other Vertebrates

As far as is known there are no endemic amphibians or reptiles in the Sudd, and the roles played there by the various species have not been studied, but have been studied in other localities, for example the detailed study by Cott (1961) of the Nile Crocodile in Uganda. The mammals of the Sudd show varying degrees of adaptation to swamp conditions. The Hippopotamus, well known for its habit of emerging from the water to graze on land at night in other parts of Africa, often feeds during the day while remaining in the water, and consumes plants such as *Najas* and *Vossia*.

Various antelopes occur in and around the Sudd: three examples will suffice to show how they vary in their relationship to swamp conditions. The Sitatunga (*Tragelaphus spekei*) is the most aquatic of the antelopes, with long, splayed hooves adapted for walking in swamps. It feeds in the permanent swamps, and does not make any major migrations. *Kobus megaceros*, the Nile (or Mrs Grey's) Lechwe, is endemic to the Sudd, the Machar Marshes and some tributaries of the Sobat, and makes local movements related to the flood cycle. In general it does not live in the permanent swamps, but follows the waterline of the river flooded grasslands, often wading in shallow water and feeding mainly on grasses. Further away from the permanent swamp the White-eared Kob (*Kobus kob leucotis*) makes long seasonal migrations over hundreds of kilometers, from wet season quarters in southern grasslands east of Bor and Juba to spend the dry season near the River Sobat. The Kob feeds in the grasslands, mainly on *Hyparrhenia* and associated grasses.

Many other herbivores, well known from the African plains, occur on the margins of the Sudd. Elephants make local movements into the wetlands as the water recedes, and even giraffes have been seen wading about in water. Carnivores in the swamps have been little studied, because they are so difficult to see; but the Marsh Mongoose, *Atilax paludinosus*, is seen occasionally, and is probably quite common. It will eat almost anything it can catch, including fish, such as *Protopterus* and *Clarias*, as well as crabs and mussels.

The birds associated with the swamps are dealt with elsewhere (Green, this volume), but the shoebill *Balaeniceps rex* merits special mention in relation to the Sudd, because its lifestyle is linked strongly to aspects of swamp ecology (Fig. 3). The shoebill avoids the main channels and very tall vegetation, preferring smaller channels and pools, frequently surrounded by *Typha*. Much of its diet consists of the air-breathing fishes *Protopterus*, *Polypterus* and *Clarias*, which often predominate when oxygen is deficient in the water. The fish are not stalked, but are ambushed by

Fig. 3 The shoebill (*Balaeniceps rex*), a typical inhabitant of the Sudd and other White Nile swamps and marshes (photograph kindly made available by Pat Morris)

a bird that has been standing motionless beside the water, waiting for a fish to surface for a gulp of air. When the shoebill strikes, its whole body falls forward in an all or nothing attempt to scoop up the fish in its enormous bill. There is no possibility of an immediate second strike if the fish is missed. The nest is usually built on a platform of floating vegetation (Guillet, 1978), and in hot weather the hatched young are kept cool by the parents bringing water back in their bills and showering it over the chicks. In 1978, Guillet estimated the total population to be about 1,500, but in 1983 Mefit-Babtie produced an estimate of 6,000, based on an aerial survey of the Jonglei area alone. The total population of shoebill in the Sudd must be higher than this estimate because it did not include the swamps along the Bahr el Ghazal, where the species is most easily seen through the reduced papyrus fringe. It is possible that the shoebill population was favoured by the expansion of the permanent swamps following the exceptional rains of the early 1960s. No other large bird has its lifestyle so closely linked to the ecology of the swamp, and if a single species can serve as an icon of the Sudd, then the shoebill must be a prime candidate.

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The Kyoga Catchment

Jim Green

Abstract Lake Kyoga is a complex, shallow lake, which breaks into satellite lakes in the east. The eastern end receives inflows from Mount Elgon and the northern province of Karamoja. The main inflow to the western part of the lake comes from Lake Victoria. The outflow falls over 400 m before joining the outflow from Lake Albert. The vegetation is complex, with a fringe of papyrus, which also occurs as floating islands, and extensive areas of water lilies (*Nymphaea*). Since 1988 The Water Hyacinth (*Eichhornia*) has invaded the lake and influenced the distribution of some of the submerged plants. The water chemistry and phytoplankton vary along a gradient from east to west, with high conductivity and domination by Cyanobacteria in the east, and lower conductivity and domination by *Melosira* in the west. The zooplankton is dominated by cyclopoid copepods, although two species of diaptomids are also present. Cladocera occur in much smaller numbers, with *Moina micrura* the most frequent. Snail hosts of *Schistosoma* are present in the lake, and transmit disease to man and cattle. The precise number of fish species in Lake Kyoga is not known, but some of the satellite lakes have at least 60 species of haplochromines, as well as members of other families. The satellites are important because some have not yet been invaded by the Nile Perch, so that they can serve as conservation areas for endemic species.

1 Introduction

The region north of Lake Victoria is often regarded as a swamp through which the Victoria Nile flows on its way to join the outflow from Lake Albert. Figure 1 shows that the situation is much more complicated. The Atlas of Uganda (1962) shows the Kyoga catchment covering 57,672 km^2, with an extensive area in the northeast (Karamoja) draining down into Lake Bisina (formerly Lake Salisbury). Swift flowing streams on the western side of Mount Elgon (alt. 4,324 m) provide a habitat not found elsewhere in the

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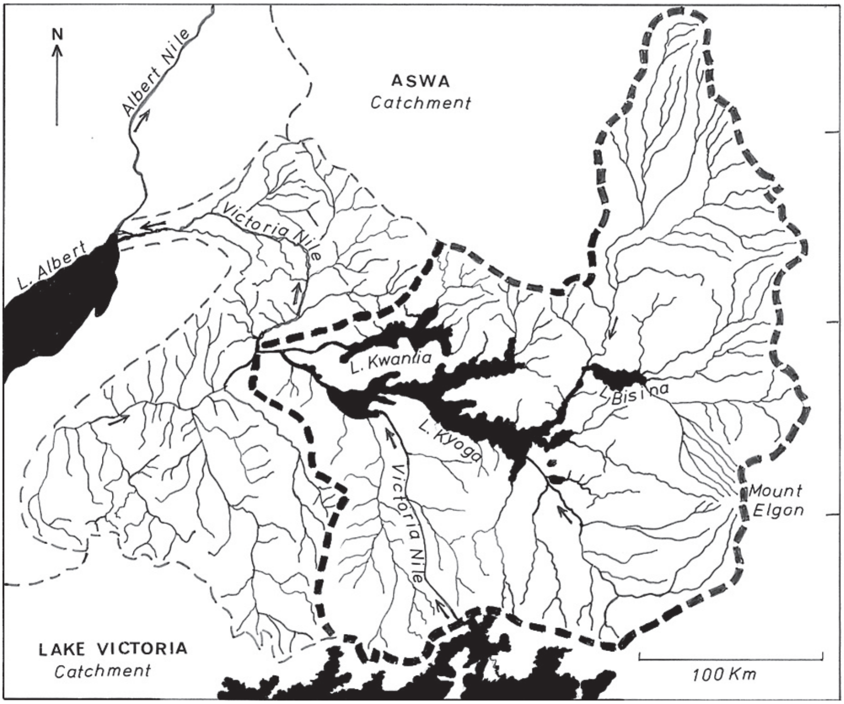

Fig. 1 Lake Kyoga and its catchment. The bold broken line encloses the catchment. The fine broken line encloses the Victoria Nile catchment. Note that the Victoria Nile between Lake Victoria and Lake Kyoga is included in the Kyoga catchment. Rivers have been omitted from the Aswa and the Lake Albert catchments. Based on the hydrology map in the Atlas of Uganda (1962). The outline of Lake Kyoga in Fig. 2 is based on the 1956 version of the Entebbe map published by D survey, War Office and Air Ministry. Figure 3, of the eastern end of Lake Kyoga and the satellite lakes, is based on a combination of images, post 2005, from Google Earth and National Geographic Map Machine. Figures 1–3 together give some indication of the variability of open water in the region

catchment; they change into slower, meandering streams at lower altitudes and flow into the swamps around Lake Bisina and the satellite lakes at the eastern end of Lake Kyoga.

The Victoria Nile leaves Lake victoria over the Owen Falls, where the construction of a dam has caused a backup of water inundating the Ripon Falls, which lay about 3 km to the south. Below the Owen Falls the river flows through a rocky gorge, and successively over the Bujagali Falls, Kijabirwa Falls, Buyala Falls, and the Busawaka Falls. When the Victoria Nile enters Lake Kyoga it has fallen through 98 m, but when it reaches the northern end of Lake Albert it has fallen another 418 m, so the overall barrier between Lakes Albert and Kyoga is much greater than that between Kyoga and Victoria. This is reflected in the fish faunas of these lakes (cf. p. 209).

The area of open water varies seasonally, and from year to year. When Worthington surveyed the lake in 1928 he found that most of the lake was less than 4 m deep, and the maximum he found was 5.7 m. In 1962, after a period of heavy rain, I found some areas with a depth of 6.3 m, and during the El Nino of 1997/1998 the lake level rose by 2 m, and the volume doubled. The Hydromet Survey (1974) found that a depth of 10.7 m occurred in a limited area, when the water level was at its maximum. With this degree of variability it is difficult to give a precise figure for the area of the lake, but it varies around 2,600 km^2. When the level is low the open water is broken into separate bodies divided by swampland, particularly at the eastern end (cf. Fig. 3).

2 Origin and Age

The basins of Lakes Victoria and Kyoga appear to have originated during the Mid-Pleistocene when the land along the eastern side of the Western Rift was uplifted, causing a reversal of rivers that originally flowed westward. Ponding back the Katonga and Kagera rivers led to the formation of Lake Victoria, while, further north, Lake Kyoga was formed by ponding of the Kafu. The early Lake Kyoga was not connected to Lake Victoria, but had it own westward flowing outlet which probably joined the Albert Nile. Outflow from Lake Victoria, via the Victoria Nile, through Lake Kyoga, did not begin until some time between 7.4 and 5.8 thousand years ago (Johnson et al., 1998).

3 Biota

Most of the shoreline is fringed with floating papyrus, which becomes extensive in bays. Floating islands break away during windy weather, and can drift for considerable distances. They are often large enough to support camps of fishermen. These drifting islands can sometimes cause blockage of the main channel, and during 1917 all steamer services between Namasagali and Masindi Port were suspended for several months. Extensive areas of the lake are covered with water lilies (*Nymphaea* spp.) which hamper the setting of nets.

An addition to the floating vegetation occurred in 1988, when the Water Hyacinth, *Eichhornia crassipes*, invaded the lake (Twongo, 1996). This plant also drifts in response to wind, and tends to accumulate in sheltered bays. When abundant it can have a deleterious effect on submerged macrophytes such as *Ceratophyllum* and *Myriophyllum*. The Water Hyacinth can also create areas with water of low oxygen content, making them unsuitable for some fish, such as the Nile Perch, *Lates niloticus*.

The complexity of Lake Kyoga is also reflected in its water chemistry, which shows local variations. Mungoma (1988) found a fairly consistent trend in the conductivity, from 168 µS in the east to 106 µS in the west. Evans (1962) found an even greater range, from 300 µS in the east to 100 µS in the west. This drop was attributed to decreases in silicate and sulphate. There was also a marked difference in the dominant phytoplankton. In the east the cyanobacterium *Lyngbya limnetica* was abundant, but in the west diatoms of the genus *Melosira* were dominant. Evans (1962) gives a list of the species found in the main body of Lake Kyoga.

Green algae, such as *Ankistrodesmus*, *Scenedesmus* and *Dictyosphaerium* were well represented, but a range of Cyanobacteria, such as *Anabaena*, *Anabaenopsis*, *Merismopedia* and *Microcystis* were also present.

A transect of the zooplankton in Lake Kyoga was made in 1962, and accounts of the Rotifera and Cladocera were published (Green, 1967, 1971). Seven sites were sampled from east to west along the northern arm of the lake. Twenty-one species of rotifers were found, and the most abundant were *Lecane bulla* (23% overall mean), *Keratella tropica* (18%) and *Brachionus caudatus* (15%). Four other species of *Brachionus* were found, but none exceeded 8%. The overall numbers of rotifers were low, with a mean of 7,732 m^{-2}.

Although 11 species of Cladocera were found, only four were of numerical significance. *Moina micrura* was the most abundant, with 2,715 m^{-2}, *Diaphanosoma excisum* and *D. sarsi* together made up 600 m^{-2}, while *Ceriodaphnia cornuta* only made up 172 m^{-2}.

Both the Rotifera and Cladocera were greatly outnumbered by the copepods and their larval stages. Calanoid copepodids and adults averaged about 10,000 m^{-2}, cyclopoids about 34,000, and combined nauplii 30,000. This dominance by the copepods was consistent throughout the transect (Fig. 2). Because of the abundance of copepodids and nauplii it was not feasible to get differential counts of the species, but by examination of the adults the following species were found:

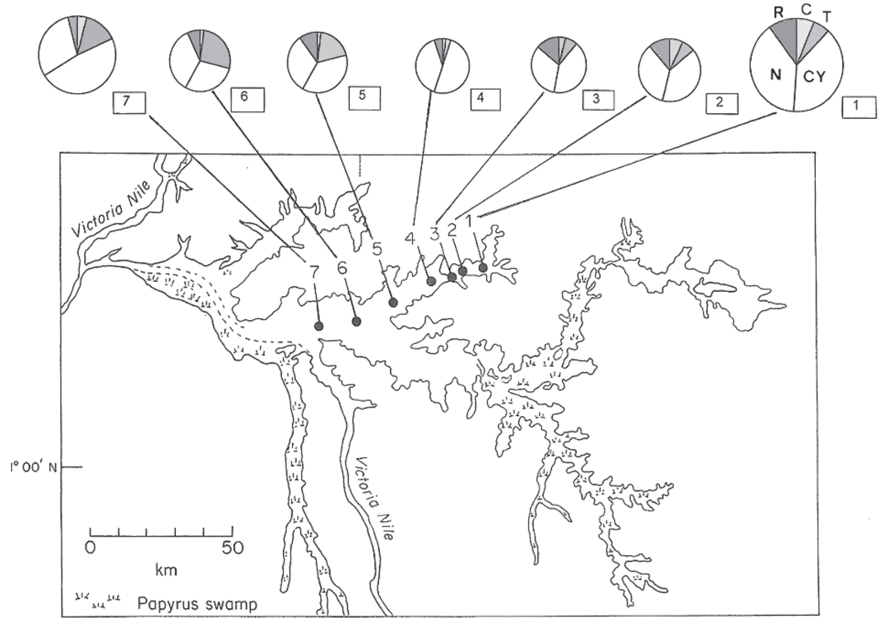

Fig. 2 Zooplankton transect of the northern arm of Lake Kyoga, November 1962. The diameter of each circle is proportional to the number of zooplankters in 1 m^3 of water (max. 28,000; min. 13,000). CY – cyclopoids; T – *Thermodiaptomus* and *Tropodiaptomus*; N – combined nauplii; R – Rotifera; C – Cladocera

Calanoida

Thermodiaptomus galebi
Tropodiaptomus processifer

Cyclopoida

Tropocyclops tenellus
Mesocyclops ogunnus
Thermocyclops neglectus

All these are known from other parts of the Nile system, but it is only recently that *Thermodiaptomus galebi* has been confirmed in Lake Albert, where it is rare (Lehman et al., 1998).

Worthington (1929) made the first significant observation on the molluscs of Lake Kyoga, when he noted the presence of *Lanistes carinatus,* a species known from Lake Albert, but not from Lake Victoria. Mandahl Barth (1954) recorded fifteen species of gastropods and three species of lamellibranchs from the lake and remarked that other species were almost certain to be present, in view of the small numbers and geographical restrictions of the samples from the lake. The gastropods included *Biomphalaria sudanica,* transmitter of *Schistosoma mansoni,* and *Bulinus globosus,* transmitter of *S. haematobium*. Another species, *Bulinus ugandae*, does not transmit *S. haematobium,* but does transmit the allied *S. bovis*, a parasite of cattle.

Other groups of invertebrates appear not to have been studied in any detail. There are isolated records in the literature, but they have not been gathered into a coherent account.

4 Fishes of Lake Kyoga

The first attempt at a comprehensive survey of the fish fauna of Lake Kyoga was that of Worthington (1929). He found that many of the species were the same as those in Lake Victoria, but there were a few Kyoga species that were found in Lake Albert and not in Lake Victoria. In addition he described six new species, three of which were in the genus *Barbus*.

Worthington included 16 species of haplochromines in his list: a more modern estimate would be four or five times this figure. His idea that the Kyoga species were the same as those in Lake Victoria is only partly true, and a number of new species have been recognised in Lake Kyoga. In 1922 Tate Regan described *Haplochromis orthostoma* from Lake Salisbury (now L. Bisina). Greenwood (1967) gives two other records from the same area in 1958 and 1966, and describes specimens from Lake Victoria, which were originally thought to be conspecific, as a new species *H. parorthostoma*. In 1980 both species were placed in the new genus *Pyxichromis*. New species are still being found in Lake Kyoga, so that it is difficult to give a precise figure for the number known from the lake. The situation has been complicated by the introduction of the Nile Perch, which flourished at the expense of the haplochromines, and certainly eliminated some of them.

In recent years there has been some relief for the smaller fishes, brought about by the invasive water weed *Eichhornia crassipes*. This has covered large areas, and beneath dense aggregations there is a reduction in available oxygen, making the area unsuitable for the Nile Perch (Willoughby et al., 1996). In extreme cases, dense *Eichhornia* renders an area suitable only for air breathers, such as *Protopterus* and *Clarias*.

Another factor mitigating the effects of predation by Nile Perch in Lake Kyoga is the breaking up of the lake into satellite lakes during periods of low water (Fig. 3), and when papyrus swamps consolidate they can form permanent barriers between bodies of open water. These smaller water bodies serve as refuges for species that are vulnerable to predation in the open waters of Lake Victoria, or even in the main Kyoga Lake. The importance of these satellite lakes has been emphasised by Mwanga et al. (2001). Table 1 shows that the estimated number of Haplochromine species in the main lake has fallen below 50, but remains over that number in the small lakes lacking Nile Perch. Small lakes with Nile Perch have fewer species of haplochromines; thus Lake Nakuwa (Fig. 3, Table 1) has many fewer species than

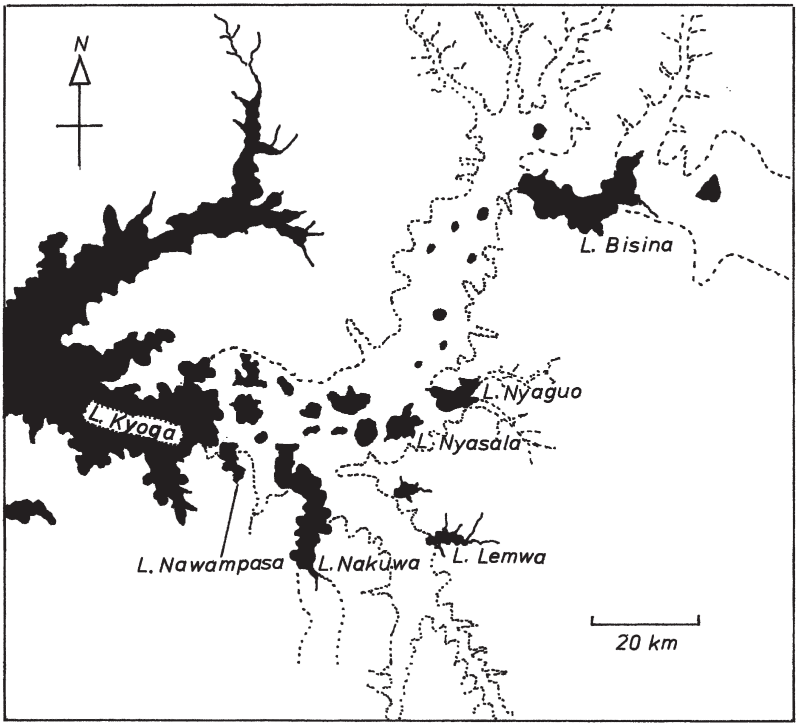

Fig. 3 The eastern end of Lake Kyoga and some of the satellite lakes. The named lakes are those included in Table 1. The broken lines indicate approximate limits of papyrus swamps. Stream systems, shown in Fig. 1, have been omitted

Table 1 Estimated numbers of haplochromine species in satellite lakes in the Kyoga catchment (data from Mwanja et al., 2001)

Lake	Haplochromine spp.	Nile Perch
Kyoga (main)	<50	Dominant
Nawampasa	>60	Absent
Lemwa	>50	Absent
Bisina	>30	Rare
Nyaguo	>50	Absent
Nakuwa	<5	Dominant
Nyasala	<30	Dominant

Lake Nawampasa. Similar results were obtained by Mbabazi et al. (2004), who found only 14 species in the main lake, but 37 species in the satellite lakes. The overall message is that species thought to be extinct are surviving in the Kyoga satellites. These small lakes clearly rate the highest conservation priority, but there are practical difficulties in enforcing regulations in an area like the Kyoga catchment. These difficulties are increased by the value of haplochromines as aquarium fish. Some of the Kyoga forms are particularly attractive and brightly coloured, selling for up to US $50 a piece. The temptation to overfish is obvious, and from various exchanges on the Internet it appears that unscrupulous collectors are overexploiting Lake Nawampasa. Lake Kyoga has become one of the most vulnerable parts of the whole Nile system, but has important conservation potential if action can be taken soon.

5 Streams on Mount Elgon

Mount Elgon has an annual rainfall of about 1,900 mm. Much of this water flows off the mountain via incised river valleys. The swift flowing streams have rocky beds, with little vegetation, mainly mosses and liverworts, although species of the family Podostemaceae occur in several of the streams. The invertebrates in these streams have been studied in detail by Williams and Hynes (1971). The dominant forms are the mayflies, *Afronurus*, *Baetis* and *Centroptilum*, the caddis *Cheumatopsyche*, and various Simuliidae and Chironomidae. The stonefly *Neoperla spio* is also common. There is a general tendency for an increase in diversity as one descends down the mountain, until one reaches the flat country, where the streams become sluggish, and the species characteristic of the upper reaches disappear. The Simuliidae are abundant in some of the streams, and 17 species have been identified in the area. The species are distributed according to their preferences for a combination of current speed and altitude, resulting in an altitudinal zonation (Fig. 4). The beetles of the family Elminthidae also show a marked vertical zonation, with 15 species covering an even greater range than the Simuliidae (Fig. 5). Although these streams are generally fast flowing there are occasional pockets of calm water where silt can

Fig. 4 Altitudinal zonation of *Simulium* species in streams on Mount Elgon. Only the six most abundant species, out of 17, are shown (data from Williams & Hynes, 1971)

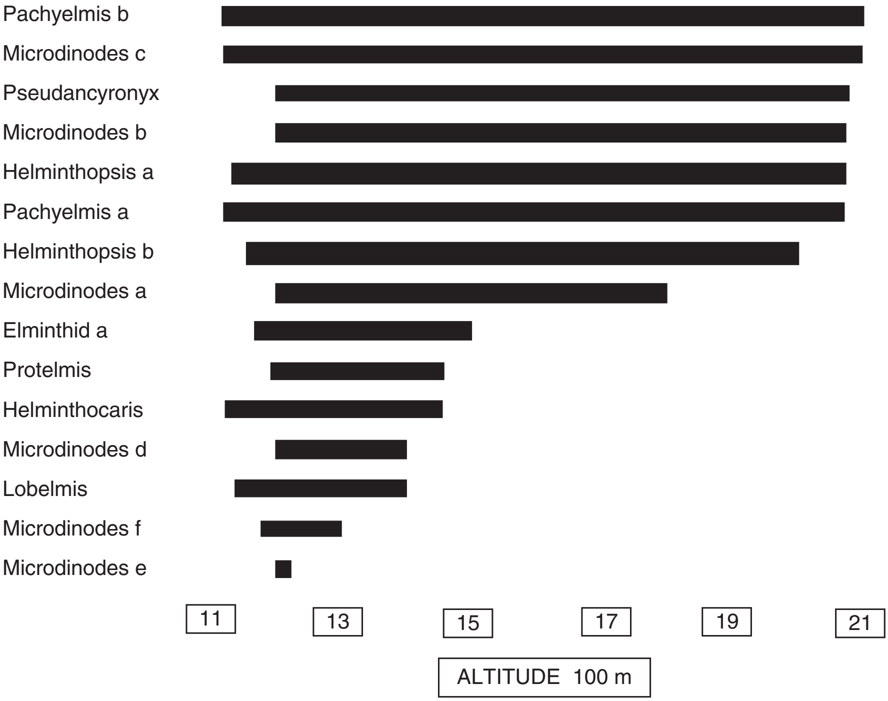

Fig. 5 Altitudinal zonation of elminthid beetles in streams on Mount Elgon (data from Williams & Hynes, 1971)

accumulate. Some of the stream dwelling invertebrates were found mainly in these silted areas: the trichopteran, *Anisocentropus*, and the oligochaete, *Bothrioneurum*, are good examples. The fauna is thus not only determined by altitude, but also by the local current flow.

The Manafwa River is one of the streams studied by Williams & Hynes (1971). Prof. P. Denny and I also sampled it in August 1987 and May 1990, close to its inflow into the swamp near Butaleja, where it is very different from a mountain stream. In this region it is a typical lowland tropical stream, flowing gently, with well developed vegetation. Samples taken with a 55 µm meshed plankton net revealed a rich microflora and microfauna. At least 20 genera of algae were present, and 50 species of rotifers were found, dominated by *Lecane bulla* and *L. luna*. Cladocera were represented by *Diaphanosoma excisum*, *Ceriodaphnia cornuta*, *Macrothrix triserialis*, *Ilyocryptus spinifer* and *Grimaldina brazzai*, while the copepods included *Tropocyclops confinis* and *Afrocyclops gibsoni*. The testate rhizopods included several species of *Arcella*, *Difflugia*, *Centropyxis* and *Euglypha*. This sort of assemblage could be found in the swamps anywhere along the Nile, from Lake Kyoga to the northern end of the Sudd and beyond. The transformation from mountain torrent to sluggish lowland stream occurs over a distance of about 60 km, and there is a corresponding change in the aquatic community from a unique assemblage (possibly paralleled in the Ruwenzori streams?), to one which may recur at intervals over a thousand or more kilometres.

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Lake Victoria

John T. Lehman

Abstract Lake Victoria, source of the White Nile, has shown itself to be a fragile ecosystem, sensitive to the variations in yearly climate and to the influences of man. Water balance is controlled mainly by over-lake precipitation and evaporation, which vary greatly from year to year according to cloud cover and surface radiation balance. Although the basin is 400,000 years old, the modern lake dried completely during the last glacial maximum, and it has had a permanent outflow for only the last 11,000 years. Despite its youth, the modern lake was the site of explosive speciation that produced over 500 species of haplochromine cichlids occupying at least 11 trophic guilds. Beginning in the twentieth century, overexploitation of the native fish stocks for an export market, introduction of alien species, and eradication of much of the species-rich biota led to the loss of both biodiversity and stability. Later in the century, nutrient enrichment and climate warming contributed to deoxygenation of deep water habitats and promoted the rise of nuisance Cyanobacteria and other changes in the lower food web. The lake now behaves as a light-limited, nutrient-saturated ecosystem that is becoming as biologically sensitive to radiation balance as is its water budget.

1 Physical Features

Lake Victoria and the clouds above it have drawn the attention of scientists and geographers ever since they became known as the source of the Nile's base flow. At 68,460 km^2 surface area, Lake Victoria ranks third in lake area globally, after the Caspian Sea and Lake Superior (Herdendorf, 1990). Numerous islands fringe the shore (Fig. 1), with combined surface area of about 1,500 km^2. The basin is moderately shallow, having mean and maximum depths of only 40 and 68 m, respectively (Johnson et al., 2000). Three riparian nations share the shoreline: Uganda, Kenya, and Tanzania. The lake's land catchment area occupies 194,200 km^2 (Piper et al., 1986), including parts of the

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three riparian states as well as Rwanda and Burundi. The ratio of catchment land surface to lake area is only 2.8, thus contributing to a relatively long water retention time and susceptibility to climate change. There are 23 identifiable drainages affluent to the lake (Okonga et al., 2006), but only one effluent: the White, or Victoria Nile. In recent decades the surface elevation has fluctuated within 2 m centered at 1,135 m a.s.l. (Fig. 2).

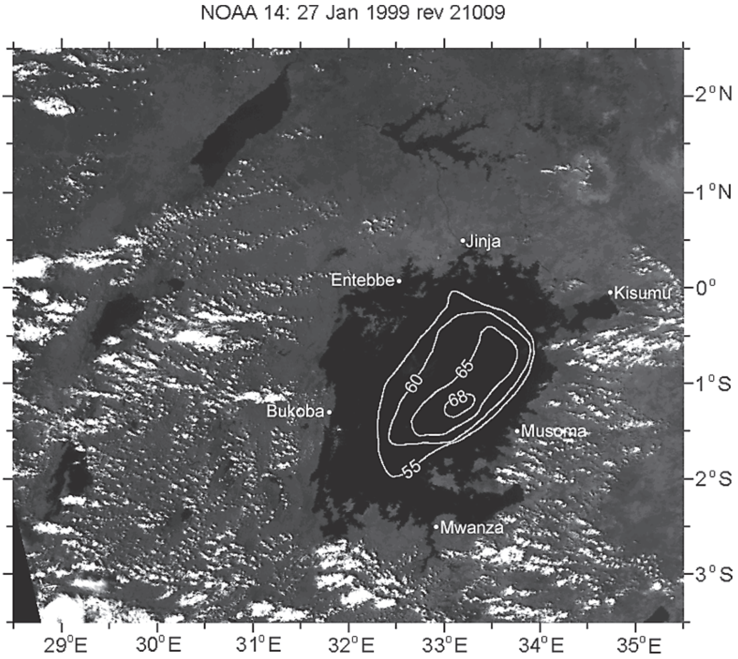

Fig. 1 AVHRR channel 2 (near-IR) from NOAA 14, 27 January 1999. Sites of daily weather observations are indicated (offshore depth contour lines are courtesy T. C. Johnson)

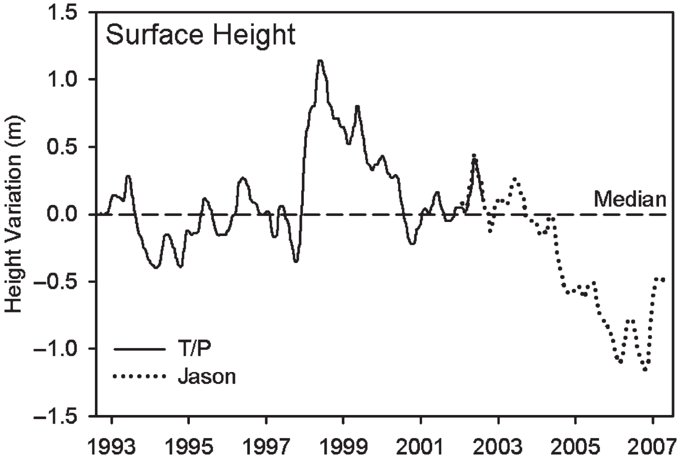

Fig. 2 TOPEX/POSEIDON (T/P) and Jason-1 satellite radar altimetry (http://www.pecad.fas.usda.gov). Data smoothed by 5-point moving median filter

2 Geological History

Seismic reflection profiles and estimated sedimentation rates date the origin of the lake to 400,000 years ago (400 ka; Johnson et al., 2000), the result of uplift along the western arm of the East African Rift Valley. Regional tilting resulted in the flooding of previously westward flowing river valleys still evident in a comparison of the west lake margin with those of the north, east, and south (Fig. 1). The lake floor itself is flat, the result of sedimentary infilling of underlying irregularities. Three major desiccation events have been identified, potentially corresponding with glacial–interglacial cycles. The most recent arid event culminated in complete desiccation of the basin, with rehydration commencing only 14.6 ka (Johnson et al., 2000). In this sense the modern lake is a youth compared to its ancient Rift Valley neighbors to the south, Tanganyika and Malawi; even so, the lake rivaled or surpassed its neighbors in the richness of its cichlid species flock (Seehausen, 2002).

Three fossil beaches, at 3, 12, and 18 m above modern lake level, represent stages in the evolution of the Holocene lake (Kendall, 1969). The high-water beach marks the origin of the Victoria Nile, which Johnson et al. (2000) place at 14.2 ka. The lower beaches may represent pauses in the rate of erosion of the outlet (Temple, 1967), or a return to closed-basin conditions from 13.6 to 11.2 ka during the Younger Dryas (Johnson et al., 2000). Stable isotope and biogenic silica profiles from sediment cores indicate that permanent outflow commenced at 11.2 ka. The age of the lowest beach (3 m above present) is well constrained by the presence of charcoal dated to 3.7 ka (Stuiver et al., 1960), so it seems to mark a former stage height of the Holocene lake.

3 Climatic Factors and Hydrology

Lake Victoria experiences two rainy seasons each year. The ‘long rains’ occur from March to May and the ‘short rains’ are from October to November. Seasonal climate is governed by migration of the intertropical convergence zone (ITCZ), which separates two relatively dry air masses, the northeast monsoon and the southeast monsoon, and the Congo Air Boundary, which separates moist westerlies from more arid easterlies (Nicholson, 1996). The rainy seasons correspond with periods of atmospheric instability as the ITCZ crosses the lake twice yearly. The lake also exhibits a strong diurnal pattern of cloudiness and rainfall that is controlled by a nocturnal land breeze system. At night, land breezes gather moisture and heat from the warm lake surface water and converge at the lake center, inducing upward air movement (Flohn & Fraedrich, 1966) with strong thunderstorms. Low elevation southeasterly winds play an important role in the rainfall pattern by displacing the center of night-time convergence toward the northwest (Nicholson et al., 2000; Nicholson & Yin, 2002), and they also seem to contain enough moisture to contribute to rainfall totals (Anyah et al., 2006). Overlake precipitation estimated by radar through the National Atmospheric and Space Administration (NASA) Tropical Rainfall Measuring Mission (TRMM) as reported by Anyah et al. (2006)

are generally consistent with estimates from thermal infrared assessment of cloud temperatures (e.g., Nicholson & Yin, 2002). Convection and rainfall are greatest during pre-dawn hours over the western and particularly the northwestern part of the lake. In the eastern part of the lake, convection and rainfall develop maximum intensity in the late afternoon to early evening.

The White Nile discharge from Lake Victoria controls the levels of Nile base flow into Sudan and Egypt. There has long been interest in the water balance of the lake, since it became known to European science after Speke's (1967, 1969) visits in 1859 and 1861 and its circumnavigation by Stanley (1878) in 1875. As early as 1929 Uganda, Sudan, and Egypt concluded international agreements regarding Nile flow rates (Crul, 1995). Numerous hydrological investigations reviewed by Yin and Nicholson (2000) pointed to annual rainfall totals in the range of 1,700 to 1,800 mm year^{-1} and annual evaporation rates of 1,500 to 1,600 mm year^{-1}. More recent estimates by Okonga et al. (2006) place precipitation at 1,860 mm year^{-1}. Both rainfall and evaporation exceed tributary inflows and discharge by four- to fivefold, which means that estimation errors in either of the large terms can control the accuracy of water balance calculations. Evaporation has been the more problematic of the two. Rates have typically either been measured empirically using evaporation pans at shore-based or island sites, or they have been calculated using energy balance models. The former method suffers from lack of open-lake observations; the latter method requires accurate assessment of over-lake atmospheric conditions, particularly cloud cover. The diurnal pattern of cloud cover caused by the land/lake breeze system as well as increased cloudiness during high rainfall years controls evaporation to a sufficient degree to contribute to dramatic rises and falls in lake level (Yin & Nicholson, 2000; Nicholson & Yin, 2002).

Regional differences in air temperature and moisture are evident in a comparison of six sites encircling the lake (Fig. 3). The data represented in Fig. 3 were calculated from data archives of the Global Historical Climate Network (GHCN, http://www.ncdc.noaa.gov/oa/climate/climatedata.html) that include monthly mean as well as minimum and maximum temperatures from early in the twentieth century at some sites, in addition to Summary of Day (SOD) records from 1957 to the present (http://www.ncdc.noaa.gov/cgi-bin/res40.pl?page = gsod.html). Median values by month for all data of record are reported in Fig. 3. Mean daily air temperatures range from 22°C at Entebbe to 25°C at Musoma. Drier conditions in the south are evident in the low dew point temperatures that in some cases are lower than the median monthly minimum air temperatures.

Prior to 1956, lake level fluctuation was regulated naturally by discharge at Ripon Falls near Jinja, Uganda. Discharge was directly controlled by lake level (Piper et al., 1986). Since 1956, outflow has been regulated by the Owens Falls dam, subsequently renamed the Nalubaale dam, a hydroelectric facility with 180 MW capacity. A discharge rating curve known as the 'agreed curve' (Piper et al., 1986) was established by treaty between Uganda and Egypt, the ultimate recipient of most of the Nile's water. The 'agreed curve' restricts discharge to a range of 300 to 1,700 m^3 s^{-1} depending on lake stage height in order to mimic the natural discharge characteristics. Lake level responds to the seasonal rains,

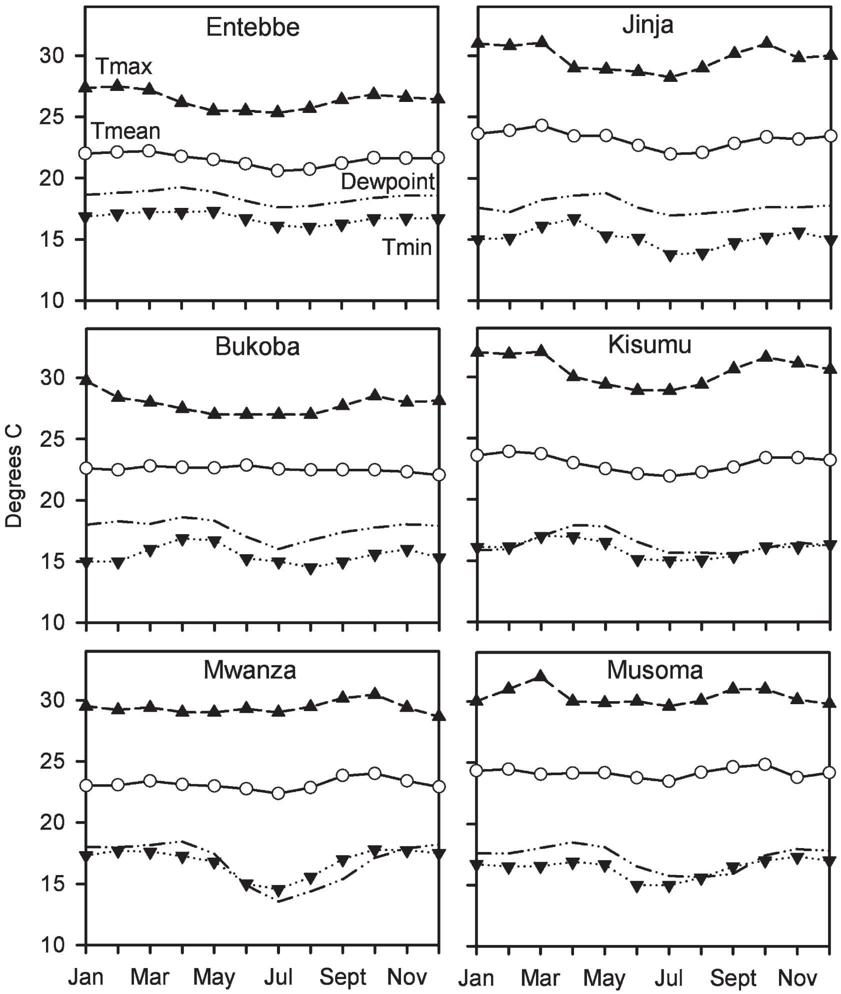

Fig. 3 Air temperature and moisture from six sites encircling the lake (see Fig. 1) (data taken from the Global Historical Climate Network[http://www.ncdc.noaa.gov/oa/climate/climatedata.html], plus Summary of Day records from 1957 to the present [http://www.ncdc.noaa.gov/cgi-bin/res40.pl?page = gsod.html]). Shown are median values by month for all data of record

typically rising during the main rains in April to a maximum in May or June, before falling to its annual minimum in October.

Interannual variations in rainfall and evaporation are able to effect striking changes in lake level, such as a famous rise of more than 2 m following unusually heavy rains in late 1961 and 1962 (Beadle, 1981). The operating rule ‘agreed curve’ was adjusted to maintain lake levels at the elevated stage height. More recently, lake levels rose during 1998 by about 1 m, which has been ascribed to enhanced rainfall and reduced evaporation during the strong El Niño year of 1997 to 1998

(Birkett et al., 1999). In 2002, Uganda began operation of a second hydroelectric facility, the Kiira power station with 200 MW capacity, about 1 km downstream from the first. Subsequent declines in lake level (Fig. 2) have been ascribed in part to overly ambitious power generation and departure from the 'agreed curve' (USDA, 2005; Okonga et al., 2006). From 1950 to 2000 the long-term mean discharge at Jinja, Uganda had been 1,046.2 m^3 s^{-1} (Okonga et al., 2006), implying a lake draw-down rate of 482 mm $year^{-1}$. From 2001 to 2004 discharge rose to 1,201.9 m^3 s^{-1}, or 554 mm $year^{-1}$. Given the dominance of precipitation and evaporation in the lake water budget, and given the mean water retention time of 80 years (i.e., 40 m mean depth, draw-down = 0.5 m $year^{-1}$), it is clear that variations in rainfall and evaporation exert profound constraints on the capacity for power generation at the lake outlet.

In addition to interannual variation, the lake has been subject to regional trends in climatic change during the twentieth century (Lehman, 1998; Lehman et al., 1998b). Climate variable anomalies calculated from the GHCN SOD data set after adjusting for long-term median monthly values show that not only have mean daily air temperatures increased significantly at four of six sites around the lake over the last 50 years (Fig. 4), but dew point temperatures have increased, as well, at five of the sites (Fig. 5). More striking still is the decrease in atmospheric transparency at all sites (Fig. 6). These factors have likely played a role in some of the profound physical and chemical changes within the lake that will be described later.

4 Radiation Balance

Net incoming solar radiation at the lake surface and net outgoing long wave radiation have been compiled over a 22 year period, from July 1983 to June 2005 based on satellite observations of surface radiation balance (http://eosweb.larc.nasa.gov/PRODOCS/srb/table_srb.html). Monthly mean values (Table 1) show only modest seasonality but a high degree of interannual variability. Net radiation gain is greatest from February to April, and is lowest from June to August. For February and March as well as August and September, interannual differences in radiative flux exceed the average annual variation. These differences are largely a consequence of interannual variations in cloud cover (Table 2). The mean annual radiation balance at the lake surface is consistent with a mean annual evaporation rate of 1,833 mm $year^{-1}$, assuming average water temperature of 25°C and no net heat conduction (i.e., a Bowen ratio of 0). The standard deviation of net radiation balance averages 10% of the mean, thus potential evaporation rates are subject to the same percentage level of variation.

5 Limnology

Many of the limnological investigations of Lake Victoria have been in support of studies of the changing fisheries of the lake. The lake experienced dramatic changes during the twentieth century (Table 3) many of which were anthropogenic.

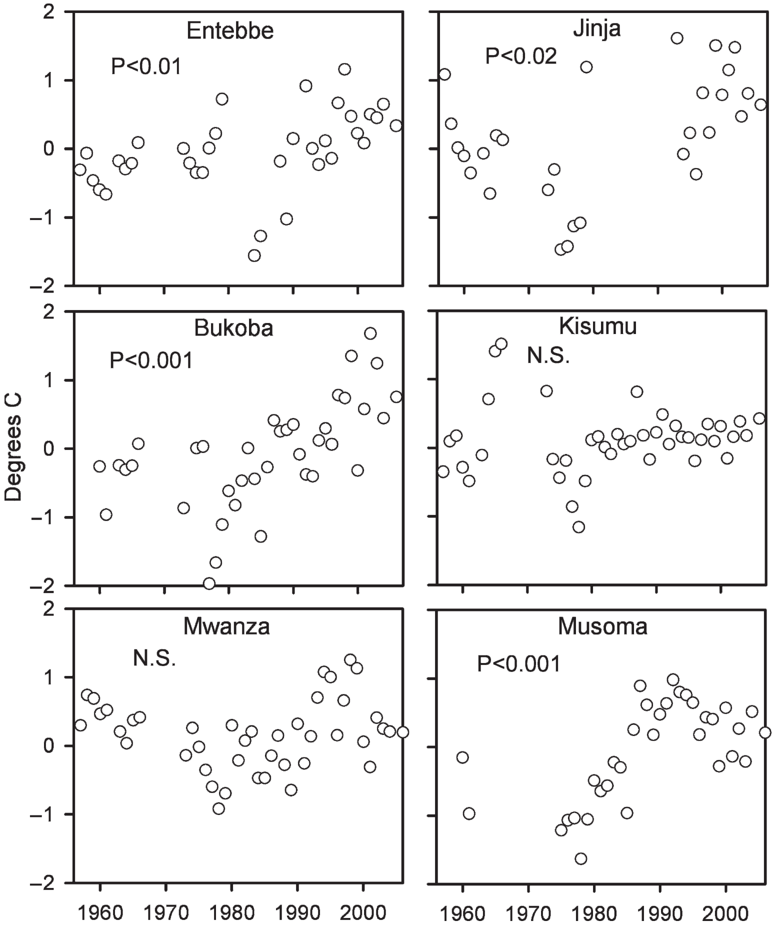

Fig. 4 Mean daily air temperature anomalies by year from six sites (see Fig. 1). Anomalies calculated after adjusting for seasonal effects by subtracting long-term median monthly values. Significance levels of linear regression are listed

In particular, the fish community has been transformed from its native state of remarkable species richness to a much simpler, largely introduced fauna that appears to be unstable under prevailing exploitation regimes.

5.1 Historical Conditions

The first systematic biological survey of Lake Victoria was the Fishing Survey conducted in 1927 and 1928 by Graham (1929). That survey also included the first physical and chemical measurements of the lake, as well as observations of the zooplankton (Worthington, 1930, 1931). The indigenous fishes of Lake Victoria

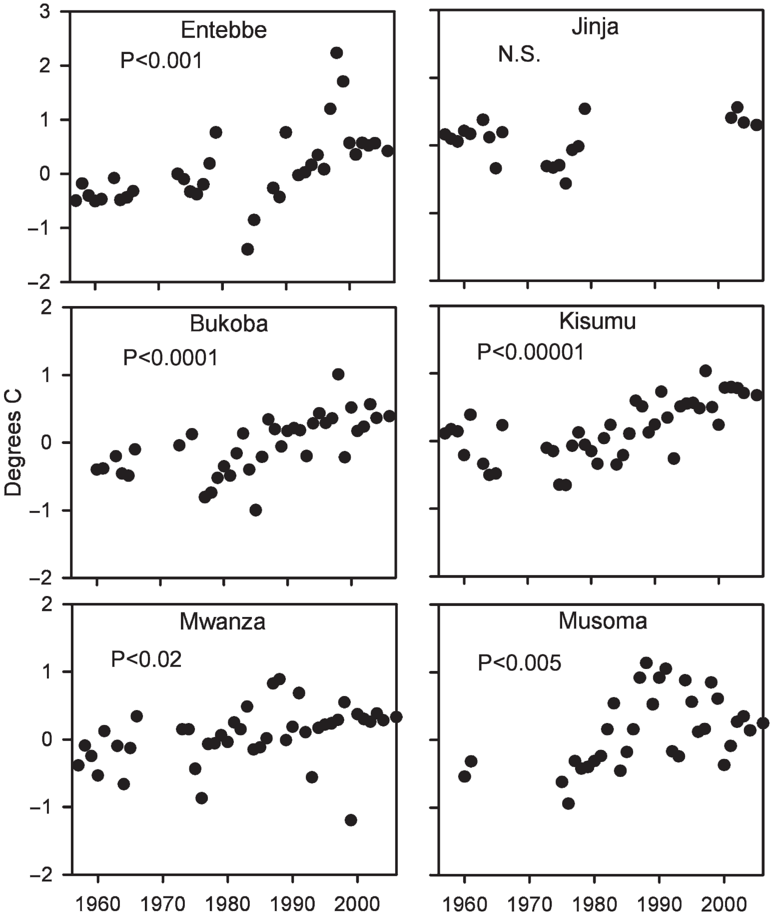

Fig. 5 As Fig. 4, but for dew point temperatures

belonged to 50 non-cichlid species (Lowe-McConnell, 1975) and over 500 cichlid species (Seehausen et al., 1997a) consisting of two tilapiines (*Oreochromis esculentus* and *O. variabilis*) and the rest haplochromines, the result of explosive speciation (Greenwood, 1965). *Oreochromis* occupied shallow water habitats nearshore; lake-wide surveys (Kudhongania & Cordone 1974) demonstrated that the offshore demersal ichthyofauna, estimated at 700,000t, was dominated by relatively small haplochromines and was devoid of large top predators. The species-rich haplochromine species flock exhibited extreme trophic radiation made possible through extensive morphological and behavioral adaptations, and its members were distributed lake-wide at all depths (van Oijen et al., 1981; Goldschmidt & Witte, 1992). As many as 11 trophic groups had been recognized, and even within a single trophic group, species exhibited niche differentiation by segregating according to space, time, or specific foods (Goldschmidt et al., 1990).

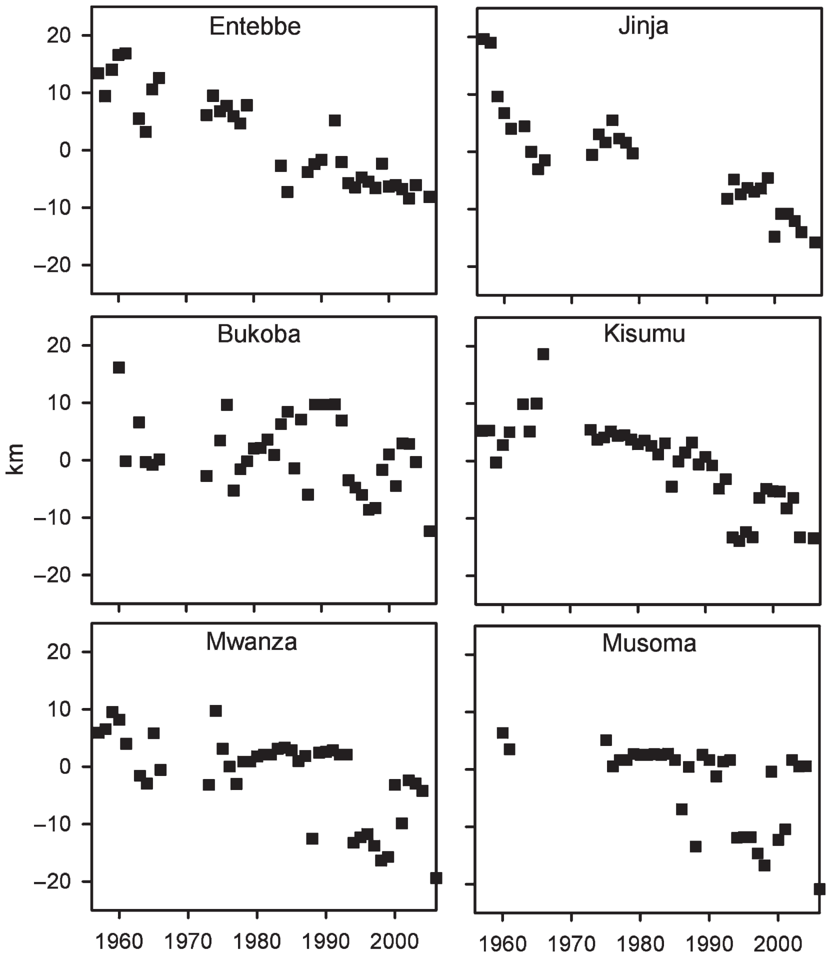

Fig. 6 As Fig. 4, but for atmospheric transparency. All linear regressions are statistically significant at P ≤ 0.05

After World War II research greatly expanded with the establishment of the East African Fisheries Research Organisation (EAFRO) in 1947 at Jinja, Uganda. Later named EAFFRO (East African Freshwater Fisheries Research Organisation), the organization established additional sites in 1975 at Kisumu, Kenya, and Mwanza, Tanzania (Crul, 1995). In a parallel development, the East Africa High Commission established the Lake Victoria Fisheries Service to oversee fishery production and management, with vessels based at Entebbe, Uganda as well as Kisumu and Mwanza. EAFRO established close working relationships with members of the Freshwater Biological Association of the UK, leading to a number of important limnological studies (Fryer & Talling, 1986).

Table 1 Net incoming short wave radiation (SWnet, W m^{-2}) and net outgoing long wave radiation (LWnet, W m^{-2}) at lake surface from NASA's Surface Radiation Budget (SRB) dataset for the open water of Lake Victoria: 0° to 2° S, 32° to 34° E; n = 22 years

Month	SWnet (SD)	LWnet (SD)	Total (SD)	Min	Max
Jan	184.3 (17.1)	–49.1 (6.0)	135.2 (13.7)	108.2	154.1
Feb	215.0 (20.0)	–51.9 (6.5)	163.1 (16.0)	125.5	190.1
Mar	226.3 (24.1)	–48.7 (4.4)	177.7 (21.3)	126.2	203.4
Apr	196.7 (18.2)	–45.3 (3.9)	151.4 (16.4)	121.5	172.2
May	188.6 (13.3)	–49.4 (4.4)	139.2 (12.2)	109.8	159.9
June	185.5 (17.6)	–57.1 (6.3)	128.4 (12.6)	104.2	147.4
July	185.7 (17.9)	–62.9 (7.1)	122.8 (12.1)	95.3	138.2
Aug	182.6 (16.8)	–61.0 (5.1)	121.5 (14.1)	86.5	144.9
Sept	211.3 (19.3)	–58.4 (6.0)	152.9 (15.7)	112.5	188.9
Oct	190.5 (17.2)	–47.8 (3.9)	142.7 (16.8)	114.1	168.3
Nov	173.9 (16.2)	–42.4 (3.4)	131.6 (15.1)	102.9	154.0
Dec	182.9 (14.2)	–45.5 (4.1)	137.4 (12.1)	114.5	162.5

Table 2 Cloud cover (percent) for the same dataset and time period as in Table 1

Month	Cloud Cover (SD)	Min	Max
Jan	70.3 (7.9)	57.3	84.0
Feb	68.0 (8.2)	53.1	86.5
Mar	74.3 (5.9)	62.4	83.8
Apr	76.8 (3.8)	69.5	82.1
May	67.8 (5.6)	56.0	79.0
June	57.0 (9.7)	34.0	70.5
July	54.1 (10.0)	31.2	76.9
Aug	58.2 (8.1)	38.1	78.1
Sept	64.9 (6.1)	52.6	77.0
Oct	76.9 (4.2)	68.9	85.5
Nov	78.9 (3.2)	73.1	85.4
Dec	71.3 (5.5)	62.8	82.9

Several investigations conducted from the 1920s to the 1960s, before the heavy floods of 1961 to 1962, provide an essential historical reference for the condition of the lake (Worthington, 1930, 1931; Fish, 1957; Newell, 1960; Talling, 1957a, b, 1966; Talling & Talling, 1965). Studies demonstrated that the lake was a warm monomictic basin that was thermally stratified through most of the year with mean temperature generally between 24°C and 25°C. The vertical temperature gradient in the offshore was at most 1.5°C, only slightly greater than the diurnal temperature gradients that developed at protected nearshore sites (Talling, 1957b). Cooling commenced in May, coincident with reduced net radiation balance (Table 1); the lake became isothermal by July, and cooled to a minimum temperature of about 23.5°C in August, although Talling (1966) cites results from surveys earlier in the century that suggest a minimum temperature of 23°C. Weak thermal stratification was re-established in September; by December a distinct thermocline was identifiable between 30 and 60 m, its exact depth subject to the action of internal waves.

Table 3 Key dates and events in the Lake Victoria ecosystem during the past century

Year	Event	References
1899	Regular recording of lake water levels commences	Beadle, 1981
1901	Completion of railroad from Mombasa to Kisumu, Kenya	Pringle, 2005a
1905	Introduction of flax gill nets with opportunity to transport fish to Nairobi markets	Kudhongania et al., 1996
1921	Yield of *Oreochromis esculentus* in severe decline	Graham, 1929
1920s	Introduction of non-selective beach seines	Graham, 1929
1927	Fishery Survey undertaken	Graham, 1929; Worthington, 1930
1929	Graham recommends that introduction of large predatory Nile perch from Lake Albert should not be attempted without prior careful study	Graham, 1929; Worthington, 1996
1952–1953	Introduction of synthetic fiber gill nets and the outboard motor; fish community dominated by small *Haplochromis* spp.	Kudhongania et al., 1992
1953	EAFFRO approved introducing 4 tilapiines: *Oreochromis leucostictus*, *O. niloticus*, *Tilapia rendalli* (formerly *T. melanopleura*), *T. zillii*	EAFFRO, 1967
1954	Nile perch first introduced, unofficially	Amara, 1986
1960	Nile perch appear in fishery catch	Pringle, 2005a
1961–1962	Heavy rains and flooding; lake level rises 2 m	Beadle, 1981
1962–1963	Extensive deliberate stocking of Nile perch	Ogutu-Ohwayo, 2004
1973	Fishmeal plant established in Mwanza; commercial trawling for haplochromines begins	Kudhongania et al., 1992
1970s	Nile perch proliferated; catch rose steadily to 500,000 t year^{-1} by 1989	Pringle, 2005b
1975	*Lates* significant in Uganda	Kudhongania et al., 1992
1977	*Lates* significant in Kenya	Kudhongania et al., 1992
1978	*Lates* significant in Tanzania	Kudhongania et al., 1992
	Large haplochromines depleted; catch rates fall	Witte and Goudswaard, 1985
1986	*Microcystis* blooms noted offshore	Ochumba and Kibaara, 1989
1989–1990	Extensive changes in limnological condition, including chlorophyll, transparency, oxygen, silica, and algal flora	Hecky, 1993
1989	*Eichhornia crassipes* reported in Uganda and Tanzania waters; rapid expansion to nuisance dimensions	Twongo, 1996
1995	Biocontrol weevils *Neochetina* spp. introduced	Ochiel et al., 1999
1998	*Eichhornia* reached peak areal coverage, ca 174 km^2; most severe in north and on protected bays	Albright et al., 2004
1997–1998	1.7 m rise in lake surface height; water hyacinth declined; lake level receded by 2001	Albright et al., 2004
2000	Yield of Nile perch fishery in decline	Ogutu-Owayo, 2004; Pringle, 2005b
2001–2004	Lake level declined more than 1 m; excessive power generation implicated	Okonga et al., 2006

Thermal stratification was associated with partial deoxygenation of the offshore hypolimnion from January to June (Fish, 1957; Talling, 1957a, 1966). Within 5 m of the bottom sediments, oxygen decreased to less than 30 µM (1 mg L^{-1}), but Talling (1966) reported only one incident of complete anoxia at 60 m depth in February 1961. Surface waters exhibited oxygen concentrations close to saturation, ranging from 90% to 103% of saturation.

Concentrations of nitrate in the surface from 0 to 20 m remained less than 1 µM throughout the year, but in the deepest water of the hypolimnion during April, nitrate achieved a maximum of 5 µM. Dissolved inorganic phosphate was typically present at less than 0.5 µM in the surface waters except during isothermal mixing in August when it rose to 0.7 µM. During stratification, phosphate episodically could exceed 2 µM in the low oxygen regions near the lake bottom. Total P in the euphotic zone (0 to 20 m) ranged from 1 to 1.6 µM. Talling (1966) reported dissolved Si levels of about 70 µM in the euphotic zone most of the time, except for the mixing period in August when levels decreased to 50 µM. Maximum concentrations near bottom exceeded 100 µM during stratification.

Algal standing crop, measured as particulate chlorophyll *a*, ranged from 1.2 to 5.5 mg m^{-3}, with maximum levels achieved during isothermal mixing in August (Talling, 1966). Much of the biomass consisted of diatoms, particularly two heavily silicified species of the genus *Aulacoseira*, plus *Cyclostephanos*, *Stephanodiscus*, and *Nitzschia*. Green light of ca 560 nm was the most penetrating spectral component, with attenuation coefficient of about 0.3 m^{-1}, thus implying that about 1% of surface incident light could penetrate to 15 m.

5.2 Fishery Transformation

Lake Victoria's transformation from artisan to commercial fisheries began with the establishment of a railhead at Kisumu in 1901, thus providing an outlet to the Nairobi markets (Table 3). Traditional basket trap, hooks, and other simple fishing gear were replaced by flax gill nets, and wholesale exploitation of the native *Oreochromus* stocks commenced. Graham's (1929) report recommended that gill nets be restricted to 12.7 cm (5 in.) minimum mesh to give refuge to first reproducing individuals, but the regulation was subsequently abandoned as catches diminished. Introduction of non-selective beach seines in the 1920s further decimated juvenile and breeding stocks of the favored tilapiines and other table fish.

Avid anglers had been advocating the introduction of Nile perch (*Lates niloticus*) into Lake Victoria since at least the 1920s (Worthington, 1996) to consume the small, bony haplochromine 'trash fish' and to provide a large game fish. Graham (1929) resisted the argument and called for careful study elsewhere before any such dramatic step was contemplated for Victoria. However, with the creation of the Lake Victoria Fisheries Commission in 1949 there was renewed interest in supplementing the waning commercial fishery. EAFFRO scientists continued to oppose introduction of *Lates*, citing the prospect of ecosystem disruption (Pringle, 2005a).

However, they approved introduction of four exotic tilapiines (Table 3) to rehabilitate the main fishery. Of these, only *O. niloticus* ultimately proliferated, and the native species all but disappeared (Goudswaard et al., 2002).

After the construction of the Owen's Falls dam in 1954, putatively sealing off Lake Victoria from the Victoria Nile below it, Uganda Game and Fisheries Department (UGFD) officials began stocking the Victoria Nile and Lake Kyoga above Lake Albert with *Lates* from Lake Albert. Previously, Murchison Falls above Lake Albert had blocked the possibility of natural upstream dispersal. Amara (1986) has reported that the officials also released some Nile perch into Lake Victoria. UGFD steadfastly denied the claim and instead argued that the fish entered Victoria through inactive turbines of the hydroelectric facility (Pringle, 2005a). In either event, the large predators started to appear in fishery catch in 1960, and extensive deliberate stocking commenced in 1962 and 1963, using stocks from Lake Albert (Uganda) and Lake Turkana (Kenya) (Ogutu-Ohwayo, 2004).

Despite a potential for prolific reproduction, it took more than a decade for Nile perch to become significant components of the commercial catch (Table 3). In the meanwhile, Tanzania implemented commercial trawling operations for demersal haplochromines to use in fishmeal production. By the time that *Lates* became established in Tanzanian waters in 1978, the haplochromines had been largely decimated by trawling (Witte & Goudswaard, 1985). Elsewhere, however, it was clear that the rise of Nile perch coincided with collapse of haplochromine stocks, and that as predicted, *Lates* was preying on the smaller fish (Ogutu-Ohwayo, 1990). Haplochromines in the sublittoral and offshore waters almost disappeared completely, and about 60% were believed to have become extinct (Witte et al., 1992a, b). Annual yields of Nile perch climbed from 100,000 t in the late 1970s to 500,000 t by 1989. Fish processing plants were constructed around the lake and a lucrative export market developed.

By the 1980s the species-rich fish community of Lake Victoria had become effectively reduced to three components: the introduced Nile tilapia, the introduced Nile perch, and a native small cyprinid, *Rastrineobola argentea*. Stocks of the latter species increased as haplochromines were suppressed by Nile perch (Wanink, 1991, 1999). There is evidence that *Rastrineobola* extended its range of vertical distribution downward in the absence of haplochromines and added macrobenthos to its diet (Wanink & Witte, 2000). By the late 1980s *Rastrineobola* emerged as the only vertebrate zooplanktivore of any abundance, whereas before the rise of Nile perch more than 25% of the commercial trawling catch had been zooplanktivorous haplochromines (Goldschmidt et al., 1993).

Juvenile Nile perch less than 4 cm in length subsist on cyclopoid copepods, but larger calanoid copepods become significant components of the diets of fish at 3 to 4 cm in length (Katunzi et al., 2006). At about 5 cm the diet shifts from copepods to midge fly larvae (Diptera, mainly *Chaoborus*), and then to a mixture of *Rastrineobola*, anisoptera nymphs, the atyid shrimp *Caridina nilotica*, and small Nile perch. *Caridina* often dominated the diets of fish up to 60 cm (Hughes, 1986, 1992). Fish from 60 to 100 cm eat mainly *Rastrineobola* and Nile perch juveniles; fish larger than 100 cm consume tilapiines plus juvenile *Lates*

(Ogutu-Ohwayo, 2004). Evidence from diet studies is consistent with stable isotope analyses (Campbell et al., 2003) that show increasing degrees of piscivory in progressively larger fish.

Shortly after its introduction and until 1982, condition factor (a scaled ratio of weight to cube of length) exceeded that of the native source population of Lake Albert, which was attributed to the excellent forage provided by Victoria haplochromines. With the collapse of the haplochromine stocks, condition factors in Lake Victoria fell below that of the native habitat, prompting calls for restrictions on human exploitation of *Lates*' new forage base, *Rastrineobola* and *Caridina* (Ogutu-Ohwayo, 2004). Moreover, owing to the fact that females mature at a larger size and greater age than do males (Hughes, 1972), heavy exploitation of *Lates* began to skew the sex ratio at first reproduction to a preponderance of males.

During the 1980s, fishing pressure on the tilapiines eased as the fishery became concentrated on Nile perch. Both population density and individual sizes of *O. niloticus* rebounded, but the native *Oreochromis* species did not recover, which was attributed to their inferior competitiveness compared to the introduced species (Goudswaard et al., 2002). These authors ascribe coexistence of *Lates* and *Oreochromis niloticus* to spatial segregation in habitat use, such that most Nile tilapia frequent shallow, nearshore regions less than 2 m in depth whereas piscivorous Nile perch prefer deeper water. There is also evidence that the body morphology of *O. niloticus* makes it difficult for *Lates* to swallow (El Gamal, 1992).

Nile perch have been regarded as relatively sensitive to low levels of dissolved oxygen since Fish (1956) demonstrated that their blood hemoglobin did not saturate with oxygen unless their gills were exposed to at least 156 μM O_2 (5 mg L^{-1}). Experiments show that the fish begin stress-induced irrigation of their gills at the air-water interface at roughly 90 μM O_2 (Schofield & Chapman, 2000), renewing speculation that potential prey might find refuge in hypoxic environments. Wanink and Witte (2000) indeed reported morphological adaptations for life at low oxygen levels among *Rastrineobola* after Nile perch became established, such as increased number of gill filaments. However, Wanink et al. (2001) argue that these adaptations were coincident with a decrease in number of gill rakers and more likely represent an opportunistic expansion of diet breadth to include plentiful macrobenthos that do abound in hypoxic regions (Branstrator & Mwebaza-Ndawula, 1998).

As Nile perch became the focus of intense fishery exploitation pressure, stocks began to decline (Balirwa et al., 2003; Getabu et al., 2003) and recent estimates suggest that the fishery is unsustainable unless regulations are introduced (Ogutu-Ohwayo, 2004; Matsuishi et al., 2006). In the face of declining stocks of the introduced predator, some haplochromines have begun to recover (Witte et al., 2000). The resurging species represent a selected subset of the original fauna that managed to maintain a cryptic presence in various refugia including lagoons, swampy littoral regions and rocky crevices (Chapman et al., 2002). In some cases the returning species show signs of new trophic adaptations (Katunzi et al., 2003). The same is true of at least two predatory catfishes that shifted their diets from haplochromines to invertebrates or *Rastrineobola* after the Nile perch upsurge (Olowo & Chapman, 1999).

5.3 Environmental Change and Eutrophication

Comprehensive investigations of water quality and lower trophic levels in the offshore waters of Lake Victoria (e.g., Talling 1965, 1966) were interrupted in the years immediately after national independence and the political instability that followed. By the mid-1980s it was clear that algal blooms were becoming more pronounced and increasingly dominated by cyanobacteria, particularly *Microcystis* (Ochumba & Kibaara 1989) compared with earlier reports. Within the Kenyan waters of Nyanza Gulf, the main northeastern bay also known as Winam or Kavirondo Gulf, massive fish kills started to be documented in 1984 (Ochumba, 1990) and were ascribed to pollution and increased algal production.

Much of the catchment, particularly close to the lakeshore, is densely populated (Verschuren et al., 2002) and human population growth within the riparian states exceeded 3% per year during most of the twentieth century (Bugenyi & Magumba, 1993; U.N., 2005). The growing human population accelerated the rates of deforestation, agriculture, animal husbandry, industrialization, and wastewater disposal into the lake, contributing to increased biological productivity during the twentieth century (Lipiatou et al., 1996). These changes at the landscape level were superimposed on a warmer and wetter regional climate during the latter half of the century (Hastenrath & Kruss, 1992; Lehman, 1998; Lehman et al., 1998b). The result was eutrophication of a pattern familiar in temperate regions (Hecky, 1993).

By 1990, primary productivity expressed as oxygen fixed per unit area per day had doubled, and algal biomass expressed as chlorophyll-*a* had increased about fourfold from that measured by Talling (Mugidde, 1993) and depth of the euphotic zone was halved. Silica concentrations had fallen from 70 µM to less than 10 µM or sometimes even less than 1 µM in the surface waters (Hecky, 1993). Total phosphorus concentrations offshore had doubled and sulfate had decreased fivefold (Lehman & Branstrator, 1994).

Thermal stratification had become more severe compared with 30 years earlier and the vertical extent of seasonal hypolimnetic anoxia had greatly expanded (Hecky, 1993; Hecky et al., 1994). Depressed ratios of total N to total P in the hypolimnion, less than 10 to 1 by moles, were attributed to denitrification within the water column at low redox-potentials (Hecky et al., 1996).

Lake Victoria had always been remarkable for its low ambient concentrations of sulfate, 3 to 4 µM (Hecky & Bugenyi, 1992; Lehman & Branstrator, 1993), probably the lowest for any large lake. For this reason, Beauchamp (1953) had proposed that sulfate was possibly growth-rate limiting for phytoplankton. However, both in situ growth bioassay and sulfate uptake experiments demonstrated that sulfate concentrations were well above limiting levels (Lehman & Branstrator, 1994). The same was true for phosphate in the offshore, but not in the nearshore. Turnover times for phosphate offshore were about 100 h; nearshore they were about 6 min.

Bioassay experiments pointed to N as the most limiting nutrient element for phytoplankton both inshore and offshore when adequate light is available (Lehman & Branstrator, 1993, 1994), and there is evidence that iron can stimulate N fixation in the presence of adequate light (Guildford et al., 2003). However, this N limitation appears to be the proximate manifestation of a more profound biogeochemical process. Although inorganic phosphate is plentiful offshore, it is often removed to undetectable levels in the water that leaves the lake as the Victoria Nile. This phenomenon appears to be the result of an interaction between light regime and nitrogen economy. Algae in the offshore waters are susceptible to light limitation of photosynthesis owing to a vertically diminished modern euphotic zone (Mugidde, 1993). Even within the shallower waters of Nyanza Gulf, light availability can limit algal production and biomass (Gikuma-Njuru & Hecky, 2005). Nitrogen fixation is similarly light-limited offshore (Hecky, 1993). Sometimes it is light-limited inshore as well, particularly during July, the time of greatest vertical mixing (Mugidde et al., 2003). Both of these limitations by light of photosynthesis and nitrogen fixation are eased in the shallow inshore regions because maximum vertical mixing depth is physically constrained by basin morphometry. Further, denitrification is presumably lessened inshore owing to increased availability of oxygen near the sediments, with the result that total nitrogen levels rise (Hecky, 1993; Lehman & Branstrator, 1994; Hecky et al., 1996) mainly in the form of particulate matter. Particulate P also increases, at least until the inorganic P is exhausted. In this way, the lake can biologically titrate its phosphate supply long-term while consistently displaying N limitation in short-term assays.

Recent evidence now points to the likelihood that Lake Victoria is approaching a state of nutrient saturation (Silsbe et al., 2006) such that mixing depth and underwater light climate control the rates of primary production to such degree that excess phosphate can accumulate even in shallow bays. If so, interannual variations in shortwave radiation balance (Table 1) and cloudiness (Table 2) that are so important to water balance will have direct control of lakewide primary production, as well.

Analysis of a sediment core from the deepest region of the lake is consistent with anthropogenically-driven changes during the twentieth century. During most of the nineteenth century and until about 1940, the diatom flora of Lake Victoria was dominated by well silicified species of *Cyclostephanos* and *Aulacoseira* (Verschuren et al., 2002). Overall diatom production then increased, but dominance progressively shifted to *Nitzschia acicularis*, a weakly silicified species with slower sinking rates and sometimes an epiphytic growth habit. The fossil evidence is consistent with plankton counts that show *Aulacoseira* rare to absent at present, and *Nitzschia* common (Kling et al., 2001).

In addition, fossil assemblages of Chironomidae (Diptera) are consistent with establishment of seasonal deep water anoxia commencing from the 1960s onward (Verschuren et al., 2002). Diatoms and cyanobacteria are known to exhibit virtually opposite growth responses to environmental conditions (Lehman et al., 2004), particularly to water column stability and optical depth. Floral, physical, and chemical changes in Lake Victoria signify a progression driven by increased phosphorus loading and slackened vertical mixing. Regional climate trends (Figs 3 and 4) toward warmer air temperatures and higher humidity help to raise surface water temperatures and increase buoyancy that opposes deep mixing. The result has been the replacement of rapidly sinking diatoms with smaller ones, depletion of silica in the surface waters, the rise of more buoyant and in some cases diazotrophic cyanobacteria, elevated phytoplankton biomass, and reduced water transparency.

Current estimates of phosphorus loading to Lake Victoria average 11.5 mmol m^{-2} year^{-1} (24.4 kt year^{-1}) of which more than half (13.5 kt or 55%) arrives by atmospheric deposition, particularly as dryfall (Tamatamah et al., 2005). Soils of the region are rich in apatite (Reedman 1984) and relatively modest rates of erosion, including wind erosion, could easily account for the elevated phosphorus of the lake (Holtzman & Lehman, 1998). Tamatamah et al. (2005) cite runoff as contributing 9.8 kt P year^{-1}, and they attribute 1.1 kt P year^{-1} to municipal wastewater, scaling upward from earlier estimates by Scheren et al. (2000).

Nitrogen loading is dominated by N-fixation, which supplies on average 814 mmol m^{-2} year^{-1} (11.4 g N m^{-2} year^{-1}: Mugidde et al., 2003). Scheren et al. (2000) estimated atmospheric deposition through rainfall as 89 mmol m^{-2} year^{-1} (85.513 kt year^{-1}). Lower bound estimates of total diffuse runoff by Lindenschmidt et al. (1998) equal 0.6 to 9.6 mmol N m^{-2} year^{-1} (8 to 135 kg N km^{-2} year^{-1}). Scheren et al. (2000) estimated that agricultural runoff and wastewater combined deliver 35.4 mmol N m^{-2} year^{-1} (33.9 kt year^{-1}). These numbers suggest annual loading of perhaps 950 mmol N m^{-2} year^{-1}, of which more than 85% is N-fixation.

Taken together, N and P loading figures imply a N:P ratio (mol:mol) of about 80:1. The bulk of Victoria's offshore water mass has a mean total N:total P ratio of 13.5 (Guildford & Hecky, 2000) and N:P ratios in recent sediments are about 20:1 (Hecky 1993). Ratios are somewhat higher in Napoleon Gulf, near the outlet, about 45:1 (Lehman & Branstrator, 1994). Mass balance can be satisfied, therefore, only if at least 40% of the N income is lost through denitrification.

The environmental changes to Lake Victoria's primary production base and nutrient chemistry were largely contemporaneous with transformation of its fishery, but antecedent to the rise of Nile perch and collapse of the haplochromine stocks. The changes are interrelated, however. It took roughly 15 years from the first official, deliberate stocking (Table 3) until Nile perch achieved prominence in the food web. Even with *Lates*' relatively late age of first reproduction of 3+ years (Balirwa et al., 2003), the lag time is notable. Much haplochromine biomass had been distributed in the deep waters of the lake (Kudhungania & Cordone, 1974) before the rise of Nile perch. These fish became displaced as the vertical extent of seasonal anoxia grew, exposing them to the new predator. Moreover, the reduction in water transparency stemming from biomass accumulation may play a detrimental role in possible recovery of species richness in the wake of a Nile perch decline. There are indications (Seehausen et al., 1997b) that increased turbidity interferes with cichlid color vision, thereby eliminating the key mechanism for mate choice, sexual selection, and reproductive isolation.

5.4 Water Hyacinth Invasion

Water hyacinth (*Eichhornia crassipes*) was first reported in Lake Victoria in 1989, though it is believed to have been present somewhat earlier (Twongo, 1996). By 1995 the floating weed infested 80% of the Uganda coastline, forming floating mats from 15 to 50 m wide, and at times clogging the turbines at the Nalubaale dam (Williams et al., 2005). Efforts to control the weed during the early 1990s centered on manual removal (Albright et al., 2004) and were of limited success. Beginning in 1995, biocontrol weevils of the genus *Neochetina* were introduced (Ochiel et al., 1999) as part of a more comprehensive program of integrated pest management. During the El Niño year of 1997 to 1998 the weed reached its high mark of abundance and then precipitously declined. This collapse has been attributed to light limitation during the cloudy conditions and heavy rains that led to significant rise in lake level (Fig. 2), as well as to physical dislodgement of the littoral mats that accompanied lakeshore flooding (Albright et al., 2004; Williams et al., 2005) to much greater degree than to biocontrol.

Eichhornia has high requirements for both nutrients and light (Williams et al., 2005), the former of which are in increasing supply within the modern lake. The prospect of resurgence in the nuisance weed is therefore real (Ogwang & Molo, 2004), although the weevil populations have become well established, raising the possibility of cyclical and spatially disjoint *Eichhornia* outbreaks in the future.

5.5 Zooplankton Community

General features and species composition of the Lake Victoria zooplankton community have been described (Lehman, 1996). The crustacean zooplankton community of present day Lake Victoria is dominated in both numbers and biomass by small-bodied cyclopoid copepods (Mwebaza-Ndawula, 1994; Branstrator et al., 1996). Mean standing crops measured during 1992 from monthly samples at an offshore reference station (62 m depth) assuming a C to dry mass ratio of 0.5 were 1,430 mg C m^{-2} for adult and copepodid Cyclopoida, 766 mg C m^{-2} for adult and copepodid Calanoida, and 75 mg C m^{-2} for Cladocera. Owing to the variety of sampling gear and mesh sizes used by investigators over the years, and owing to a historical emphasis on numbers rather than biomass, it is not possible to say whether the community has changed significantly from that of the 1950s (Rzóska, 1957) or from the time of the Nile perch upsurge in the 1980s (Mavuti & Litterick, 1991). There have been suggestions that the dominance by cyclopoids is a change from conditions in the 1920s (Wanink et al., 2002), but that is not at all clear. Worthington (1931) had collected plankton over a 24-h period in 1927 from a deep site offshore and reported 50% calanoid copepods and 39% Cladocera by counts, but his net had an aperture of ca 640 µm ('15.7 meshes per cm,' p. 416), and could not properly census the microcrustacea: 'the catch contained more of the larger Crustacea in proportion but fewer of the very small organisms' (ibid).

Two important changes likely did arise from the food web transformations caused by Nile perch. First, *Caridina nilotica*, an atyid shrimp increased significantly despite its status as a prey item in the diets of both *Rastrineobola* and juvenile Nile perch (Goudswaard et al., 2006). Between 11% and 53% of the native haplochromines were zooplanktivores (Witte, 1981), and at least 13 species were specialized for feeding on *Caridina* (Greenwood, 1981; Witte & van Oijen, 1990). In addition, several piscivorous haplochromines included adult shrimp in their diets, and juvenile cichlids from virtually every trophic guild fed on juvenile *Caridina* when available (Goudswaard et al., 2006). The latter authors estimate that predation pressure on the juvenile shrimp became reduced with the collapse of the haplochromines, but that predation on the adults has continued or accelerated. Both Lehman et al. (1996) and Goudswaard et al. (2006) point to the size and age structure of offshore *Caridina* populations as evidence that there is heavy predation on the adult shrimp. Goudswaard et al., further suggest that one factor contributing to the long interval between Nile perch introduction and its rise to prominence (Table 3) could have been haplochromine predation on *Caridina*, which kept its population low and limited foraging prospects for the smallest Nile perch.

Fryer (1960) characterized *Caridina* as an epibenthic detritivore, but Worthington (1931) collected specimens from midwater plankton tows and Lehman et al. (1996) demonstrated that only 14% and 9% of animals at a 64-m offshore site were epibenthic during day and night, respectively. First estimates of the shrimp's lake-wide secondary production based on bioenergetics modeling (Ignatow et al., 1996) indicated that it consumed the equivalent of only about 0.2% of primary production, but that its production exceeded the elevated fishery yields of the peak Nile perch years by more than 10-fold, and with birth rates that permit potential population doubling times of one month (Mbahinzireki et al., 1998). More recent experimental assessments of *Caridina* growth rates (Hart, 2001) suggest that its production may be larger than these initial estimates, by at least 20%. These estimates point to *Caridina* as a most significant forage resource for Lake Victoria fisheries.

The second development of significance was the appearance of a large bodied *Ctenodaphnia* in offshore plankton collections from 1992 (Branstrator et al., 1996). Subsequently identified as *Daphnia magna* (Jonna & Lehman, 2002), the large-bodied cladoceran had not been reported from any previous plankton collection. Specimens as large as 2 mm were encountered, and they co-existed with the slightly smaller *Daphnia longispina*. Presence of such large and conspicuous herbivores can only be ascribed to at least temporary relaxation in the rate of zooplanktivory by visual predators. However, predation pressure on the herbivores was not so low that they could achieve abundances sufficient to permit them to exert grazing control over the phytoplankton (Lehman & Branstrator, 1993; Branstrator et al., 1996).

Diel vertical migration by Lake Victoria zooplankton was first documented by Worthington (1931), and is practiced by Crustacea including *Caridina*, by *Chaoborus*, and by fish (Lehman et al., 1996; Goudswaard et al., 2004). Zooplanktivorous haplochromines and *Rastrineobola* migrate upward at night to pursue migrating zooplankton and third or fourth instar *Chaoborus*.

Studies with stable isotopes of N and C have elucidated two major food chains operating in the Nile perch era (Branstrator et al., 2003). One of these is a trophic path from *Caridina* to juvenile *Lates*. The other leads from copepods and Cladocera to *Rastrineobola* and *Chaoborus*. The isotope evidence favors the conclusion that *Caridina* feeds on suspended detritus and associated microflora (Hart et al., 2003). Thus, its incursion of predation risk during nocturnal vertical migrations may reflect a quest for higher quality suspended particulates near surface than it encounters at depth (Branstrator et al., 2003).

Dipterans of the Chaoboridae and Chironomidae represent another important source of secondary production accessible to the fisheries of Lake Victoria. The resident dipteran taxa have been characterized as having life cycles of 2 lunar month duration, with pupation and adult emergence shortly after the new moon (MacDonald, 1956). Two cohorts exist at any time, 180° out of phase, such that an emergence occurs every month. Larvae of *Chaoborus* remain planktonic during their first two instars, but by their third week of life, as larvae enter instar III, they adopt diel migratory behavior that causes them to burrow in mud during the day and to rise upward at night. The larvae are ambush invertebrate planktivores that use tactile mechanoreceptors to identify potential prey. Chironomidae remain benthic and benthivorous through their fourth larval instar before rising to the surface as pupae. These dipteran life cycles impose a strong cyclic pattern on benthic biomass and production. The effect of this lunar periodicity on planktonic biomass is also substantial. Lehman et al. (1998a) reported offshore biomass of *Chaoborus* ranging from 0.3 to 230 mg C m^{-2} during 1994. When the biomass data are plotted against days before new moon, it is clear that biomass of the population compounds rapidly in the last two weeks of the lunar month (Fig. 7). As the animals grow larger, the intensity and duration of moonlight wane, helping to reduce their conspicuousness to visual predators.

Under the influence of lunar periodicity, *Chaoborus* seem to exhibit net secondary production rates that are on the order of 300 mg C $month^{-1}$, which is roughly of the same magnitude as that of *Caridina*. Like *Caridina*, *Chaoborus* production greatly exceeds fishery yields, and the animals represent a viable forage base. The occurrence of spectacular, massed lake fly emergences, however, suggests that their life history strategy successfully evades vision-oriented hunters until their short-lived adulthood is achieved.

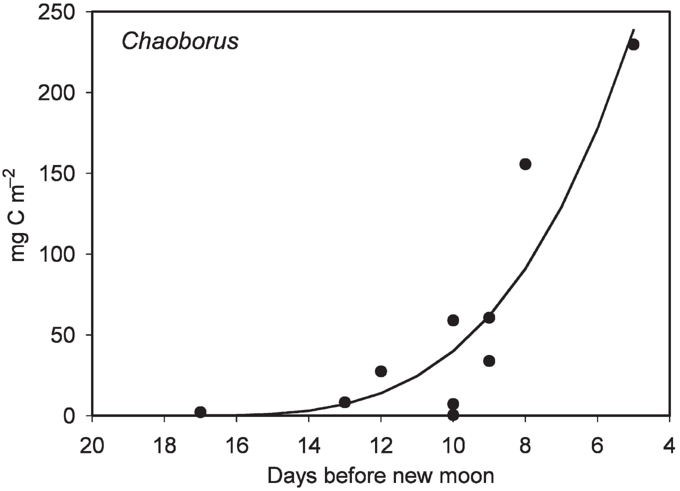

Fig. 7 Standing crop biomass estimates for *Chaoborus* at an offshore reference station during 1994 plotted against days before the next new moon (data from Lehman et al. (1998a: Table 4, p. 142)). Trend line is illustrative only and is a power function of time ($day^{3.68}$; $r^2 = 0.84$)

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Rwenzori Mountains (Mountains of the Moon): Headwaters of the White Nile

Hilde Eggermont, Kay Van Damme, and James M. Russell

Abstract The Rwenzori Mountains, Ptolemy's legendary Mountains of the Moon, were created in the late Pliocene (less than 5 Ma BP) and stretch along the border between western Uganda and Democratic Republic of Congo. The landscape has been sculptured by repeated growth of glaciers, resulting in numerous lakes and six separate mountains rising over 4,500 m asl. Apart from being considered the (highest) source of the White Nile, the range is also renowned for its high level of endemicity, especially with regard to the terrestrial biota. In this chapter, we sketch the history of exploration, and summarize the main characteristics of Rwenzori's terrestrial and aquatic ecosystems. We also point out some highlights in the paleo-climatic history of the range.

1 Introduction: General Features

The Rwenzori Mountains straddle the equator along the border between Uganda and the Democratic Republic of Congo, extending north–south for about 110 km and east–west for about 50 km (Fig. 1). Rising gradually from the highland plains of Uganda, the mountains fall steeply on the west to the Semliki River, the outflow of Lake Edward and a major tributary of Lake Albert, one of the sources of the White Nile. Geologically the mountains are young, created in the late Pliocene (less than 5 Ma BP) by an upthrust of crystalline rocks (mainly gneiss, amphibolite, granite and quartzite) that rose from within the western rift to divide palaeolake Obweruka and create present-day Lakes Albert and Edward. Hence, the range itself is not of volcanic origin although numerous craters (crater-lakes) of more recent age are found in the surrounding area (south-western Uganda; see Melack, 1978; Kizito et al.,

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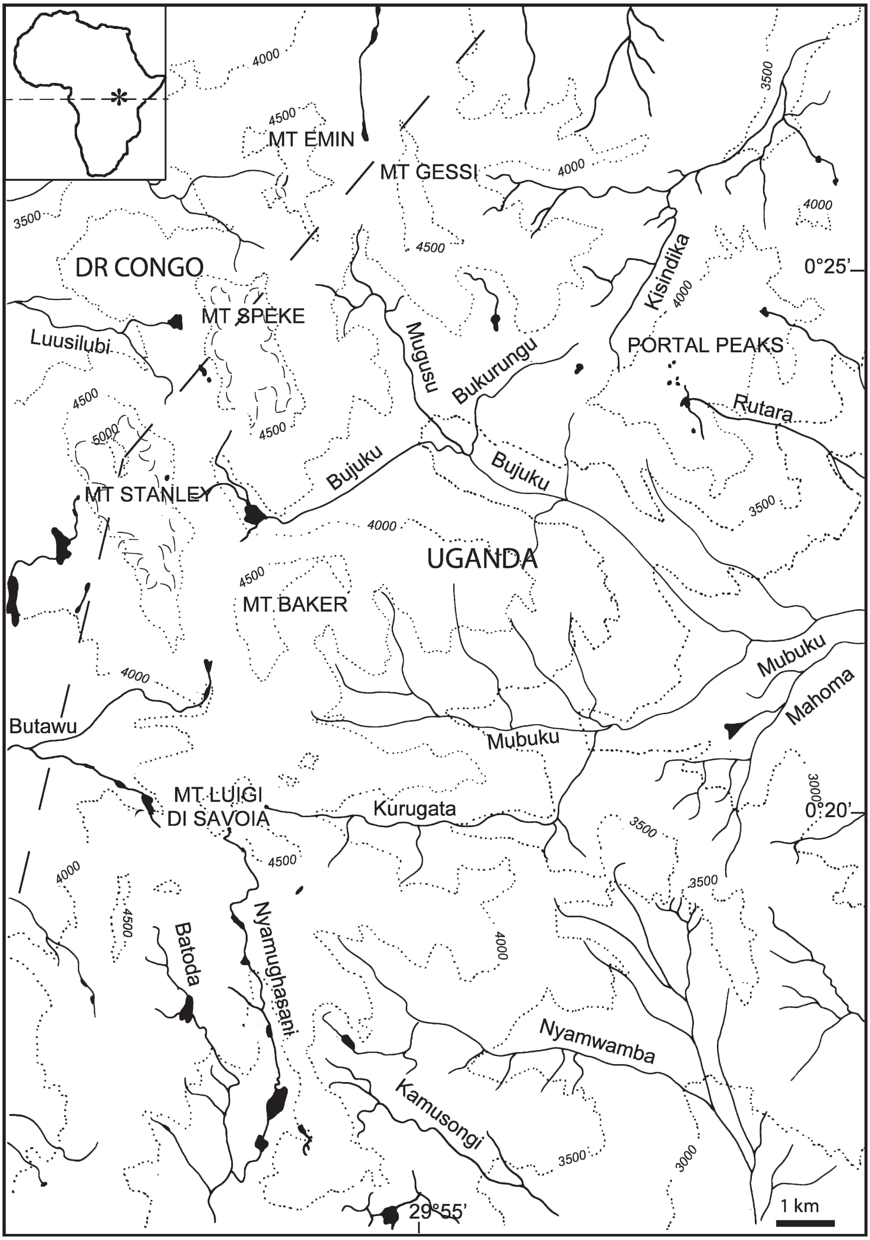

Fig. 1 Map of the Rwenzori Mountains, showing glaciers, river drainages and location of lakes (orig.)

1993). The uplifted mountain range has subsequently been sculptured by rivers and repeated growth of glaciers (Section 4; Fig. 1), resulting in six separate mountains rising over 4,500 m: Mts. Stanley (5,109 m), Speke (4,889 m), Baker (4,842 m), Gessi (4,715 m), Emin (4,791 m) and Luigi di Savoia (4,626 m). Each of these consists of several peaks, the highest being Margharita on Mt. Stanley. All mountains were glaciated until historic times, but ice caps on Mts. Gessi, Emin and Luigi di Savoia have now completely disappeared. The range is dotted with numerous lakes, mainly occupying glacially-excavated and moraine-dammed basins formed after the last glacial period (Osmaston, 1989; Section 4). In 1992 the upper western slopes (~375 km^2) were incorporated in the Parc National Albert, now renamed the Parc National des Virunga as it includes the Virunga volcanoes, 200 km to the south. The remaining three-quarters (~996 km^2), lying in Uganda, were protected as forest reserve until 1991 when it became the Rwenzori Mountains National Park (RMNP). In 1994, the range was gazetted as a UNESCO World Heritage site.

The heavy rainfall together with the melting of glaciers from the peaks provides a significant source of water into the Nile river system. Hence, the range is often claimed to be the most important source of the Nile. The Victoria Nile and Lake Victoria contribute far more water than the Rwenzoris, and the tributaries of the Kagera River, which flows into Lake Victoria, reach considerably farther south from the mouth of the Nile. Other important freshwater bodies in the White Nile drainage include Lakes Kyoga, Albert, Edward and George. Yet, the Rwenzori are certainly the highest source of the (White) Nile, and in many respects the most spectacular. A popular version of the history of the exploration of the Nile is presented in Moorehead (1960) and Yeoman (2004).

Climate data on the range are summarized in Temple (1961) and Osmaston (1965). Due to its great extent and height, the range acts as a large condenser drawing up hot moist air from the surrounding plains and precipitating it as snow, rain and mist. The Rwenzori are wetter than other East African mountains, with annual rainfall varying with altitude from 2,000 to 3,000 mm, and being heaviest on the eastern slope, which faces the prevailing winds. On the Uganda side heavy rain can occur any time of year, but the most rainy periods are from mid-March to May and from September to mid-December (Temple, 1961; Osmaston, 1965). The equatorial position of the mountain range creates daily air temperature oscillations between −5°C and 20°C in the Alpine and Nival zones, an order of magnitude greater than the seasonal variation in maximum daytime temperature. Occasional night-time freezing occurs from ~3,000 m altitude (the present-day boundary between Bamboo and Ericaceous zones); at 4,000 m (the Ericaceous–Alpine zone boundary) freezing occurs on 80–90% of the nights (Rundel, 1994).

Rwenzori, as a cool, moist island rising from the dry tropical plains, has encouraged the development of a unique variety of animals and plants, including numerous endemic species (see Sections 3 and 4). The lower slopes are the home of the Bakonzo people who have lived and cultivated there for centuries, depending on the forest for resources and hunting, besides developing a strong religious and social tradition connected with the mountains. More recently, they have supplied manpower for supporting scientific expeditions and tourists, and for building trekking facilities.

Popular accounts and scientific publications on the Rwenzori are numerous. Interesting and attractive books produced in the last 50 years include ‘Africa’s Mountains of the Moon’ by Yeoman (1989) and the recently published ‘Guide to the Rwenzori’ by Osmaston (2006), including an extensive bibliography. Other significant contributions are collated in the proceedings of the 1996 Rwenzori Conference (Osmaston et al., 1998a).

2 History of Exploration

For centuries, legend and rumour had told of the existence of snowy mountains that fed the Nile. About 1,800 years ago, C. Ptolemy depicted the Rwenzoris on a map and called them the 'Lunae Montes' (The Mountains of the Moon), a name now in popular use. The modern era of their exploration did not begin until 1888, when H. M. Stanley traveled along the western foot of the Rwenzori (while on a mission to rescue Emin Pasha from Southern Sudan), and brought back the first unequivocal evidence of the existence of the range (Stanley, 1890). He had the name ready: 'Rwenzori' (which is spelled in a number of ways), is a colonial-era corruption of 'Rwenzururu' meaning 'place of snow' ('rwe nzururu'). The range is also locally known as 'Gambaragara' which means 'the great leaf in which clouds are boiled'. Both names clearly describe the striking characteristics of Rwenzori's climate (wet and misty) and reflect the mountains' importance to the water supplies of the Bakonzo. There were several major scientific and climbing expeditions on the Rwenzori between 1889 and 1905, mostly by colonial Administrators (H. Johnston), Natural Historians (G. F. Scott Elliott, J. E. S. Moore, F. Stuhlmann), adventure seekers (G. W. Stairs; D. W. Freshfield), and geologists (J. J. David), after whom many passes in the range are named. In 1906, two major expeditions were launched. The first, by the British Museum, made extensive collections of animals and plants, many previously unknown to science (e.g., Woosman, 1907, 1909; Ogilvie-Grant, 1908; Heron, 1909; Oldfield, 1910). The other was a world renown expedition led by Prince Luigi di Savoia (the Duke of the Abruzzi) to climb and map all the major peaks and accomplish significant scientific objectives (de Filippi, 1908; Pluth, 1996).

The 1920s and 1930s were marked by several major scientific expeditions. E. Nilsson made the first important contribution to Rwenzori's Quaternary glacial history (Nilsson, 1931); a Belgian expedition explored the Congo side of the range under X. de Grunne (1933, 1937); and the British Museum expanded their natural history collections (Natural History Museum London, 1939–1957). Between 1926 and 1932, G.N. Humphreys made seven expeditions in previously unknown parts of the range (Humphreys, 1927, 1933), and took the first aerial photos. 1952 was marked by a joint British–Ugandan–Belgian expedition, achieving a major geological survey of the range (e.g. McConnell, 1952), the first glaciological studies (e.g., De Heinzelin, 1953; Bergstrøm, 1955), and extensive collections of insects and plants (e.g. Ross, 1955a, b; Kimmins, 1959). In 1955, complete coverage of the eastern slopes of the range with vertical aerial photographs was obtained, leading to the 1:50,000 maps currently available (Wielochowski, 1994). In the same year, De Heizelin and colleagues conducted basic geographic surveys on the Congo side (De Heinzelin & Mollaret, 1956; Mollaret, 1961). 1957–1961 marked Makerere's first involvement, with a series of glaciological expeditions to study the conditions of the glaciers and the climate of the range (e.g. Whittow, 1959; Temple, 1967). Most expeditions since the mid-1950s have focused on specific physical and climatic processes (e.g., Mölg et al., 2003; Taylor et al., 2006), climate and vegetation history (Livingstone, 1962, 1967; Russell et al., 2008), ecosystem functioning (e.g., Eggermont et al., 2007), ecology (e.g., Hedberg, 1964), and problems caused by both visitors and local people (e.g. McCall, 1988; Howard et al., 1996). A systematic overview (from 470 BC until 2006) of Rwenzori's discovery and exploration, and the origins of its place names are given in Pluth (1996), and Osmaston (1998b, 2006).

3 Terrestrial Ecosystems

3.1 Flora

The Rwenzori, like other tropical mountains, have a range of exotic vegetation organized in discrete vegetation belts distributed across the altitudinal gradient (Hedberg, 1951, 1957, 1964, 1969, 1986; Fishlock & Hancock, 1932; Hauman, 1933; Robyns, 1948; Loveridge, 1968; Schmitt & Beck; 1992). The montane forest zone extends from about 1,800 to (2,200) 2,400 m, and varies from dense forest (mainly confined to valley bottoms and ridge tops), through bracken or shrub dominated areas with scattered trees, to grassy glades. Common trees include *Albizia* spp., *Dombeya* spp., *Olea* spp., *Podocarpus milanjianus*, *Prunus africana* and *Symphonia globulifera*. The bamboo zone, which is dominated by *Sinarundinaria alpina*, reaches its upper limit at about 2,600 (2,800) m on the west and 3,000 m on the east side. The Ericaceous zone (Fig. 2a), extending from the end of the bamboo up to (3,800) 3,900 m, is characterised by broad-leaved trees (*Hypericum* spp. or St. John's Wort, *Hagenia abyssinica* and *Rapanea rhododendroides*), arborescent heathers (*Erica* spp.) draped with *Usnea* spp. (Old Man's beard, a lichen), flowering shrubs (typically *Helichrysum guilelmii*), scattered tree groundsel (mostly *Senecio longeligulatus*), and giant lobelias (chiefly *Lobelia stuhlmannii*). The dominant mosses are *Breutelia stuhlmannii* and *Sphagnum* spp. Common plants in the Alpine zone (Fig. 2b) include *Carex runssoroensis* tussocks, as well as *Helichrysum stuhlmannii* (everlasting flower) and *Alchemilla* spp. (Ladies Mantle). Most celebrated in this zone are the so-called 'giant rosette' plants of the genera *Senecio* and *Lobelia* (primarily *S. adnivalis*, *S. friesiorum* and *L. wollastonii*), which are well-developed in ravines and other sheltered or well-watered sites. Almost all rock surfaces in the Nival zone (Fig. 2c–d), if not overlain by glaciers, are covered by lichens of the genera *Umbilicaria* and *Usnea* (see the Umbilicarietum of Zahlbrucker & Hauman, 1935) and mosses, such as *Rhacocarpus humboldtii* forming bright orange carpets. The different vegetation zones are not always clearly separated, and transition zones with mixed types are common throughout the range (Fig. 2a). Moreover, at a given altitude the vegetation can vary greatly according to microclimate and edaphic conditions (soil depth, moisture, stability and fertility) in the different valleys.

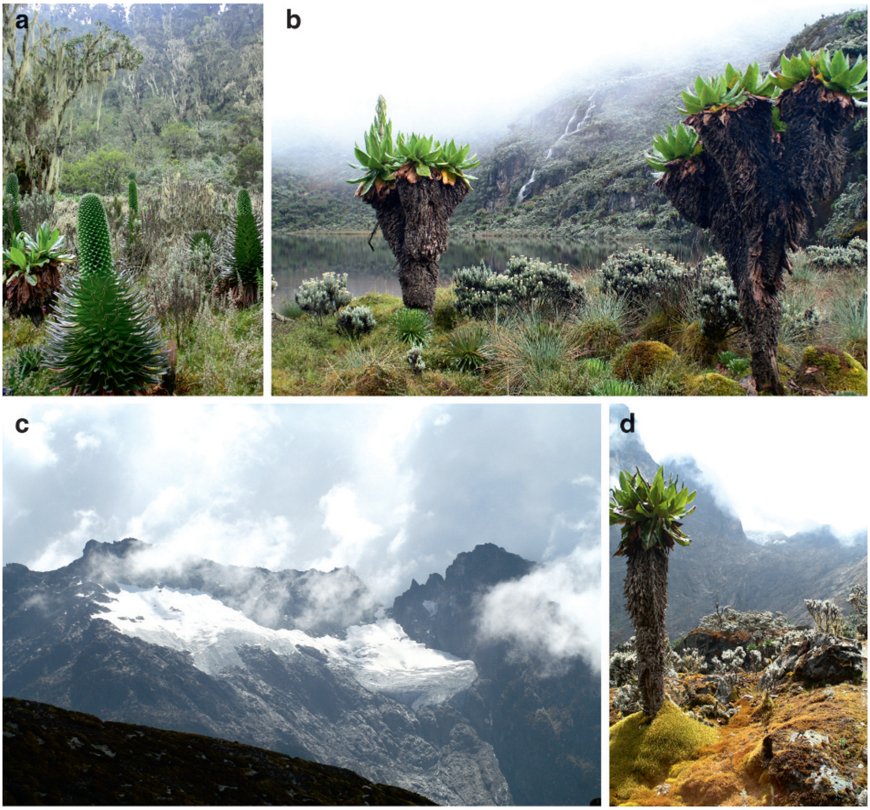

Fig. 2 Scenery and vegetation cover in the Rwenzori Mountains: (**a**) Ericaceous vegetation mixed with tree groundsel (*Senecio*) and *Lobelia* (Mutinda valley). (**b**) View on Lake Batoda, surrounded by tree groundsels, *Carex runssoroensis* tussocks and *Helichrysum stuhlmannii* (everlasting flowers) scrub. (**c**) Glacial retreat on Mt. Speke (picture taken from Lake Irene at 4,487 m elevation, July 2006). (**d**) Transition between Alpine and Nival zone, with tree groundsel and *Rhacocarpus humboldtii* forming bright orange carpets (photographs by H. Eggermont) (*see Color Plates)*

Survey work by Howard (1991) and Howard et al. (1996) indicates that Rwenzori has ~ two-thirds fewer species of trees and shrubs compared to other montane and/or forested national parks (Kibale, Semliki, Bwindi and Elgon) in Uganda. However, it remains to be seen whether this also applies to other floristic groups, especially in the forest zone adjoining a former rainforest refugium in DR Congo. The afroalpine vascular flora of Rwenzori is certainly impoverished (~half the number of species) compared with Mts. Elgon, Kenya and the Afroalpine region of South Ethiopia. Yet, in terms of endemic species, the mountain range is remarkably diverse (ranking second highest in East Africa after Mt. Elgon), with the highest level of endemicity recorded in the Afroalpine zone (e.g. 15 out of the 98 vascular plant species; WWF and IUCN, 1994). The large number of endemic species and vicarious taxa developed under geographical isolation from other highland regions in Africa (for details see Hedberg, 1969, 1986). Osmaston (1998b) further suggested that the evolution of endemic species and subspecies in the Afroalpine zones may not have been a steady adaptive response to the environment, but instead resulted from glacial cycles that repeatedly compressed and stressed Afroalpine populations then allowed for their rapid expansion and speciation. Whatever the case may be, speciation contributes to the ecological diversity in the Rwenzori. For example, the *Dendrosenecio adnivalis* woodlands on the west side are dominated by the subspecies *friesiorum* which is endemic to the west, while subspecies *adnivalis* is confined to the east slopes.

A striking feature on the Rwenzori and other high African mountains is the abundance of Palearctic plant genera in the Ericaceous and Alpine zone, while they are almost totally absent further down in the forest. Some geographers have proposed a well-founded theory that African mountains were almost void of vegetation above the timberline until land contact was established between the European and African plates in the Middle Miocene about 18 Ma BP, and again 13 Ma BP. Then a mass migration of cool-climate-tolerant plant genera started, resulting in a colonisation of the African high-altitude areas. This process took place fairly recently in an evolutionary sense, and the temperate Eurasian plant genera are still easily recognisable. However, as said earlier, many species are already local African endemics.

3.2 Fauna

The major inventories of vertebrate and/or invertebrate species were carried out during the British Museum expeditions of 1905–1906 and 1935–1936, and more recently by Salt (1987), Howard et al. (1996), Behangana (1998), Kerbis et al. (1998) and Willard et al. (1998). A common pattern in these studies is that of decreasing species diversity (and number) with elevation, related to the extreme temperature regime above 3,000 m. Comparable to the situation for plants, Rwenzori's fauna is relatively species-poor compared to other Ugandan National Parks, especially in the montane forest zone (see Howard, 1998 for a thorough comparison), even when differences in sampling are taking into account. The low overall number of taxa may be due to the long isolation of the Rwenzori as well as the absence of low to mid-elevation forests in the different valleys. Yet, Rwenzori is exceptionally rich in endemics: it harbours at least 1 hawkmoth, 6 butterflies, 19 bird species and 12 small mammals that occur only here and/or in a few other highlands on either side of the Albertine Rift (including the Rwenzori hyrax *Dendrohyrax arboreus ruwenzorii* and Rwenzori Leopard *Panthera pradus ruwenzorii*). Twelve species are on the IUCN Red List of Threatened Animals including the 'vulnerable' Moon striped Mouse (*Hybomys lunaris)*, the 'vulnerable' Rwenzori Horse-shoe Bat (*Rhinolophus ruwenzori*), the 'near threatened' Rwenzori Otter Shrew (*Micropotomogale ruwenzori*) and the 'least concern' Rwenzori Turaco (*Ruwenzorornis johnstoni*) (IUCN, 2006).

4 Aquatic Ecosystems

4.1 Former Glaciations and Modern Glaciers

The modern landscape of the Rwenzori has been sculptured by a sequence of Pleistocene glaciations (reviewed in Osmaston, 1989), also found on other East African Mountains. In the earliest glaciation, termed the Katabarua Stage, ice caps extended over 500 km^2 (which is nearly half the area of RMNP) and left wide spreads of long frontal moraines (mainly on the East of the range), extensive sheet moraines (particularly on the west and north-west), and small cirques (on the north). In the next two major glaciations (Rwimi Basin Stage) the valley glaciers reached as low as 2,000 m, and reached 3,000 m during the most recent Mahoma Stage, thereby forming the modern drainage system and leaving behind conspicuous moraines. The Mahoma Stage is well-dated to ca 15,000–20,000 yr BP, coincident in timing with the Last Glacial Maximum (LGM), but the other Rwenzori glacial advances have not been directly dated. Cosmogenic nuclide dating of glacial sediments on Mts. Kenya and Kilimanjaro indicates two major glacial advances in East Africa prior to the LGM; one at ca 400,000 yr BP, and a second ca 270,000 yr BP, roughly coincident with glacial conditions during Marine Isotope Stages 10 and 8, respectively (Shanahan & Zreda, 2000). Stage 6 glacial deposits are generally lacking from Eastern Africa. Assuming this timing hold for the Rwenzori, the Katabarua stage could be Stage 10, and the Rwimi Stage 8.

Lesser moraines indicate younger retreat stages or minor readvances during the Omurubabo Stage ca 10,000 yr BP. Our knowledge on the history of the modern glaciers starts at about 200 years ago (Lac Gris Stage, ca 100–700 yr BP), when the glaciers extended to a set of frontal moraines at an altitude of about 4,300 m. This stage corresponds to the maximum extent of glaciers in Europe (and probably elsewhere), at the end of the ‘Little Ice Age’ (AD 1850). At that point, Rwenzori glaciers occupied about 10 km^2. The next observations of Rwenzori glacier extent were made during the Abruzzi expedion (1906) when glaciers were photographed and mapped; their termini had retreated slightly but, according to Kaser and Noggler (1996), had probably diminished in area by no more than 3.5 km^2. The next reliable inventories were made in the 1950s (Bergstrøm, 1955; Whittow & Shepherd, 1958; Whittow, 1959; Whittow et al. 1963) and 1960s by Makerere University (Temple, 1967, 1968), early 1990s when total area was estimated as 1.68 km^2 (Kaser & Noggler, 1991, 1996; Talks, 1993), a reduction of more than 80% since 1850. Taylor et al. (2006) recently estimated the total remaining area from field surveys and satellite imagery as only 1 km^2. Glaciers have disappeared completely on Mts. Emin, Gessi and Luigi, and now only remain on Mts. Speke, Baker and Stanley (Fig. 2c). Thus, a continuing trend of glacial recession from 1906 onwards is evident (reviewed in Kaser, 2002), except for a brief period of glacier advance in the early 1960s coinciding with a period of anomalously high precipitation in East Africa. If this rate of retreat is continued, no permanent ice will remain after 2025. The period of glacial readvance in the 1960s, in part, has fueled considerable debate as to whether twentieth century glacial recession is driven primarily by warming of the middle troposphere due to anthropogenic greenhouse gases (Hastenrath & Kruss, 1992; Gaffen et al., 2000; Taylor et al. 2006), or a long-term decrease in humidity since the late nineteenth century (Hastenrath, 2001; Kaser et al., 2004). Sadly, lack of continuous and proximate meteorological observations in the African mountains prevents direct analysis of climatic factors driving the recession, but efforts are underway to obtain these data using remote loggers and meteorological stations (Eggermont et al., unpublished). Moreover, on-going research mountains (Brown University, US; Ghent University, Belgium) involving multi-proxy analysis of lake sediment records from seven Rwenzori mountain lakes will likely shed more light on the controlling factors of deglaciation.

4.2 Lakes

4.2.1 Limnology

Until recently, limnological surveys in the Rwenzori Mountains have remained sparse and/or incomplete. In the 1950s, De Heinzelin and his colleagues conducted basic surveys of eight lakes on the Congo side of the Rwenzori range (De Heinzelin & Mollaret, 1956; Mollaret, 1961). Subsequent studies focused only on four lakes on the Ugandan side, located along tourist routes in the Bujuku-Mubuku river drainage (Löffler, 1964, 1968a, b; Livingstone, 1962, 1967). Cholnoky (1964) visited seven lakes in the remote Kamusongi and Nyamughasana valleys to inventory their lacustrine diatom flora, but did not collect morphological, physical or chemical data on the lakes. The most extensive limnological survey has been carried recently (in July 2005 and 2006) by Eggermont et al. (2007) who described the physical and chemical limnology of 17 lakes and 11 permanent pools in the Batoda, Bujuku, Butawu, Kamusongi, Mahoma and Nyamughasani river drainages on the Ugandan side of the range (Fig. 3a–e).

With few exceptions the Rwenzori lakes were formed by glacial activity. During the Last Glacial Maximum (LGM, 21,000 yr BP) the local snowline extended down to 3,000 m (Mahaney, 1989), but since most lakes are located above 3,700 m they are probably of Holocene age; at least some of their basins were formed only following glacier retreat after the Little Ice Age (De Heinzelin, 1962). Most lakes were created after a glacial valley was dammed by terminal or recessional moraines, but those above 4,200 m occupy glacially-scoured basins. Some of the latter are quite young (i.e. ~60 years or less; Osmaston, 2006), as their basin was exposed by recent glacier regression. Examples include Lake Ruhandika at the foot of Speke glacier (Fig. 3e), and Lake Irene below Stanley glacier. All rock pools above 4,400 m are also formed by glacial scouring below the headwall of former glaciers; those at lower elevations are marsh or river features. Lake Bujuku (Fig. 3d) appears to be dammed by a landslide off the North slope of Mt. Baker rather than a moraine (Livingstone, 1967). Lake Mahoma is located at 2,990 m within the LGM terminal

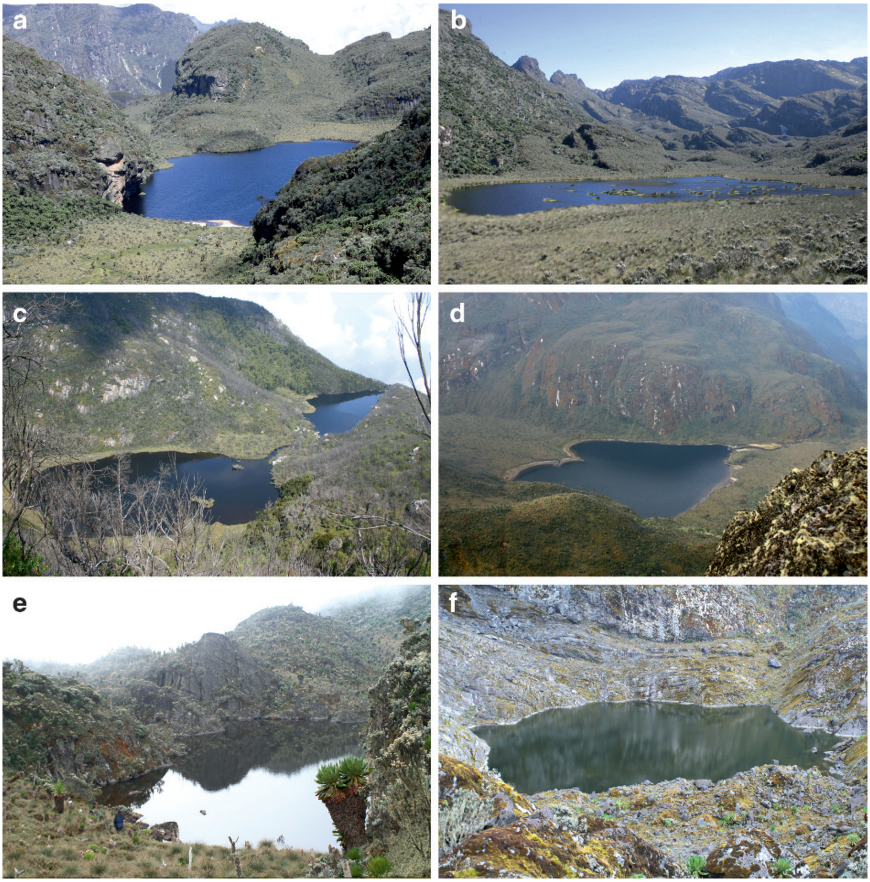

Fig. 3 Images of selected Rwenzori mountain lakes on the Ugandan side of the range: (**a**) Lake Batoda at 4,017 m asl in the Batoda valley. Tree groundsel forest covers most of the slopes, and *Carex runssoroensis* tussocks most of the bog surface. (**b**) Lake Bigata at 4,010 m asl in the Nyamugasani valley. The lake is surrounded by *C. runssoroensis* tussocks and *Helichrysum stuhlmannii* (everlasting flowers) scrub. Floating islands of tussocks dot the lake surface. (**c**) Middle (*left*) and Lower Kachope (*right*) at 3,840 m asl in the tributary valley of the Butawu. The slopes are covered with tree heathers, tangled undergrowth and scattered tree groundsel. Part of the vegetation is burned, likely caused by armed conflict in the area. (**d**) Lake Bujuku at 3,849 m asl in the Bujuku valley, with tree groundsel and *C. runssoroensis* covering the catchment. Streams from Speke glacier and former East Stanley Glacier have built a delta into the lake. (**e**) Lac du Speke at 3,822 m in the Luusilubi valley (DR Congo), surrounded by steep rocky cliffs and tree groundsel forest. (**f**) Lake Ruhandika at 4,341 m asl, where the terminus of the Speke glacier stood in the 1950s. Since then, the glacier has retreated about 600 m and greatly thinned, leaving this small lake in front of it. The lake is surrounded by bare rock, moss, liverworts and lichens (photographs by H. Eggermont) (*see Color Plates)*

moraine, and is extraordinary in that its size, shape, and depth all suggest that unlike any other lake in the African tropics (Livingstone, 1967) its basin was formed after the thawing of a block of ice detached from the retreating glacier (i.e., a kettle lake; Wetzel, 1983). Lakes dammed by moraines or land-slides in steep valleys are typically long-drawn between in- and outflow, whereas lakes in glacially-scoured and the Mahoma kettle are more circular and lack a well-defined inlet. Most moraine-dammed lakes have a single major inflow, in some it is supplemented by several smaller inflowing streams that drain the local catchment. Lac Vert (DR Congo) is almost certainly the deepest (37 m) and largest (>11 ha) lake in the Rwenzori, while Ruhandika (Uganda) is likely the smallest (3 m deep, ~0.01 ha).

As regards their physical–chemical properties, the lakes on the Uganda side of the range generally consist of two types (Eggermont et al., 2007): (1) lakes located near or above 4,000 m, with at least some direct input of glacial meltwater and surrounded by rocky catchments or alpine vegetation; and (2) lakes located mostly below 4,000 m, remote from glaciers and surrounded by Ericaceous vegetation and/or bogs. The former group are mildly acidic to neutral clear-water lakes (surface pH: ~5.80–7.82; Secchi depth: 120–280 cm) with often above-average dissolved ion concentrations (18–52 μS cm^{-1}). These lakes are (ultra-) oligotrophic to mesotrophic (TP: 3.1–12.4 μg l^{-1}; Chl*a*: 0.3–10.9 μg l^{-1}) and phosphorus-limited (mass TN/TP: 22.9–81.4). The latter group are mildly to strongly acidic (pH: 4.30–6.69) waters stained by dissolved organic carbon (DOC: 6.8–13.6 mg l^{-1}) and more modest transparency (Secchi-disk depth: 60–132 cm). Ratios of particulate carbon, particulate nitrogen and chlorophyll-*a* in these lakes indicate that organic matter in suspension is primarily derived from the lakes' catchments rather than aquatic primary productivity. As regards their mixing regime, most Rwenzori lakes can be classified as discontinuous warm polymictic (*sensu* Lewis, 1983), whereas a minority is continuous warm polymictic or even meromictic. Since key features in the Rwenzori lakes' abiotic environment are strongly tied to temperature and catchment hydrology, these Afroalpine lake ecosystems can be expected to respond sensitively to climate change and glacier melting.

4.2.2 Biology

Cholnoky (1964) investigated the diatom flora of seven lakes and three small pools in the remote Nyamughasani and Kamusongi valleys. He recorded a total of 139 species, with an average of 60 species per lake. These were predominantly extra-tropical or cosmopolitan forms (>70% of total diatom richness), and some nine taxa (or 6.5% of total diatom richness) may be endemic to the Rwenzoris (e.g. *Achnanthes adamsii*, *Fragilaria adamsii* and *Navicula adamsii*) or the East African Mountains (one species: *Achnanthes kenyae*). At least 30 taxa were found to be widely distributed among the sites, including *Achnanthes affinis*, *Eunotia pectinalis*, *Fragilaria strangulata*, *Navicula soehrensis* and *N. subtilissima*. Cholnoky noticed considerable variation in diatom composition between lakes, even though he only samples lakes in one valley, with several species being confined to only one lake or to a particular habitat. Ongoing research by C. Cocquyt (National Botanical Garden of Belgium) on an elaborate set of samples from 17 lakes and 11 pools scattered throughout the mountain range (cf. Eggermont et al., 2007) will permit determination of the main factors structuring Rwenzori's diatom distribution, and hopefully elucidation of biogeographical patterns. Preliminary results already suggest that the diatom communities of tea-stained lakes and surrounding swamps are fairly different from those in the clear-water lakes in the Alpine zone, and they confirm the predominance of cosmopolitan forms (the remaining being mainly African and Afrotropical elements). As regards other algae, there might be a striking variety of Desmidiaceae linked to the presence of moorlands and *Sphagnum*-bogs as is the case on Mt. Kenya, but hitherto no such studies have been conducted in Rwenzori. Among the submerged plants on African high-mountain lakes, *Crassula* sp. (mainly *C. aquatica*) and *Subularia* sp. are most prevalent, often forming crops of meander-like patterns. Generally speaking, lakes above 4,600 m lack any higher vegetation.

Vertebrates are completely absent in Rwenzori lakes. Invertebrates, on the other hand, are common but poorly diverse relative to other tropical lakes. Among the Crustacea, Malacostraca (isopods, amphipods and freshwater crabs) are absent; micro-crustaceans (cladocerans, ostracods and copepods) are ubiquitous. Ongoing study by Van Damme (Gent University) indicates that cladocera dominate the open water with the chydorid *Chydorus sphaericus* being the most abundant species. So far, *Daphnia* has been found only in Lakes Bujuku (*D. curvirostris*) and Mahoma (*D.* cf. *obtusa*). The benthic chydorids *Alona guttata* and *A. rustica* appear to be restricted to the littoral zone of tea-stained lakes (<4,000 m asl) and surrounding *Carex-Spaghnum* swamps. Current study (F. Fiers, Royal Belgian Institute of Natural Sciences) points out that copepods are common throughout the study region, but most diverse in the littoral zone of tea-stained lakes. *Elaphoidella damasi* and *Paracyclops altissimus* are the most widespread, and – together with *Maraenobiotus* cf. *brucei* – the only species remaining in clear-water lakes and pools at high elevation. Contrastingly, Löffler (1968b) cites the cyclopoids *Paracyclops fimbriatus*, *Ectocyclops hirsutus*, *Thermocyclops hooki* and the harpacticoid *Elaphoidella damasi*. Ostracods (one species: *Candonopsis bujukuensis*) have been found only in the littoral zone of tea-stained lakes. Crustacean biodiversity in Rwenzori (at least 9 Cladocera, 12 Copepoda and 1 Ostracoda) appears to be generally lower compared to Mt. Kenya (10, 16 and 5, respectively), but we strongly believe that further investigation of available study material will reveal more species. Taxonomic uncertainties have so far complicated proper biogeographical assessment, but the majority are likely local (tropical African) or cosmopolitan elements. There is no evidence for endemic crustacea; however, the range seems to harbour at least some local subspecies, especially among copepods. Chironomidae (Insecta: Diptera) are fairly common in the benthos of both near- and offshore locations; thus far, 18 taxa have been recorded in Rwenzori lake sediments (Eggermont, unpublished data). There appears to be a strong altitudinal (and thus temperature) gradient in chironomid species distribution, with a faunal transition zone coinciding broadly with the Ericaceous zone (ca 3,000–4,000 m, where night-time freezing becomes increasingly more common). Despite efficient dispersal, an estimated 40% of total species richness appears to be restricted to the specific habitat of cold holomictic lakes in the Alpine and Nival zones (>3,800 m), and can thus be considered true Afroalpine elements. The question of endemism among Afroalpine Chironomidae at either a local, regional or continental scale remains largely unanswered at this time, but taking into account the restricted occurrence of glacier-fed lakes and tarns on Africa's highest mountains, the chironomid fauna of tropical cold-water ecosystems is potentially unique on a continental scale (Eggermont & Verschuren, 2007). Otherwise common aquatic insects like Coleoptera and Hemiptera are absent in most Rwenzori standing-waters. Other groups such as Rotifera, Oribatida, Hydracarina, Tardigrada, Oligochaeta and Nematoda are abundant in nearshore locations and swampy areas, but these faunas still need to be investigated. Only one freshwater clam (*Pisidium ruwenzoriense*) has thus far been recorded (Pilsbry & Bequaert, 1927); this species is likely endemic.

4.3 Rivers

4.3.1 Hydrology

Rivers and streams draining the Rwenzori Mountains are generally small and of low stream order (Fig. 1), yet they constitute a vital source of water for Lakes George, Edward, and Albert. Principal rivers are the Nyamwamba, Mubuku, and Ruimi Rivers; they debouch into Lake George. The Nyamugasani River drains into Lake Edward, and the Butawu and Lamya Rivers join Lake Edward's outflow, the Semliki, en route to Lake Albert. These rivers are generally steep, rapidly flowing, rocky torrents above ~1,200 m elevation, but slow and flatten considerably as they reach the lowland plains and swamps on the rift valley floor. High precipitation rates in the mountains, together with the Rwenzori's impermeable, crystalline bedrock, result in high runoff rates and efficiencies relative to the adjacent lowlands (Russell & Johnson, 2006). River gauge data collected in the 1960s indicates that the eastern slopes of the Rwenzoris contribute about 1 billion $m^3\ y^{-1}$ of water to Lake George, about 50% of that lake's water income (Viner & Smith, 1973). Runoff from the Rwenzoris comprises about 20% of the total surface runoff to Lake Edward, outflow from which merges with about 1.5 billion $m^3\ y^{-1}$ of water derived from surface runoff from the western slopes of the Rwenzoris in the Semliki River (Russell & Johnson, 2006), the largest river draining into Lake Albert other than the Victoria Nile. In short, the Rwenzori rivers comprise a vital water resource for western Uganda.

The potential impacts of the complete loss of the Rwenzori glaciers, expected to occur within the next few decades (Taylor et al., 2006), on river discharge is unclear. Discharge data collected at 4,000 m elevation from the Mubuku River suggests that glacial melt may contribute significantly to dry season flow (Kaser & Osmaston, 2002), thereby decreasing the amplitude of seasonal changes in high elevation river discharge. However, the water inputs from glacial melt to Rwenzori rivers likely becomes insignificant relative to precipitation at lower elevations.

In spite of the potential for significant river ecosystem changes resulting from climate and environmental variability, the physical chemistry and biota of the Rwenzori rivers remain poorly studied. Recent surveys of rivers draining the Ugandan side of the mountains (Busulwa & Bailey, 2004) show that the rivers' conductivities increases with decreasing elevation, with average values of ~200 µS cm^{-1} in the lowlands, similar to other rivers in the region. The rivers are well oxygenated even in the lowlands where anthropogenic activities might strongly affect river ecosystems. However, industrial activities on the rivers, particularly metal mining activities, may still seriously alter Rwenzori's river chemistry and ecology in the lowlands (Denny et al., 1995).

4.3.2 Biology

At least 16 fish species (six families) occur in the Rwenzori Mountains, and their distribution is mainly limited by altitude (for details see Busulwa, 1998). Many indigenous fish species are present between 900 and 1,500 m. The most common are cyprinids such as *Varicorhinus rwenzorii, Barbus alluaudi*, *B. somereni*, *B. perince* and *B. apleurogramma*. Other species include the fast flowing catfish, *Amphilius jacksonii*, the swamp catfish *Clarias alluaudi*, two or three species of Cyprinodontidae and various Haplochromine at the very lowest sites. Cyprinid (large *Barbus*) species are the only species extending above 1,500 m. Brown and rainbow trout were introduced in the mountain in the 1930s. Although they may have survived up to the 1980s, very few or no individuals are present today. Given sufficient food supply, the most plausible reason is that they may not have found areas for successful breeding (typically small stones and gravel).

Previous inventories of the invertebrate fauna along Rwenzori river systems (Bailey et al., 1994; Bailey & Busulwa, 1996) mainly focused on Coleoptera, Diptera, Ephemeroptera, Trichoptera and Plecoptera. Lack of sufficient taxonomic resolution in these studies hampers evaluation of faunal distribution and diversity patterns, but so far results point to an overall low species richness, particularly at higher altitude, and maybe three unknown Coleoptera species. Pentecost et al. (1997) studied the epilithic algal communities between altitudes of 900 and 4,500 m along the Bujuku–Mubuku River systems. They found that it consisted predominantly of diatoms (43 species), mainly the cosmopolitan *Achnanthes minutissima* var. *affinis*, *A. lanceolata*, *A. linearis*, *Navicula decussis*, *Fragilaria capucina* var. *mesolepta* and *Gomphnema angustatum*. Some diatom zonation along the altitudinal gradient was evident, with *Caloneis* cf. *alpestris*, *Cymbella naviculiformis*, *Eunotia bilunaris*, *Frustulia rhomboides* and *Surinella linearis* confined to the upper regions, whereas *Cocconeis placentula*, *Cymbella aspera*, *Denticula* sp., *Diploneis* sp. and *Surirella biseriata* occurred only in the lower reaches. Overall, diatom species richness and diversity appeared to be low and negatively correlated with altitude. This was mainly attributed to higher turbulence (physical instability) and lower solute concentrations in the upper regions, and only partly to water temperature. Green algae (*Draparnaldia*, *Stigeoclonium* and *Spirogyra* sp.) were infrequently recorded and mainly confined to downstream sites. Cyanobacteria (at least six species) were also occurred, including the rarely recorded *Desmonema wrangelii*, and their abundance appeared to increase with altitude.

5 Paleoclimatology

During the 1950s, growing interest in the climate history of tropical Africa and its effects on species distribution pushed scientists to look for appropriate climate archives. Hedberg (1954) recognised the importance of the Rwenzori for pollen studies, namely its strategic location by the equator, the variety of lakes and bogs suitable for pollen analysis, its interesting glacial history, and a small flora with plants organised into relatively simple pattern of zoned communties. However, the peat sequence he retrieved near Lake Bujuku was too short to reveal any changes other than edaphic ones of very local significance. Given deficient archive quality of bog sediments in Rwenzori (for details see Osmaston, 1958), efforts then shifted to fossil analysis of lake sediments which shed some light on the postglacial vegetation history of Rwenzori. Livingstone (1962, 1967) cored three glacial lakes (Lakes Mahoma, Lower Kitandara and Bujuku) and showed that Pleistocene climatic changes in the tropics and associated changes in the vegetation had been comparable in magnitude to those of temperate regions, and synchronous with northern latitudes during the latest Pleistocene. According to Livingstone, the first important change since deglaciation was the shift from relatively open vegetation to closed montane forest about 12,500 yr BP, reflecting generally drier climate prior to this date. The second important change, starting about 3,000 yr BP, was an increase in grass pollen at the expense of montane forest which likely reflects human agricultural activities and/or a cooling and drying climate. These changes are comparable in trend and timing to climate changes experienced throughout much of tropical Africa during the late Pleistocene and Holocene (e.g. Gasse, 2000).

During recent years, lake-based paleoclimatology in East Africa moved to a multi-proxy approach (e.g. Verschuren et al., 2000; Ryner et al., 2007). Ongoing multi-proxy paleoclimate reconstruction in the Rwenzori Mountains (Brown University, US; Gent University, Belgium; http://www.geo.brown.edu/georesearch/esh/Rwenzori.htm) is very promising: First, the study will produce new records of Holocene climate variability to assess the coherency and spatial extent of climate changes within Africa and their relationships to global climate variability, solar forcing, and modes of tropical ocean circulation and temperature. Secondly, it will provide baseline data to evaluate ongoing and future climate and environmental changes in this sensitive, alpine tropical area. Finally, by providing climate records of temperature and rainfall that can be compared against independent records of tropical glaciation, results will be important to ongoing studies evaluating the sensitivity of tropical glaciers to climate change.

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Nilotic Lakes of the Western Rift

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Abstract The nilotic lakes associated with the Western Rift are separated from the more southerly lakes Kivu and Tanganyika by the Virunga volcanoes. They include three small lakes in the Kigezi highlands, and three large lakes, George, Edward and Albert in the valley. The small lakes have poor fish faunas (mostly introduced), and have shown major changes in their zooplankton and *Xenopus* populations over the last sixty years.

Lake George is shallow and eutrophic, with a permanent dense phytoplankton dominated by Cyanobacteria, and zooplankton dominated by *Thermocyclops* although some Cladocera are present in smaller numbers. Lake George, in common with Lake Edward, lacks the nilotic genera *Lates* and *Hydrocynus*, but both lakes have many more species of cichlids than Lake Albert.

Lakes Edward and Albert are much deeper than Lake George, and their phytoplankton is not dominated continuously by Cyanobacteria. The zooplankton associations in both lakes show changes between inshore and offshore, which in Lake Albert have been shown to be related to predation by inshore fishes. The littoral associations of invertebrates in these lakes are very diverse, particularly the insects, with, for instance, over 100 species of aquatic Coleoptera recorded from Lake Edward. Some aspects of these lakes have been little studied: the interstitial fauna of Lake Albert includes two species of Syncarida, but is otherwise unknown. Parasites and epibionts, particularly of invertebrates, are, apart from trematodes, poorly known.

1 Introduction

The western branch of the Great Rift Valley contains three major lakes forming a reservoir system stabilising the flow of the White Nile. The lakes are interconnected, and are fed by rivers from smaller lakes in the Kigezi highlands (Fig. 1). Some basic features of this system are given in Table 1. The salient biological features of these lakes are considered in sequence, starting with the highest.

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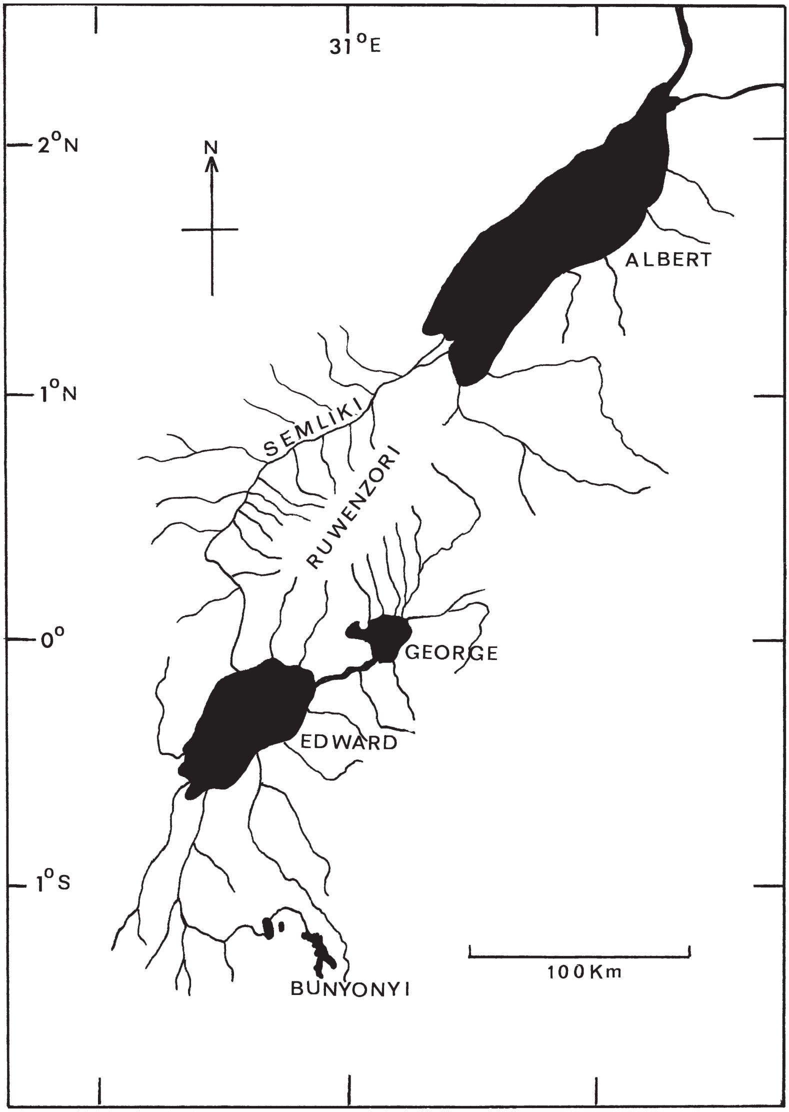

Fig. 1 Map showing connections from Lake Bunyonyi down to Lake Albert

Table 1 Basic data on lakes on the Western Rift branch of the Nile

Lake	Altitude M	Area km^2	Max. depth M	Conductivity µS cm^{-1} 20°C
Bunyonyi	1,973	56	40	233–286
Mulehe	1,806	5	6	252–260
Mutanda	1,792	29	56	225–235
George	913	250	3.5	200
Edward	912	2,325	117	900
Albert	619	5,600	58	675–735

2 Age and Origin

The formation of the Western Rift started in the Miocene, but the present forms of the lakes have much more recent origins. The lakes of the Kigezi highlands were formed when lava flows from the Virunga volcanoes blocked tributaries of the Rutshuru River about 18,000 years B.P.

A lake was present in the Edward basin in the early Pleistocene, and its fauna included nilotic fishes, such as *Lates* and *Hydrocynus*. These were eliminated by volcanic activity about 9,000 B.P. There appears to have been an earlier, temporary, connection with Lake Victoria, possibly via the Katonga valley and other rivers now incorporated into Lake Victoria. This connection was severed by continued uplifting of the western edge of the Victoria Basin, but before this severance a 'superflock' of cichlids developed and formed the ancestors of the numerous species that now inhabit Lakes Victoria, Edward, George, and possibly even Lake Kivu before it was isolated by the Virunga eruptions (Snoeks, 1994). This implies that the cichlids survived the effects of volcanic activity, while the nilotic fishes did not.

Lake Albert seems to have passed through five phases: an overflowing period about 28,000 to 25,000 B.P., a closed period 25,000 to 18,000, open again 18,000 to 14,000, closed 14,000 to 12,500, and finally open with its present connection to the Nile at about 12,500 B.P. (Hamilton, 1982). The productivity of Lake Albert is thought to have increased after 5,000 B.P. due to increased flow of nutrients via the Semliki River (Hecky & Degens, 1973).

3 Lake Bunyonyi

Worthington (1932) gives a good description of Lake Bunyonyi as it was in 1931. Since that time there have been many changes. The vegetation of Lake Bunyonyi has been studied in detail by Denny (1973). The sheltered bays have extensive floating swamps of *Cyperus papyrus* and *Cladium jamaicense*, but other shores have a much wider range of plants. Particularly notable are the beds of blue flowering *Nymphaea coerulea*. Table 2 lists the species recorded by Denny. One of the interests in this list is the occurrence of particular species at an altitude of 1973 m and the fact that some, such as *Cyperus papyrus* and *Nymphaea coerulea* also occur in the Nile Delta.

In 1931, the phytoplankton was sparse, with *Botryococcus* and a few diatoms (*Synedra*), but by 1961 *Microcystis* and *Anabaenopsis* were more evident, and in 1990 the dominant forms were *Microcystis* and *Ceratium*.

The zooplankton has also shown dramatic changes. In 1931, *Daphnia curvirostris*, *D. laevis*, *Ceriodaphnia reticulata* and *Metadiaptomus aethiopicus* were present, but by 1962 all these species had disappeared, and *Thermocyclops* had increased (Green, 1965a). Samples taken in 1975, 1990 and 2001 have not contained any *Metadiaptomus*, *Daphnia laevis* or *Ceriodaphnia reticulata*. However a single

Table 2 Macrophytes recorded from Lake Bunyonyi, altitude 1973 m (after Denny, 1973)

Emergent species	Floating-leaved species
Carex pseudocyperus	*Lemna minor*
Cladium jamaicense	*Nymphaea caerulea*
Crassocephalum vitellinum	
Cyperus immensus	*Potamogeton* x *bunyonyiensis*
..nudicaulis	*..thunbergii*
..papyrus	*Spirodela polyrhiza*
Hydrocotyle mannii	
..ranunculoides	
Leersia hexandra	
Mentha aquatica	
Phragmites australis	Submerged species
..mauritianus	*Ceratophyllum demersum*
Polygonum pulchrum	*Chara* sp.
..salicifolium	*Hydrilla verticillata*
Pycnostachys coerulea	*Lagarosiphon* sp.
Pycreus lanceus	*Potamogeton pectinatus*
Rumex abyssinicus	*..schweinfurthii*
Scirpus costatus	*Utricularia vulgaris*
Thelypteris squamigera	
Typha latifolia	

specimen of *D. curvirostris* was found in 1990 among thousands of *Moina micrura* and *Thermocyclops*. In 2001, no *Daphnia* were found, in spite of an intensive search (Green, personal observation). The presence of a single *D. curvirostris* in the 1990 samples indicates a very small population persisting somewhere in the lake, perhaps mainly as resting eggs, which hatch at irregular intervals. The hatchlings would provide a mechanism for testing the suitability of the environment. If they survive and reproduce they could produce a significant population, but this does not appear to have happened yet.

When Worthington & Ricardo (1936) studied the vertical migration of zooplankton in Lake Bunyonyi they found that juvenile *Caridina nilotica* formed, numerically, about 0.4% of the mid-lake plankton. The adults were found among vegetation around the margins of the lake. Gordon (1933) described the extraordinary variation in the rostrum of *Caridina* in Lake Bunyonyi. In some individuals the rostrum was shorter than the eye, and lacked either dorsal or ventral teeth. In others the rostrum was several times the length of the eye and bore numerous ventral as well as dorsal teeth. Intermediates between these extremes were also found. Gordon (1933) regarded all the forms as variants of *C. nilotica*. A recent study (Richard & Clark, 2005) has redescribed *C. nilotica*, and separates all the Bunyonyi forms from it, describing four new species: *C. bunyonyiensis*, *C. gordonae*, *C. pseudonilotica*, and *C. subventralis*. Some of these species are probably not confined to Lake Bunyonyi, because Green (1965a) found wide variation in the rostrum of *Caridina* in Lake Mutanda resembling the range found by Gordon. The question of the range of variation in *Caridina nilotica* will require the application of molecular methods before it is settled.

Lake Bunyonyi was originally fishless, but in 1919 the small catfish *Clarias carsonii* was introduced, and by 1928 dried fish were being exported from the lake to Kampala. *Oreochromis niloticus* was introduced into the lake in 1928, and various other introductions are listed in the Annual report of the East African Fisheries Research Organisation for 1953. They include *Oreochromis esculentus* and some Lake Victoria *'Haplochromis'*. None of these later introductions produced a sustainable fishery. The latest introduction is the crayfish *Procambarus clarkii*, which is now abundant.

Not least of the changes in Lake Bunyonyi are those found in the clawed toads of the genus *Xenopus* (Tinsley, 1981). In 1925, a sample of 86 *Xenopus* from Lake Bunyonyi contained 85 *X. laevis bunyoniensis* and one *X. wittei*. Other samples taken between 1925 and 1935 contained only *X. laevis bunyoniensis*, but in 1972 only *X. wittei* was found.

In 1931, *Xenopus* was abundant in L. Bunyonyi, and Worthington records it as part of the food chain leading to otters (*Lutra macullicollis* and *Aonyx congica phillipsi*). The former species was abundant in the open lake, while the latter, much larger, species was found in the swamps. Both species are now rare in the lake.

These biological changes have taken place against the background of a permanently stratified lake, with a lack of oxygen below about 7 m from the surface (Denny, 1972). There is some evidence that phosphate has increased in the lake. Talling and Talling (1965) recorded 93 μg l^{-1} PO_4 P at a depth of 35 m in 1961, while Denny (1972) found 480 μg l^{-1} at 30 m and 610 μg l^{-1} at 37 m. Eutrophication, caused by the expanding human population, could explain the changes in the phytoplankton, and possibly, the zooplankton, but the changes in the *Xenopus* population may be more related to the retreat, or even extinction of one species in response to invasion by other species. The otters were probably reduced by hunting for their fur.

4 Lake Mulehe

Lake Mulehe is the smallest and shallowest of the Kigezi lakes. Its surface is about 14 m above that of Lake Mutanda. Water drains through a swamp into Lake Mutanda, and this flow is sometimes visible as a blue-green patch on the eastern side of that lake. In 1961, the phytoplankton was dominated by *Melosira*, together with *Synedra*, *Oscillatoria* and *Coelastrum* (J. Talling, personal communication). In 1975, *Melosira* was accompanied by *Microcystis* and *Pediastrum*, and in 1990, the dominant forms were *Microcystis* and *Ceratium*.

The zooplankton showed little change between 1962 and 1990. The only noteworthy event was the disappearance of *Ceriodaphnia reticulata* between 1962 and 1975 (Green, 1976). In 1962, Lake Mulehe had the most productive fishery of the Kigezi lakes. About 30 canoes were operating, and producing good catches of introduced *Oreochromis*. In 1990 only three canoes were operating, and the catches were poor. Carp (*Cyprinus carpio*) have been introduced into the lake, and, according to the local people, flourished for a few years, but are now scarce.

Xenopus population changes in Lake Mulehe parallel those in Lake Bunyonyi. In 1934 all the specimens collected were *X. laevis bunyoniensis*, but in 1975 this species had disappeared and was replaced by two other species: *X. wittei* and *X. vestitus*. These two species can be distinguished by their pigmentation and their differing calls (Kobel et al., 1996). Both were sometimes found in the same trap set in Lake Mulehe, and probably invaded the lake from the nearby mountain ridges, where they occur in small water bodies (Tinsley, 1981).

5 Lake Mutanda

Lake Mutanda is the deepest of the Kigezi lakes. It receives water from the Ruhezaminda River, which drains from the Ruhuma Swamp, which in turn receives the outflow from Lake Bunyonyi. Water also flows from Lake Mulehe through a swamp into Lake Mutanda.

The River Kaku flows out of Lake Mutanda and joins the Rutshuru, which eventually flows into the southern end of Lake Edward.

In 1962 the phytoplankton of Lake Mutanda contained the desmids *Staurastrum* and *Closterium*, together with *Pediastrum* and *Coelastrum*, but in 1990 the dominant form was *Ceratium* accompanied by small amounts of *Microcystis*, and by 2001 *Microcystis* was dominant. These changes are consistent with eutrophication.

The crustacean zooplankton of Lake Mutanda in 1962 was remarkably similar to that of Lake Bunyonyi in 1931 (Green, 1965a). Three species of *Daphnia* were present, together with *Ceriodaphnia reticulata* and *Metadiaptomus aethiopicus*, all of which disappeared between 1962 and 1975 (Green, 1976), reflecting the change in Lake Bunyonyi between 1931 and 1962. These crustaceans have not re-appeared in samples taken in 1990 and 2001. The crustacean zooplankton of both Lakes Bunyonyi and Mutanda have converged to a simplified version, dominated by *Thermocyclops oblongatus* and *Moina micrura*, which is similar to that found in Lake Mulehe in 1962.

Lake Mutanda has also had introductions of various fish, including *Oreochromis* and *Cyprinus* but none has developed into a long-term sustainable fishery. The *Xenopus* population in Lake Mutanda has also changed, from *X. laevis bunyoniensis* in 1934 to *X. vestitus* in 1969, although a single *X. laevis bunyoniensis* was found together with 218 *X. vestitus* in 1975 (Tinsley, 1981). Originally all three lakes were populated by *X. laevis bunyoniensis*, but this species was replaced by *X. wittei* in Lake Bunyonyi, and *X. vestitus* in Lake Mutanda, while both species invaded Lake Mulehe.

6 Lake George

The Western Rift is interrupted by the Virunga volcanoes, separating the drainages to the Congo and the Nile. The first insight of this was gained by Speke (1863) who wrote “I found these hills to be the great turn point of the Central African watershed". Lake George, a truly equatorial lake, bisected by the equator, was studied intensively by an IBP team between 1966 and 1972. Their results were summarised by Greenwood (1976), based mainly on papers published by the team (e.g. Burgis et al., 1973; Lock, 1973; Viner & Smith, 1973; Ganf, 1974a, b).

The remarkable feature of Lake George is the lack of any marked seasonal change (Ganf & Viner, 1973). During the six years of the IBP study the level did not vary by more than 0.1 m. Beadle (1981) attributed this to the structure of the outlet to the Semliki River from Lake Edward, where rocks form a barrier which acts like a spillway, maintaining a constant lake level. Table 1 shows that the conductivity of Lake George is much lower than that of Lake Edward. This difference is maintained by the slow flow in the 30 km long Kazinga Channel, mainly towards Lake Edward. While the outflow to the Semliki prevents the level from rising, the constant supply of water via streams from the Ruwenzori Mountains prevents the level of Lake George from falling. These streams supply approximately 2.8 times the mean volume of Lake George per year (Viner & Smith, 1973), giving a theoretical retention time of 130 days.

Another unchanging aspect of Lake George is the consistently large population of Cyanobacteria (*Microcystis* and *Anabaenopsis*), which form 70–80% of the phytoplankton. The general lack of seasonality includes solar radiation and the species composition of both phytoplankton and zooplankton. In contrast, diurnal changes are marked. On a typical day the 2.5 m water column starts with a uniform temperature of 25°C. By 14.00 h the top 30 cm can reach up to 35°C. Oxygen concentration in the water column at dawn is near 100% saturation, but by 16.00 h the top 20 cm may reach 230% saturation. The stratification usually breaks down near dusk under the influence of evening breezes. The Cyanobacteria tend to be evenly distributed in the water column at dawn, but by mid-afternoon there is a reduction in the numbers near the surface and an increase near the bottom. The even distribution is restored when the sun goes down.

The zooplankton of Lake George shows no marked seasonal changes, either in composition or abundance. *Thermocyclops crassus* forms about 80% of the zooplankton biomass, while the cladocerans, *Moina micrura*, *Daphnia barbata* and *Ceriodaphnia cornuta* are relatively minor constituents in the open water (Burgis, 1973). Figure 2 compares the standing crop biomass of *T. crassus* in Lake George with that of *Cyclops abyssorum* in a temperate eutrophic lake in Scotland. The relative stability of the Lake George population contrasts strongly with the sharp seasonal peak in Loch Leven.

The horizontal distributions of both phytoplankton and zooplankton are influenced by wind induced water movements. Figure 3 shows that both are most abundant in midlake and show more or less concentric reductions towards the lake margins (Burgis et al., 1973).

The macrophytic vegetation of Lake George was studied in detail by Lock (1973). He listed 53 species from the lake margins and surrounding swamps, but recorded no submerged macrophytes in the main body of the lake. The reduction of light penetration by the dense phytoplankton is thought to be the main factor restricting rooted macrophytes to the margins of the lake. Free floating macrophytes

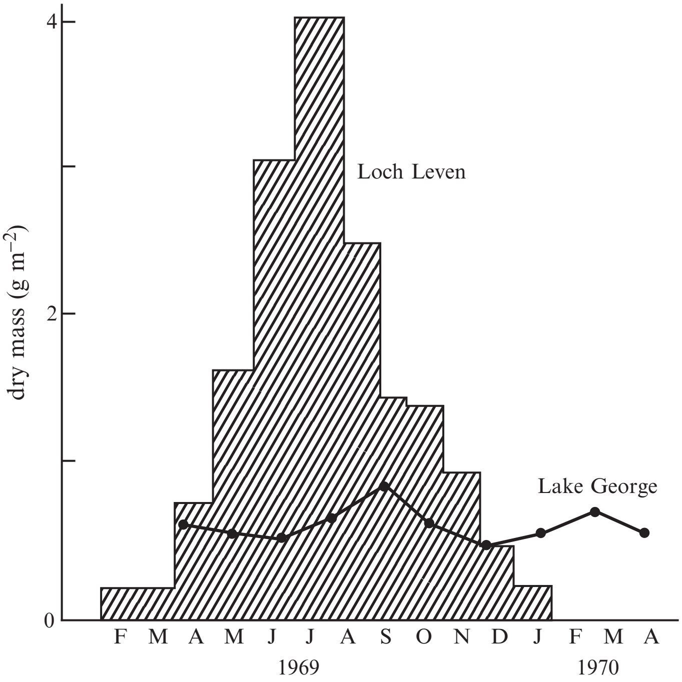

Fig. 2 Standing crop biomass of *Thermocyclops crassus* in Lake George, compared with that of *Cyclops abyssorum* in Loch Leven, Scotland (after Burgis, 1974)

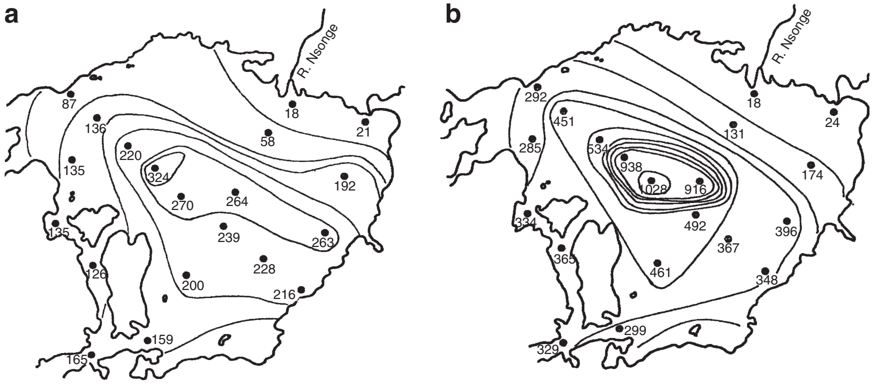

Fig. 3 Biomass density of plankton at 20 sites around Lake George on 9 December 1969. A – phytoplankton as µg chlorophyll a per litre; contours at 50 µg intervals. B – zooplankton as µg dry mass per litre; contours at 100 µg intervals (after Burgis et al., 1973)

are not restricted by phytoplankton, and on Lake George *Pistia stratiotes* formed the basis of a plant community that could result in the formation of small floating islands. Clumps of *Pistia* became overgrown by *Hydrocotyle ranunculoides*, and the duckweeds *Lemna* and *Spirodela* grew between the *Pistia* plants. In Hamukungu Bay the community developed further, with the additions of *Enhydra fluctuans*, *Leersia hexandra*, *Ludwigia stolonifera* and *Marsilea minuta*. These floating islands were however very small in comparison to those found on Lake Kioga, where the islands incorporate substantial amounts of Papyrus, and are strong enough to support fishermen.

In recent years *Pistia* has diminished in abundance on Lake George (Mary Morris, personal communication). This may be due in part to heavy metal pollution from the Kasese mines which lie about 9 km north of the lake (Denny et al., 1995). There have also been fluctuations in the hippopotamus population, partly caused by an outbreak of anthrax. These population changes are reflected in variations in erosion of the shoreline, and when populations are low there are increases in the floating grasses along the Kazinga channel.

Along the northern shore of Lake George, where rivers descend from the Rwenzori, there are extensive swamps. The largest of the swamps, with an area over 100 km^2, has six inflowing rivers, and is dominated by *Cyperus papyrus*, but in the centre has a wet *Ficus* forest, which appears to be floating, with water visible between the trees, when viewed from the air. We know nothing of the microflora and fauna of this area.

The invertebrate fauna of the marginal vegetation has not been examined, but the benthos in the main lake has been studied by Darlington (1977). Most of the lake bottom is covered with a layer of soft organic mud, inhabited by larval Diptera. Two species of *Chaoborus* are the most abundant (McGowan, 1974), while several species of chironomid larvae, including *Procladius brevipetiolatus* and *Chironomus imicola*, are also widespread. Oligochaetes, ostracods and hydracarines are also present, but have not been identified. Only one mollusc, *Melanoides tuberculata*, is present in the main body of the lake, but along the Kazinga Channel there are twelve additional species, including three lamellibranchs: *Mutela rostrata*, *Corbicula africana* and *Sphaerium victoriae* (Mandahl-Barth, 1954). In shallow water the presence of *Hippopotamus* can limit the numbers of molluscs: Mandahl-Barth found that whenever his dredge was filled with hippopotamus dung it contained no molluscs, or at most a few *Melanoides*.

Table 3 shows the mean densities of benthic invertebrates in midlake and inshore. There is a clear differentiation of the faunas, with ostracods most abundant in midlake, and oligochaetes, hydracarines, *Tanypus* larvae and *Melanoides* more abundant inshore.

The fishes of Lake George have been studied by Greenwood (1973), Dunn (1975) and Gwahaba (1973, 1975). The overall list of fish species includes 33 species, 21 of which are cichlids. The feeding habits of these cichlids are diverse. The two most important species feed on phytoplankton. By far the most numerous species is *Enterochromis nigripinnis*, with approximately 30,000 fish per hectare (biomass ca 6 g m^2). The much larger *Oreochromis niloticus* was less evenly distributed,

Table 3 Lake George: comparison of midlake and inshore benthic invertebrates (data from Darlington, 1977)

	Mean no./m^2		% Total biomass	
	Midlake	Inshore	Midlake	Inshore
Chaoborus, larvae & pupae	3,825	2,136	34	14
Procladius brevipetiolatus	1,537	4,417	17	12
Tanypus sp.	–	1,357	–	17
Chironomus imicola	657	289	18	4
Oligochaetes	1,234	6,177	18	41
Ostracods	12,218	375	9	<1
Daphnia barbata	5,889	318	2	<1
Copepods	2,143	1,559	1	<1
Melanoides tuberculata	–	72	–	8
Hydracarines	–	303	–	4

with about 75 fish per hectare (biomass 2.5 g) in midlake, and 900 fish per hectare inshore, with a biomass of 12 g m^2. This inshore biomass formed the basis of a commercial fishery, which flourished during the 1960's,with a factory dedicated to preparation and marketing. As commercial fishing intensified, the size of the fish gradually decreased, but the numbers caught increased, probably because smaller meshed nets were used. This process could not continue indefinitely, and eventually the factory closed, and now lies in ruins.

Other cichlids utilise a range of different foods available in Lake George (Dunn, 1975). For instance: *Yssichromis pappenheimi* preys on zooplankton, *Labrochromis mylodon* preys on molluscs (mainly *Melanoides*), while *Lipochromis taurinus* feeds on the embryos and fry of other cichlids. Perhaps the most interesting of the Lake George cichlids is *Thoracochromis petronius*. This species is almost confined to the Kashaka Crater Bay, where it feeds on insects in a rocky marginal area; a habitat not found elsewhere in the lake.

An occasional feature of the ecology of Lake George is the occurrence of storm driven deoxygenation. This does not affect the whole lake, but can result in substantial mortality of fish. Gwahaba (1973) records a storm in September 1971, which killed about 150,000 *Oreochromis niloticus*, but he estimated at that time this was only 4% of the total biomass of that species. Such fish kills do not occur every year, so the fish populations are not seriously endangered by this form of mortality.

Another potential threat to the fishes in Lake George is the copper mine at Kilembe to the north of the lake. The mine opened in 1959 and closed in 1978, but during that period the tailings gave rise to metal enriched soil deposits which were washed towards Lake George during the wet season. Denny et al. (1995) showed that copper and cobalt were passing into the lake through the swamps along its northern border. The concentrations of these metals were highest in the north in both sediments and plankton. There are some indications that this pollution may be diminishing. Denny et al. found a copper concentration of 749 $\mu g\ g^{-1}$ and cobalt at 89 $\mu g\ g^{-1}$ in sediment near the northern edge of the lake in September 1992.

At the same place in 2000 Lwanga et al. (2003) found copper at 270 µg g^{-1} and cobalt at 57 µg g^{-1}. This may indicate that the pollution washing out from the tailings is diminishing with time since the mine closed in 1978.

Lwanga et al. (2003) also showed that heavy metals were passing through the food chain, and accumulating in fish livers. *Oreochromis leucostictus* had the highest concentration (189 µg g^{-1} dry weight) of copper in its liver, but only 0.2 µg g^{-1} dry weight in its flesh (muscle). These figures indicate that the flesh would be safe for a man to eat, but not the liver. A comparison of these data with earlier data from Denny et al. (1995) shows that here again there has been a decrease. In April 1991 the livers of *O. leucostictus* had a copper concentration of 571 µg g^{-1} dry weight, while in May 2000 the figure was 189 µg g^{-1}. This decrease is similar to that in the sediments, and indicates that, as long as the mining does not resume, the pollution will gradually diminish. Recent work by Hartwig et al. (2005) and Owor et al. (2007) shows that most of the contaminants settle soon after entering the lake, and that at present Lake George is highly resilient.

7 Lake Edward

Lake Edward is the deepest of the lakes in the western group of Nile sources. Damas (1937) described it as 'a veritable paradise', and contrasted the abundance of life with the relative poverty he had seen on Lake Kivu, 150 km to the south. The relatively high conductivity (ca 900 µs cm^{-1}) of Lake Edward is not easy to explain (Lehman, 2002), and is only one of the marked contrasts with Lake George. The conductivity of Lake George is kept low by inflowing streams from the Rwenzori, and a net outflow via the Kazinga Channel to Lake Edward. The sources of the extra ions in Lake Edward have not yet been precisely identified. The saline crater lakes around the northern end of the lake are probably relevant, but underground seepage into the lake has not been established. The elevated conductivity of Lake Edward is not sufficient to induce any marked reduction in biodiversity of either plants or animals.

Verbeke (1957) described three major associations of marginal vegetation around Lake Edward, but also pointed out that variation was considerable. The Lemneto-Pistietum is typical of calm water down to a metre in depth. A typical association would include *Lemna*, *Azolla*, *Pistia*, *Ceratophyllum* and *Utricularia*. Additional forms such as *Jussiaea repens* and *Hydrocotyle ranunculoides*, interweave to bind the association together. In deeper water, around 2 m, the association includes *Ceratophyllum*, *Vallisneria* and *Najas*, and in the deepest vegetated zone *Potamogeton pectinatus* becomes dominant.

The invertebrates associated with the aquatic macrophytes in Lake Edward are considered in detail by Verbeke (1957), and his work should be consulted for a thorough systematic and quantitative account. Some generalisations emerge: Fig. 4 shows the relative abundance of major groups. The shallow water is dominated by carnivorous water beetles (Dytiscidae), but this is also the zone where mosquitoes

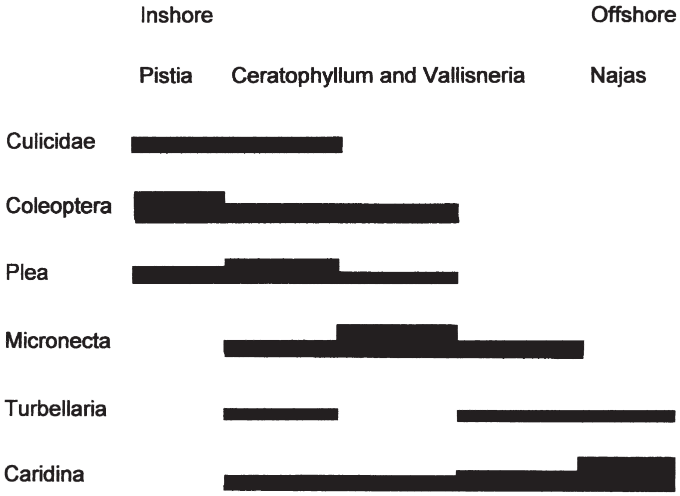

Fig. 4 Zonation of invertebrates in relation to vegetation in shallow water around Lake Edward (based on data from Verbeke, 1957)

(Culicidae) are most abundant. The middle zone has an abundance of *Micronecta*, while the deeper vegetation is populated mainly by *Caridina*. An outstanding feature of the invertebrate associations in the marginal vegetation of Lake Edward is the richness of coleopteran species. Guignot (1957) records 69 species of Haliplidae and Dytiscidae from the lake, while Balfour-Browne (1950) adds 41 species of Palpicornia (Hydrophilidae, etc.), and Brinck (1955–1956) adds five species of Gyrinidae. It is possible that these numbers may increase, because the present records are from a relatively limited number of sites around the lake.

Aquatic Hemiptera are also abundant in Lake Edward: at least 30 species have been recorded (Poisson, 1949). The genera best represented are the notonectid, *Anisops* (6 spp.), and the corixid, *Micronecta* (6 spp.). These are relatively small forms, but also present is the giant *Lethocerus cordofanus* (= *Belostoma nilotica*), ranging up to 80 mm in length.

Mosquito larvae also flourish in the shallow marginal waters. Wolfs (1957) records 13 species, including three of *Anopheles* and five of *Culex*. The larvae of *Taeniorhynchus* have their siphons modified to pierce plant tissues, and the two species found in Lake Edward are well known to be associated with *Pistia stratiotes* (Hopkins, 1952), and the larva of *T. africanus* has also been found attached to the underside of *Lemna* (Connal, 1928–1929). The margins of Lake Edward also have a range of Trichoptera. Jacquemart (1957) lists 15 species, some of which occurred mainly near river outflows. This number of species is lower than that found in Lake Albert (24), but higher than in Lake Kivu (7). The Trichoptera play a small role in the food web of Lake Edward, but they do form part of the diet of several species of fish, such as *Barbus altianus*, *Clarias gariepinus*, *Mormyrus caschive* and *Astatotilapia nubila*. The Ephemeroptera of Lake Edward have not been studied in detail, but Verbeke (1957) found that *Povilla* larvae were important in the diet of several fish species.

Table 4 Ostracoda in Lakes Edward and George (data from Lowndes, 1936; Klie, 1944; Lindroth, 1953 with nomenclature according to Martens, 1984)

	Edward	George
Physocypria capensis	+	−
.. *bullata*	+	−
Candonopsis africana	+	−
Cypris decaryi	+	−
.. *latissima*	+	+
Hemicypris fossulata	+	+
Heterocypris congenera	+	−
.. *obliqua*	+	+
Strandesia unicolor	+	−
Stenocypris stagnalis	+	−
.. *junodi*	+	−
Cypridopsis affinis	+	−
Sarscypridopsis clavata	+	−
.. *pygmaea*	+	−
Zonocypris glabra	+	−
Oncocypris worthingtoni	+	+
Cypretta tenuicauda	−	+
Centrocypris horrida	−	+
Limnocythere michaelseni	+	−
.. *coelebs*	+	−

Entering deeper water, beyond the limits of rooted vegetation, there is a marked change in the fauna. Chironomid larvae become important, and the larvae of *Chaoborus anomalus* are numerous, migrating up and down in the water column, and emerging in enormous numbers of adults at regular intervals through the year. Below 40 m the fauna diminishes. No molluscs occur below this depth, although a few ostracods range down to 50 m. The ostracods of Lake Edward so far recorded are more diverse that those known from Lake George (Table 4) but there is a need for further study of this group in this part of the Nile, particularly in Lake Albert.

The phytoplankton of Lake Edward is much sparser than in Lake George, but still has a high proportion of Cyanobacteria, including *Microcystis flos-aquae*, *Anabaenopsis tanganyicae* and *Lyngbya lagerheimii* (Rich, 1933). A more characteristic feature found by Rich was the abundance of the diatom *Surirella biseriata*. Examination of the sediments of Lake Edward shows that diatoms were much more abundant in the past, but the main species was *Stephanodiscus damasii* (Gasse et al., 1983).

The zooplankton of Lake Edward differs from Lake George in the presence of *Daphnia longispina* and *D. monacha* instead of *D. barbata* (Green, 1971). *Diaphanosoma excisum* and *Ceriodaphnia cornuta* also form significant parts of the cladoceran zooplankton, which shows changes in composition in deeper water (Fig. 5). *Moina micrura* is important inshore, and decreases in deeper water, while

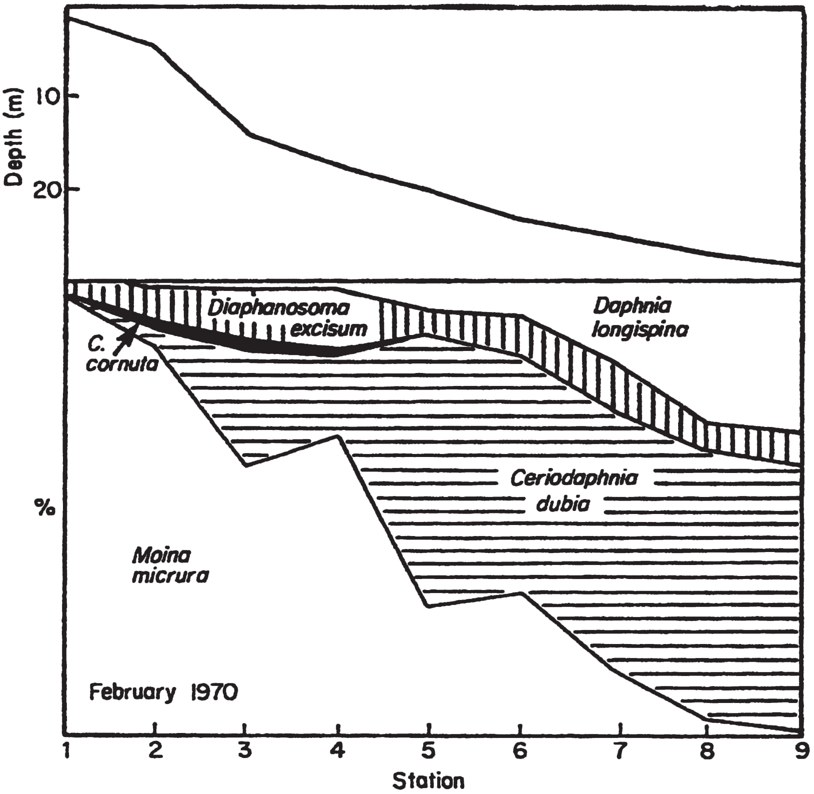

Fig. 5 Variation in the percentage composition of the planktonic Cladocera in Lake Edward in relation to depth (after Green, 1971)

Table 5 Lake Edward: numbers of zooplankters in vertical hauls at four stations from the Uganda shore, 3 November 1962

	8.5		19		24.5		29.5	
Depth (m)	No. m^2	%	No. m^2	%	No. m^2	%	No. m^2	%
Cladocera	5,416	6	20,786	30	59,586	36	78,956	28
Cyclopoida	55,712	60	36,127	51	67,137	40	119,837	43
Nauplii	29,637	32	13,150	18.6	38,349	23	77,487	28
Rotifera	1,471	2	141	0.2	622	0.4	1,273	0.4
Chaoborus lv.	0		240	0.3	467	0.3	1,951	0.7

Daphnia longispina and *Ceriodaphnia dubia* become more abundant. The relative importance of the major groups of zooplankton is shown in Table 5. Cyclopoids, mostly *Thermocyclops oblongatus* and *Mesocyclops* spp. are the most abundant group throughout, but the Cladocera steadily increase in numbers in the deeper water. These samples were taken from relatively shallow water, which probably had oxygen available down to the bottom. Below 40 m there is no oxygen in Lake Edward, and in a series of samples taken in March 1964 by Prof. L. Beadle, no Cladocera were found in vertical hauls between 70 and 50 m, but in the top 30 m *Daphnia longispina*, *D. monacha* and *Ceriodaphnia dubia* were abundant.

The young of many species of fish feed on zooplankton, but in Lake Edward a specialised zooplanktivore has arisen in a genus normally found among vegetation in shallow water. Adults of *Aplocheilichthys pelagicus* live in deep open water, and feed on *Daphnia*, *Ceriodaphnia*, cyclopoids and *Chaoborus* (Worthington, 1932). There has also been a radiation of cichlids in Lake Edward, resulting in about 60 species, one of which, *Yssichromis pappenheimi* (which also extends into Lake George) feeds on zooplankton. The general impression of the cichlid radiation in Lake Edward is of a muted version of the explosive radiation that occurred in Lake Victoria, with, for instance, only one piscivore and only one paedophage.

The non-cichlid fishes of Lake Edward are more remarkable for those missing, rather than those present. The absentees include genera such as *Lates*, *Alestes*, *Citharinus*, and *Hydrocynus*. Some of these have been found as fossils within the Lake Edward catchment, and their extinction has been attributed to volcanic activity about 8,000–10,000 years ago. They were prevented from recolonising the lake from Lake Albert by the waterfalls on the Semliki River. A similar fate eliminated the Nile Crocodile from Lakes Edward and George, but in recent years crocodiles have appeared in both lakes and the Kazinga Channel. It is not known if they made their own way there via the Semliki, following forest clearance along its banks, or whether they were introduced by man.

8 Lake Albert

Lake Albert has a larger surface area than Lake Edward, but is not so deep (cf. Table 1).

The water temperature varies between 27°C and 29°C, and thermal stratification is limited. During the windiest period, from May to August the water is well mixed to the bottom of the lake. In calmer periods some stratification occurs, but without sharp thermoclines (Evans, 1997). During these periods the oxygen in deep water is reduced, but rarely falls to zero: so for much of the year aerobic life is possible in the deepest parts of the lake.

The seasonal and spatial distribution of the phytoplankton in Lake Albert has been studied by Evans (1997). He listed about 75 species, but found the diatoms *Stephanodiscus* (*Cyclostephanos*?) and *Nitzschia* were dominant for most of the year, over most of the lake.

Anabaena flos-aquae showed seasonal and regional peaks of abundance, particularly in the northern half of the lake. Evans considered that phosphate was not limiting, but, based on data provided by Holden (1963), nitrogen deficiency was limiting the growth of the phytoplankton.

The zooplankton of Lake Albert shows great spatial and temporal variation. Figure 6 gives a simplified view of the spatial variation of cladocerans based on annual means. In midlake *Daphnia monacha* is the most abundant cladoceran, but also occurs in smaller numbers at inshore sampling sites. The distribution of this species and the helmeted form, *D. lumholtzi* was considered in detail by Green (1967a). The main conclusion was that inshore fish predation was the major factor governing the distributions of the two forms; in particular the absence of intense predation

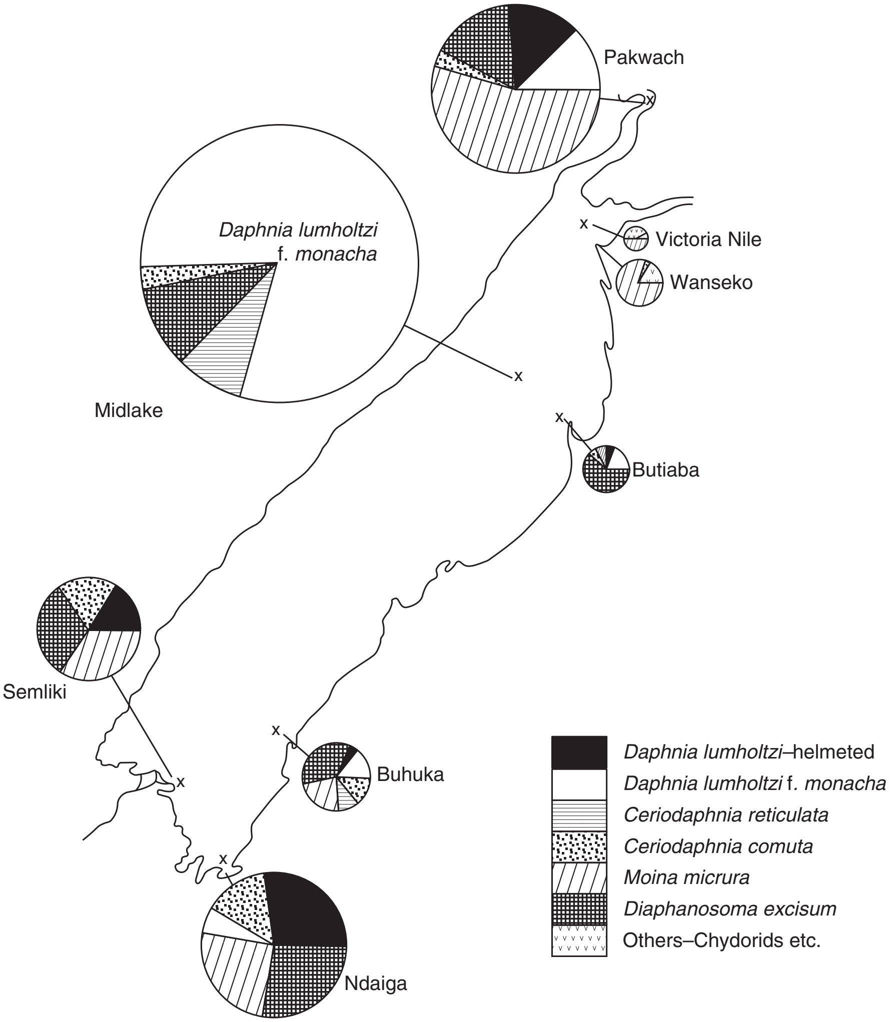

Fig. 6 Total Cladocera and their mean annual percentage composition at eight sites in Lake Albert. The area of each circle is proportional to the number of Cladocera under 1 m^2 (after Green, 1971)

in midlake allows the development of large numbers of *D. monacha*. The large population of daphnids in midlake helps to explain (by competitive elimination) why there are so few rotifers in the open water. Rotifers are much more abundant inshore, where cladocerans are sparser, as at the mouth of the Semliki River (Green, 1967b). Plankton samples taken along transects of the lake show that the cladoceran zooplankton can be divided into an offshore group: *Daphnia monacha* and *Ceriodaphnia reticulata*, and an inshore group: *Moina micrura* and *Daphnia lumholtzi*. Overlapping these two groups were *Diaphanosoma excisum* and *Ceriodaphnia cornuta*. Lehman et al. (1998) have shown that *Diaphanosoma mongolianum* is also present: this may explain the wide overlap by *Diaphanosoma* of the inshore and offshore groups. Diaptomids are rare in Lake Albert, with few records of *Thermodiaptomus galebi* (Lehman et al., 1998).

In addition to the large population of *Daphnia monacha* in midlake there are even larger numbers of cyclopoid copepods. *Thermocyclops (neglectus)* and *Mesocyclops (aequatorialis* and *ogunnus)* are both present (Lehman et al., 1998), and, including all the copepodid stages, can number up to 370,000 m^{-2}. These form the main food of the small cyprinid fish *Mesobola bredoi*, which is endemic to the lake (Howes, 1984). A notable feature of the midlake plankton of Lake Albert is the consistent presence of young *Caridina nilotica*, in numbers ranging up to 15,000 m^{-2}. Adult *Caridina* are abundant inshore near the outer edges of the vegetated zone, but the larval forms become truly pelagic and occur in large numbers 20 km from the shore. In the same region the larvae of *Chaoborus anomalus* are present, ranging up to 2,000 m^{-2}.

Caridina forms a major part of the diet of the Tiger Fish, *Hydrocynus forskalii*, in offshore waters, but inshore, particularly in the lagoons, this fish is mainly piscivorous, including at least six species of fish in its diet (Holden, 1970). Its larger relative, *Hydrocynus vittatus* is scarcer, but preys on fish, mainly in the southern shallows of the lake. *Hydrocynus* forms part of a food chain exploited by native fishermen. They use bundles of grass and brushwood to entrap small *Haplochromis*, which act as bait to catch *Hydrocynus*, which in turn are used as live bait on large hooks to catch large *Lates*. In Lake Albert a female *Lates* averages about 27 kg, but can get up to 90 kg, while males average about half the weight of the females.

Lates niloticus is the top predatory fish in Lake Albert, but can fall prey to large crocodiles. Baker (1866) records his men recovering half of a fish, weighing 50 pounds, the other 50 pounds having been bitten off by a crocodile.

Figure 7 presents a simplified food web for Lake Albert. The groups enclosed in boxes each have an estimated number of species; these indicate that a complete food web would be extremely complicated. The molluscs for instance include both gastropods and lamellibranches with their very different feeding methods. The insects are even more complicated, with an estimated 200 species, ranging from mosquito larvae to predatory coleopterans. The diagram shows only a representative sample of 10 species of fish. At present about 46 fish species are known from Lake Albert, and their diets range from phytoplankton through zooplankton, insect larvae, molluscs and other species of fish.

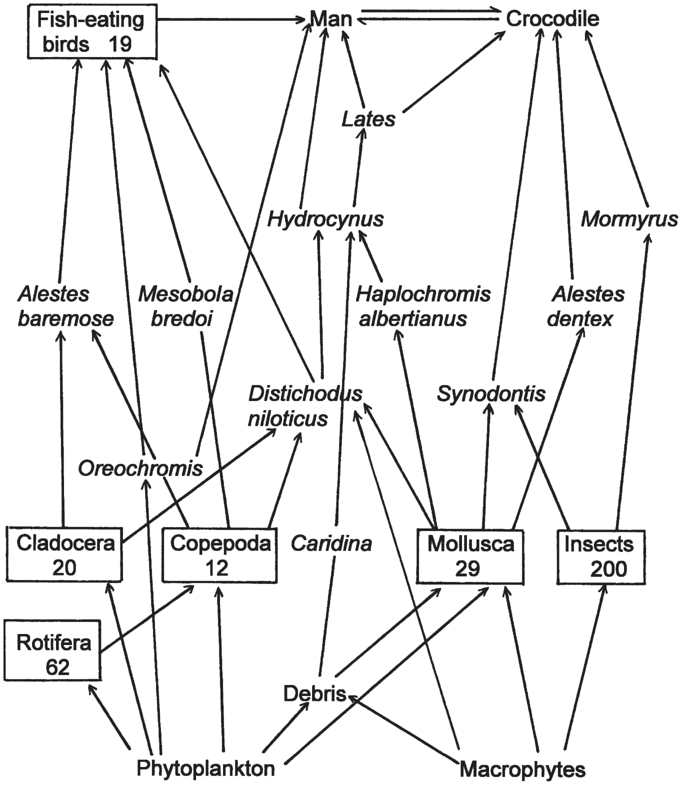

Fig. 7 Simplified food web for Lake Albert, indicating the major links, many minor links are omitted, and only 10 of the 46 species of fish are included. The numbers in boxes estimate the number of species, and, hence, links (original)

Complications in the food web are also introduced by changes in diet with age. This is most spectacularly shown in *Crocodylus niloticus*. Cott (1961) showed that young crocodiles eat a lot of insects, including giant aquatic Hemiptera, predatory Coleoptera, and Odonata (particularly *Brachythemis leucosticta* in Lake Albert). As the crocodile grows it includes larger animals in its diet. When 2–3 m in length it feeds mainly on fish, but also includes molluscs, reptiles, birds and mammals. The last group becomes increasingly important as the crocodile grows beyond 4 m in length. Over all animal groups Cott lists about 200 species as prey of *C. niloticus*, making any food web into an indecipherable tangle.

The benthos of Lake Albert has not been studied in detail, but the data available at present indicate that it may contain more species than Lake Edward. There are more species of molluscs and Trichoptera in Lake Albert, and Guignot (1957) records 92 species of Haliplidae and Dytiscidae in the lake, while Lake Edward has 69.

One feature that may enhance the biodiversity in Lake Albert is the development of sandspits along the eastern shore. These produce sheltered bays, some of which become lagoons, more or less separated from the main body of the lake, providing vegetated areas for fish and amphibians, which in turn provide food for a great diversity of birds. Reptiles are also common in the lagoons. The snakes include *Natriciteres olivacea*, *Grayia smythii* and *Naja melanoleuca*; the last two species frequently feeding on fish. When Worthington studied Lake Albert in 1931, the large turtle *Trionyx triunguis* was quite abundant, but is now rarer. The smaller *Pelusios chapini* (recently separated from *P. subniger*), also occurs in Lake Albert, but it is shy, elusive, and rarely seen. The Nile Monitor lizard, *Varanus niloticus*, swims well, and is common around the lake, acting as predator, scavenger and robber of crocodile nests. The last activity carries some risk, and *Varanus* has been found in crocodile stomachs.

The most widespread and abundant frog around the lagoons is *Dicroglossus occipitalis*, a large species, capable of prodigious leaps in the shallow water, and liable to eat anything that it can swallow, including smaller frogs.

The sandspits also provide a habitat that has been little studied in Lake Albert: the interstitial. A small start was made in 1962 by digging a hole near the waters edge on Kaiso spit. The water accumulating in the hole was passed through a plankton net and two species of Syncarida were found. They were originally described as species of *Parabathynella* (Green, 1964), but, in a detailed revision of the Parabathynellidae, Schminke (1973) placed them in separate, newly created, genera, so that they are now known as *Cteniobathynella bakeri* and *Heterodontobathynella ninianae*, but nothing more is known of their biology and distribution. Another indication of the greater diversity of animal species in Lake Albert compared to Lake Edward is found in the Crustacea parasitic on fish. Table 6 compares the two lakes; a part of the difference is probably due to the absence of some hosts from Lake Edward. For instance, *Opistholernaea longa* is specific to fish of the genus *Lates*, and *Lamproglena hemprichii* occurs on *Hydrocynus*. Both these fish hosts are absent from Lake Edward. For a detailed discussion of the biology and distribution of parasitic Crustacea in the inland waters of Africa see Fryer (1968).

Table 6 Parasitic Crustacea in Lakes Albert and Edward (data from Fryer, 1968)

	Lake Albert	Lake Edward
Ergasilus kandti	+	−
Lamproglena monodi	+	+
..elongata	+	−
..hemprichii	+	−
Lernaea barnimiana	+	+
Opistholernaea longa	+	−
Argulus africanus	−	+
..rhipidiophorus	+	+
..cunningtoni	+	−
Dolops ranarum	+	+

Table 7 Branchiura parasitic on fishes in Lake Albert, and occurrence of the epibiotic peritrich, *Epistylis* (Ep)

Fish host	*Argulus cunningtoni*	*Argulus rhipidiophorus*	*Dolops ranarum*
Hydrocynus lineatus	−	+	−
..forskali	−	+	−
Alestes baremose	−	+	−
Bagrus bayad	+	+	+
..docmak	−	−	+ (Ep)
Disticodus niloticus	+	−	−
Auchenoglanis occidentalis	+	−	+ (Ep)
Labeo horie	+ (Ep)	−	−
Synodontis schall	+	+	+
Clarias lazera	+	+	+ (Ep)
Lates niloticus	+ (Ep)	+ (Ep)	+ (Ep)

A final complication in assessing faunal diversity is the existence of parasites and epibionts. Comparative data on parasites in the lakes of the western rift have not been assembled, although there are scattered records in the literature, and Tinsley (1981) gives a good account of the parasites found in *Xenopus* in the Kigezi lakes.

Peritrich ciliates are often found attached to other organisms, both animals and plants. In Lake Albert a species of *Epistylis* was found attached to both *Argulus* and *Dolops*, which in turn were attached to fish. Table 7 shows that *Argulus* and *Dolops* occur on a wide range of fish, and although *Epistylis* is not restricted by the fish host, it does occur more frequently on *Dolops* than on *Argulus*. The two species of *Argulus* sometimes occur on the same individual fish, together with *Dolops*, and on one large *Lates* all three were found together with the copepod *Lernaea barnimiana* (Fig. 8). This copepod anchors its head into the tissues of the fish, and its elongated body projects outside. A 'necklace' of peritrichs was found around the body of the copepod near the point at which it emerged from the host. This phenomenon has been noted by other workers on parasitic copepods (Cunnington, 1914; Capart, 1944; Fryer, 1956), but the peritrichs were not identified. The specimens from *Lernaea* in Lake Albert were studied alive, and found to be a remarkably large species of *Rhabdostyla*, with a body length of about 500 µm instead of the more usual 50 to 80 µm (Green, 1965b). Examination of other 'necklaces' from other parts of Africa show that other genera, such as *Epistylis*, are often involved, and sometimes more than one species of peritrich can be found on a single parasitic copepod. Similar infestations of peritrichs can also occur on free-living flatworms, annelids, molluscs, crustaceans and insects. If a study was made of the epibionts of invertebrates in Lake Albert one would expect to find at least 40–50 species, and, in view of the findings by Lust (1950) in Germany, a good proportion would occur on the aquatic Coleoptera and Hemiptera, which together number over 100 species in the lake.

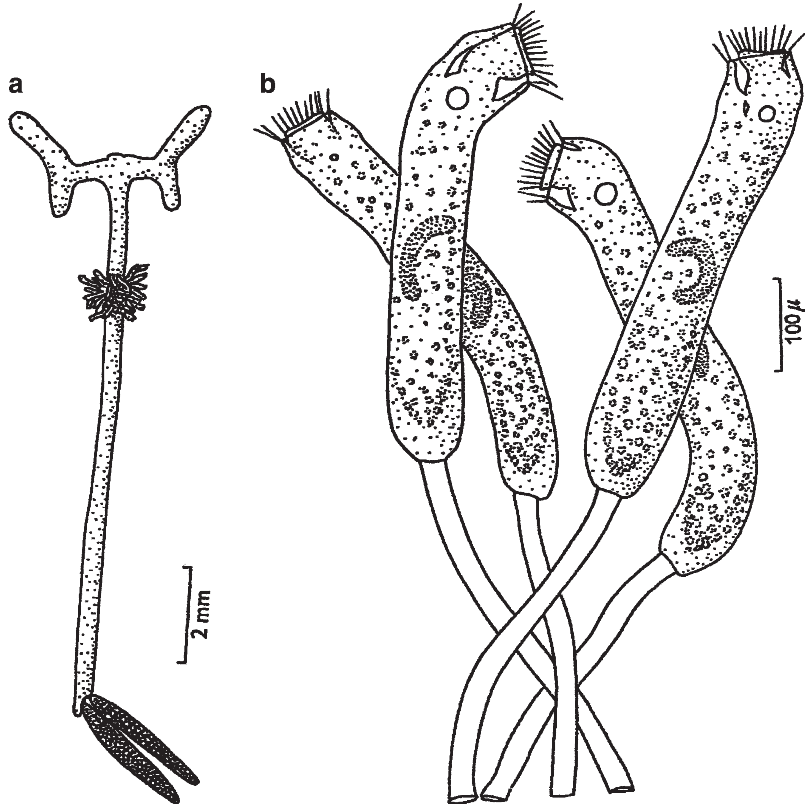

Fig. 8 A, Adult female *Lernaea barnimiana*, a parasite of *Lates niloticus* from Lake Albert; note the ‘necklace’ of peritrichs. B, The peritrich *Rhabdostyla elongata*, zooids in open feeding condition (after Green, 1965b)

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Lake Turkana and Its Link to the Nile

Thomas C. Johnson and John O. Malala

Abstract Lake Turkana is a large, closed-basin lake in the northern Kenyan rift that occasionally overflowed first to the Indian Ocean and then, after about 1.3 million years ago, into the Nile drainage basin. The lake lies in a broad, arid depression surrounded by late Cenozoic fluvial, lacustrine, and volcanic sequences. The climate of the Turkana basin is hot and arid, with extended periods of unusually intense diurnal winds. Seasonal variability in air temperature and rainfall is much subdued compared to the other great lakes of East Africa. Lake temperatures range between 24.5°C and 30°C, the salinity is about 2,500 mg/l, and the entire water column is oxygenated throughout most years. The lake's hydrological budget is dominated by Omo River input and by evaporation. Primary production in the lake is about 700–800 gC/m^{2}y, and is typically limited to the upper 6 m of the turbid water column. Lake level has fluctuated more than 100 m in response to climate change. Analyses of sediment cores from within the modern lake and of lake deposits exposed onshore indicate that Lake Turkana overflowed into the Nile in the early Holocene (11.5–7.8 and 7.4–4.3 kyr), at 102 kyr, and at 195 kyr, with possible links at 123 and 172 kyr as well. Geochemical composition of much older (2.8–0.7 Ma) lacustrine sediments exposed to the east of the lake also suggest periodic overflow to the Nile, but the exact timing of these events are yet to be worked out. Additionally, Lake Turkana very likely was much lower than its present level during the last ice age and at other times of weakened African monsoon, perhaps even completely desiccated.

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1 Introduction

Lake Turkana is a large, closed-basin lake in the northern Kenyan rift that in wetter times overflowed periodically, first to the southeast into the Indian Ocean prior to 1.9 million years ago (Ma) and then to the northwest into the Nile drainage basin. Turkana is the most remote of the great lakes of the East African Rift Valley, occupying a desert setting and offering little to attract the population densities that have enveloped the great rift valley lakes to the south. The lake's water is slightly saline, making it unsuitable for agriculture or human consumption. Nevertheless, the lake is home to a rich aquatic ecosystem that reflects earlier communication with the Nile Basin and subsequent evolution to the arid conditions of today. This chapter summarizes the geological setting and limnology of Lake Turkana with emphasis on its periodic linkage to the Nile River system.

2 The Turkana Basin

Turkana lies in a broad, arid depression between the Ethiopian Rift to the northeast and the Kenyan Rift to the south. It is the largest lake in the eastern arm of the Rift Valley, with a length of about 250 km and average width of 30 km. The drainage basin occupies 146,000 km^2 and extends from the Kenyan highlands near the equator on the south to a broad expanse on the Ethiopian Plateau north of the lake (Fig. 1) (Butzer, 1971). Most of the western shore and the northern half of the eastern shore of the lake is draped with Pliocene and Quaternary fluvial sands and gravels with interbedded lake deposits, while much of the remaining shoreline comprises Miocene – Pliocene volcanic sequences (Morley et al., 1999).

A multi-channel seismic survey conducted on the lake by Project PROBE (Duke University, USA) in the early 1980's revealed a series of six half grabens underlying the lake floor, exhibiting roughly north–south orientations and alternating directions of dip, or "polarity," away from their respective arcuate border faults (Dunkelman et al., 1988). More than 3 km of sediment fill these grabens, displaced locally by four Pliocene to Recent volcanic centers that are equally spaced along the lake axis. These are the "barrier" at the south end of the lake and the three small islands (South, Central and North) within the lake (Dunkelman et al., 1988). Acoustic basement consists of Miocene – Pliocene volcanic sequences similar to those exposed across much of the surrounding landscape.

Lake Turkana has a mean depth of 35 m and a maximum depth of about 120 m. The lake floor slopes gradually from the shoreline towards the offshore basins throughout most of the lake, with bathymetric contours rather evenly spaced towards the deeps (Fig. 2). High resolution seismic profiles display evidence for erosion or non deposition where the water is shallower than 35 m due to surface wave activity, with the exception of the Omo River delta where the high sediment influx overwhelms the erosional impact of wind-generated waves (Johnson et al., 1987). The seismic profiles display abundant evidence for normal faulting, even in the most recent sediments (Johnson et al., 1987; Dunkelman et al., 1988), indicating that the Turkana basin remains tectonically active

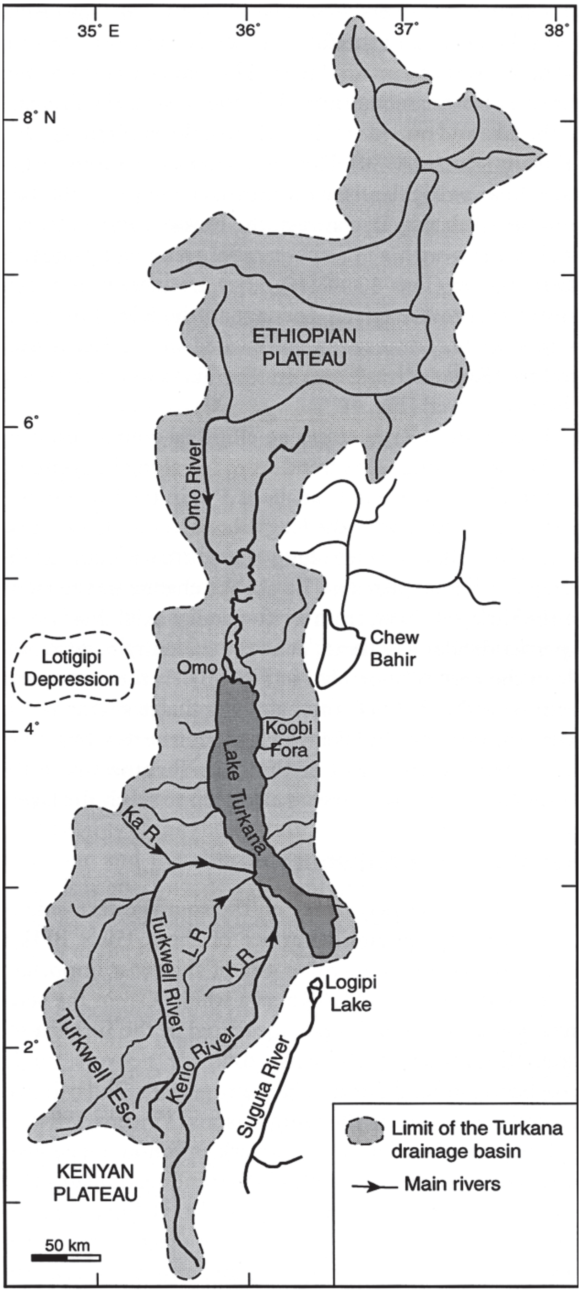

Fig. 1 The drainage basin of Lake Turkana (from Vetel et al., 2004)

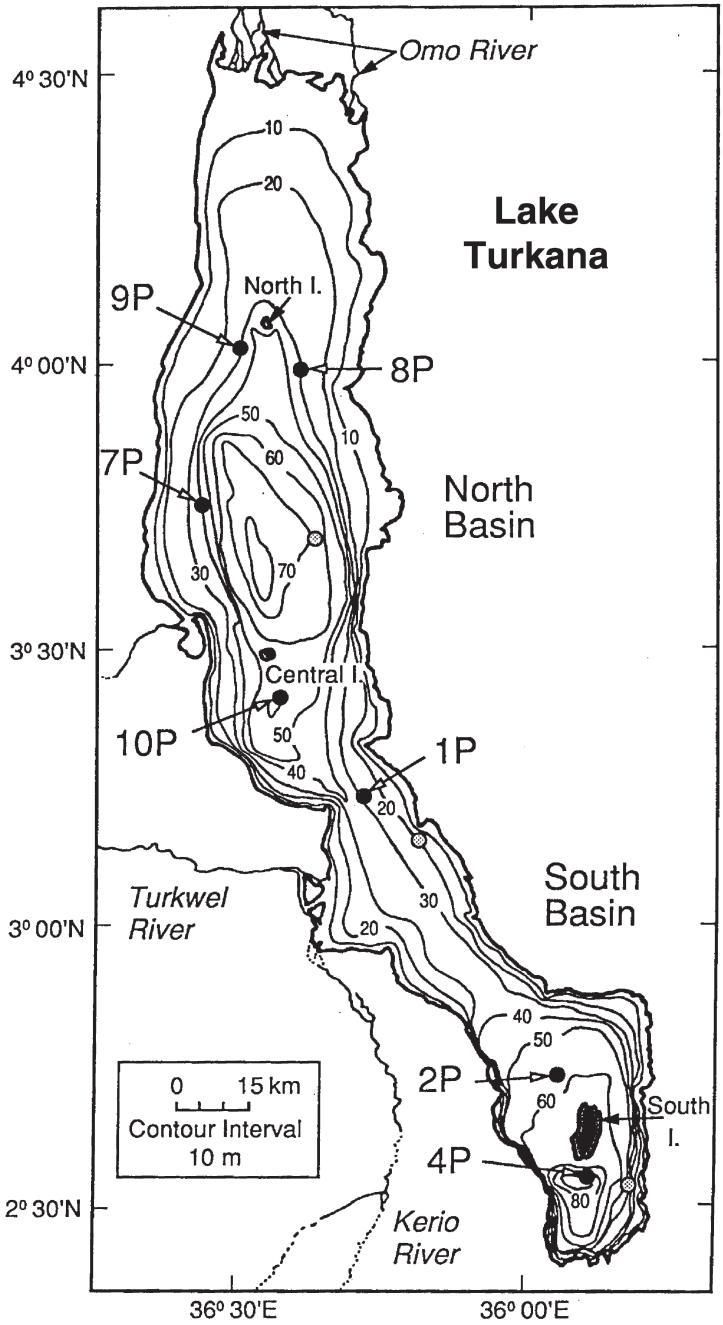

Fig. 2 Bathymetric map of Lake Turkana, depicting sediment core locations. Bathymetric contours are in meters below lake surface in 1984. Reprinted from Halfman et al. (1994) with permission from Elsevier

today. An analysis of river drainage network anomalies, coupled with seismic reflection data from west of the south and central basins of the lake, revealed recent faulting across a 60 km – wide zone onshore as well (Vetel et al., 2004).

3 Climatic Setting

The climate of the Turkana basin is characterized by hot, arid conditions, with extended periods of unusually intense diurnal winds. Seasonal variability in air temperature and rainfall is much subdued compared to the other great lakes of East Africa. Mean maximum and minimum air temperatures recorded in 1973–1975 at Ferguson's Gulf were 32.5°C and 26.0°C, respectively (Ferguson & Harbott, 1982). Air temperatures are slightly warmer in the winter months than in the summer, presumably due to the cooling influence of occasional rains and clouds when the Intertropical Convergence Zone (ITCZ) passes overhead. Mean annual rainfall in the Turkana Depression is about 200 mm/y (Nicholson et al., 1988), while the annual evaporation rate is about 2,300 mm/y (Ferguson & Harbott, 1982). The lake survives only because of the fresh water delivered by the Omo River from the Ethiopian Highlands, where annual rainfall is in the range of 800 to 1,200 mm/y. The Omo River accounts for 80–90% of freshwater input to the lake (Yuretich & Cerling, 1983), with the remainder derived primarily from the seasonal input of the Turkwell and Kerio Rivers that drain the Kenyan highlands and enter the lake midway along its western shore (Fig. 1). The rains on the surrounding highlands are highly seasonal, and reflect the dynamics of the ITCZ, which migrates to the north over the Ethiopian Highlands during boreal summer and to the south of Lake Malawi during boreal winter. Most of the Ethiopian Plateau experiences one rainy season a year centered on July-August, while the Kenyan highlands to the south of Turkana, and the lower elevations to the east of the Ethiopian Plateau, have two rainy seasons centered on April and September (Nicholson et al., 1988). So freshwater input from the major rivers is highly seasonal and impacts the lake's ecosystem dramatically even though the local climate shows little seasonality.

The winds over Lake Turkana are unforgettable. When we were conducting field work on the lake in 1984, the air was calm in the late morning hours and into the afternoon. The wind would begin to blow around sundown and by midnight was blowing steadily at 80 km/h and gusting to 110 km/h. The winds would continue, often peaking at sunrise before dissipating abruptly to the calm conditions of the daylight hours. When I revisited the lake in 1992 the diurnal winds were not as intense, and they were strongest in the late morning and early afternoon rather than during the night. Ferguson & Harbott (1982) reported mean wind speeds in 1973–1975 of about 295 km/24 h near Ferguson's Gulf on the west central shore of the lake, and 760 km/24 h at Loiengalani on the eastern side of the south basin, almost always out of the south and east. They noted the tendency for strong daily winds to last for 9 or 10 h, and over the roughly 2 years of measurements found the timing of intense winds to vary, but most often center around the late morning hours. The pronounced diurnal pattern of winds likely arises from interactions between local thermal circulation patterns and the prevailing trade winds over the region.

4 Limnological Considerations

The limnology of Lake Turkana has rarely been investigated due to the lake's harsh and remote setting and a lack of local infrastructure to support the logistical needs of a scientific field program. E. B. Worthington led the first limnological survey of the lake as part of the Cambridge Expedition to the East African lakes in 1930–1931. Their focus was on the lake fisheries, which showed close similarity to the fauna of Lake Albert, but with significant divergences from Nilotic fauna (Worthington, 1996). The team was surprised by the unusual immensity of Nile perch recovered from the lake. The only other extensive limnological surveys to be conducted on the lake were the Lake Turkana Project 1972–1975 (Ferguson & Harbott, 1982; Hopson, 1982) and a limnological study carried out as part of a fisheries project in 1985–1988 (Liti et al., 1991). Most of the discussion of the limnology of the lake presented here is derived from the latter two expeditions.

Surface water temperatures in Lake Turkana ranged from about 27°C to 30°C throughout the years in 1973–1975, while bottom water temperatures exhibited only minor seasonal fluctuations between 24.5°C and 26.5°C (Ferguson & Harbott, 1982). The lake was about 1°C warmer in 1987–1988 (Liti et al., 1991). The lake exhibits weak thermal stratification during the spring months, followed by more uniform temperature structure due to wind mixing at other times of the year (Fig. 3). The south basin of the lake is typically 1°C–2°C cooler than the north basin, due to upwelling in the south driven by the southerly winds, and northward transport of the warm surface waters.

The lake's hydrological budget is dominated by Omo River input and by evaporation. The seasonal drop in lake level when river input is at a minimum implies an annual evaporation rate of about 2,300 mm, or 17.5×10^{9} m^3/y (Yuretich & Cerling, 1983). Total river inflow to the lake, derived from mass balance assuming direct rainfall on the lake surface of 180 mm/y and negligible exchange of lake water with ground water, is estimated at 16×10^{9} m^3/y (Yuretich & Cerling, 1983).

While the lake circulation has not been measured directly with current meters, the horizontal and vertical distribution of conductivity clearly indicate a prevailing counterclockwise pattern of circulation, at least in the north basin, as well as substantial vertical mixing of the water column in the south basin (Fig. 4). Ferguson and Harbott (1982) speculated that surface waters flow primarily in a northwesterly direction over most of the lake, with the exception of southwards flow along the eastern and western shores of the north basin, balanced by counter currents in the opposite direction at depth. This has not been verified by direct observation.

A unique aspect of Lake Turkana among the great lakes of the Rift Valley is that its waters are usually well oxygenated at all depths. Throughout the 1973–1975 years of measurement, near-surface waters typically contained 7.5–8 mg/l O_2 and

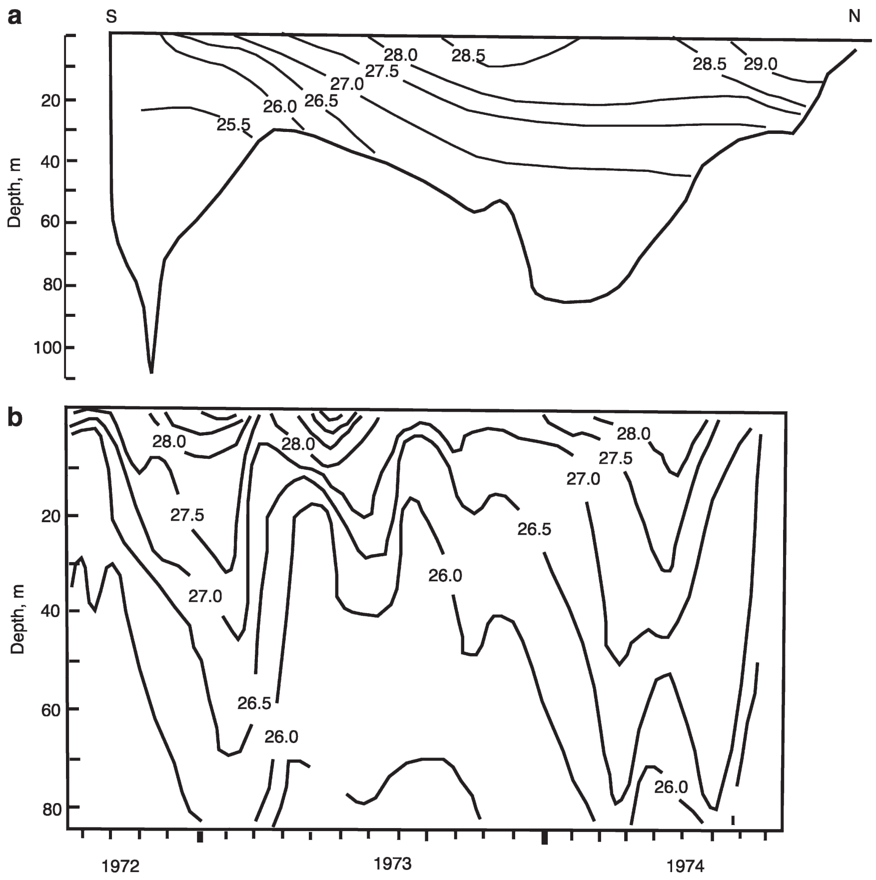

Fig. 3 (**a**) Temperature structure along the north–south axis of Lake Turkana in March 1975. (**b**) Temporal variability in the thermal structure at a station just north of Central Island from August 1972 to August 1974 (both figures modified from Ferguson & Harbott, 1982, with permission of the UK Department of International Development)

bottom water concentrations varied between 4 and 5.5 mg/l (Ferguson & Harbott, 1982). The absence of anoxia in the deeper reaches of the water column was likely due to effective mixing by the intense wind field and the relatively shallow mean depth of the lake. However in 1987–1988, dissolved oxygen concentrations at 70 m depth dropped briefly to 2.4 mg/l in June 1987 and to 0.2 mg/l in May 1988 during periods of thermal stratification (Liti et al., 1991).

Lake Turkana is a brackish Na-HCO$_3$ lake with a salinity of about 2,500 mg/l, dominated by Na$^+$, HCO$_3^-$, and Cl$^-$ ions, and a pH averaging 9.1 (Cerling, 1979; Yuretich & Cerling, 1983). The salinity is much lower than might be expected, given the lake's closed-basin status for roughly the past 4,000 years (discussed below). Yuretich & Cerling (1983) attribute the relatively low salinity of Turkana waters to cation removal by sediment–water reactions, such as Na$^+$ uptake by

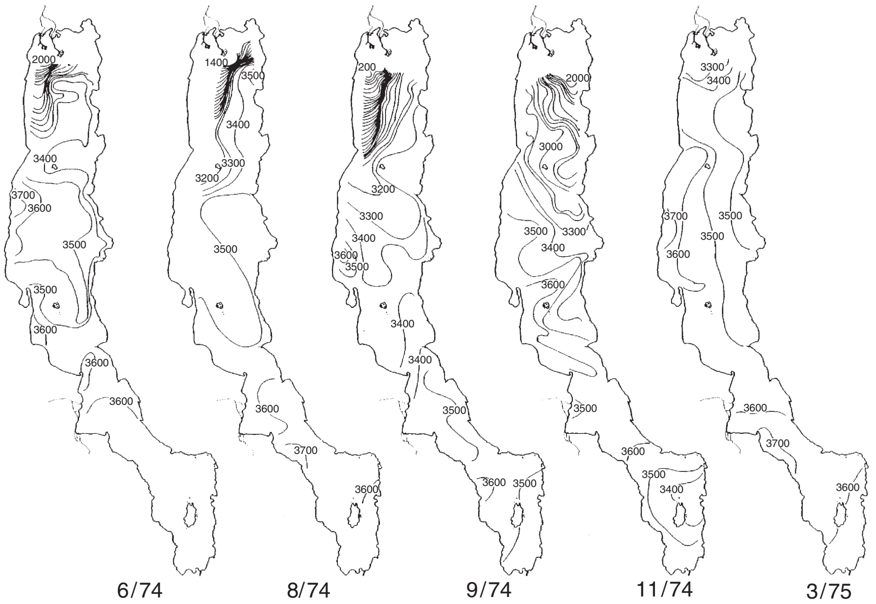

Fig. 4 Surface water conductivity on five occasions between June 1974 and March 1975. Reprinted from Ferguson and Harbott (1982) with permission of the UK Department of International Development

smectite, Mg^{++} incorporation into a silicate phase, and Ca^{++} precipitation in calcite, as well as by burial of solutes in pore water. The few measurements of dissolved nutrients that have been made in the lake show it to be a N-limited system, with dissolved NO_3^- concentrations much less than 1 mg/l and dissolved PO_4^{3-} of about 2 mg/l (Ferguson & Harbott, 1982; Liti et al., 1991).

The phytoplankton of Lake Turkana are dominated by the blue-green alga *Microcystis aeruginosa* and the green alga *Botryococcus braunii*, with occasional high concentrations of the diatom genus *Surirella* (Harbott, 1982; Liti et al., 1991). Lake Turkana waters are highly turbid due to wind turbulence and substantial sediment input from the Omo River, and frequent aeolian depositional events. The photic zone is consequently restricted to the upper 6 m of the water column. During the months of high river input, phytoplankton concentrations are higher in the northern part of the lake than in the south, presumably due to river-supplied nitrate. Despite evidence for upwelling in the south basin, algal concentrations were always found to be much lower than in the central and north basins, and algal blooms were never observed in the southern part of the lake (Harbott, 1982). Primary production in the lake, based on very few measurements of oxygen production, is estimated to be about 700–800 gC/m^{2}y (Liti et al., 1991).

The zooplankton community is dominated by protozoan *Heliozoa* and *Ciliata* in terms of numbers of individuals, and by carnivorous and omnivorous crustaceans, primarily the Calanoid, *Tropodiaptomus banforanus*, and the Cyclopoid, *Mesocyclops leuckarti* (Beadle, 1981). The identities of both taxa were later revised and changed to *Tropodiaptomus turkanae*, an apparent endemic of the lake (Maas et al., 1995), and *Mesocyclops ogunnus* Onamabiro. *Mesocyclops leuckarti* does not occur in Africa, and is replaced in the Nile basin by about seven species, of which at least *M. ogunnus* and *M. salinus* occur in Turkana (Dumont, 2009). Small, detritus-feeding prawns dominate the benthos and provide an important food source for the lake's fish population. Of the 48 species of fish identified in Lake Turkana by Hopson and Hopson (1982), 30 are found throughout the soudanian region, 22 of which are also found in Lake Albert and 8 in the Nile (Beadle, 1981). Ten species are endemic to Lake Turkana, a relatively small number when compared to Lakes Victoria, Malawi and Tanganyika to the south that are each home to hundreds of endemic species of fish (Beadle, 1981). The low degree of endemism and the prevailing soudanian character of Turkana fish populations reflects the relatively recent hydrological tie to the Nile flowage. The fisheries of Lake Turkana has undergone dramatic and unpredicted change in recent decades, a reflection of a highly variable system responding to both fishing pressure and a fluctuating lake level that impacted nearshore nurseries and other environmental factors (Kolding, 1992).

5 Turkana's Past Connection to the Nile

Lake Turkana, like other closed basin lakes in arid regions, is considered an "amplifier lake" in terms of its dramatic response to climate variability (Street-Perrott and Roberts, 1983). Relatively minor swings in rates of evaporation and rainfall can generate substantial rise or fall in lake level and in water chemistry. Such changes can lead to dramatic shifts in lake biota, as well as in the composition of sediments accumulating on the lake floor.

The most recent fluctuations in the hydrological budget of Lake Turkana are apparent from radar altimetry measurements of the lake elevation, monitored at least bi-monthly since 1992 from Topex/Poseidon and Jason satellite systems (Fig. 5). Over this time period lake level has fluctuated by over 5 m, from its lowest level in 1996 to its highest level in 1999. The level of Lake Turkana closely parallels the levels of Lakes Victoria and Tanganyika over the same time interval. All three lakes rose dramatically in the 1998 El Nino year when heavy rains fell throughout tropical East Africa, responding primarily to the sea surface temperature (SST) field in the Indian Ocean (Goddard & Graham, 1999). SST's in the west central Indian Ocean tend to be relatively warm compared to the eastern equatorial region during El Nino years (Goddard & Graham, 1999), leading to enhanced advection of moisture over tropical East Africa and relatively intense rainfall.

A hydrological history of the Turkana basin is derived, at least qualitatively, from the composition of sediments recovered in cores from the offshore basins of the modern lake. These sediments consist of laminated to thinly bedded, calcareous silty clay (Yuretich, 1979). The laminae are typically 0.3–0.5 cm thick and are defined by calcite-rich light layers between calcite-poor dark layers. These couplets are not varves, but rather represent on average 1.5–2 years duration, and perhaps reflect the influence of the biennial oscillation on rainfall on the Ethiopian Plateau (Halfman

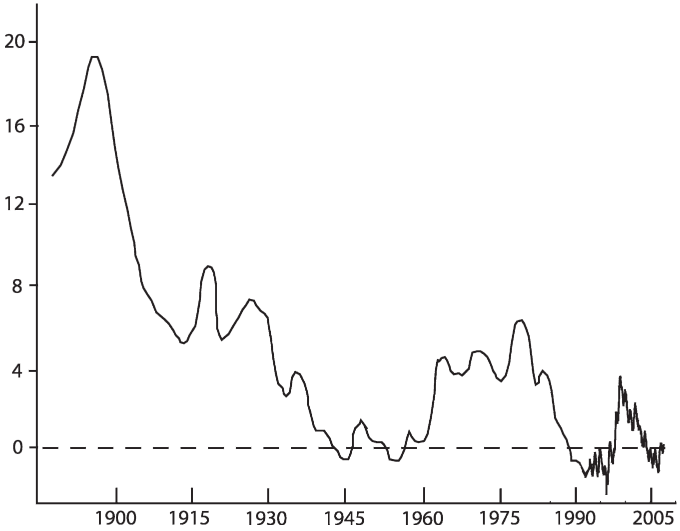

Fig. 5 The history of lake level fluctuations from 1893 to 2006, based on historical ground survey to 1990 (from Kallqvist et al., 1988; measurements by the Kenya Marine Fisheries Institute (1988–1994); and on TOPEX/Poseidon satellite radar altimetry, from Global Reservoir and Lake Elevation Data Base, Eastern Africa, U.S. Department of Agriculture Foreign Agricultural Service web site (http://www.pecad.fas.usda.gov/cropexplorer/global_reservoir/gr_regional_chart.cfm?regionid=eafrica&region=&reservoir_name=Turkana). Lake level is in meters, based on an arbitrary datum of about 361 m asl

et al., 1994). Laminations are preserved in the sediment, despite the oxygenated bottom waters, because of the unusually high sedimentation rates and the prevalence of epifaunal detritovores living on the lake floor rather than infaunal invertebrates that would more effectively destroy sedimentary structures (Cohen, 1984).

The sedimentary calcite consists of ostracod shells and endogenic, arrowhead-shaped crystals of low-Mg calcite about 2–5 µm in length. The profiles of carbonate content in Turkana sediment cores reflect dilution by varying input of detrital siliciclastic sediment derived primarily from the Omo River, and is a rough measure of rainfall on the Ethiopian Plateau (Fig. 6) (Halfman et al., 1994). The 12 m long piston cores from Turkana span at most only 5,400 years, due to the high sedimentation rate in the lake. A stacked carbonate record bears crude resemblance to the Nile discharge record of Hassan (1981) that spans the past 1,500 years (Fig. 6), and displays significant periodicity of 76, 32, 22, 18.6 and 11 years (Halfman et al., 1994).

Diatoms are not well preserved in the upper few meters of Turkana sediment cores due to the high pH of the lake waters and its impact on the preservation of biogenic silica (Johnson, 2002). However Core LT84-2P recovered from the south basin of the lake displays increasing abundance of diatoms with depth, and a major shift in diatom species abundances 7.6 m below the lake floor. Below this level, the diatom assemblage is dominated by *Aulacoseira* (formerly *Melosira*) species indicating freshwater conditions, and above, dominance of salt tolerant genera *Thalassiosira* and *Surirella* (Fig. 7) (Halfman et al., 1992). The age of this transition

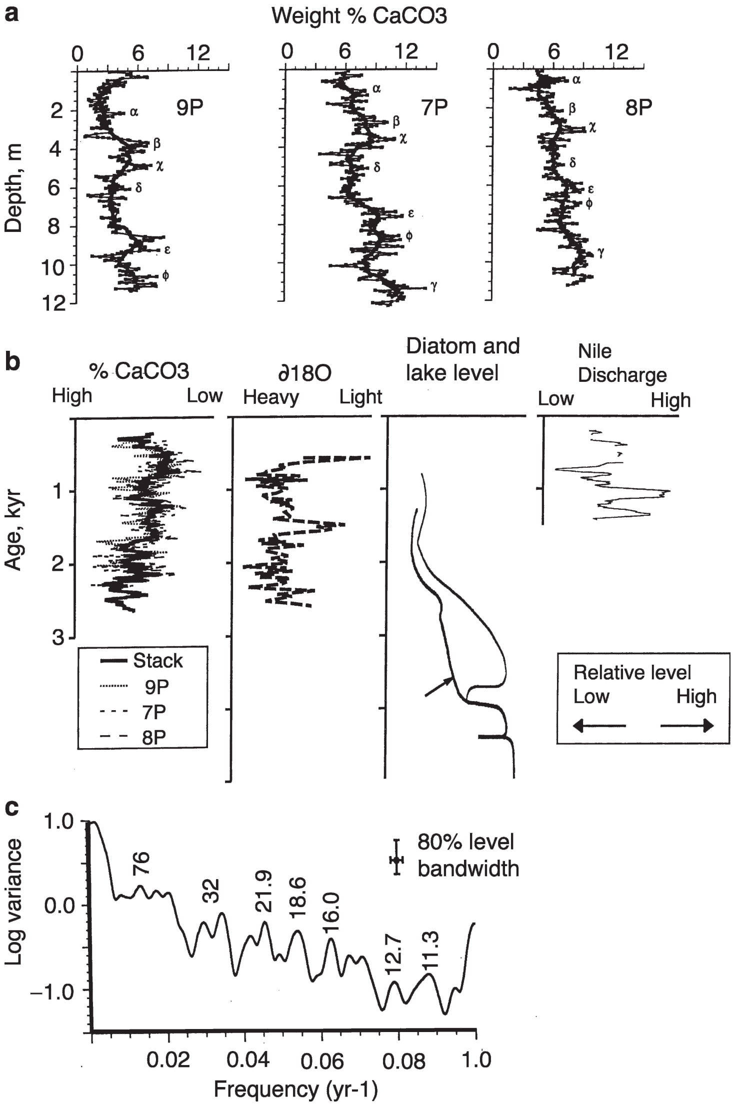

Fig. 6 Abundance of calcite in sediment cores from Lake Turkana reflect past changes in river input to the lake, with high calcite abundance reflecting low river input. (**a**) Weight % calcite versus depth in cores from the northern basin. Core locations are depicted in Fig. 2. (**b**) Various measures of hydrologic change vs. radiocarbon age from Lake Turkana and the Nile River: calcite abundance, δ18O of calcite, and diatom indicators of salinity in the south basin core 2P (see text and Fig. 7), and dated beach ridges (see text and Fig. 8). Nile River discharge data are from (Hassan, 1981). (**c**) Power spectra of stacked %$CaCO_3$ profiles plotted against age in Turkana cores, showing decadal scale cyclicity in the lake's hydrological regime. Modified from Halfman et al. (1994) with permission from Elsevier

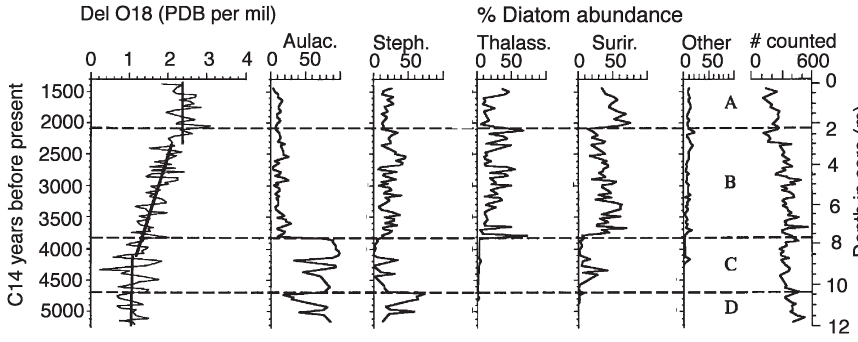

Fig. 7 δ18O of endogenic calcite and the relative abundances of the major diatom genera versus age in core LT84-2P (location in Fig. 2). Reprinted from Halfman et al. (1994) with permission from Elsevier

is 3,900 ^{14}C ybp, or 4,320 Cal ybp, and it signals the last time that Lake Turkana was an open basin lake, with outflow to the Nile.

The oxygen isotopic composition of the $CaCO_3$ in micrite and ostracodes has been analyzed in Turkana sediment cores, as further evidence of the hydrological history of the lake. δ^{18}O of lacustrine calcite varies with temperature and with the isotopic composition of the lake water. Temperature variability in tropical lakes has relatively minor impact on oxygen isotopic composition compared to the effect of shifts in lake water isotopic composition that result from either evaporative fractionation or to changes in the composition of source water through time. The relationship between the isotopic composition of calcite and lake level history is not simple (Ricketts & Johnson, 1996), but with appropriate modeling a reasonable estimate of past lake level can be derived (Ricketts & Anderson, 1998). The δ^{18}O profile of micrite in the same piston core analyzed for diatoms, described in the previous paragraph, is quite variable throughout the core, and undergoes a pronounced shift to heavier values over the span from 3,900 to 2,200 ^{14}C ybp (4,320–2,320 Cal ybp) (Fig. 7) (Ricketts & Johnson, 1996). This prolonged shift to heavier values cannot be explained by the abrupt drop in lake level at 4,320 Cal ybp, but must indicate a 2,000 year long adjustment in climate over the Ethiopian Plateau that was manifested in part by a corresponding shift in the isotopic composition of rainfall in the region (Ricketts & Johnson, 1996).

The most accurate history of lake level fluctuations is derived from a series of radiocarbon dates on mollusk shells recovered from shoreline deposits exposed in the basin above present lake level, especially to the north and east of the lake. These beach strandlines with early to mid Holocene ages lie as high as 460 m above sea level, or 10 m higher than the sill that would allow Turkana water to drain westward into the Sobat catchment and the Nile (Butzer, 1980). The elevation of Lake Turkana today is about 360 m asl. There is considerable variability in radiocarbon dates from the relict shoreline deposits but, when taken together, appear to cluster into two, possibly three, phases of lake high stands in the Holocene (Butzer

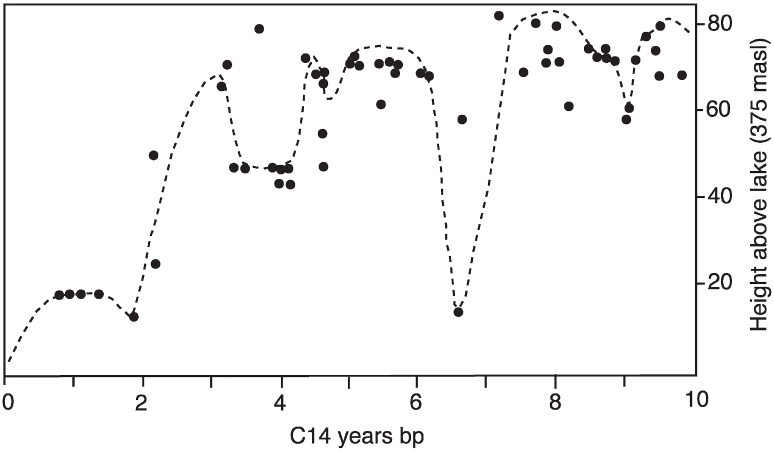

Fig. 8 A curve of Lake Turkana level versus radiocarbon age for the past 10,000 years, based on radiocarbon dates on relict shoreline deposits. Modified from Owen et al. (1982) with permission from the Nature Publishing Group

et al., 1972; Owen et al., 1982). The first, lasting from 10,000 to 7,000 ^{14}C ybp (11,500–7,800 Cal ybp), includes several dates from beach ridges at elevations corresponding to overflow conditions (Fig. 8). A brief low stand, defined by only one date at 380 m asl, is identified at 6,600 ^{14}C ybp (7,500 Cal ybp). This precedes the second phase of high lake level that spans the interval of 6,500–4,200 ^{14}C ybp (7,400–4,700 Cal ybp). Lake level then dropped to about 420 m asl. There is one radiocarbon date of 3,250 ^{14}C ybp suggesting a final brief period of overflow into the Nile (Fig. 7) (Butzer et al., 1972; Owen et al., 1982), but this is not compatible with the diatom data from Core LT84-2P (Fig. 7), nor with core data reported by Barton and Torgersen (1988). This suggests that the date is erroneous, and that the last time of Turkana overflow to the Nile was around 4,300 to 4,700 Cal ybp, based on the diatom record in LT84-2P and dated beach deposits, respectively.

The history of lake level fluctuations in the Turkana basin prior to 11,500 Cal ybp is not as well known as it is for the Holocene. No lake high stands have been identified for Turkana for the period 35,000–10,000 ^{14}C ybp (Owen et al., 1982). However the Kibish Formation includes some older, flat lying deltaic deposits and interbedded tuffs at the drainage divide between the Turkana and Nile catchments (Fig. 9). The formation has been divided into four members, each representing at least one interval when Lake Turkana was high enough to contribute outflow to the Nile. The uppermost Member IV has been radiocarbon dated and included with the early Holocene deposits described previously. Alkali feldspars extracted from pumice clasts from tuffs in Members I and II have been dated by ^{40}Ar/^{39}Ar, at 196 ± 2 and 104 ± 1 kyr, respectively (McDougall et al., 2005), which coincide with ages of sapropels S7 (195 kyr) and S4 (102 kyr) in the eastern Mediterranean Sea. The sapropels are distinct, organic-rich horizons with an absence of benthic faunal remains that have been attributed to high Nile discharge to the Mediterranean, which

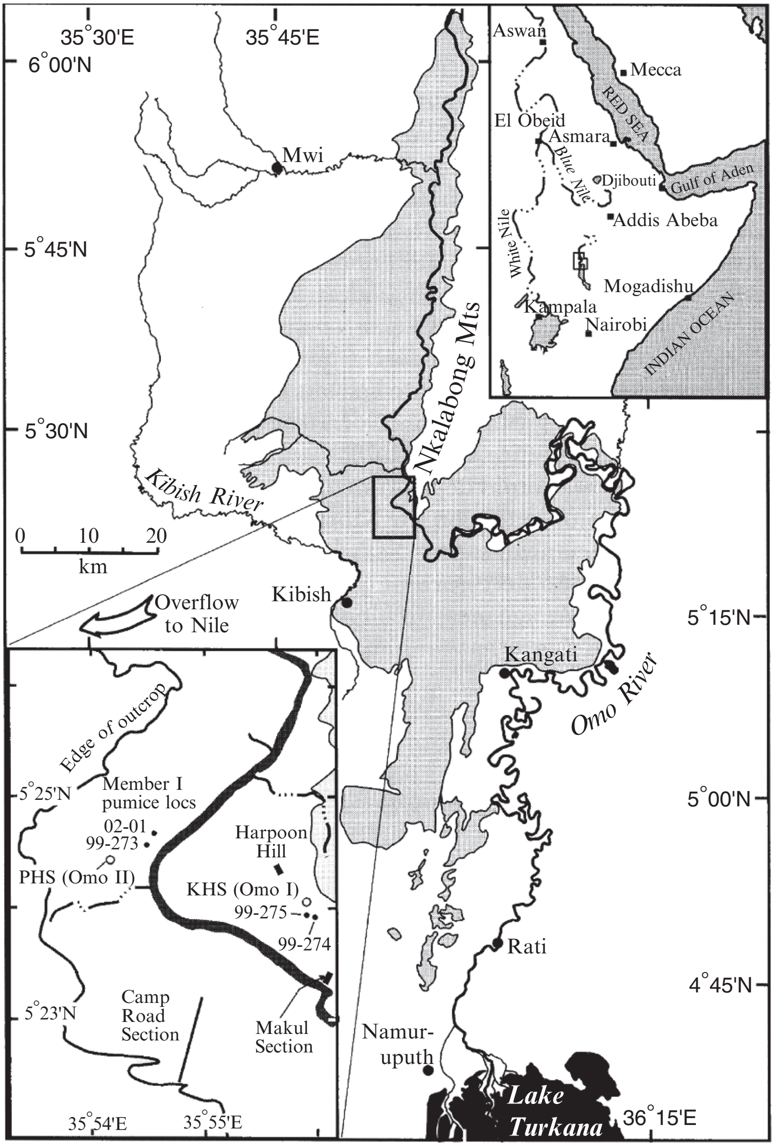

Fig. 9 A map of the Kibish Formation (shaded area) north of Lake Turkana. Reprinted from McDougall et al. (2005) with permission from the Nature Publishing Group

caused intense stratification in the upper water column and suboxic conditions on the sea floor (Rossignol-Strick et al., 1982). Member II of the Kibish Formation has two siltstone sequences separated by a disconformity. These likely coincide with S5 (119–123 kyr) and S6 (172 kyr), or with two phases of S5 (McDougall et al., 2005). The tie between sapropel formation in the Mediterranean and the high stands of Lake Turkana lead to speculation that there are more high stand deposits in the Turkana basin to be found and dated, but at present we can only be sure of Turkana links to the Nile in the early Holocene, at 102 kyr, and at 195 kyr, with possible links at 123 and 172 kyr as well.

Plio-Pleistocene lake deposits are also exposed to the east and west of the present lake. The lacustrine clays are interbedded with conglomerates, sands and silts of alluvial and fluvial origin. Stratigraphic correlations have been drawn across the Turkana basin based on interbedded tephras of distinct composition, many of which have been dated by the ^{40}Ar/^{39}Ar method (Feibel et al., 1989; McDougall & Brown, 2006). Cerling (1979) analyzed lacustrine clays and silts in the Koobi Fora Formation east of the lake to determine the paleochemistry of past lake high stands, based on fossil assemblages, exchangeable cations on clay minerals, and presence or absence of certain authigenic minerals. At the time of his analysis the age of the deposits was not well known, but they are now dated at about 4.2–0.7 Ma (Feibel et al., 1989). Cerling determined that the presence of molluscs in lacustrine deposits indicates relatively freshwater conditions, with alkalinity in the range of 0.5–16 meq/l (Cerling, 1979). Under these circumstances, Lake Turkana was likely overflowing. Feibel (1994) concluded that the lake overflowed to the southeast to the Indian Ocean from the late Miocene until at least 1.9 Ma, based primarily on an abundance of fossil stingray spines in lacustrine and fluvial deposits that are of early Pleistocene age (1.9–1.3 Ma). Subsequent tectonics in the basin shifted the direction of Turkana outflow during humid times from a corridor to the Indian Ocean to the Nile drainage system.

We have no record of how much lower Lake Turkana may have stood than at its present level. It is likely that it was reduced to a much smaller body of water during the last ice age and in earlier times of weakened summer monsoons, and perhaps was completely desiccated. New results from the Lake Malawi and Lake Bosumtwi Drilling Projects, and from a core from Lake Tanganyika, indicate widespread megadrought conditions in tropical Africa prior to 75 kyr – far drier than during the last glacial maximum at 21 kyr (Scholz et al., 2007). Lake Malawi was about 500 m lower than today around 110 and 130 kyr, and 350 m lower than present around 75 and 100 kyr. Such extreme aridity during precessional minima in summer insolation may have extended as far north as the Ethiopian Plateau. If so, Turkana may have completely dried out. This could mean that the soudanian biota that are found in Turkana today are the remnants of only the most recent flooding of the Turkana basin between 10,000 and 4,000 years ago.

6 Conclusions

Lake Turkana is a closed-basin lake that relies primarily on inflow from the Omo River for its existence in the hot, arid depression of northern Kenya. It is a slightly saline lake that has a well-mixed water column and an oxygenated lake floor. Sedimentation rates are high in the lake, typically on the order of 0.2–0.5 cm/y, due to high river discharge of sediments from the extensive drainage basin. The lake has stood 100 m higher than present under wetter conditions in the past, at which times the water was of low salinity and the lake spilled into the Nile River catchment, at least in the last 1.3 million years. The most recent outflow from Turkana to the Nile occurred in the early Holocene, from about 11,500 to 7,800 Cal ybp, and again from about 7,400 to 4,300 Cal ybp. At present we have no evidence for Turkana outflow to the Nile between 11,500 ybp and 104,000 years ago. High stand deposits in this age range may become revealed with further field work in the region. Prior to 104 kyr, a few high stand deposits have been dated that appear to coincide with Mediterranean sapropels, dating as far back as 195 kyr. The history of lake level fluctuation prior to this time is unknown. There are thick sequences of lacustrine shale that have been imaged seismically and sampled in oil exploration wells in the Lokichar Basin southwest of the lake, and the lake itself overlies 3.5 km of sediment up to 4.3 million years old. There is still much to be learned about the hydrological history of the Turkana basin and its past tie to the Nile River.

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Part III
Climates and Hydrology

Nile Basin Climates

Pierre Camberlin

Abstract The climate of the Nile Basin is characterised by a strong latitudinal wetness gradient. Whereas the areas north of 18° N remain dry most of the year, to the south there is a gradual increase of monsoon precipitation amounts. Rainfall regimes can be divided into nine types, among which summer peak regimes dominate. In the southern half of the basin, mesoscale circulation features and associated contrasts in local precipitation patterns develop as a result of a complex interplay involving topography, lakes and swamps. Precipitation changes and variability show up as three distinct modes of variability. Drying trends since the 1950s are found in central Sudan and to some extent the Ethiopian Highlands. The equatorial lakes region is characterised by occasional very wet years (e.g. 1961, 1997). The interannual variations are strongly, but indirectly influenced by El-Nino/Southern Oscillation. Sea surface temperature variations over other ocean basins, especially the Indian and South Atlantic Oceans, also play a significant role. Projections for the late twenty-first century show a 2–4°C temperature increase over the basin, depending on the scenario, but rainfall projections are more uncertain. Most models tend to predict a rainfall increase in the equatorial regions, but there is little consistency between models over the tropical regions.

1 Introduction

It is well known that the river Nile has the world's longest stretch under arid conditions: along 3,000 km of its course, rainfall does not exceed 150 mm annually. However, due to its great latitudinal and altitudinal extent, the Nile basin displays large variations in precipitation receipt. These contrasts, which clearly show up in the mean climate fields, also manifest in time as large year-to-year or longer-term fluctuations.

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2 Mean Climate

2.1 Drivers of the Nile Basin Climates

2.1.1 General Circulation and Its Forcings

The Nile basin extends over 35 degrees of latitude, from the equatorial zone (4° S) to the northern subtropics (31° N). This results in highly contrasted climatic conditions, dominated by the Hadley circulation. The Hadley circulation is fuelled by a north–south energy gradient between a zone with excess energy (to the south of the basin, shifting to the central part with the northern summer heating) and a zone with a deficit (to the north of the basin). The excess energy originates from high solar radiation gains, low terrestrial radiation losses due to an extensive cloud cover, and a high atmospheric moisture content (latent heat). The deficit in the north, mainly the Sahara desert, is related to lesser solar radiation gains (in the northern winter), to high terrestrial radiation losses due to cloudless skies, and to a dry atmosphere (low latent heat content).

The excess surface energy induces relative low pressure and rising motion, as well as a low-level wind convergence, the Intertropical Convergence Zone (ITCZ). The ITCZ is located southward outside the Nile basin in the northern winter, and gradually shifts to the north to reach the central part of the basin by mid-summer (Fig. 1). Rising motion within the ITCZ results into widespread precipitation.

Reciprocally, the energy loss at higher latitudes is accompanied by diverging low-level winds, subsidence and permanent dryness. The northern part of the Nile basin is therefore capped by high-pressure systems, namely the Libyan and Arabian Highs, during much of the year (Fig. 1). In summer they weaken and are partly replaced by surface heat lows, though subsidence still prevails higher in the troposphere.

Winds systems reflect the dominant influence of the Hadley circulation. The Libyan high drives north-westerly winds in Egypt, turning to north-easterly in northern Sudan, during most of the year (Fig. 1). Occasionally, in winter, the northernmost part of the region along the Mediterranean is affected by disturbances associated with upper troughs in the mid-latitude westerly circulation. To the south, the dry north-easterly trade winds combine with those originating from the Indian Ocean to reach southern Sudan and Uganda. From March, the ITCZ starts shifting northward, and south-westerly monsoon winds, originating from the South Atlantic and the Congo basin, appear in southern Sudan. The lake Victoria basin dominantly remains under the influence of easterlies, gradually getting a southerly component from April onwards. Further north in Egypt, rising temperatures induce surface desert depressions, which drive extremely hot and dusty southerly *khamsin* winds across Egypt, causing sudden heat waves in spring (e.g., 41°C in Cairo in early April 2003). By June, the monsoon winds reach central Sudan (16° N, Fig. 2) and the western slopes of the Ethiopian Highlands. From the end of June, due to the deepening of the Indian monsoon low further east, the south-westerly monsoon

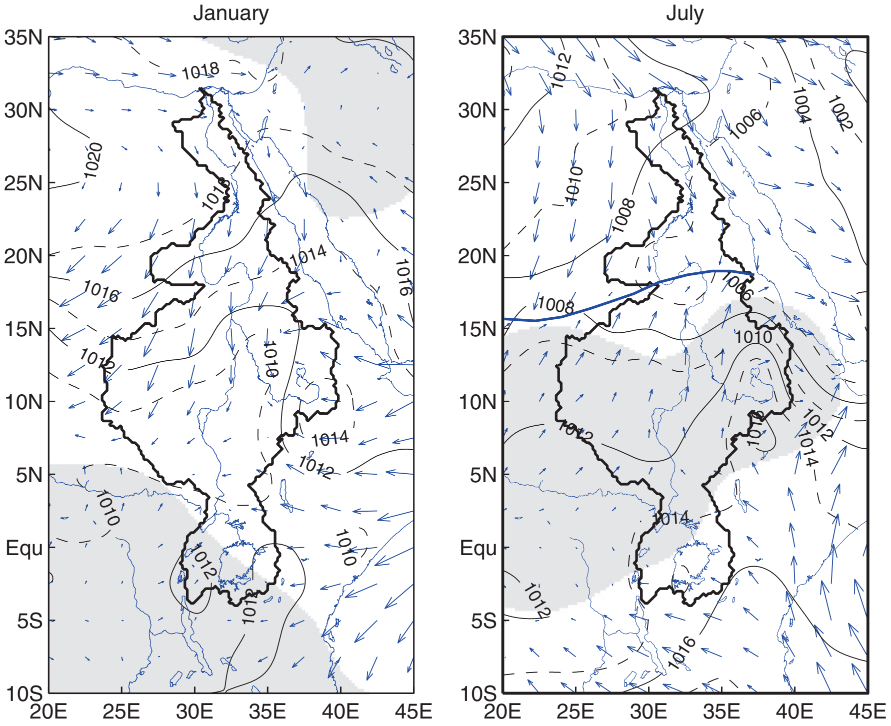


Fig. 1 Mean surface winds and sea-level pressure over North-East Africa in January and July. Data: Long-term mean (1968–1996) NCEP-NCAR reanalysis (Kalnay et al., 1996). Data over areas of complex topography should be considered as approximate. *Bold line*: July Intertropical Front surface location as deduced from the shift from northerly to southerly winds. *Shading*: regions of mean ascending motion at 400 hPa

spills over the Ethiopian Highlands to reach the southern Red Sea, where it is channelled until it joins the main Indian monsoon flow in the Arabian Sea. However, a distinct feature of the ITCZ in tropical North Africa, including the Nile valley, is that in summer the surface southerly winds tend to penetrate far to the north due to the Saharan heat low. Mean July temperatures range between 26°C and 33°C in Egypt and northern Sudan (Shahin, 1985). The surface heat low causes the "Intertropical Front" (ITF), which separates the monsoon winds from the northerly trade winds, to show a tilt with height (Hastenrath, 1991). In July–August, at the time of its northernmost location, the ITF is found around 17–19° N at the surface in the Nile valley (Fig. 1), and a few hundreds of kilometre further south at 1,500 m. South of lake Victoria, diverging south-easterly winds from the Indian Ocean induce dry conditions. Starting in September, the retreat of the ITCZ to the south tends to be faster than its northward shift (Osman & Hastenrath, 1969).

In the upper troposphere, the winds are also characterised by a seasonal reversal. In winter strong westerlies, forming the Subtropical Westerly Jet (SWJ), are found

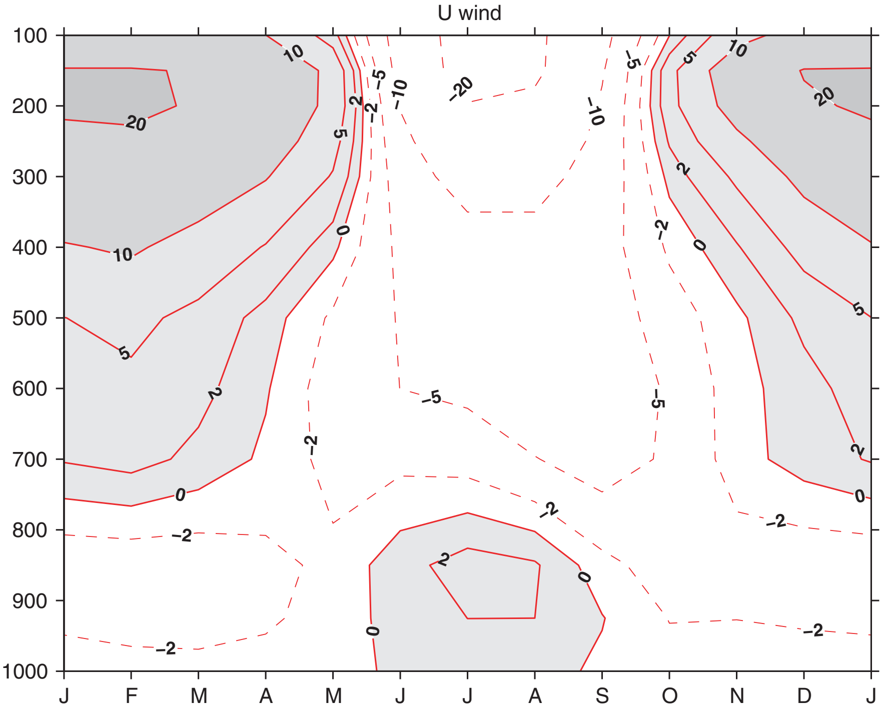


Fig. 2 Time–height distribution of mean zonal winds above central Sudan (15° N, 32.5° E), in m.s^{-1}. Data: Long-term mean (1968–1996) NCEP-NCAR reanalysis. Positive (negative) values indicate westerlies (easterlies)

over much of the Nile basin (Fig. 2). The variations of their latitudinal location and the waves which develop in the westerly flow affect winter weather conditions in the northern part of the basin. In particular, cut-off lows in the eastern Mediterranean will induce cloudy or possibly rainy conditions over northern Egypt. Cold fronts sweeping behind Mediterranean depressions result into a significant temperature drop, and sometimes the instability created by the passage of cold air over the warm desert surface produces widespread dust-storms (Tucker & Pedgley, 1977). The SWJ persists until May, after which the westerlies are replaced by easterlies (Fig. 2). They take the form of a jet (Tropical Easterly Jet, TEJ), which originates from Asia as a result of the summer monsoon. Maximum winds are found in July–August at 150 hPa near 10–15° N over Sudan, with velocities decreasing from 25 to 10 m s^{-1} from east to west (Hulme & Tosdevin, 1989; Segele & Lamb, 2005).

2.1.2 Regional and Local Factors

Among the factors which regionally modify the general circulation pattern, the most important one is topography. The highlands which bound the Nile basin to the east, from Eritrea to Kenya, restrict the penetration of the easterlies from the Indian Ocean. An exception is the gap between the Ethiopian Highlands and the Kenya Highlands, where strong easterlies prevail throughout the year (Turkana Jet; Kinuthia & Asnani, 1982). Mountain ranges also set up their own circulation and generate their own climate. A strong daytime horizontal flow is directed towards the heated mass of the Ethiopian Highlands, while it is suggested that the nearby Sudanese plains exhibit subsidence (Flohn, 1965; Pedgley, 1971).

Some of the Great Lakes of East Africa also tend to develop their own circulation, in the form of lake breezes induced by the small diurnal temperature variations of the lakes (around 25°C for lake Victoria) compared to the surrounding areas. This is most evident for lake Victoria, whose circular geometry encourages daytime breezes diverging from the lake to the warmer surrounding land, and night-time land breezes converging to the warmer middle part of the lake (Fraedrich, 1972). These breezes interact with slope circulation, especially to the north-east of the lake which is bordered by the Western Kenya Highlands (Okeyo, 1987). The joint effect of lake and upslope breezes enhances afternoon convection. The strong updraughts are responsible for a high frequency of hail around Kericho and Nandi Hills in Kenya (Alusa, 1986). An important aspect is also the interaction with the large-scale circulation (Asnani & Kinuthia, 1979; Anyah et al., 2006). The latter in the middle and upper troposphere is predominantly easterly, thus the convective clusters associated with low-level convergence and instability tend to drift westwards. This explains asymmetries in the rainfall distribution on either side of the mountain ranges or lakes.

The influence of regional features (topography, waterbodies, land cover) over atmospheric circulation is best studied by numerical modelling. The overall influence of the East African Great Lakes was assessed by Bonan (1995) using a general circulation model, but regional models are needed to adequately resolve the local topographical features. For East Africa, Sun et al. (1999a, b) assessed the ability of the NCAR RegCM2 model to simulate the region's climate. It was subsequently shown that taking into account three-dimensional lake dynamics is necessary to satisfactorily reproduce climate conditions over lake Victoria itself (Song et al., 2004). Anyah et al. (2006) then performed sensitivity experiments showing the key role played by the Kenya Highlands on the diurnal circulation and associated rainfall distribution over the lake Victoria basin. For the Nile basin as a whole, Mohamed et al. (2005) used the RACMO regional model to evaluate the components of the water cycle. The study enabled to confirm that in June–September the low-level moisture advection towards the Ethiopian Highlands and Bahr-el-Ghazal region is mainly of Atlantic origin, whereas in Uganda and east of the Bahr-el-Jebel (White Nile) the Indian Ocean is the major moisture source. However, regional models still have some difficulties in reproducing some aspects of climate variation. For instance, while moisture convergence and associated rainfall is well simulated in June–September over the Ethiopian Highlands and Uganda north of lake Victoria in the RACMO model (Mohamed et al., 2005), the March–May rains over East Africa are strongly underestimated.

2.2 *Spatial and Temporal Distribution of Rainfall*

2.2.1 Mean Annual Rainfall

The mean annual rainfall for the Nile basin is low (630 mm over the period 1961–1990), but it is spatially very contrasted. As much as 28% of the basin receives less than 100 mm annually (Fig. 3), and part of it experiences hyper-arid conditions. However, a substantial area exhibits sub-humid conditions (34% between 700 and 1,300 mm), as displayed on the frequency distribution plot.

Spatially, there is a very gradual decrease of rainfall amounts from south to south in the central part of the basin (about 100–140 mm per degree of latitude; Fig. 4). North of about 18° N, from northern Sudan all across Egypt, rainfall is negligible (below 50 mm a year), except for a small increase along the Mediterranean coast (Alexandria 180 mm). Precipitation in excess of 1,000 mm is restricted to two areas: the equatorial region from south-western Sudan to most of the lake Victoria basin, and the Ethiopian Highlands. Even in these two areas, precipitation amounts are contrasted, with maxima around 2,100–2,300 mm near Gore, south-western

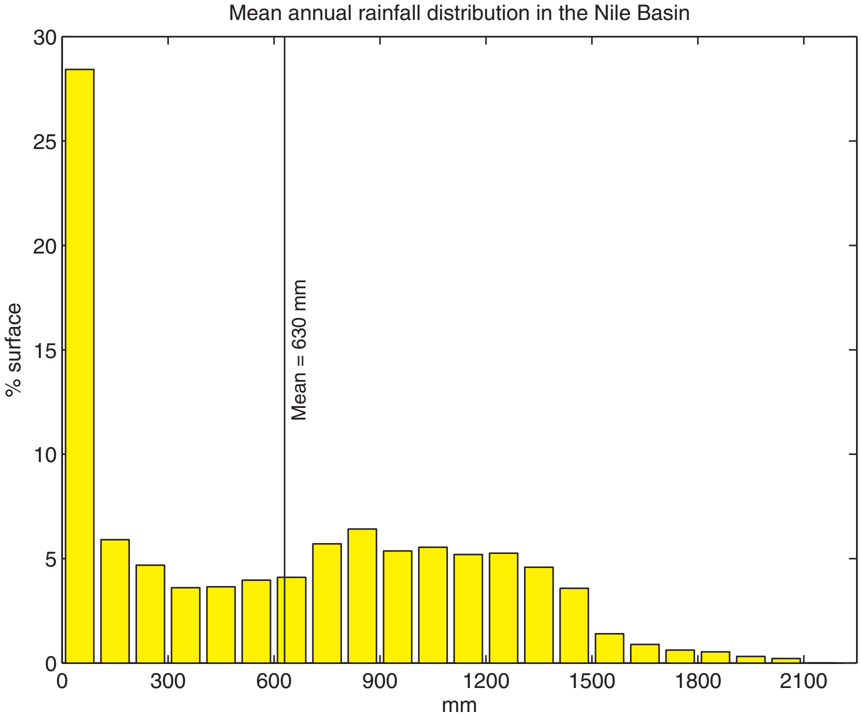


Fig. 3 Frequency distribution of mean annual rainfall in the Nile basin (1961–1990 average), as a percentage of the total surface area. Data: Climate Research Unit CRU CL 2.0 climatology at a 10’ resolution (New et al., 2002)

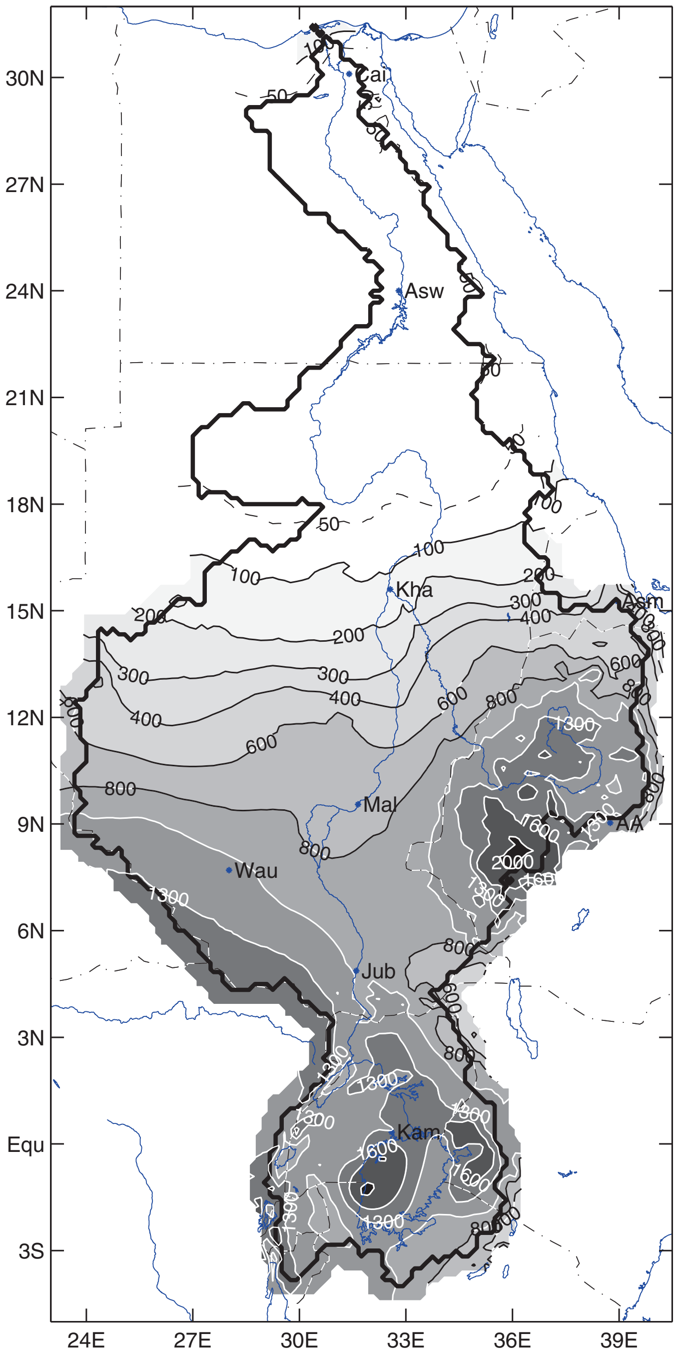


Fig. 4 Mean annual rainfall map of the Nile basin (1961–1990). Data: Climate Research Unit CRU CL 2.0 climatology at a 10’ resolution (New et al., 2002). Isohyets in mm

Ethiopia, 2,200 mm over the western part of lake Victoria, 2,000 mm on the western slopes of Mt Elgon. Localised values over 2,500 mm are found on Mount Rwenzori (Osmaston & Kaser, 2001), and perhaps over 3,000 mm on the western slopes (Leroux, 1983). Parts of the Western Rift Valley (lake Edward, lake Albert), north-eastern Uganda, and areas to the west and south of lake Victoria get less than 900 mm (Fig. 4).

This general distribution reflects the latitudinal movement of the ITCZ, which never reaches Egypt and northernmost Sudan, stays only briefly in central Sudan but longer further south. In wet areas, regional and local enhancements of rainfall are found on the west-facing slopes, mainly as a result of orographic lifting of the moist south-westerlies or westerlies. In the Great Lakes region in the south, local wind systems associated with the lakes and the complex topography of the Rift system explain the variable rainfall amounts. Rain shadows are found over lakes Albert and Edward in the Western Rift, while the maximum over the western part of lake Victoria results from the nocturnal convergence which takes place over the lake, generating thunderstorms which subsequently drift westward. The increase of rainfall with elevation is far from being universal; moisture convergence or orographic uplift (the latter possibly resulting into mid-slope maxima or windward/leeward rainfall asymmetries) are actually of much greater importance in both Ethiopia and the Equatorial Highlands (Oettli & Camberlin, 2005).

2.2.2 Seasonal Rainfall Distribution

The seasonal distribution of the rains is illustrated by the typology shown in Fig. 5, which is based on mean monthly rainfall for the period 1961–1990. The classic division of the basin into three rainfall regimes (arid, tropical and equatorial, from north to south) remains valid, but a further separation into nine types is useful. The northernmost part of Egypt receives some winter rains characteristic of the Mediterranean margins (type 1). The rest of the country, as well as northern Sudan, are totally dry throughout the year (type 2). At around 18° N a summer rainfall peak starts to appear (type 3), but the mean rainfall for the wettest month (August) remains very low. It increases in types 4 and 5, while the rainy season becomes longer (for type 5, 4–6 months above 50 mm at 10–13° N in central Sudan). In southern Sudan (type 6), the rainy season lengthens further, but though the peak is still in August, rainfall tends to level off during summer. This contrasts with type 7, covering much of western Ethiopia, where the rainfall regime is very similar to type 6, except for a strong increase in the middle of the rainy season, in July–August. This increase is likely to be related to the moist monsoon south-westerlies becoming thicker (Segele & Lamb, 2005), and overflowing the warm surface of the Ethiopian plateau, which results into enhanced convective instability. Equatorial regimes are found further south, with two peaks (the main one in April) separated by two drier seasons, in connection with the twice-a-year passage of the ITCZ over the region (Nicholson, 1996). In much of Uganda and Western Kenya (type 8), the northern winter is the

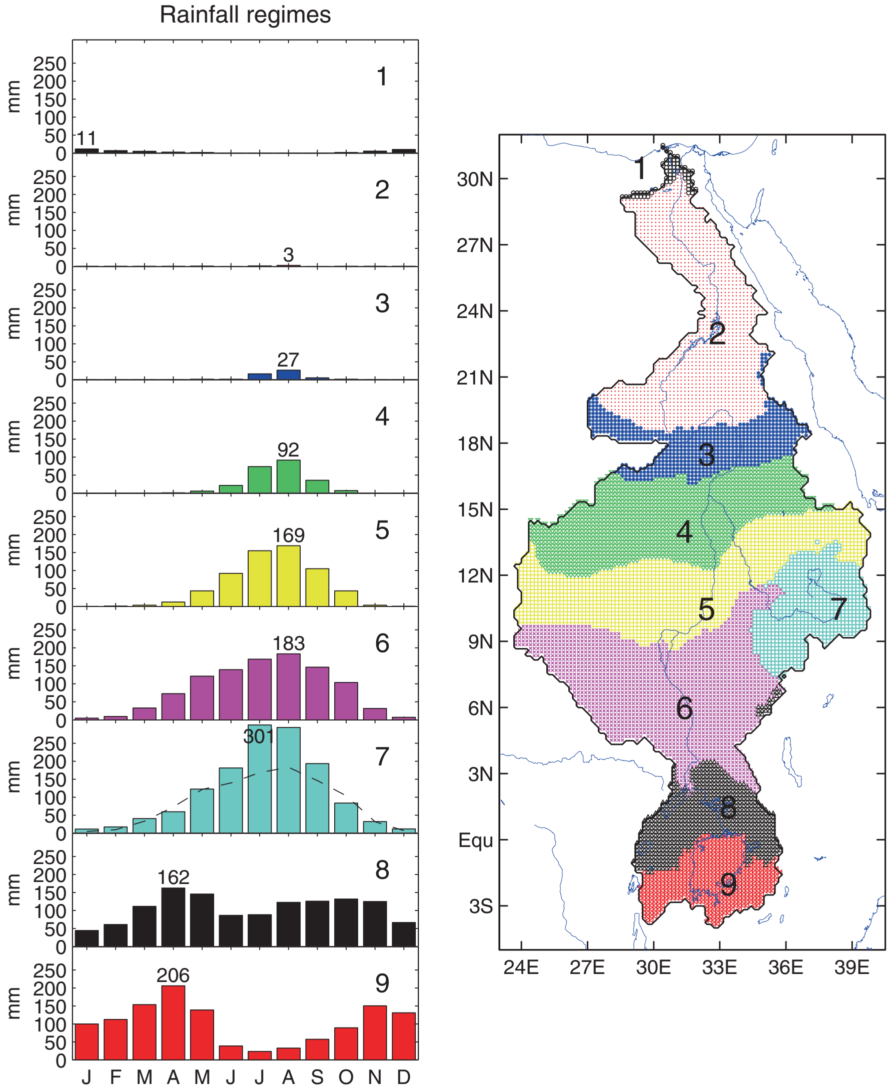


Fig. 5 Typology of rainfall regimes for the Nile basin. Based on a hierarchical cluster analysis of mean monthly rainfall for 1961–1990 (CRU CL 2.0 data). Figures in each panel indicate the maximum monthly rainfall. For type 7, type 6 is shown as a dashed line for comparison

driest season. After the March–May rains, rainfall remains quite high for six consecutive months till November. Over lake Victoria and its catchment in Tanzania, Rwanda and Burundi (type 9), it is the northern summer which becomes the driest season, whereas there is only a relative decrease between the "short rains", peaking in November, and the "long rains", peaking in April.

2.2.3 Small-Scale Temporal Organisation of Rainfall

The modalities of within-season variations in rainfall depend on the region. Apart from northern Egypt, the effect of extra-tropical disturbances on rainfall in the Nile basin is limited. Upper troughs remain generally rainless over Sudan, though over eastern equatorial Africa, cases of interactions with moist easterlies have been reported, giving enhanced rainfall. In Sudan during the summer rains, a pronounced periodicity around 4–5 days, except in dry years, is found in daily precipitation (Hammer, 1972, 1976), and is suggested to be associated with easterly waves activity. As recently demonstrated by Mekonnen et al. (2006), dynamic components of easterly waves are weak in the region, compared to West Africa. However, a 2–6 day convective variance as strong as in West Africa suggests an initiation of the waves by convective activity, on the western side of the mountains of Sudan (Darfur) and Ethiopia (see also an example in Desbois et al., 1988). Though most storms developed over Ethiopia drift westward due to the Tropical Easterly Jet of the upper troposphere, many decay before reaching the Nile Plains (Pedgley, 1969). In equatorial East Africa, organised weather systems are even more difficult to detect. Synoptic disturbances have been identified, but little is still known about their behaviour and relationship with rainfall, partly because the effects of topography make them difficult to follow (Nicholson, 1996). Emphasis has been given to incursions of moist westerlies from the Congo basin, to explain wet spells in the region. However, this is challenged by Anyah et al. (2006) who demonstrated through numerical modelling that rainfall over the lake Victoria basin is much less sensitive to changes in moisture entering the region from the west than from the east. It is likely that it is more the zonal wind convergence associated with westerly wind anomalies propagating from the Congo basin, rather than the moisture amount, that is instrumental in rainfall variability. At longer timescales, the 30–60 day "Madden–Julian" oscillation (MJO), which strongly modulates convection over the Indo-Pacific region, has also a moderate effect on intra-seasonal rainfall variability in Eastern Africa (Pohl & Camberlin, 2006).

Rainfall intensities may be high, though not as extreme as in many parts of the tropics. Maximum 24-h precipitation, though an imperfect indicator, shows that highland locations do not necessarily tend to have the highest intensities, despite their high mean rainfall amounts (Potts, 1971; Griffiths, 1972). A generalised map of 100-year 24-h extreme rainfall for the lake Victoria catchment area, based on Gumbel-I distribution, provides values generally comprised between 110 and 150 mm (WMO, 1974). As an illustration of the poor relationship between mean and extreme rainfall, in Uganda, the return period for a 100 mm daily fall is 4 years at the dry station of Moroto, and between 10 and 30 years for most wetter stations across the country, while at the highland station of Kabale (1,800 m) it is even as long as 170 years (Potts, 1971). The differences result from the respective parts played by convective and orographic rainfall, and the lesser precipitable moisture over high ground. In the northern part of the Nile basin, the computation of extreme rainfall probabilities is difficult due to rainfall events becoming much less frequent. However, very high intensities are possible. In the Nile Plains at Khartoum, a 201 mm 24-h record, resulting into extensive damages and human deaths, was recorded on 4 August 1988 (Hulme & Trilsbach, 1989), while the record of the previous 90 years was only 88 mm. On shorter time spans, very high peak rainfall rates may be found throughout the basin.

As in most other continental regions, rainfall generally peaks in the afternoon, especially over mountain areas (Desbois et al., 1988; Ba & Nicholson, 1998), but quite contrasted patterns are found across the basin. These diurnal regimes reflect the regional wind systems and their daytime evolution. The afternoon maximum is sharp over the Ethiopian Highlands and in northern Uganda and western Kenya (Fig. 6). Asmara (Eritrea), on the plateau, gets one third of its rainfall between 1500 and 1800 local time (LT). This maximum shifts to the evening hours further west, as the main convective cloud clusters move westward in the direction of the prevailing upper easterlies. An early morning maximum is even found in the central plains of Sudan. At Kosti 52% of the August rainfall occurrences occur between 0000 and 0900 LT (Pedgley, 1969). The weakness of the afternoon maximum is suggested to be due to subsidence, as a result of the daytime circulation which develops between the Nile Plains and the Ethiopian Highlands (Pedgley, 1971). Further south over the western part of lake Victoria, the morning peak is even more pronounced (Fig. 6). It results from the build up of the night-time convergence in the middle of the lake, the associated thunderstorms then drifting westward (Asnani & Kinuthia, 1979; Ba & Nicholson, 1998; Anyah et al., 2006).

3 Climate Variability and Change: Present and Future

3.1 Space–Time Patterns of Rainfall Variability

The region shows relatively coherent areas of rainfall variability. For the period 1951–2000, 44% of the space–time variance (for all areas receiving at least 100 mm annual rainfall) can be accounted for by three regional modes of variability, as deduced from principal component analysis (Fig. 7). Region 1 corresponds to the northern part of the summer rainfall belt (centred around 15–16° N), from northern Darfur to Kordofan and the Ethiopian–Eritrean border, with a southward extension along the Nile valley. It is characterised by heavy rains in the 1950s and early 1960s, followed by much drier conditions throughout the last three decades of the twentieth century, except for relatively isolated wet years like 1980, 1988 and 1998–1999. The second region is located further south, describing the latitudes 7–14° N but not continuously from Sudan to Ethiopia. Areas best represented are Darfur and the Ethiopian–Sudanese border area. Like for region 1, a marked rainfall decrease is evident, but the shift from wetter to drier conditions is delayed to the late 1970s, and a partial recovery occurs in the late 1990s. Region 3 comprises much of the equatorial regions, as well as the south-westernmost part of Ethiopia. It is dominated by a skewed distribution of annual rainfall, with some occasional very wet years like 1961, followed by 1951, 1963, 1982 or 1997. There is a tendency for the 1960s to stand out as wetter than average.

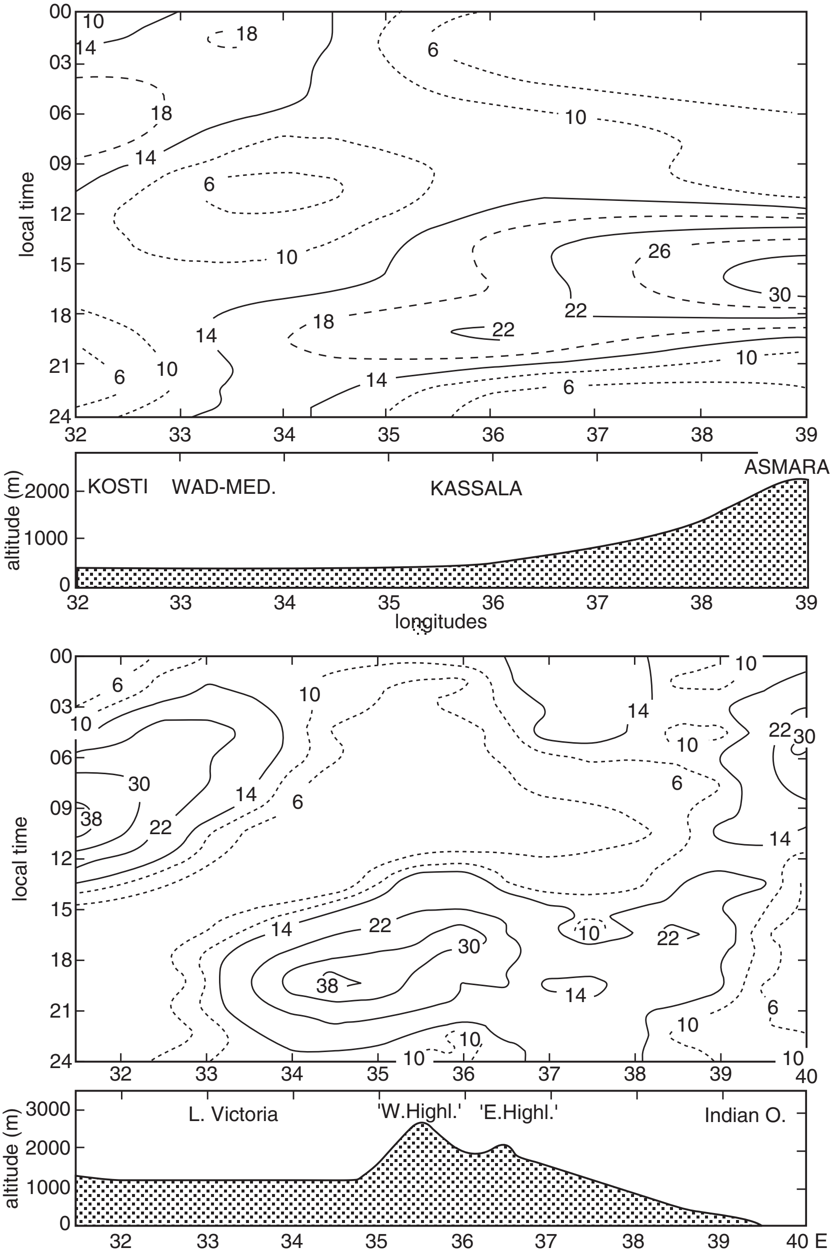


Fig. 6 Mean diurnal distribution of precipitation along west-east cross-sections. *Top*: cross-section from the Nile Plains to the Ethiopian Highlands, around 15° N (3-hourly rainfall amount or occurrence as percentage of the total for May–October). *Bottom*: cross-section from the lake Victoria west coast to the Indian Ocean, around 0–5° S (3-hourly rainfall occurrence as percentage of the annual total) Data from Pedgley (1969; 1971), Tomsett (1975)

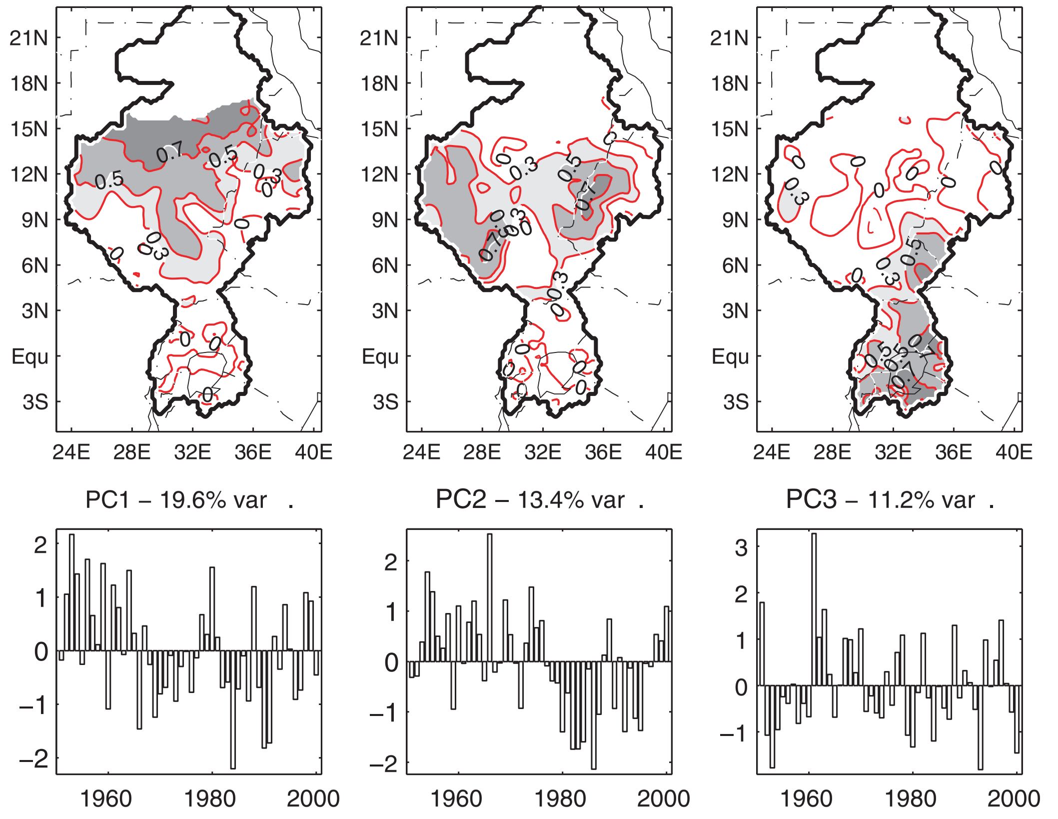


Fig. 7 Space–time patterns of the interannual variability of annual rainfall amounts, for 1951–2000. First three principal components (with a varimax rotation) of the correlation matrix. *Map shadings*: areas whose rainfall is significantly correlated (5% confidence level) with the corresponding time-series (*bottom*). Figures are correlation values

This description of space–time rainfall variations leaves out smaller size areas, like the central part of the Ethiopian Highlands and parts of southern Sudan. This is partly because the timescale retained (annual) combines different seasons and is not fully relevant for those areas where different climate signals, with a different spatial extension, are consecutively found during the year. For instance, part of the Ethiopian Highlands displays spring rains which are unrelated to those found at the same time in equatorial regions. Additionally, the main Ethiopian rains in summer show similarities with both the Sudano-Sahelian belt further west, and the equatorial regions, at this time of the year. However, on an annual basis, the equatorial region is dominated by the interannual variations of the northern autumn "short rains". On average the latter are not as wet as the spring "long rains". However, the "short rains" display a much larger amplitude in their interannual variability than the rest of the year (Nicholson, 1996; Black et al., 2003). In addition, they are spatially much more coherent than the "long rains" (Camberlin & Philippon, 2002). Therefore, the "short rains" dominate the interannual signal in equatorial rainfall and lake levels (Bergonzini et al., 2004).

A key feature of the last decades over part of the Nile basin is the downward rainfall trend, whose spatial pattern is shown in Fig. 8. Over the period 1951–2000, the linear trend is particularly pronounced in most of northern Sudan (around 50% precipitation decrease). It is also highly significant in Darfur (15–50% decrease). Other regions of significant decrease include central Sudan (10–40%) and south-western Ethiopia (20–35%). The equatorial region exhibits localised areas of rainfall decrease, like in West Nile (Uganda), but the overall rainfall is stable during 1951–2000. Small increases are restricted to isolated pockets around Addis-Ababa and the lake Victoria shorelines.

In Sudan, the rainfall decrease which started in the second half of the 1960s resulted into a much shorter rainy season in the 1970s and 1980s, particularly due to an earlier end, while all classes of daily rainfall amounts have seen a lesser occurrence (Hulme, 1988). As in the West African Sahel, the rainfall recovery in the 1990s is only a partial one, this decade remaining drier than the 1950s and early 1960s. In Ethiopia, previous evidence of decreasing rainfall is mixed (Conway & Hulme, 1993; Conway, 2000; Funk et al., 2003; Seleshi & Zanke, 2004): several studies failed to detect any systematic downward trend while others did. Conway et al. (2004) noted that Addis-Ababa rainfall shows little trends, but this station was found to be unrepresentative of the rest of the Ethiopian Highlands. In the latter, a drying trend is actually shown if only the summer monsoon rains are considered, and the 1950s and 1960s included. Several wet years in the 1990s additionally contribute to dampen the trend, but it remains very significant in south-western Ethiopia. The coherence between central Sudan rainfall and that recorded over part of the Ethiopian Highlands (Atbara basin), as shown by region 1, replicates the correlation found in annual rainfall for the corresponding sub-basins in Conway and Hulme (1993). Further south, the association between western Ethiopia and south-western Sudan precipitation (region 2), corroborates the correlation found by Sutcliffe and Parks (1999) between the river flows of the Blue Nile and the Jur at Wau (Sudan).

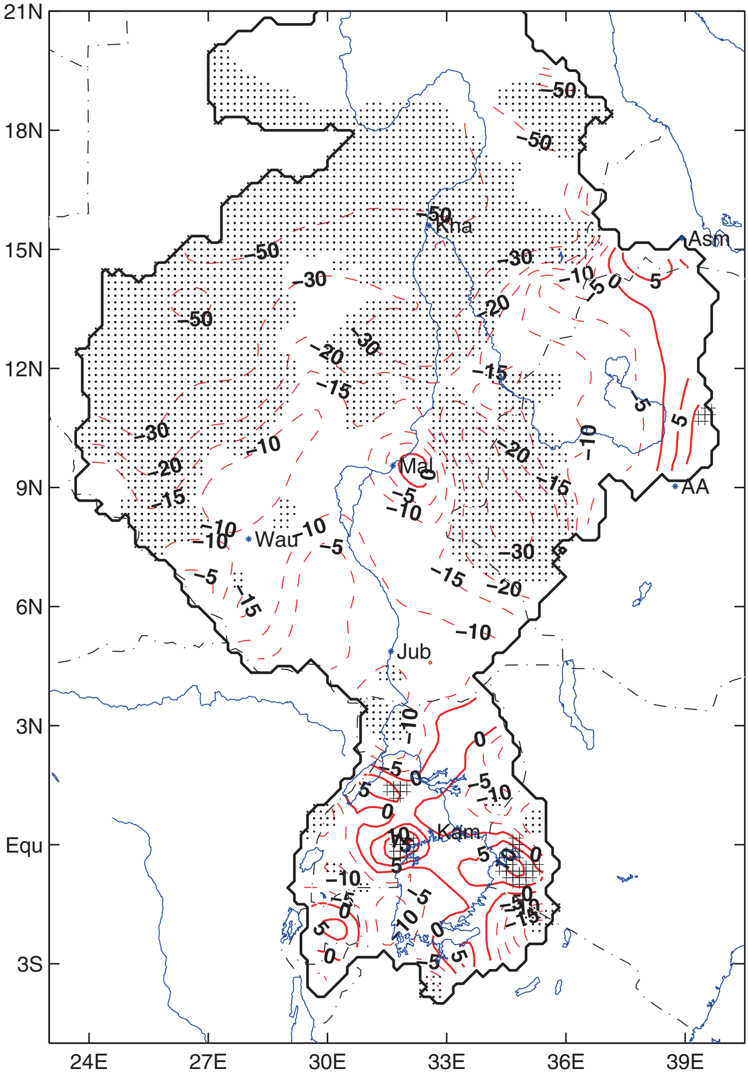


Fig. 8 Percentage change in annual rainfall between 1951 and 2000 (slopes of the linear trend as a percentage of the mean rainfall). Data: interpolated rainfall series based on the CRC rainfall data base and CRU rainfall climatology. *Dashed*: rainfall decrease; *solid*: rainfall increase. *Dots*: significant decrease; *cross-hatching*: significant increase (Spearman's ranks correlation, 95% confidence level)

3.2 Causes of Rainfall Variability

One of the main causes of climate variability in the tropics, the El-Nino Southern Oscillation (ENSO), has for long been found to affect the Nile basin, as demonstrated by Nile flows interannual variations (Bliss, 1925). However, studies on

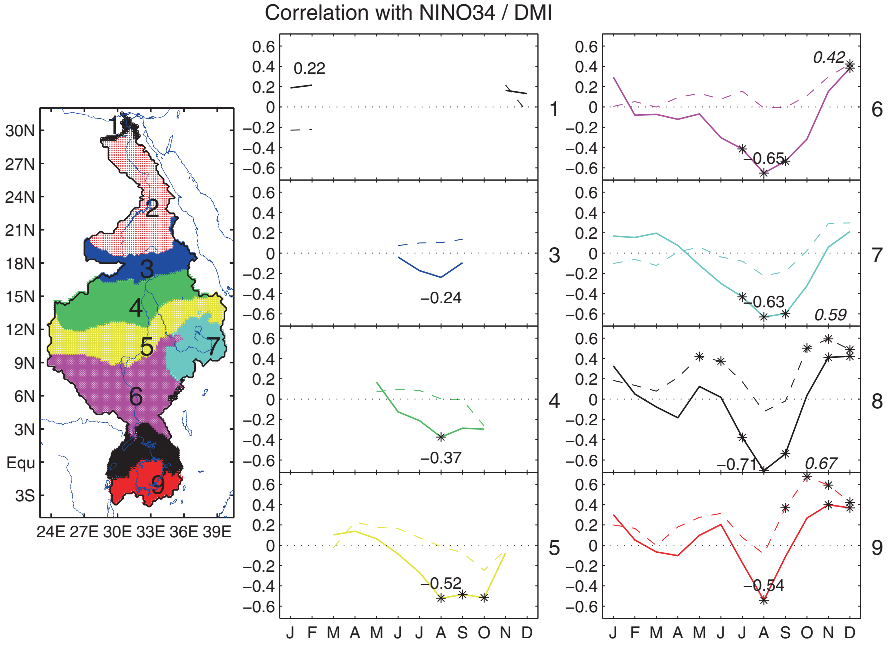
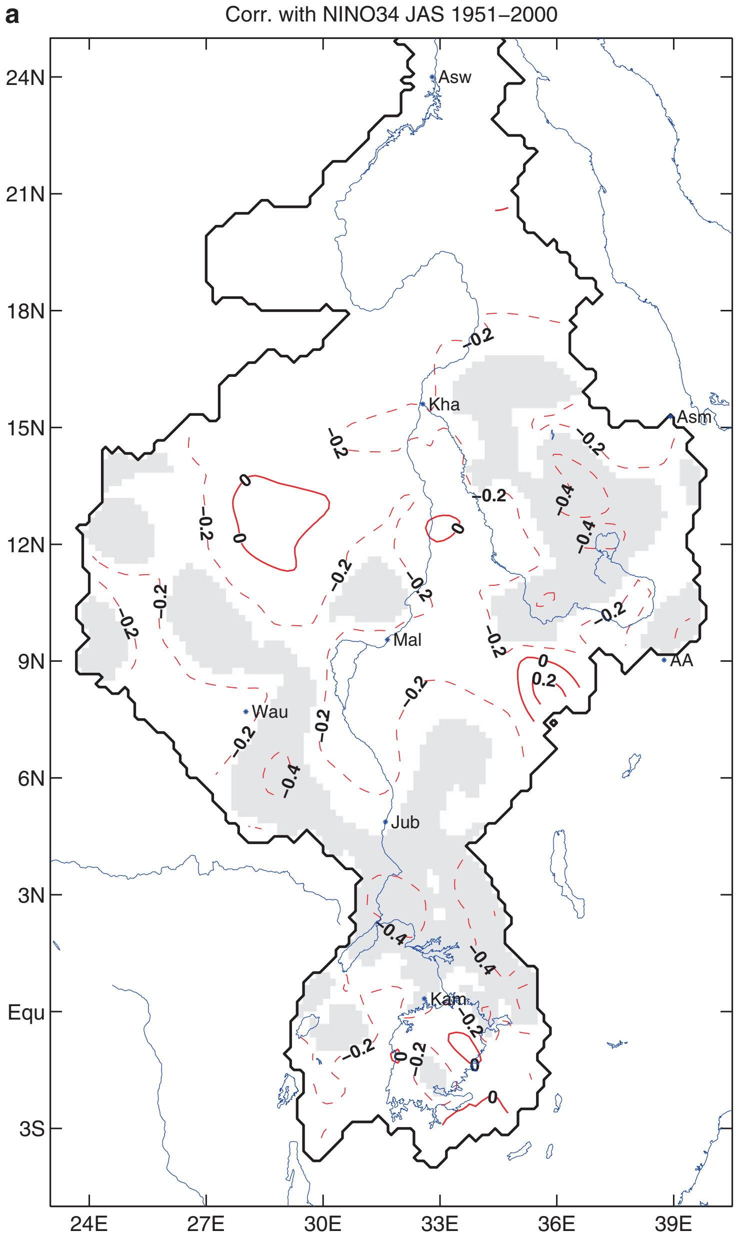


Fig. 9 Correlations between rainfall in the Nile basin and the Nino 3+4 index (*solid line*) and the Indian Ocean Dipole Mode Index (*dashed line*). Period: 1951–2000. The computation uses 3-month averages (e.g., the correlation for July stands for June–August rainfall vs June–August Nino 3+4), for all months with a mean rainfall above 5 mm. Figures indicates the maximum correlation. Stars: significant correlations at the 99% level

the regional rainfall response to ENSO did not emerge until the late 1980s. This response is seasonally dependant (Fig. 9).

The main ENSO signal is found during the northern summer, at which time a negative correlation is found with the Nino 3+4 index, depicting lower than normal rainfall in years of higher sea-surface temperatures (SST) in the eastern equatorial Pacific (i.e., El-Nino years). The summer signal is consistent over most parts of the basin where rains are found during this season (Fig. 10). This includes most of Sudan and Ethiopia, but the largest regional correlations (−0.71 for July–September 1951–2000) are found further south in Uganda and Western Kenya. Significant correlations between ENSO and rainfall have been documented by Osman & Shamseldin (2002) for Sudan (annual rainfall), by Haile (1990), Beltrando & Camberlin (1993), Seleshi & Demarée (1995), Seleshi & Zanke (2004), Segele & Lamb (2005) & Korecha & Barnston (2007) for Ethiopia (main July–September rains as well as rainy season length), and by Ogallo (1988), Camberlin (1995), Indeje et al. (2000) & Philipps and McIntyre (2000) for Uganda and Western Kenya (July–September). All conclude to some summer rainfall reduction in El-Nino years.

However in October–December, the correlation with ENSO switches signs, becoming positive (Fig. 9). At this time of the year, precipitation, mostly restricted



a Corr. with NINO34 JAS 1951–2000

Fig. 10 Correlation maps between interpolated rainfall and climate indices. Period: 1951–2000. *Dashed* (*solid*) *lines*: negative (positive) correlations. *Shading*: correlations significant at the 95% level (**a**) Nino 3+4 and July–September rainfall

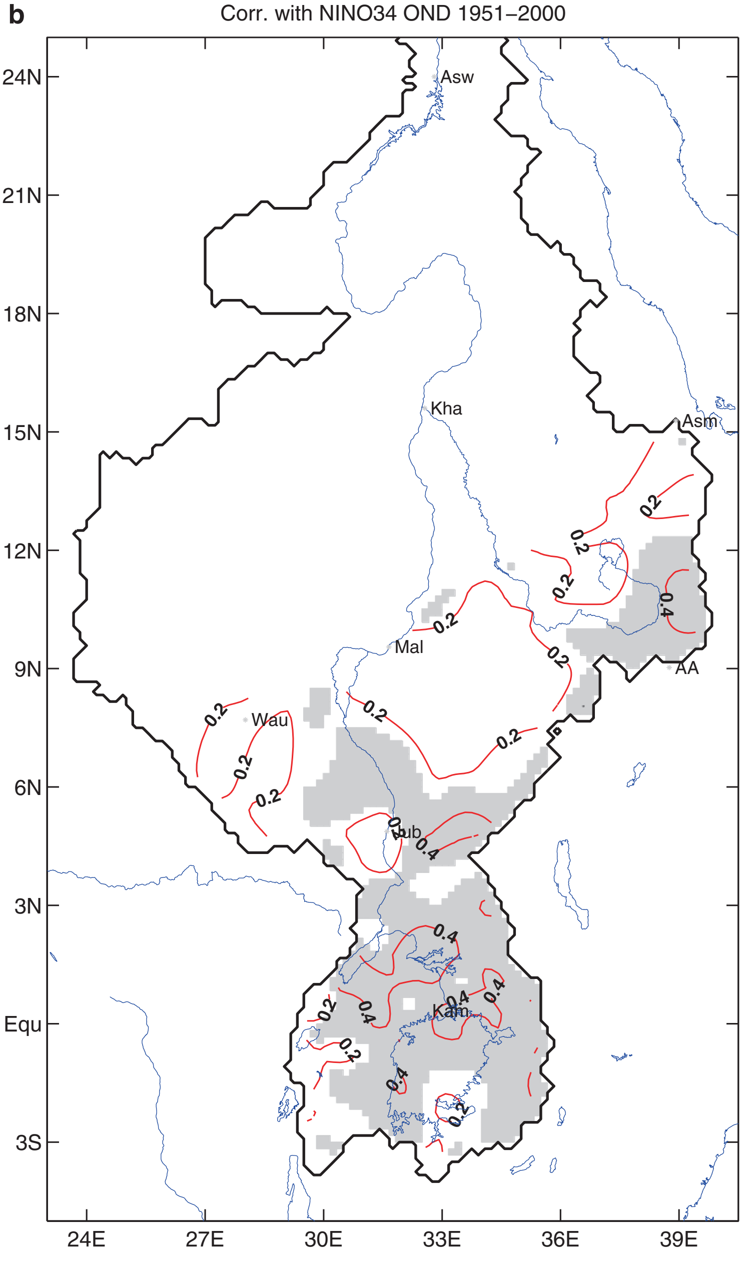


Fig. 10 (continued) (**b**) Nino 3+4 and October–December rainfall

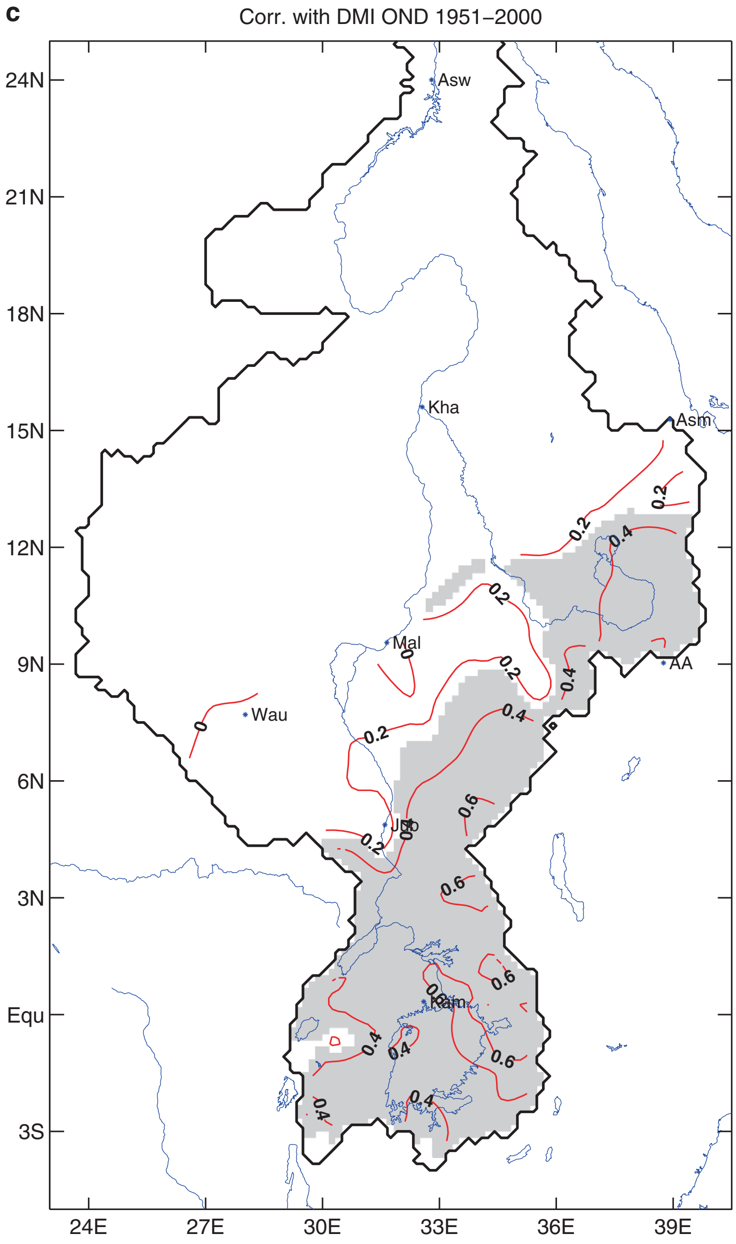


Fig. 10 (continued) (**c**) Indian Ocean Dipole Mode Index and October–December rainfall.

to the equatorial regions, is higher than normal in El-Nino years. This pattern is typical of Eastern Equatorial Africa during the "short rains" of October–December (Ogallo, 1988; Hastenrath et al., 1993; Nicholson & Kim, 1997; Nicholson & Selato, 2000; Mutai & Ward, 2000; Indeje et al., 2000). Following Saji et al. (1999) and Behera et al. (2005), the ENSO signal in the East African "short rains" may only be an indirect manifestation of anomalous Walker-type (east–west) circulation in the Indian Ocean, associated with zonal SST gradients. Though most of the years which record abundant "short rains" in Eastern Africa are El-Nino years, like 1965, 1972, 1977, 1982, 1997 and 2006 in the last four decades, there exist a few cases of high rainfall which can solely be explained by anomalous SST and circulation in the Indian Ocean. This is best shown in the year 1961 (Flohn, 1987; Kapala et al., 1994; Hastenrath & Polzin, 2003), whose exceptionally heavy rains resulted from a strong warming (cooling) in the western (eastern) Indian Ocean, in the absence of El-Nino conditions. Thus the October–December rains exhibit a higher correlation with the zonal SST gradient in the Indian Ocean than with the Nino 3+4 index (Figs 9 and 10), in agreement with Saji andYamagata (2003), though in many cases it is ENSO which originally triggers off the Indian Ocean dipolar events. During other seasons (including summer), zonal SST gradients in the Indian Ocean have virtually no role in rainfall variability over the Nile basin.

Though the summer rains in the Nile basin are partly dependant on ENSO, a stronger connection exists with the Indian monsoon (Camberlin, 1995, 1997). Averaged over Ethiopia, Eritrea, Sudan, Uganda and Western Kenya (i.e., roughly the part of the Nile basin receiving summer rains), July–September rainfall during 1953–1988 is correlated at −0.89 with Bombay pressure, an indicator of the Indian monsoon intensity. Droughts (heavy rains), and not only those occurring at times of El-Nino (La-Nina) events, therefore tend to occur simultaneously in the Nile basin and in India. This is because a deepened monsoon low increases the pressure gradient with the South Atlantic Ocean, resulting into strengthened moist south-westerlies/westerlies in Ethiopia, Sudan and Uganda. An additional factor is the strengthened Tropical Easterly Jet associated with an intense Indian monsoon, known to enhance rainfall in the Sahelian belt (Hulme & Tosdevin, 1989; Fontaine & Janicot, 1992; Grist & Nicholson, 2001).

Both teleconnections with ENSO and the Indian monsoon fail to account for the downward rainfall trend experienced in the central part of the basin in the 1970s and 1980s. This trend is actually similar to that found further west in the Sudano-Sahelian belt of West Africa. Land cover changes, associated in particular with overgrazing, and which were earlier thought as being a possible trigger of the drought (Charney, 1975), are now considered only as an amplifier of ocean-induced rainfall variations. Inter-hemispheric SST variations are actually seen as the key player in the long-term rainfall evolution (e.g., Folland et al., 1986; Ward, 1998; Giannini et al., 2003). In particular, the cooling of the North Atlantic ocean in the late 1960s, combined with the warming of the Southern Hemisphere oceans (including the Indian Ocean) is likely to have resulted into a reduced northward excursion of the ITCZ and/or more rainfall over the tropical oceans than over the African continent. A negative correlation was noted between and Indian Ocean SST and both Sudan rainfall (Osman & Shamseldin, 2002) and Ethiopia rainfall (Seleshi & Demarée, 1995; Gissila et al., 2004; Korecha & Barnston, 2007). This prompted these authors to define seasonal prediction models, including Indian Ocean SST as well as ENSO as predictors. However it should be noted that the negative correlation with Indian Ocean SST is mainly a manifestation of common trends, as evidenced for the Sahel as a whole (Giannini et al., 2003). South Atlantic SST also exhibits a warming trend. A small contribution of this basin to summer rainfall variability is demonstrated for Sudan and Ethiopia. The South Atlantic warming is not only a component of that of the Southern Hemisphere, but it also occasionally has a separate incidence on monsoon depth, like in 1984 where the devastating drought which affected Ethiopia and Sudan can be related to exceptionally high SST in the Gulf of Guinea. The main evaporative regions that contribute to summer rainfall in the eastern Sahel are actually central Africa and the Gulf of Guinea, and not the Indian Ocean (Druyan & Koster, 1989). The higher moisture content which prevails in warm years is largely counterbalanced by the reduced northward excursion/monsoon depth which results from the unfavourable meridional energy gradients.

Other causes of rainfall variability are not well known. This particularly applies to the northern spring (March–May) rainy season in the equatorial part of the basin. Its interannual variability is spatially poorly organised, and the above-mentioned sources of climate variability account for only a small part of rainfall fluctuations (Camberlin & Philippon, 2002). The zonal gradient between the Atlantic and Indian oceans and the associated anomalous westerlies play a part, and so do interactions with the upper tropospheric extratropical circulation. A North Atlantic Oscillation (NAO) signal is found over the southernmost part of the basin during the December–February dry season (McHugh & Rogers, 2001), suggesting unseasonable rainfall in negative NAO years, though the teleconnection mechanisms are not well understood. In Ethiopia, an 11-year cycle was previously identified in rainfall and associated with sunspot numbers and solar activity (Wood, 1977; Seleshi et al., 1994). Evidence of similar oscillations in the equatorial lakes region is still inconclusive.

3.3 Projected Climate Changes

The drying trend which affected much of the Nile basin in the 1970s and 1980s, added to potential climate effects associated with increasing greenhouse gases concentrations in the global atmosphere, have prompted speculations about the future of the Nile basin climate.

In the 1990s, twenty-first century projected climate changes for the Nile basin were focused upon in a series of studies dedicated to the assessment of water resources, based on a direct use of General Circulation Models (GCM) experiments. Strzepek et al. (1996) used three GCM (UKMO, GISS and GFDL) to evaluate future changes in the Nile water resources, under a doubled CO_2 hypothesis. A 15–17% increase in the basin-averaged rainfall was found for the first two models, and a 5% increase for the latter. Expected temperature rises ranged from 3.1°C to 4.7°C. A more detailed assessment, based on interpolated data from six GCMs, provided contrasted projections (Yates & Strzepek, 1998). While for the equatorial lake region almost all the models gave an increase in annual precipitation (0% to 26%), the projections for the Blue Nile catchment were between −9% and +55%. Temperature rises were more consistent among the models, as well as spatially. Inter-model differences in precipitation were also pointed out by Conway and Hulme (1996), who used the GFDL and GISS models as well as a weighted ensemble mean from seven GCM experiments. Whereas all the experiments showed a temperature increase slightly under 1°C by 2025 with respect to 1961–1990, and fairly identical in the Blue Nile and lake Victoria areas as well as in all the four trimesters considered, precipitation projections were more contrasted. Increases dominated over lake Victoria, but large disparities in the Blue Nile region highlighted the difficulty for most models to simulate precipitation. More recently, McHugh (2005), based on the four models out of 19 which best simulate East African rainfall, showed a projected rainfall increase in the equatorial regions, mainly due to a rise in DJF and MAM rainfall.

Other studies considered more diverse greenhouse gases emission scenarios (SRES scenarios), but the outcome is not markedly different from that derived from earlier studies. Hulme et al. (2001), analysing ten experiments from seven coupled models, obtained a median temperature rise of 0.12–0.18°C per decade under scenario B1 (low emission scenario) to 0.3–0.6°C per decade under scenario A2 (high emission scenario) for the Nile basin region. In each case the rise is less in the equatorial region, and higher in northern Sudan. Inter-model differences are moderate for temperatures, but not for precipitation. This is particularly so for the summer rains. While a majority of decreases (exceeding natural variability) are projected for much of eastern Africa, in Ethiopia the trend is negative in some models, and positive in others (Hulme et al., 2001). In the northern winter (DJF), whatever the scenario, there is a more robust tendency for increased rainfall in Ethiopia and Uganda, but this is during the low rainfall season in most parts of the region.

The projections shown in the third assessment report (IPCC, 2001), and confirmed in the 2007 fourth assessment report, give an average temperature increase for the Nile basin region of around 2°C (B1 scenario) to 4°C (A2 scenario) for the years 2090–2099. Confidence in the projections remains lower for precipitation. The only two consistent trends projected using ensemble model experiments correspond to an increase in northern winter (DJF) rainfall in eastern equatorial Africa, and a decrease in the Eastern Mediterranean (in Egypt, from already very low rainfall amounts).

The expected temperature rise is to be compared with the actual changes during the twentieth century. Studying a greater eastern Africa region, from Sudan to Mozambique, King'uyu et al. (2000) found a general minimum (nighttime) temperature warming, especially in the northern part of the region, which corresponds to the Nile basin. The geographical patterns of the trends are very complex. However, for East Africa as a whole, a rise of about 0.4°C is found in the last four decades of the twentieth century (Hulme et al., 2001), though it should be recalled that the 1960s stand out as an unusually wet and cold decade. A significant rise (decrease) in hot (cold) extremes is also found in Uganda (New et al., 2006). For Egypt, decreasing temperature trends were found over the observation period 1941–2000 for annual, maximum, winter and autumn temperatures, and increasing trends for minimum, winter and spring temperatures (Domroes & El-Tantawi, 2005). Increasing trends prevailed in summer (Hasanean & Abdel Basset, 2006). For the recent period 1971–2000 all trends were positive except maximum temperature (Domroes & El-Tantawi, 2005). In Addis-Ababa in Ethiopia, Conway et al. (2004) showed increasing trends in annual minimum and maximum temperatures from 1951 to 2002 (0.4°C per decade and 0.2°C per decade, respectively). On the whole, while a majority of warming trends are found in the region in the last 50 years, the patterns are spatially and temporally variable, though becoming increasingly clear in the last decades. Observed rainfall trends have been discussed above. They are characterised by the pronounced decrease of the 1970s and 1980s in Sudan and parts of the Ethiopian Highlands, with a partial recovery since then, and have been shown to result from hemispheric SST variations.

The fact that the region is subject to large natural climate variability makes the observation of climatic trends of the last few decades a poor indicator of the climate conditions expected for the Nile basin during the twenty-first century. This can only be assessed through numerical modelling. However, the problem with GCM projections is that they are made at coarse resolutions (typically at a scale of 2.5° latitude and longitude) so that, in a region like the Nile basin which has a complex topography and contrasted land surface properties, the associated regional circulation features are very poorly resolved. To date, there have been few attempts to address this problem, though the current development of a regional climate model tuned to North-East Africa (e.g., Mohamed et al., 2005; Anyah et al., 2006) will be an important step towards higher resolution climate projections. Alternatives are the use of statistical downscaling methods, which rely on the definition of empirical models relating present-day rainfall and temperature variations to large-scale atmospheric patterns. The latter are generally better simulated than precipitation by the GCMs, hence by using the projections of dynamical variables under enhanced greenhouse conditions, it might be feasible to estimate rainfall changes and their spatial distribution. However, this requires a prior understanding of the factors which determine current rainfall variations in the Nile basin region.

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The Hydrology of the Nile Basin

John V. Sutcliffe

Abstract The hydrology of the Nile is discussed through a description of the various tributaries, ranging from Lake Victoria and its numerous tributaries, through the lower Lakes Kyoga and Albert which contribute inflows to the White Nile in different periods. A major feature of the Lake Plateau is the great increase in outflows between the periods before and after 1961–1964. The lake-fed inflow to the Bahr el Jebel where it enters the Sudd wetland is supplemented by the highly seasonal flow of the torrents, and half the inflow is lost by inundation of the wetlands and subsequent evaporation. The contributions of the Bahr el Ghazal and Sobat tributaries to the White Nile are discussed. The Blue Nile provides the greater part of the flow of the main Nile, but its contribution is more seasonal than that of the White Nile, being the residual of seasonal rainfall on the Ethiopian highlands. The regimes of the Atbara and the main Nile lead to a discussion of the Aswan High Dam and the variability of the tributary flows over the period of records.

1 Introduction

The main characteristic of the Nile basin is its variability; this is to a large extent a result of its size and its length. The topography varies from a region of lakes and moist and forested uplands, through an area of swamps filled with papyrus and seasonal grasslands to a single channel flowing through arid desert, joined by tributaries from a mountainous region. This topographic variety is matched with a variety of climate; its behaviour in time has been equally variable. Superimposed on seasonal variety, the climate has undergone periods of relatively wet and dry rainfall, which have persisted over a number of years. These changes have been

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magnified by the unusual regime of Lake Victoria into periods when the flow of the White Nile has doubled and persisted for some years. These changes have resulted in changes in vegetation downstream, which have impinged on the economy of large areas. Discussion of the hydrology of the Nile basin must deal with different tributaries in turn before the regime of the whole basin can be understood.

1.1 Geography of the Basin

The Nile, as the longest river in the world, extends over a very wide range of latitude, from 4°S to 32°N, and has a total catchment area of nearly 3 million km^2. However, (Said, 1993) the present river course is a recent development. The longitudinal profile (Fig. 1) includes a number of flat reaches linked by steep connecting channels. Rushdi Said describes how the Lake Plateau drained west towards the Congo before the formation of the African Rift led to the presence of Lake Victoria in the depression between the two arms of the Rift, and the reversal of west-flowing rivers like the Kagera, Kafu and Katonga. Both Lake Victoria and the Sudd basin of the southern Sudan were closed basins until they overflowed to the north through Jinja and the Sabaloka gorge north of Khartoum some 12500 years ago.

The furthest tributary of the Nile (Fig. 2) is the Kagera, which drains the mountains of Rwanda and Burundi, before flowing into Lake Victoria through a series of lakes and swamps alongside the channel. A number of other tributaries drain the forested escarpment to the northeast of the lake; these two sources contribute

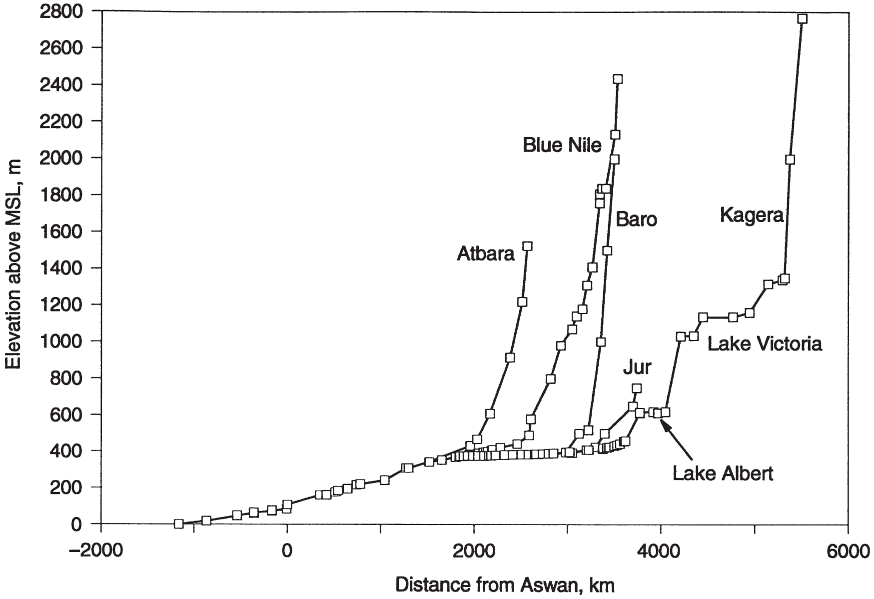

Fig. 1 Profile of the Nile and its tributaries (after Sutcliffe & Parks, 1999)

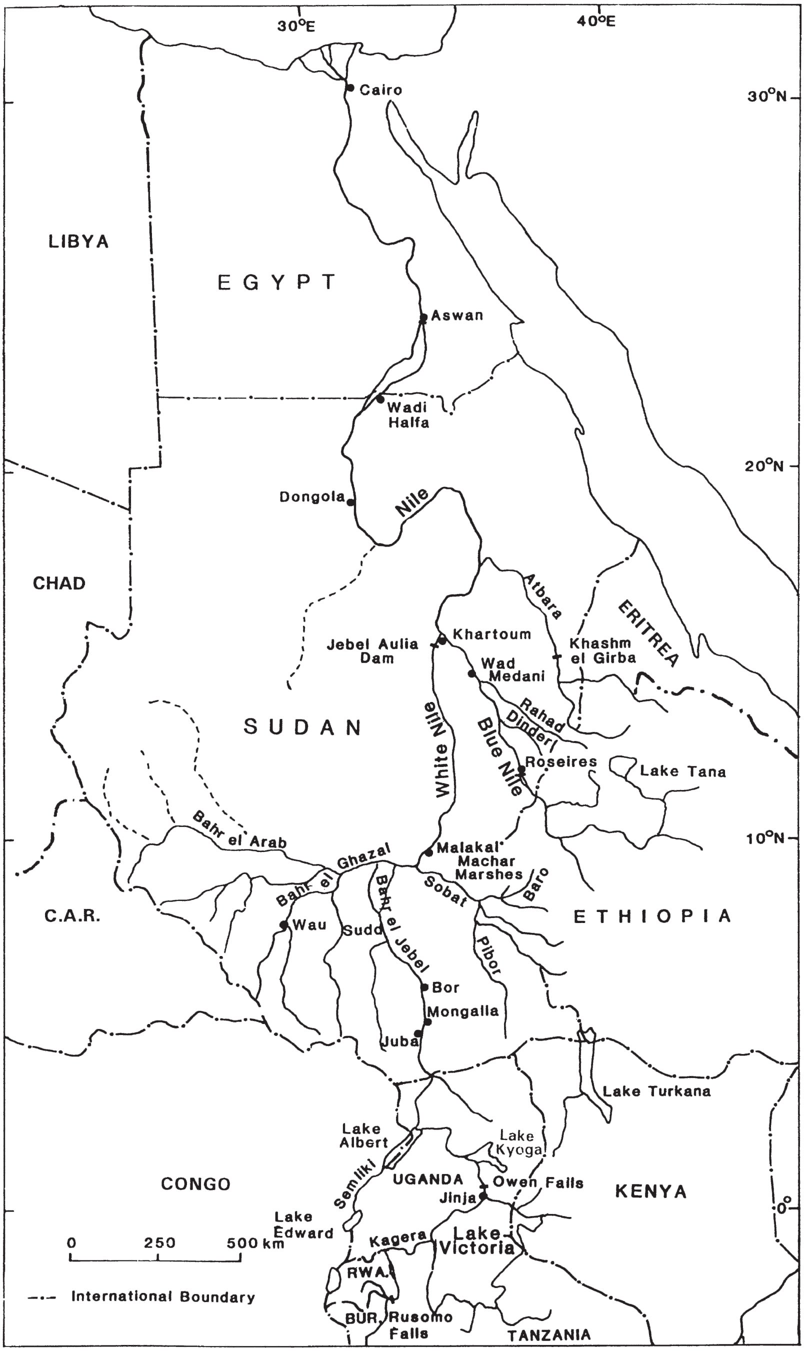

Fig. 2 Key sites of the Nile basin (after Sutcliffe & Parks, 1999)

most of the lake inflow, though other tributaries drain the Serengeti plains and the swamps of Uganda.

The Victoria Nile below the lake is confined to a single channel which leaves the lake at Jinja and reaches Lake Kyoga after about 100km. This lake is relatively shallow and grass-filled; in some periods the lake causes a net loss of water and in other periods inflow to the lake provides a net gain.

The Kyoga Nile flows from the lake towards the western arm of the Rift Valley through a succession of level reaches and swamps, interrupted by rapids and falls, leading to the Murchison Falls and Lake Albert which it enters through a swamp near its northern end. This lake, unlike the lakes upstream, is located within the Rift Valley with steep sides. It also receives the inflow of the river Semliki which drains Lake Edward and the Ruwenzori mountains. The Albert Nile or Bahr el Jebel then flows towards Nimule in a flat reach through swamp vegetation.

At Nimule the river enters the Sudan, turns to the northwest and flows in a steeper channel towards Juba and Mongalla. Here the Bahr el Jebel enters a large swamp known as the Sudd or ‘blockage’. Between Lake Albert and Mongalla the river receives a number of tributaries known as the torrents, which provide seasonal and sediment-laden flows to supplement the less variable outflow from the East African lakes.

Below Mongalla the channel is inadequate to carry the high flows occurring during the flood season, and the alluvial channels are built up above the flood plain. The excess flows leave the river through small channels through the banks, or spill over the banks at higher flows; they then inundate large areas on either side of the main channel. In the southern part of the swamps the flood plain is limited by higher ground on either side, but further north there is no lateral limit to flooding. High river flows from the torrents coincide with rainfall within the swamps. The maximum extent of flooding occurs after the end of the rainfall season, when net evaporation is high, and water is lost by evaporation. The outflow from the swamp is only about half the inflow, and the seasonal variation of the inflow has been damped out. The large volumes evaporated within the swamps led to various proposals made from 1904 onwards to reduce these losses by various means, including a canal, so that hydrological attention has been focussed on this region. However, the complexity of the channel system and the problems of estimating evaporation from swamp vegetation have made the water balance of the region difficult to solve.

Below the Sudd the White Nile turns to the east at Lake No, where the Bahr el Ghazal enters from the west. Although this tributary drains a wide area with relatively high rainfall, the various tributaries spill into a succession of swamps, and the contribution to the main river is negligible.

The final tributary of the White Nile is the Sobat, whose tributaries the Baro and Akobo drain the southwestern Ethiopian highlands; the Pibor also receives occasional runoff from a wide area of the southeastern Sudan. These rivers spill into the Machar marshes and other wetlands, whose location along the Ethiopia–Sudan border has made detailed investigation difficult.

The course of the White Nile below the Sobat to its confluence with the Blue Nile near Khartoum is confined to a single channel with no inflow except in exceptional years. The steady outflow from the Sudd is supplemented by the seasonal contribution of the Sobat.

Two-thirds of the annual discharge of the main Nile at Khartoum is contributed by the Blue Nile and its tributaries the Dinder and Rahad. The Blue Nile drains a large area of the western Ethiopian highlands, where rainfall is concentrated in a single season and the river flows are highly seasonal. The upper river flows through Lake Tana, but only a small fraction of the inflow occurs above this site. As the rainfall depends on the seasonal migration of the ITCZ (InterTropical Convergence Zone), the length of the rainfall and runoff season decreases from south to north from the Sobat basin to the Blue Nile and the Dinder and Rahad.

The main Nile flows north from Khartoum through the Sabaloka gorge and is joined some 300 km north by the Atbara which drains the northern Ethiopian highlands and part of Eritrea; the runoff season is even shorter than the Dinder and Rahad, and the river is dry for much of the year. Below the Atbara mouth the river flows in a series of loops through an arid region of successive cataracts, where the river flows are reduced by evaporation before entering Egypt within the reservoir of the Aswan High Dam.

1.2 *Climate*

The climate of the Nile basin is extremely variable. Table 1 illustrates the average rainfall totals and seasonal distributions of various tributary basins of the system. It shows how the regime varies from the bimodal rainfall of the East African Lake Plateau, to a single rainfall season over the Sudd region. The rainfall season

Table 1 Average monthly rainfall over parts of the Nile basin (mm) (after Sutcliffe & Parks, 1999)

Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Year
Lake Victoria basin (excluding the lake)												
75	90	134	194	145	61	47	68	72	89	111	100	1,186
Lake Kyoga basin												
38	64	108	176	159	99	89	127	121	120	109	66	1,276
Lake Albert basin												
27	55	95	149	137	81	87	128	134	142	121	58	1,214
Lake Albert to Mongalla												
9	25	62	122	154	131	150	162	139	135	68	23	1,180
Mongalla to Lake No												
2	6	25	70	119	121	147	141	125	90	19	6	871
Bahr el Ghazal basin												
4	12	39	90	143	162	186	205	174	118	31	5	1,169
River Baro basin												
18	25	61	118	198	207	220	244	202	125	63	22	1,503
Pibor, Akobo, Veveno basin												
4	12	33	89	122	118	155	165	123	88	35	10	954
Ethiopia												
14	28	57	91	125	137	237	243	167	73	34	21	1,227
Lower Blue Nile basin												
0	0	0	2	8	24	84	109	44	8	0	0	279
Main Nile												
0	0	0	0	2	1	12	18	3	0	0	0	36

From *The Nile Basin*, vol. VI, supplement 7.

continues to shorten to the north, to the relatively dry regime of the lower Blue Nile and the arid main Nile reach.

Compared to the size of the basin, the total flow of the Nile is comparatively low; the average annual runoff from the whole basin is only about 30 mm. This runoff is very variable across the basin; the areas which make significant contributions are quite small. They are largely confined to the East African lake region, where rainfall is high and spread between two rainfall seasons, and to the Ethiopian highlands where high rainfall within a short season and steep slopes result in relatively high and concentrated runoff. The climate and runoff regimes are discussed further under individual tributaries.

1.3 The Hydrometric Network

Although Nilometers had been used to measure flood levels on the Nile for thousands of years, the first modern staff gauges were installed at Aswan and Khartoum in the 1860s. Scientific river flow measurement began about 1900, when staff of the Survey of Egypt measured discharges of the Blue and White Niles using Price current meters. The Sudan branch of the Egyptian Irrigation Service was formed in 1905 to erect gauges on the different tributaries of the Nile. By 1912 gauges had been installed at most of the important sites within the Sudan. In 1915 Dr H. E. Hurst became head of the Physical Department, who established a comprehensive network of gauges throughout the basin, including the East African lake system, and published in '*The Nile Basin*' descriptions of all the different basins and summaries of all gauge levels, discharge measurements and 10-day flows (Hurst et al., 1933). By 1953 the number of river discharge stations had reached a maximum of over 150 stations, but gradually the number of records published has decreased as the responsibility for maintaining stations was taken over by upstream hydrological services or as conditions in the southern Sudan made access difficult. Nevertheless the sixty or so volumes and supplements of '*The Nile Basin*' present an unparalleled record of the behaviour of the river system over most of the 20th century. Since 1967 a number of international organisations have carried out investigations in the East African basin, and a series of conferences held in different basin countries have led to informal exchange of technical findings. These activities, along with support from multi-lateral agencies such as the World Bank, have helped contribute to the establishment of the Nile Basin Initiative in 1999.

2 East African Lake Plateau

2.1 Lake Victoria Basin

It has been pointed out (Flohn & Burkhardt, 1985) that the true source of the Nile is not the outfall of Lake Victoria at the Ripon Falls, nor the headwaters of the Kagera in the highlands of Rwanda and Burundi, but the nocturnal cloud above the lake which provides most of the inflow to the lake. Therefore improved estimates of the lake rainfall in addition to tributary inflows have provided an essential element to the understanding of the lake water balance.

The contributions of the various tributaries are discussed before dealing with rainfall and evaporation over the lake. The Kagera is the major tributary contributing to Lake Victoria, and its basin contains a large number of small lakes and swamps. With a basin area of 60,000 km^2, it drains, with its tributaries the Ruvuvu and Nyabarongo, much of Rwanda and Burundi as well as parts of Tanzania and Uganda. The basin rises above 2,500 m in the west, with peaks up to 4,500 m; the annual rainfall is less than 1,000 mm in the east but rises to 1,800 mm in the west. There are two rainfall seasons, in February–May and September–November, but the runoff, which reaches a peak in April in the upper reaches, is delayed by lakes and swamps formed by drainage reversal to May at Rusumo Falls, and by further lakes and swamps to July at Kyaka Ferry above the mouth of the river; at this point the mean runoff is only 136 mm compared with rainfall of 1,170 mm. The feature of the flow series, which has been measured since 1940, was a marked rise to higher flows after 1961; this increase is reflected in the lake levels and outflows.

Although the Kagera provides the largest tributary inflow to Lake Victoria, a large number of other rivers flow into the lake and together contribute twice the flow of the Kagera. The flows of these other tributaries are available from various dates; four of the major tributaries in the northeast of the lake have been measured since 1956, and nearly complete tributary flows for the period from 1969 to 1978 were obtained by the WMO Hydrometeorological Survey. This Survey was established to investigate the cause of the rise in the lake after 1961. The total flows of the four tributaries were compared with the total tributary runoff (excluding the Kagera) by the Institute of Hydrology in 1985 and monthly multipliers were calculated to complete the inflow series for the whole period 1956–1978.

The annual totals, including the Kagera, are shown in Table 2, where the totals are also expressed as mm over the lake surface of 67,000 km^2. Although the average tributary inflow of 343 mm is only about 15% of the total lake supply, which is dominated by the rainfall component, the runoff is much more variable than the rainfall itself, because runoff coefficients increase with rainfall amount. The variability of the tributary inflow is about three times that of the rainfall, and this component is important to the water balance of the lake.

The rainfall over the lake surface provides the largest component, on average about 85%, of the input to the lake water balance. However, it is not easy to estimate this rainfall as the only regular measurements have been taken around the lake peri-meter. Only eight stations have been measured regularly since 1925 or earlier, and these have been used in various studies of the lake water balance. The problem is complicated by evidence from the timing of rainfall on different shores, and by some rainfall measurements on islands, which together suggest that rainfall on the lake surface is higher than at lakeside stations. A model (Datta, 1981) has explained this by convergence and lifting of westerly land breezes and prevailing easterlies, which give rise to convection storms in the morning on the western shore and in the evening on the eastern shore. This has been estimated to double the rainfall which would have occurred if the lake were not present

Table 2 Annual water balance of Lake Victoria, 1956–1978 (after Sutcliffe & Parks, 1999)

Year	Lake rainfall (mm)	Kagera inflow ($m^3 \times 10^6$)	Total inflow: ($m^3 \times 10^6$)	(mm)	Outflow: ($m^3 \times 10^6$)	(mm)	Lake level (m)
1956	1,787	4,918	19,326	288	19,636	293	10.91
1957	1,727	6,299	18,121	270	20,112	300	11.02
1958	1,622	5,412	14,629	218	19,671	294	10.94
1959	1,702	4,730	13,310	199	18,434	275	10.84
1960	1,827	6,160	17,526	262	20,348	304	10.87
1961	2,370	4,895	21,856	326	20,577	307	11.94
1962	1,919	9,114	36,136	539	38,716	578	12.39
1963	2,121	10,941	34,664	517	44,788	668	12.91
1964	2,011	11,045	32,332	483	50,476	753	12.88
1965	1,663	7,760	17,428	260	46,878	700	12.48
1966	1,889	7,951	21,435	320	42,950	641	12.32
1967	1,752	6,421	21,448	320	37,832	565	12.31
1968	2,114	10,375	32,600	487	43,305	646	12.58
1969	1,770	8,923	21,083	315	46,006	687	12.36
1970	1,865	8,477	27,572	412	44,282	661	12.45
1971	1,639	7,030	20,139	301	39,510	590	12.17
1972	1,975	7,587	19,950	298	37,540	560	12.35
1973	1,749	7,717	19,982	298	38,467	574	12.05
1974	1,657	7,331	20,946	313	35,046	523	11.97
1975	1,826	6,082	18,968	283	33,326	497	12.04
1976	1,781	5,932	14,409	215	34,835	520	11.82
1977	1,938	6,980	29,147	435	35,999	537	12.13
1978	2,041	8,525	35,575	531	39,383	588	12.56
Mean	1,858	7,418	22,982	343	35,136	524	
SD	180	1,799	6,908	103	9,976	149	
CV (%)	9.7	24.2	30.1	30.1	28.4	28.4	

Sources: Lake rainfall and outflow from Institute of Hydrology (1993); Kagera inflow from *The Nile Basin* and WMO (1982); total inflow from Institute of Hydrology (1985).

(Flohn & Burkhardt, 1985). In an early study by the Institute of Hydrology (Piper et al., 1986) this enhanced rainfall was estimated by enhancing the deviations from the mean, but in a later study (Sene & Plinston, 1994) the lake was treated as a giant raingauge and a linear relation derived between lakeside rainfall and net lake rainfall deduced from the water balance for 1969–1978. Lake rainfall series were then deduced using constant evaporation estimates. This lake rainfall series for 1956–1978 (Table 2) shows a trend to higher rainfall, which is largely explained by an increase in rainfall in October and November after 1961/62. Extreme October–November rainfall seasons are associated with El Nino Southern Oscillation and Indian Ocean Dipole events and have caused widespread socio-economic disruption (e.g. 1961 and 1997, Conway, 2002).

The water balance is completed with outflow totals which were measured at the Ripon Falls before 1954, and after construction of the Owen Falls hydroelectric dam were controlled by agreement to maintain the natural relation between lake level and outflow. The flows could be estimated from this 'Agreed Curve' or derived from the turbine/sluice releases. Lake evaporation estimates were based on Penman estimates for stations around the lake, and the lake levels and volumes measured at Jinja.

The water balance can be illustrated by the annual balance (Fig. 3) for the period 1956–1978, which is the period when measurements of the water balance constituents

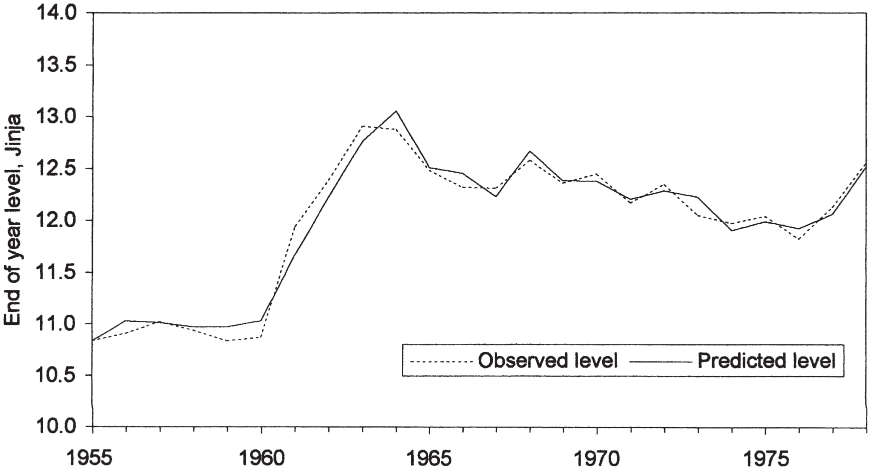

Fig. 3 Lake Victoria annual water balance, 1956–1978 (after Sutcliffe & Parks, 1999)

have been most complete. This covers the period of the lake level rise in 1961–1964, and shows that it is possible to explain the behaviour of the lake during this period. Reasonable results were also obtained by Sene & Plinston (1994) for the periods 1925–1990 and 1900–1990.

Because river flows have been measured at Aswan since 1870, and because low flows at this site are largely composed of outflows from the East African lakes conveyed by the White Nile, it has been possible to estimate lake levels by correlation with downstream flows for the period from 1870 until lake levels were measured in 1896. These modelled levels were found to correspond reasonably with levels deduced from early travellers' observations (Tate et al., 2001) and show that the rise in lake level which occurred in 1961–1964 was not unique, but that earlier rises had been followed by returns to lower levels more rapidly than after 1964 (Fig. 4).

There is also evidence from an archaeological investigation near Entebbe that the high lake level of 1964 has been near the limit of levels over a long period. Bishop (1969) has noted that "the recently recorded rise in the level of Lake Victoria between 1961 and 1964 is of interest as, at their maximum, the lake waters were within two feet of the dated beach gravel in Hippo Bay cave." He deduced that Lake Victoria had not risen to occupy the 10- to 12-foot cliff notch in the past 3,720± years; this corresponds with a Jinja gauge level of 13.85–14.45 m.

Although the Jinja levels from 1896 to 2000 reflect the water balance of Lake Victoria while the outflows corresponded to the Agreed Curve, the outflows have increased above the Agreed Curve in recent years. The natural level series can be estimated by adjusting the measured lake levels for over-abstraction on a continuous basis to those which would have occurred if the Agreed Curve had been followed. The measured levels after 2000 have been adjusted on a monthly basis to obtain the natural series illustrated in Fig. 5 (Sutcliffe & Petersen, 2007).

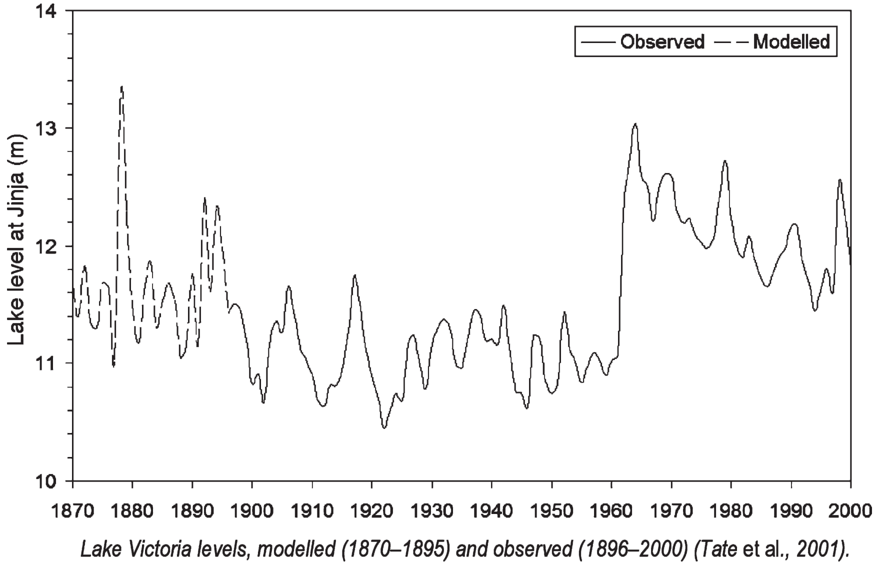

Fig. 4 Lake Victoria levels, modelled (1870–1895) and observed (1896–2000) (after Tate et al., 2001)

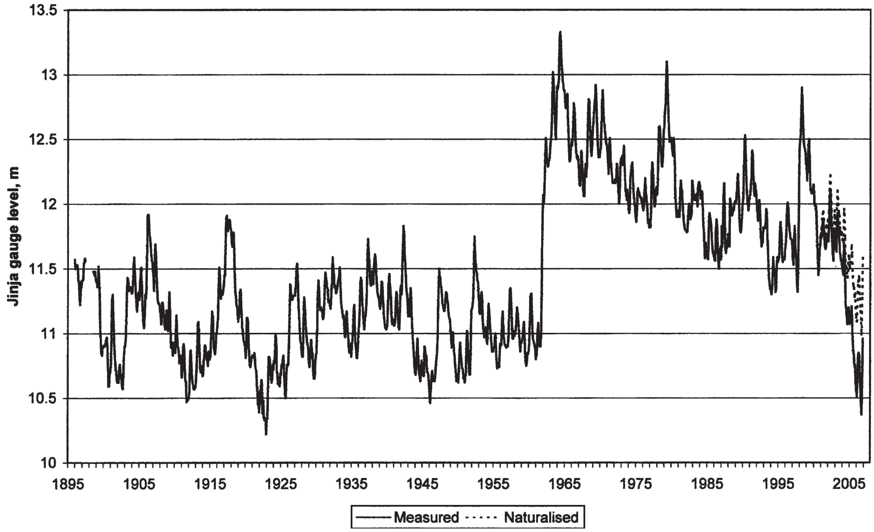

Fig. 5 Lake Victoria levels, 1896–2006 after Sutcliffe & Petersen, 2007

2.2 Lake Kyoga

The Victoria Nile flows north from the Owen Falls complex towards Lake Kyoga in a channel with a series of rapids and falls. Lake Kyoga is unique among East African lakes as it is essentially a dendritic river valley which formed the headwaters of the River Kafu flowing to the west. The formation of the Rift Valley reversed the direction of flow of the Kafu, and resulted in the Victoria Nile entering Lake Kyoga from the side and leaving to the north through Masindi Port. The lake is relatively shallow and its surface is fringed with papyrus and floating vegetation; the lake has recently been invaded with water hyacinth. The inflows to the lake correspond to the outflows from Lake Victoria, while the lake outflows have been measured at various sites; however, the most reliable estimates have been derived for the period 1940–1979 from water levels at Kamdini and discharge measurements at Kamdini, Fajao and Paraa downstream (Sutcliffe, 1996; Sutcliffe & Parks, 1999). These records show that during the period 1951–1960, before the rise in Lake Victoria levels and outflows, the outflows from Lake Kyoga are slightly lower than the inflows, whereas in 1966–1975, after the rise the outflows were 5% higher than the inflows. This is doubtless due to increased local inflow in a period of higher rainfall, but few measurements of this local inflow exist.

2.3 Lake Albert

The Kyoga Nile, in its course from Lake Kyoga to Lake Albert, first flows down the course of the River Kafu, but when it meets the reversed course of this river, turns north past Masindi Port. There are a number of rapids and falls, culminating in the Murchison Falls where the channel reaches the Rift Valley before entering Lake Albert. The topography of Lake Albert contrasts with the other lakes, as the lake lies along the course of the Rift Valley and the sides of the Rift form steep slopes rising from the lake.

Although the rainfall on the lake surface is relatively low and less than lake evaporation, Lake Albert receives the inflows of the River Semliki, which contributes some $4.5\,\mathrm{m}^3 \times 10^9$ from the basins of Lakes Edward and George and the Ruwenzori mountains. The water balance of this lake is not easy to calculate, as precise estimates of rainfall and evaporation are not available. However, it is clear that, after the rise in Lake Victoria rainfall, lake levels and outflow in 1961–1964, the inflow from the Semliki and local runoff also increased, and Lake Albert has contributed significantly to the flow of the Bahr el Jebel or White Nile after 1964. A summary of the water balances of Lake Kyoga and Lake Albert is given in Fig. 6.

The Albert Nile flows in a very flat channel confined within swamp vegetation as far as Nimule, where it turns to the northwest and flows into the Sudan; here it is known as the Bahr el Jebel.

3 White Nile Basin

3.1 Bahr el Jebel and the Sudd

The river course as far as Juba is steep and passes through several rapids. It also receives between Lake Albert and Mongalla a number of seasonal streams known as the torrents, which have steep basins and contribute spates and heavy sediment

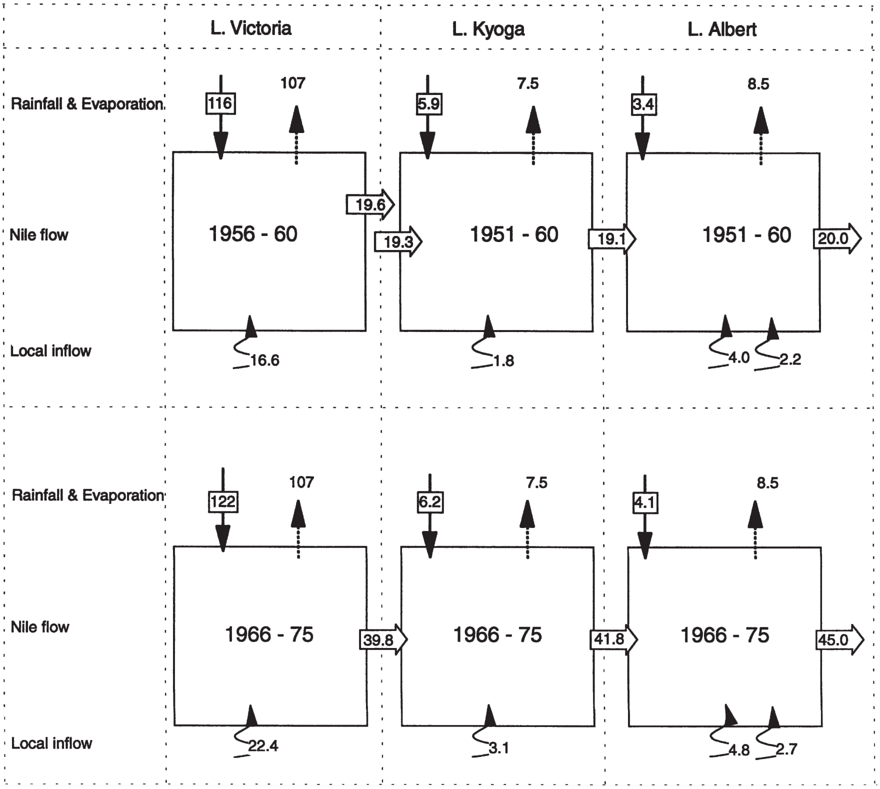

Fig. 6 Schematic balance of Lakes Victoria, Kyoga and Albert, km^3 per year (after Sutcliffe & Parks, 1999)

as a result of local rainfall between April and October. At Mongalla, where the river enters the swamps and seasonal grasslands of the Sudd, the flow is made up of the outflow from the East African lakes, which is seasonally fairly constant but has in the past been liable to severe fluctuations on a longer time scale, together with the torrents providing the seasonal high flows.

The inflows to the Sudd have been measured at Mongalla from 1905 to 1983, while the outflows have been measured as the difference between flows at Malakal on the White Nile and the inflows from the Sobat tributary just upstream from Malakal. The inflows from the Bahr el Ghazal are negligible by comparison. The outflows from the Sudd are on average only about half the inflows, so that half the inflow is lost by spill and evaporation. For this reason the hydrology of the Sudd has been a major focus of the investigations of the Egyptian Irrigation Service, since a canal to bypass the Sudd was first suggested in 1904.

Some description of the topography is necessary to understand the hydrology of the Sudd. Between Juba and Mongalla the river is incised within an even plain sloping gently north or east of north, turning west of north below Gemmeiza; this plain is flanked by scarps of a few metres marking the limit of woodland on either side; these scarps decrease in height from south to north, fading out north of Bor on the east bank and south of Shambe on the west. From Juba to Bor the river meanders in one or more channels from one side of the restraining trough to the other, dividing the flood plain into a series of isolated basins or islands. These basins are below the levels of the alluvial river banks, which are pierced by many spill channels; at the downstream limit of each basin, a large channel carries spill back into the river. Further north, there is no lateral limit to the flood plain, and spillage to the east leads to large areas of seasonally flooded grassland and permanent swamp. It is important to note that the doubling after 1964 of the base flow from the East African lakes has led to a large increase in the area of permanent swamps.

The complex flooding process is best illustrated by the study of sample basins. In 1951–1952, when river flows were very low, a number of sample reaches between Juba and Bor were surveyed (Sutcliffe, 1957, 1974). The way in which spill leaves the river can be deduced from cross-sections of the flood-plain and sections of the river bank. At moderate flows and levels, spill passes through the alluvial banks of the river through a succession of spill channels. A survey along the east bank of the river from Mongalla to Gemmeiza revealed 170 spill channels over 57 km. When river levels are high widespread spilling occurs over the banks of the main river, starting in the north of the basin where banks are relatively low and spreading upstream. When the flood-plain is inundated, the stored water flows north parallel to the river either through channels or through the swamps. A cross-section of the floodplain east of Tombe (Fig. 7) illustrates the process at this stage.

Where the river touches the high ground, a channel invariably carries upstream spill back into the river. Thus the basins of the floodplain, especially above Bor, act as a series of reservoirs which receive flood water and return water to the river downstream. The volume of water in temporary storage increases as the river rises and decreases as it falls. For example, the return channel at Gemmeiza was stagnant in March 1952 when the Mongalla basin was relatively dry, but was flowing strongly in February 1982 when the higher lake outflows caused large scale spilling into the basin. Between Juba and Bor the flooding is confined by higher ground but below Bor and Shambe these limits disappear and flooding extends further during high flows.

However, a detailed study of the basin between Mongalla and Gemmeiza enabled the volumes and levels of flooding to be deduced from inflow records at Mongalla and outflow records at Gemmeiza and Gigging on the west bank. The volumes of flooding were related directly to Mongalla inflows and thus to frequency and duration of flooding. Comparison of flooding levels and vegetation species recorded on the flood-plain cross-sections revealed how hydrological factors control the wetland vegetation. This procedure was extended to develop a simple hydrological model to describe the behaviour of the whole Sudd over the period of flow records.

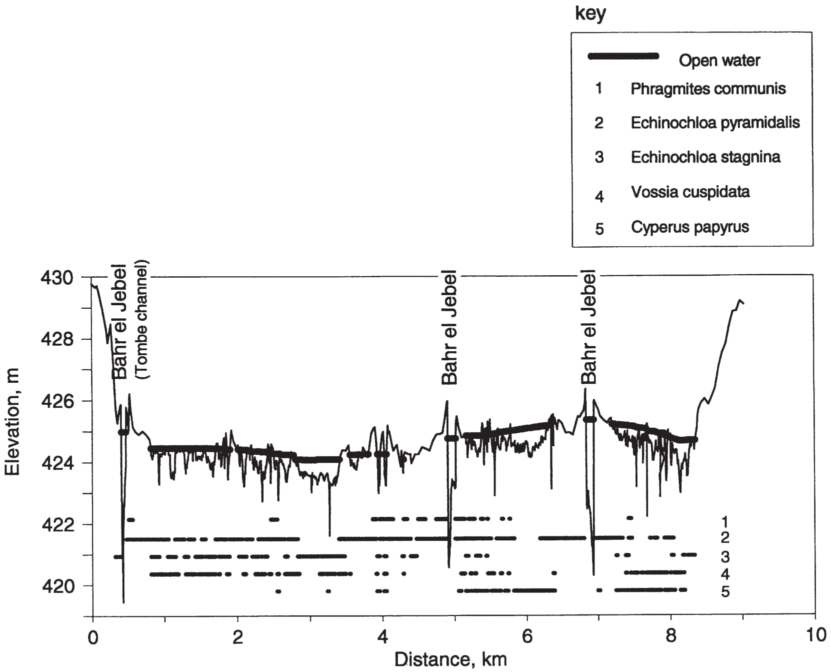

Fig. 7 Bahr el Jebel valley cross-section east from Tombe (after Sutcliffe & Parks, 1999)

3.2 Hydrological Model of the Sudd

After construction of the Jonglei Canal had begun, interest in the local effects of the canal was renewed and as a part of an environmental study a hydrological analysis of the Sudd was carried out by the Institute of Hydrology (Sutcliffe & Parks, 1987; Howell et al., 1988). The whole area of the Sudd was modelled, as flow records within the Sudd were not available after the rise in Lake Victoria and Bahr el Jebel flows after 1964. The inflows at Mongalla and outflows from the swamps were available from 1905 to 1980. Monthly rainfall records at eight stations around the Sudd were used to derive a swamp rainfall series for the same period. A reasonable estimate of swamp evaporation is vital for realistic modelling of the Sudd. Early measurements of evaporation from tanks filled with water and papyrus gave results which were too low to explain the water balance, but improved experiments by Migahid using tanks with healthy vegetation gave results which Penman (1963) suggested as showing that swamp transpiration and open water evaporation were nearly equal. Open water evaporation, estimated by the Penman method from temperature, humidity, sunshine and wind speed at Bor, corresponds to 2,150 mm/year and average values were used in the model. The model is based on the equation of continuity and treats the swamp as a reservoir receiving inflow from the river and rainfall on the flooded area. The losses include outflow, evaporation from the flooded area, and infiltration into newly flooded ground, estimated as 200 mm at the start of the wet season. A relation between volume V and area A of flooding is required, and field evidence suggested that a simple linear relation was reasonable. Thus A = kV was used which implies a constant mean depth of 1/k as the area increases; 1/k was estimated as 1 m.

The equation of continuity for a time interval dt is:

$$dV = [Q - q + A(R - E)]dy - rdA \qquad (1)$$

where V is volume of flooding, Q is inflow, q is outflow, R is rainfall, E is evaporation, A is flooded area and r is soil moisture storage, which is positive but set to zero when dA is negative. The analysis for month t, allowing for rainfall and evaporation over the mean of the initial and final values of area A, and substituting kV for A, becomes:

$$V_{i+1} = V_i + Q_i - q_i - k/2(V_i + V_{i+1})(E_i - R_i) - kr_i(V_{i+1} - V_i) \qquad (2)$$

and hence

$$V_{i+1} = V_i\,[1 + k\{r_i - (E_i - R_i)/2\}] + Q_i - q_i/[1 + k\{r_i + (E_i - R_i)/2\}]. \qquad (3)$$

Storage volumes and flooded areas were estimated at monthly intervals starting from initial estimates of 8,000 $m^3 \times 10^6$ and 8,000 km^2. These model estimates (Fig. 8) corresponded reasonably well with estimates of flooded areas derived over the years from survey maps, vegetation maps and satellite imagery. The series of

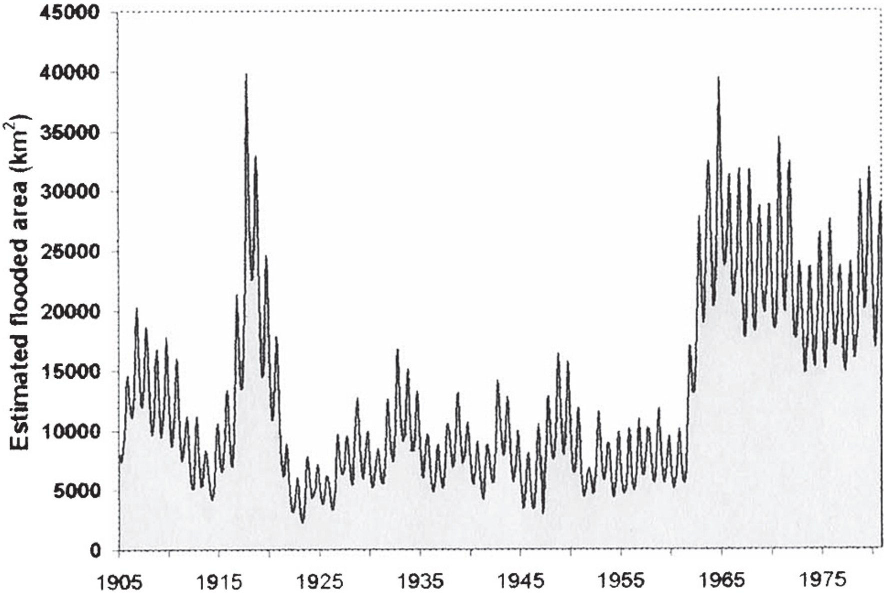

Fig. 8 Bahr el Jebel swamps: monthly estimates of flooded areas, 1905–1980 (after Sutcliffe & Parks, 1987)

monthly flooded areas show the influence of the seasonal torrents in providing areas of annual flooding and recession, which provide the important areas of dry season grazing, while the lake-fed flows of the Bahr el Jebel below Lake Albert are responsible for the more permanent swamp. The important effect of the rise in Lake Victoria after 1961–1964, when the areas of permanent swamp more than doubled, is also shown.

By substituting measured outflows from the Sudd by outflows derived from inflows over the period of records, the model could be run without measured outflows. Then the inflows were reduced by abstractions into the Jonglei Canal and the model was rerun and the flooded areas derived. This suggested that, with the Jonglei Canal operating with a constant discharge of $20\,\mathrm{m}^3 \times 10^6\ \mathrm{day}^{-1}$, the seasonally flooded areas would be reduced by some 26% in the lower flow period of 1905–1961, and by 17% in 1961–1980; the permanent swamp would be decreased by 46% and 21% respectively. The hydrological modelling also suggested that the adverse impact could be reduced by varying the canal flows seasonally; altering the canal flow to $25\,\mathrm{m}^3 \times 10^6\ \mathrm{day}^{-1}$ from November to April and $15\,\mathrm{m}^3 \times 10^6\ \mathrm{day}^{-1}$ from May to October would lead to a decrease in seasonal flooding of only 12% in the early period and 10% in the later period.

3.3 Vegetation Distribution

A similar water balance of the Mongalla basin, on the right bank between Mongalla and Gemmeiza (Sutcliffe, 1957, 1974), showed that the volume of water in transit through the basin could be related to the inflow, and therefore the volume of seasonal flooding could be deduced from the records at Mongalla. A survey of this basin carried out in 1951–1952 included 12 cross-sections of the basin, as well as a longitudinal survey of the alluvial bank of the river, transects of the vegetation and soils along the cross-sections, and studies of the use of the valley for grazing. From the recorded vegetation along each cross-section (Fig. 9), the distribution of species could be deduced along each cross-section and down the flood-plain. This revealed a distinct elevation boundary between the deep-flooded species (*Echinochloa stagnina, Vossia* and *Cyperus papyrus*) and the shallow-flooded species (*Echinochloa pyramidalis*, *Oryza* and *Phragmites*). The vegetation boundary was traced along the river profile and shown to be parallel to the high river level; it was deduced that the boundary was controlled by the maximum depth of flooding, and it was estimated from the statistics of flooding volume that this maximum depth was 1.3 m. Because papyrus was limited to the lower end of each basin, and the range of flooding increases from the lower to the upper end of each basin, it was deduced that the presence of papyrus, anchored by fragile rhizomes, is controlled by the range of flooding; the limiting vertical range was 1.5 m. These conclusions on how the hydrological conditions control the vegetation (Sutcliffe, 1957, 1974; Sutcliffe & Parks, 1996) were supported by the areal distribution of species, by similar analysis of the Aliab valley opposite Bor and by observation elsewhere in the Sudd.

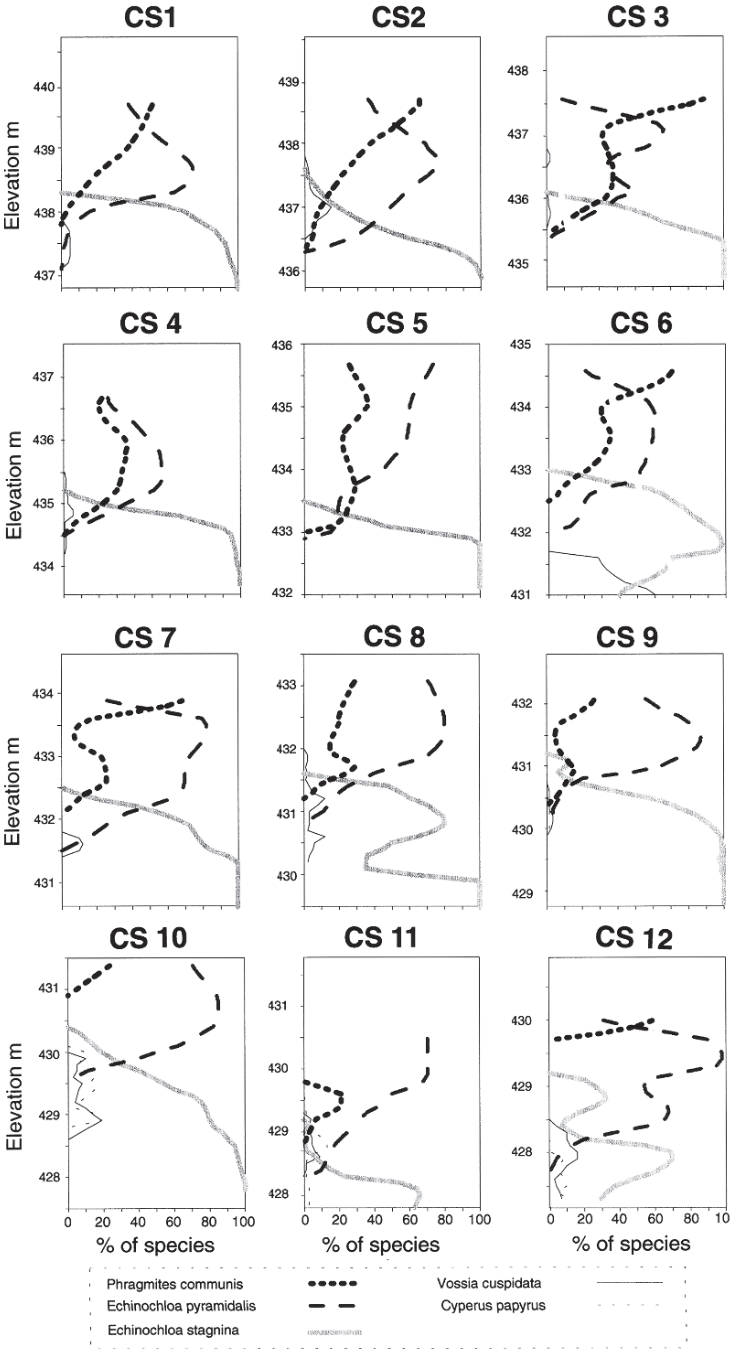

Fig. 9 Mongalla basin: vegetation and elevation on cross-sections (after Sutcliffe & Parks, 1999)

The observed changes in the Aliab valley after the rise in Lake Victoria and the doubled outflows and the resulting vegetation change support the deductions about the links between flooding and vegetation. During the 1982 hydrological study, the opportunity was taken to observe the Aliab valley from the air at low level along the survey cross-sections, armed with vegetation and topographic maps of the 1951 survey. *Vossia* and papyrus had spread over areas previously dominated by grazing grasses. The spread of key species between 1951 and 1982 is illustrated by Fig. 10. Because the seasonal torrent flow volumes had not increased after 1961, but the area of flooding had doubled, the range of flooding would have decreased to favour papyrus. In the drier Mongalla basin, by contrast, the increased flooding had resulted in the increase of grazing grasses, and cattle were observed grazing areas which had previously been dominated by *Phragmites*.

The distribution of these vegetation species on the floodplain was important because the pastoral economy relied on the dry season grazing from *Echinochloa* species and *Oryza*, while the papyrus swamp and *Phragmites* provide no grazing. The local economy was based on annual migration to the flood-plain during the dry season, and on rain-fed vegetation during the rest of the year. The maintenance of the seasonal inflow regime, with steady outflow from the East African lakes with a modest seasonal variation, and the seasonal contribution of the torrents leading to the annual inundation and uncovering of the flood-plain, were essential to the pastoral economy; alternative agriculture on the higher ground was difficult because of the frequency of either drought or excessive flooding.

The contribution of the White Nile flowing out of the Sudd has continued to be fairly constant in seasonal terms, but also reflects the increased contribution of the East African lakes; however, the losses in the Sudd, because of the greater areas of flooding, have increased disproportionately and the flows of the White Nile have not increased as much as the lake outflows.

3.4 Bahr el Ghazal

The Bahr el Ghazal tributary, which joins the Bahr el Jebel at Lake No to form the White Nile, is unusual because it has relatively high rainfall but its contribution to the flow of the main Nile is almost negligible. The annual rainfall of 1,200–1,400 mm is spread over a relatively long period between March and October, and feeds a number of individual tributaries which flow from the fairly impermeable upper plateau towards clay plains and Lake No. After soil moisture recharge, runoff occurs between June and November and averages about 60–100 mm over the gauged basins. Each of the rivers leaves the plateau in defined channels, but then meanders through flood plains in alluvial channels, with initial spill over limited areas during high flows. They converge downstream in complex swamps where spill occurs into widening flood-plains and unconstrained clay plains causing seasonally flooded grasslands and areas of permanent papyrus swamp.

River flows have been measured at a number of gauging stations sited along the main road from Juba to Rumbek, Wau and Aweil where the rivers leave the ironstone

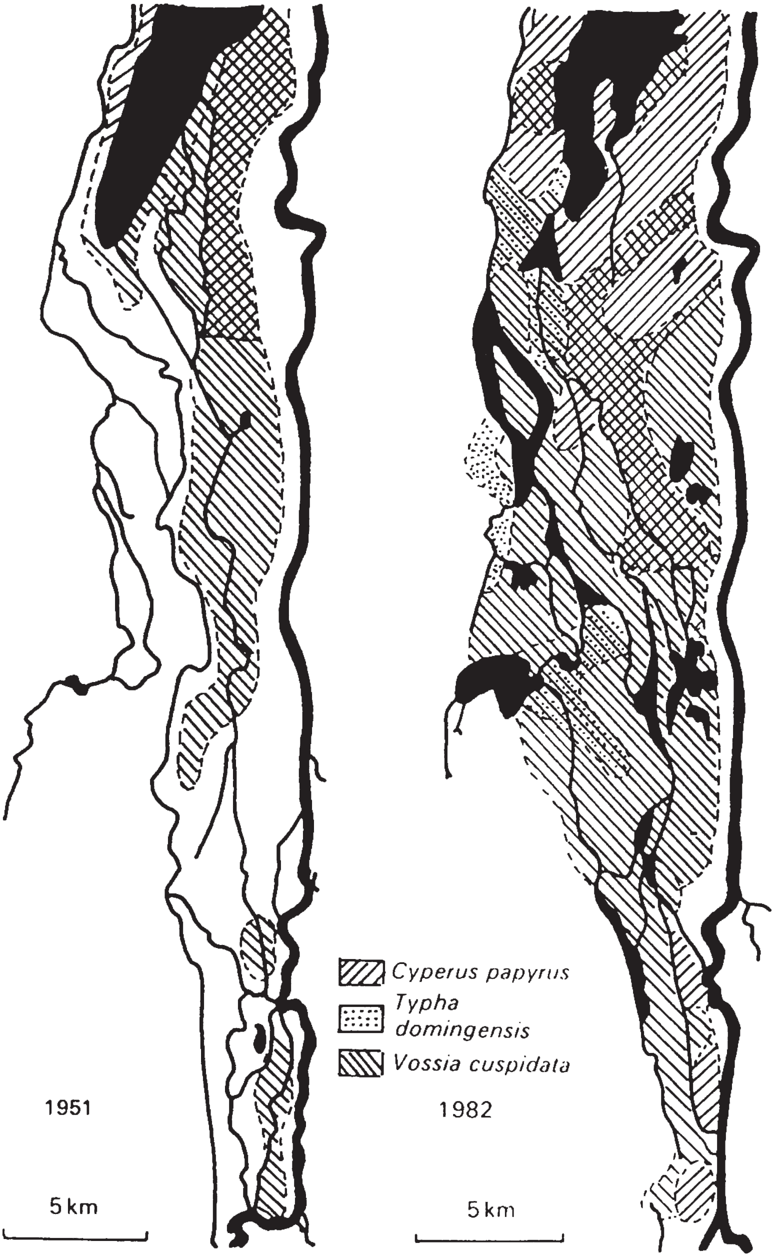

Fig. 10 Aliab valley: channels and vegetation in 1951 and 1982 (after Sutcliffe & Parks, 1999)

peneplain and enter the clay plains. These gauges were established by the Egyptian Irrigation Department and levels were read from 1932; regular discharge measurements began about 1942 and were maintained until 1961; the flows were published in '*The Nile Basin*'. After 1970 measurements at key sites were resumed by the Sudan authorities and published in yearbooks, but were discontinued about 1986. A number of estimates of the total flow of the Bahr el Ghazal tributaries have been made over the years. They vary from 12.3 $m^3 \times 10^9$ (Hurst et al., 1978) to 11.3 $m^3 \times 10^9$ (Sutcliffe & Parks, 1994), but other authors (e.g. Chan & Eagleson, 1980) have estimated considerable additional unmeasured flow by comparing measured runoff with the catchment yield simulated by a conceptual model. It is likely that measured flows have been underestimated by spill bypassing the gauging stations but the topography of the sites must limit this effect.

It is clear from these records that the increase in rainfall and river flows which occurred in the Lake Victoria basin after 1961, did not affect the Bahr el Ghazal basin. There has been a decrease in flows in the 1970s and 1980s which is more similar to the Blue Nile basin.

The wetlands of the Bahr el Ghazal system have not received the detailed attention as those of the Bahr el Jebel, but the species and the influence of the hydrological regime are likely to be similar. The seasonal distribution of the inflows and the inundation and uncovering of the floodplains are similar, but the extent of the flooding are not known so precisely. A satellite image of December 1986 (Sutcliffe & Parks, 1999) illustrates a number of isolated areas of flooding, totalling about 4,000–5,000 km^2, which is considerably smaller than the area of the Bahr el Jebel wetland of the same date. The importance of these wetlands to the local economy is underlined by the distribution of population (see Sutcliffe & Parks, 1999, Fig. 6.4). There are proposals for conservation works to reduce the evaporation losses in the Bahr el Ghazal, but these require more precise hydrological estimates than are available at present.

3.5 Sobat Basin

The Sobat flows into the White Nile from the east just above Malakal, and contributes about half the flow of the White Nile; its contribution is therefore about equal to the outflow from the Sudd. As the river derives most of its runoff from the mountains of southwest Ethiopia, its flow is seasonal and it provides the seasonal element to the flow of the White Nile. However, the river system loses a lot of spill in the region of the Sudan–Ethiopian border, where flow measurements are not complete, so its regime is known with less precision than other rivers.

There are two main tributaries of the Sobat: the Baro and the Pibor. The Baro drains an area of the Ethiopian mountains east of Gambeila, and the Pibor receives the flow of the Gila and Akobo from the mountains south of the Baro basin, but also drains a wide area of the plains east of the Bahr el Jebel which provides high runoff in some years. The upper Baro above Gambeila, where flows were measured by the Egyptian authorities from 1905 to 1959, receives runoff from a number of mountain streams which flow through deep gorges. Below Gambeila it flows towards the Pibor junction, but about 100 km above this junction it splits into the Adura and Baro which rejoin downstream; these rivers receive tributaries but also lose water through several spill channels leading towards the Machar marshes. In addition the river overtops its banks at high flows and inundates wide areas. The Machar marshes are a wetland to the north of the Baro, whose extent is little known except from satellite imagery. Outflow from these marshes sometimes reaches the White Nile.

The main contribution to the Pibor channel comes from the Gila and Akobo, which drain areas of the Ethiopian plateau rising to 2,500 m elevation. The Pibor above the Akobo junction forms the outfall for a number of ephemeral streams which drain a large area of the plain between the Bahr el Jebel and the mountains; the runoff from this area is likely to be small in most years as rainfall is low. These streams start as depressions in the southern part of the plain which are ill-defined but are filled with swamp vegetation towards the northern limit; there is evidence that in a few years there is significant inflow from these streams. This may well include the result of 'creeping flow', which has been observed on several occasions and consists of the slow movement of large bodies of water across a gently sloping and impermeable plain following heavy rain.

Although a large number of observations have been made and gauges established to study the interchange of river flows and swamps between Gambeila and Nasir, the complexity of the channel system and the intermittent nature of the flow records make it difficult to quantify the balance with any precision, but a number of estimates have been made over the years (Sutcliffe & Parks, 1999, Fig. 6.5). There have been proposals to reduce the amount of water evaporated in the Machar marshes either by regulating the river flows by means of upstream storage to reduce spill or by constructing a channel to convey water through the swamps. Satellite imagery is likely to be useful in further investigation.

Analysis of inflows and outflows in the Sobat channel and flood-plain adjacent to the Sobat channel between Nasir and the Sobat mouth has shown that losses and gains of water can best be explained by the flooding and drainage of a wide area of plain flanking the river channel. The outflows from the Sobat into the White Nile have averaged $13.5\,\mathrm{m}^3 \times 10^9$ over the period 1905–1983. There has been no significant difference between the periods before and after 1961.

3.6 White Nile

The White Nile between the Sobat mouth and the junction with the Blue Nile at Khartoum is largely self-contained and only falls about 13 m over a distance of 840 km. The flood-plain storage results in some delay in the outflows and causes losses by evaporation. The natural backing up of the White Nile during the Blue Nile flood also results in delayed outflow and increased evaporation losses. The construction of the Jebel Aulia dam above the confluence, originally designed to store water for irrigation in Egypt during the low flow season, also raises river levels upstream and has facilitated the development of irrigation upstream along the White Nile.

The inflows to the White Nile above Malakal combine two very different components. The outflows from the Sudd reflect the outflows from the East African lakes and the seasonal torrents, reduced and highly damped by losses in their passage through the swamps; however, they also reflect the rise in levels and outflows of Lake Victoria and the other lakes, so they include a muted rise after 1961–1964. They also reflect the seasonal outflows of the River Sobat, which derive from the extended rainfall season in the southern Ethiopian highlands, damped by spill of the higher flows along the river course.

Analysis of the water balance of the White Nile reach, taking account of flood-plain storage related to river levels, showed that the apparent losses and gains could be explained by inundation of the flood-plain, with associated soil moisture recharge and evaporation, and subsequent return of stored water; in some years, however, the water balance suggested that there were significant inflows during certain years when high floods occurred on the Baro, when there had been eye-witness accounts of inflow from the Machar marshes to the White Nile. There is evidence of increasing losses within the reach, which is attributed to the construction of Jebel Aulia dam and to increasing irrigation abstraction.

The flood-plain vegetation along this reach is similar to that of the Sudd, and detailed investigation near Gelhak (11°N) aided by air photography showed that the flooding process and the vegetation distribution were similar to those observed on the Bahr el Jebel.

4 Blue Nile Basin

4.1 Blue Nile

The Blue Nile (Abbay in Ethiopia), provides about 60% of the flow of the main Nile, but published information about its hydrology within Ethiopia is limited. Although some observations for Lake Tana exist from the 1930s, it was not until the late 1950s that Ethiopian agencies began regular hydrological monitoring in the basin (Conway, 2000). The Blue Nile and its tributaries rise on the Ethiopian plateau, which lies generally at 2,000–3,000 m with peaks up to 4,000 m or more. The basin is very broken and cut by deep ravines or canyons in which the Blue Nile and other rivers flow. The plateau drops steeply to the plains of the Sudan.

Lake Tana, at an elevation of 1,800 m, is a feature of the upper basin and has been studied as a possible site for storage, but only some 7.7% of the main river flow passes through the lake. The Blue Nile leaves the lake through a series of cataracts, including Tississat Falls with a drop of 50 m, and enters the ravine while receiving a series of tributaries. The Didessa and Dabus, draining the relatively humid southwest of the basin, contribute over a third of the total flow, but other tributaries drain an area of high rainfall in the loop below Lake Tana. Below the Damazin rapids at Roseires, where a reservoir was built in 1961–1966, the profile changes and the river is little below the surrounding plain. Two tributaries, the Rahad and

Dinder, enter the river from the north between Sennar and Khartoum; both streams are highly seasonal and are dry for much of the year.

The average rainfall of the Blue Nile basin above Roseires is about 1,600 mm, but it increases from 1,000 mm near the Sudan border to 1,400–1,800 mm in the upper basin and above 1,800 mm in the south. The seasonal distribution is governed by the migration of the ITCZ from south to north and back, so that the duration of the rainfall season decreases from south to north. Conway (1997) has shown that it is possible to reproduce the 1951–1987 Blue Nile flow series near the Sudan border from distributed rainfall and potential transpiration estimates, using a simple water balance model. The mean annual runoff for this period was 47.37×10^9 m^3, or 269 mm over the basin of 176,000 km^2, compared with a mean annual rainfall of 1,590 mm; the runoff coefficient is 17%. Lake Tana levels were modelled using rainfall and estimates of runoff and evaporation and observed outflows during the period 1960 to 1992 (Kebede et al., 2006). Whilst lake levels were fairly stable, outflows showed quite high variability, primarily driven by rainfall fluctuations.

Within the Sudan Blue Nile flows have been measured regularly at Roseires/ el Deim from 1912, and at Khartoum from 1900. The Dinder and Rahad flows have been measured since 1907/8, with a gap between 1951 and 1972, which has been filled by correlation with flows at Roseires. The long-term annual flow at Roseires has been 48.7 $m^3 \times 10^9$, but this includes a range from 20.7 $m^3 \times 10^9$ in 1913 to 69.8 $m^3 \times 10^9$ in 1929. During the 1980s flows were comparatively low, but after the second lowest flow of last century in 1984, flows have steadily recovered due to a sustained recovery in rainfall across large parts of the basin (Conway, 2005). The seasonal variation is very high, from average monthly flows of 15.2 $m^3 \times 10^9$ in August to 0.32 $m^3 \times 10^9$ in April. The recent period of low flows in the Blue Nile contrasts with the high flows occurring in the White Nile after 1964, following the marked rise in Lake Victoria.

Comparisons of annual flows between those at Roseires, including the Rahad and Dinder, with those of the Blue Nile at Khartoum, show that apparent losses along the course of the Blue Nile have increased fairly steadily over the years. This is almost entirely explained by abstractions for irrigation, but also includes channel losses and reservoir evaporation.

4.2 Floods

The Blue Nile has a greater potential for flooding than the tributaries of the White Nile, as flows on the latter are attenuated by lake storage or wetland spilling. This was illustrated in 1988, when heavy rainfall over Khartoum and further north was compounded by floods on the Blue Nile and Atbara; these combined to cause severe damage along the main river. The main damage in the Khartoum area was caused by a severe storm on the night of 4/5 August 1988 which recorded daily rainfall of 200 mm or more at sites in the city; an approximate estimate of the return

Table 3 Mean monthly flows at key sites ($m^3 \times 10^6$) (after Sutcliffe & Parks, 1999)

Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Year
Kagera at Kyaka Ferry (1940–1978)												
452	420	491	518	617	627	647	603	531	499	460	467	6,332
Other Lake Victoria tributaries (1956–1978)												
819	578	972	2,103	2,474	1,342	1,201	1,387	1,332	999	1,151	1,207	15,565
Victoria Nile at Jinja (1896–1997)												
2,162	1,973	2,204	2,212	2,412	2,369	2,372	2,277	2,143	2,160	2,057	2,160	26,501
Kyoga Nile at Kamdini (1940–1980)												
2,511	2,200	2,372	2,301	2,526	2,550	2,679	2,695	2,660	2,733	2,609	2,657	30,493
Semliki at Bweramule (1940–1978)												
359	292	327	363	415	371	392	417	409	423	435	419	4,622
Bahr el Jebel at Mongalla (1905–1983)												
2,534	2,180	2,327	2,360	2,767	2,663	2,920	3,317	3,295	3,244	2,975	2,751	33,332
Jur at Wau (1904–1986)												
45	17	10	19	98	212	450	818	1,115	1,149	623	176	4,730
Sudd outflow (1905–1983)												
1,515	1,318	1,392	1,280	1,262	1,188	1,227	1,284	1,328	1,444	1,379	1,473	16,091
Baro at Gambeila (1905–1959)												
257	169	163	202	454	1,154	1,946	2,590	2,971	2,022	816	440	13,184
Sobat at Doleib Hill (1905–1983)												
967	431	273	232	413	851	1,301	1,608	1,780	1,992	1,964	1,718	13,530
White Nile at Malakal (1905–1997)												
2,479	1,756	1,675	1,528	1,696	2,042	2,556	2,914	3,117	3,434	3,340	3,178	29,714
White Nile at Mogren (1911–1995)												
2,469	1,905	2,014	2,225	2,026	1,792	1,368	1,435	2,236	3,024	2,786	2,747	26,026
Blue Nile at Roseires/el Deim (1912–1997)												
762	446	364	324	612	1,659	6,763	15,228	12,111	6,484	2,559	1,348	48,658
Dinder at Mouth (1907–1997)												
0	0	0	0	0	16	318	1,005	1,009	392	51	6	2,797
Rahad at Mouth (1908–1997)												
0	0	0	0	0	2	119	346	378	228	27	2	1,102
Blue Nile at Khartoum (1900–1995)												
724	448	406	427	503	1,084	4,989	15,237	13,625	7,130	2,451	1,257	48,279
Main Nile at Tamaniat (1911–1995)												
3,099	2,302	2,378	2,555	2,490	2,860	6,398	16,151	15,584	9,996	5,067	3,810	72,691
Main Nile at Hassanab (1909–1995)												
3,146	2,320	2,286	2,428	2,359	2,690	5,937	15,607	15,859	10,460	5,351	3,894	72,337
Atbara at Mouth (1903–1994)												
17	6	1	3	8	88	1,536	5,126	3,306	770	145	46	11,052
Main Nile at Dongola (1890–1995)												
3,577	2,547	2,268	2,239	2,175	2,169	5,268	18,701	20,554	13,337	6,767	4,538	84,138
Main Nile at Aswan (Water Arriving) (1869–1992)												
3,738	2,651	2,257	2,011	1,980	1,943	4,754	18,207	21,189	14,318	7,478	4,849	85,376
Main Nile at Aswan/Dongala (1869–1995)												
3,831	2,715	2 379	2,220	2,127	2,178	5,529	19,341	21,385	14,151	7,295	4 298	88,079

period of the storm was 500 years. The river flood was also significant, with a peak level exceeded only in 1946. However, flood frequency analysis suggested that the 1988 peak flow had a return period of about 10 years, but the peak level had a return period of about 50 years. Analysis suggested that the Khartoum gauge level has risen about 0.5 m since 1902 for a typical flood flow.

It was shown during the 1988 flood that cold cloud data from satellite imagery could provide useful information on rainfall amounts, from which flow forecasts could be made (Sutcliffe et al., 1989). This has the advantage that it could be used in areas of difficult access, as it does not depend on direct rainfall measurement and transmission. This was used to develop a flow forecasting system for the Blue Nile and Atbara basins. Rainfall estimates are based on cold cloud duration below a temperature threshold, and linear regression with rainfall records. The conversion of rainfall estimates to river flows are based on conceptual models, and the transmission of the inflow flood hydrograph down the channel system is based on a dynamic flow model, which takes account of abstractions and tributary inflows. The forecasting method utilised by the Nile Forecasting System in Cairo is based on the same principles (Schaake et al., 1993).

4.3 Sedimentation

The Blue Nile, with its steep catchment and highly seasonal flow regime, carries a significant sediment load during the flood period. The annual suspended sediment load at el Deim has been estimated at 140 million tonnes. The storage available in Roseires and Sennar reservoirs is fairly limited, and has been significantly reduced since construction. The strategy for these reservoirs has been to delay filling until the peak of the flood has passed through the reservoir, as the sediment load is greatest on the rising limb of the hydrograph. Reservoir filling rules have been based on flow statistics to minimise sedimentation while ensuring that the reservoir is filled.

4.4 Atbara

The only tributary of the Nile north of Khartoum is the Atbara, which drains an area of 69,000 km^2 of northern Ethiopia and Eritrea. The upper basin, known as the Tekaze in Ethiopia, has a rainfall season which is shorter than the Blue Nile season and is largely concentrated in August and September; the mean annual rainfall of the effective part of the basin has been estimated as about 950 mm. Flow measurements near the Atbara mouth have been measured from 1903 and show wide interannual variability; seasonal patterns are similar to those of the Blue Nile but the flows at the mouth are very low for half the year.

There was some flood irrigation along the upper Atbara before the Khashm el Girba dam was built in 1960–1964 for irrigation; this dam has been subject to sedimentation.

The Atbara has suffered more severely than the Blue Nile from low flows after 1970, though the decline has been exaggerated by the effect of the Khashm el Girba reservoir on flows at the mouth.

5 Main Nile Basin

5.1 *Main Nile*

The main Nile from Khartoum to Aswan, apart from the contribution of the Atbara, is a channel through an arid landscape interrupted with six cataracts and rapids along its course. Much of the reach is underlain by Nubian sandstone, which gives way to Basement Complex northeast of a line from Atbara to Dongola; practically all the rapids and cataracts are found on the Basement Complex, including those between Atbara and Meroe and between Dongola and Wadi Halfa. Sixteen principal rapids between Khartoum and Wadi Halfa are listed by Hurst et al. (1959), with a total fall of 102 m over a length of 228 km.

The discharges of the river have been measured as inflows to Aswan reservoir and also at an upstream station; this station was sited at Wadi Halfa from 1911 to 1931, when the heightening of the early Aswan dam affected the discharge site. Flows were then measured at Kajnarty, 47 km above Wadi Halfa, from 1931 to 1962, when the construction of the Aswan High Dam made another move necessary, and at Dongola, 430 km above Wadi Halfa, from 1963. The composite record at Wadi Halfa/Kajnarty/Dongola is available from 1890, while the flows measured downstream at the Aswan reservoir commenced in 1869. These flows have been measured by various methods and standardised from time to time. They have been tabulated as ‘Water arriving at Aswan’ and also as ‘Natural River at Aswan’; the latter is adjusted for water abstracted from the Blue Nile in the Gezira main canal, and from 1963 in the Managil canal; it allows for the regulation of the Sennar reservoir and the Aswan reservoir, but not for reservoir evaporation. From 1978 the Natural River flows has included estimated evaporation from the Aswan High Dam and the Jebel Aulia reservoir, but not all the effects of upstream storage and abstractions.

The values for Water arriving at Aswan are most useful, and particularly valuable for including the low flows which derive from Lake Victoria, modified by the other lakes and the Sudd. They reveal the high lake levels in 1878 and 1895, and the marked rise in 1961–64. Later records reveal the recent decline in Blue Nile and Atbara flows, and reflect reservoir storage and abstraction in the Sudan; they also show evaporation losses within the Aswan High Dam after 1964. Comparisons between the published Water Arriving at Aswan and discharges at Dongola also show the effect of reservoir evaporation after 1965.

5.2 *The Aswan High Dam*

The concept of the Aswan High Dam arose from theoretical work related to over-year storage in the East African lakes, where the concept of ‘Century Storage’ was defined as the size of reservoir required to guarantee a supply equal to the mean inflow over a period of 100 years. The range R of reservoir storage, ignoring rainfall and evaporation, should increase over a period of N years according to:

$$\log(R/\sigma) = K \log(N/2) \tag{4}$$

with $K = 0.5$ if the inflows are drawn from a random series of standard deviation σ. However, research using Nile flows, including Nilometer records, and other physical time series, showed that the range increased with K values varying randomly about a mean of 0.73. This meant that a markedly larger reservoir would be needed to guarantee a given draft from a natural rather than a random series. This finding has become known as the Hurst phenomenon, and has given rise to advances in theoretical and practical statistics, and in turn to a branch of applied mathematics epitomised by '*The Fractal Geometry of Nature*' (Mandelbrot, 1977). This research led also to the concept and construction of the Aswan High Dam, with over a year's discharge volume allocated for over-year storage. As a result of the reservoir, Egyptian agriculture survived the droughts of the 1970s and 1980s.

5.3 Variability in Nile Flows

Because of the importance of the Nile flood to irrigation in ancient Egypt, a number of Nilometers were built to record flood levels. The longest quantitative records are from the Roda gauge on Roda Island in Cairo. The series records the annual maximum and minimum river levels for the period 622–1921 AD. Although the record has been criticised for inconsistencies of scale and zero, and suffers from some gaps and the effect of channel aggradation, the record is a useful guide to natural variability.

Systematic measurements of Nile river flows began in 1869 and the full record shows substantial decadal and interannual variability caused by the interaction of rainfall variability and the complex hydrology of the Nile (Fig. 11). The causes of decadal and extreme events are not fully understood. Extreme wet years in the White Nile system and parts of southwest Ethiopia that drain into the Sobat and Blue Nile are associated with El Nino and Indian Ocean Dipole events, and dry years in central and northern Ethiopia are associated with El Nino events (Eltahir, 1996; Sileshi & Demarée, 1995). Decadal variability such as the dry 1980s and shifts such as the humid period before 1900 remain unexplained. At present there is no clear indication from observations or climate models of future behaviour in rainfall in the basin. Some agreement exists between climate models that rainfall may show modest increases in East Africa (McHugh, 2005), but there are no emergent patterns for the Indian Ocean and its influence on extreme events in the region (Conway et al., 2007).

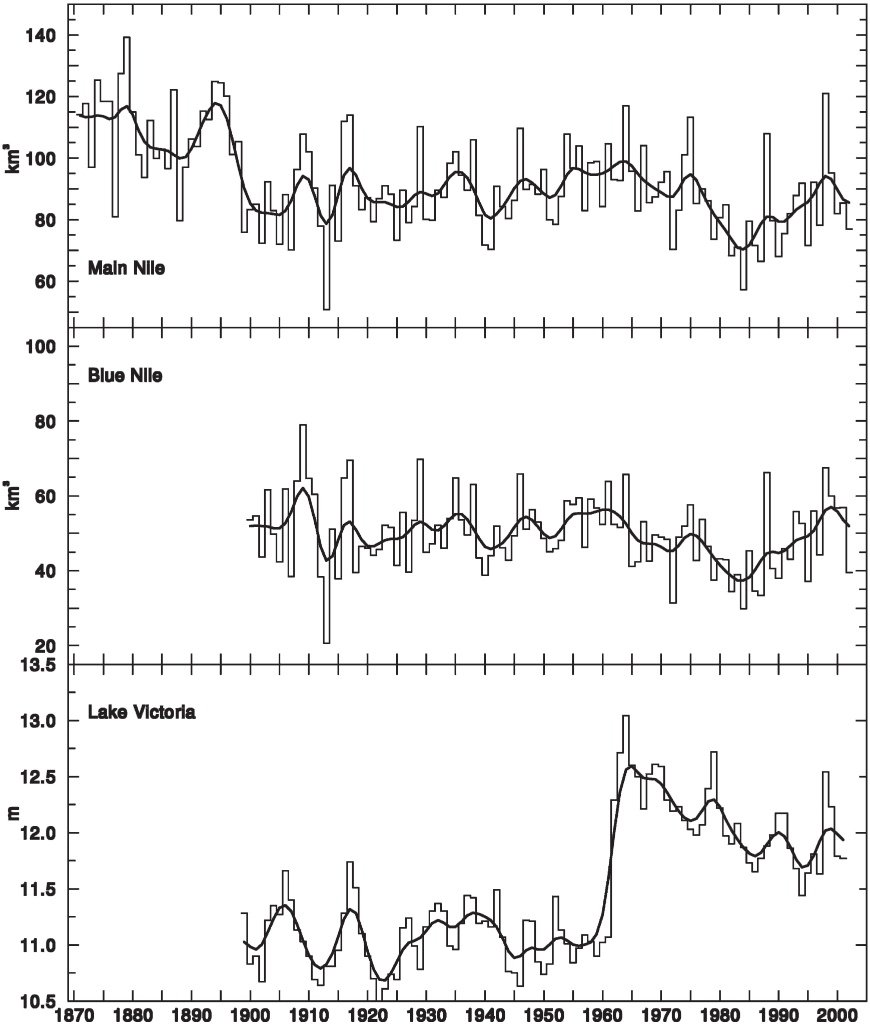

Fig. 11 Annual river flows and lake levels for various periods. Note different vertical scales. *Upper panel*: Nile flows 1870–2002 (from a combination of records at Aswan, Wadi Halfa, Kajnarty and Dongola). *Middle panel*: Blue Nile flows 1900–2002 (from a combination of Khartoum, Roseires and El Deim). *Lower panel*: Lake Victoria levels 1899–2001. *Bold line* represents 10-year Gaussian filter (reproduced from Conway, 2005)

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Part IV
Limnology and Biological Diversity

Physical and Chemical Water Characteristics

Jack F. Talling

Abstract An outline is given of the physical and chemical features of waters in the Nile system, including headwater lakes. Temperature is governed by the large range of latitude and altitude, and is mostly within 15–30°C. Differences with depth can be appreciable under conditions of low to minimal flow and in deeper water columns. They introduce a density stratification with both diurnal and seasonal components, which influences the vertical distribution of plankton and dissolved gases. A long-lasting seasonal stratification is seen only in the deeper headwater lakes, and in Lake Nasser outside the winter season. Light penetration with depth is generally low, especially in silt-laden water associated with turbulent flow and floodwater. During water storage in reservoirs it is subject to the two opposing influences of silt deposition and phytoplankton development. Another influence, that of dispersed colour of partly organic origin accompanied by Fe enrichment, occurs during passage of water through the large Sudd swamp region.

Concentrations of two gases, oxygen and carbon dioxide, are influenced by atmospheric exchange, photosynthesis of phytoplankton and submerged macrophytes, and the decomposition of organic matter, also to the limitation of vertical exchange by density stratification and mats of surface vegetation. Severe oxygen depletion at depth occurs in Lake Victoria and L. Nasser, and can affect the whole river in the Sudd swamp region. Conversely, a near-surface super-saturation of oxygen occurs by day in waters with abundant phytoplankton, conditions in which pH is often above 9.0 by the photosynthetic consumption of CO_2. Otherwise pH is generally in the range 7–9.

Salinity, as the total concentration of major ions, is extensively documented by electrical conductivity. It is strongly reduced in floodwater, but otherwise tends to increase downstream. In Egypt there are instances of relatively high salinity, induced mainly by evaporation in some laterally derived water-bodies (e.g. L. Qarun) or by the influx of seawater in some Delta lakes. The Blue and White Niles differ in cationic composition, the divalent ions Ca^{2+} and Mg^{2+} being predominant in the

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former and the monovalent ions Na^+ and K^+ in the latter – for which river there is a large and variable contribution from Lake Albert. The HCO_3^-/CO_3^{2-} complex (summed as titration alkalinity) is dominant among anions, is closely correlated with conductivity, and falls to low levels only in parts of the *Sudd* swamps.

Longitudinal and seasonal surveys have shown much variation in the major plant nutrients PO_4-P, NO_3-N, NH_4-N and Si. A major input of PO_4-P comes from the contribution of Lake Albert. Chemical exchanges between silt and water are likely to be important, with relevance for bacterial and algal communities. Floodwater is generally with considerable concentrations of these nutrients, especially NO_3-N. Subsequent falls reflect the changing character of drainage and consumption in the seasonal and spatial abundance of phytoplankton. These changes have been closely documented for the White and Blue Niles near Khartoum.

1 Introduction

Two characteristics of water from the lower Nile long attracted attention – that it was of excellent quality for drinking and irrigation, and that it seasonally contained high concentrations of silt. The systematic, scientific exploration of the general subject developed but slowly over the last hundred years. An essential element in this was a direct parallel to geographical exploration, namely the tracing upstream of sources of the materials and properties observed below. Geography and geology dictate that a blending of different types of water must occur in the headwaters and middle reaches, with contributions from dissimilar lakes and highland tributaries. These sources also have different seasonal flows, and so influence the seasonal composition of water downstream. Further seasonal influences include the annual impoundment of water by dams in the Sudan and Egypt, and the chemical activities of plankton in the impounded water. The Nile is affected by pollution, but mainly in the densely inhabited Egyptian sector (El-Sheekh, this volume). However, the extensive Sudd swamps on the Upper White Nile can introduce deoxygenation and its chemical consequences.

As in other fields of river ecology, the information is obtained by combining repeated (e.g. seasonal) observations at a few fixed sites with longitudinal surveys. In Lower Egypt, analyses of Nile water extend back at least 100 years; early information is given by Lucas (1908). Later descriptions of seasonal changes near Cairo include Aladjem (1926, 1928), Abdin (1948a), Hurst (1957), and Ramadan (1972). At Khartoum, Beam (1906, 1908) provided detailed seasonal analyses of the lower White and Blue Niles, and also a foundation for interpreting longitudinal changes down the White Nile. The latter were explored more recently by Talling (1957a), Bishai (1962), Kurdin (1968) and Prosser (1987), as were seasonal changes in the two rivers at Khartoum (Prowse & Talling, 1958; Talling & Rzóska, 1967; Abu Gideiri, 1969; Omer Badri, 1972; Hammerton, 1972d; Sinada & Abdel Karim, 1984). Chemical and physical studies of the headwater lakes were developed in part by hydrological expeditions from the lower Nile (e.g. Hurst, 1925; Graham & Black, 1925; Tottenham, 1926), in part independently of other work on the Nile; they are summarised by Talling & Talling (1965) and Beadle (1981). The water chemistry of the Nile is also discussed by Golterman (1975) in relation to general aspects of river chemistry. The following account is essentially an updated version of that published in the earlier Nile book edited by Rzóska (1976).

2 Temperature

This factor has a double significance. Absolute values (and their seasonal ranges) are of importance for chemical reaction rates, equilibria, and biological tolerances; vertical differences can regulate, through water density, the overall stratification of a water-column.

Over most of the Nile a prolonged or seasonal thermal stratification is absent, due to wind- and current-induced mixing in shallow waters. Among the headwater lakes, this is applicable to the relatively shallow L. Tana (Morandini, 1940) and L. George (Viner & Smith, 1973), and was once believed true for the deeper L. Albert also (Worthington, 1930). However, periods of stratification are probably important in the economy of L. Albert (Talling, 1963) though the vertical temperature differences are small. In Lake Victoria, an annual cycle of thermal stratification can be distinguished (Fish, 1957; Talling, 1957c, 1966), and a pronounced thermocline is present – at least seasonally – in L. Edward (Beadle, 1932, 1981; Damas, 1937). Thermal stratification appears briefly and irregularly in the downstream reservoir at Roseires (Hammerton, 1972b, c), but is annual and prolonged in Lake Nasser-Nubia (Entz, 1976) where it is eliminated by winter cooling and the entry of flood water. Prolonged stratification is lacking in the shallower reservoirs of Gebel (= Jebel) Aulia and Sennar in the Sudan, and – according to Abdin (1948b) – was absent from the old Aswan reservoir.

Even though the shallower lakes and reservoirs have frequent vertical mixing, short *diurnal* phases of thermal stratification are widespread and important. They have been studied in detail for the Gebel Aulia reservoir (Talling, 1957b), some inshore areas of Lake Victoria (Worthington, 1930; Talling, 1957b), and Lake George (Viner & Smith, 1973; Ganf, 1974b; Ganf & Horne, 1975). Diurnal changes of stratification in Lake Tana have also been described by Bini (1940) and Morandini (1940). Figure 1 shows an example from Gebel Aulia, in which the daily stratification of temperature, oxygen and pH was broken down at night by a combination of surface heat loss and wind action. Further implications were traced by Talling (1957b) for the depth-distribution of a planktonic cyanobacterium, *Anabaena flos-aquae* f. *spiroides*, and the estimation of photosynthetic productivity.

The temperatures reached depend upon factors influencing the heat (energy) budget, including radiation income (solar elevation, day length, cloudiness), surface exchange of sensible heat (air temperature), back-radiation and latent heat of evaporation. The last two components are large and increase markedly under conditions of low relative humidity, as found in the central and northern Sudan

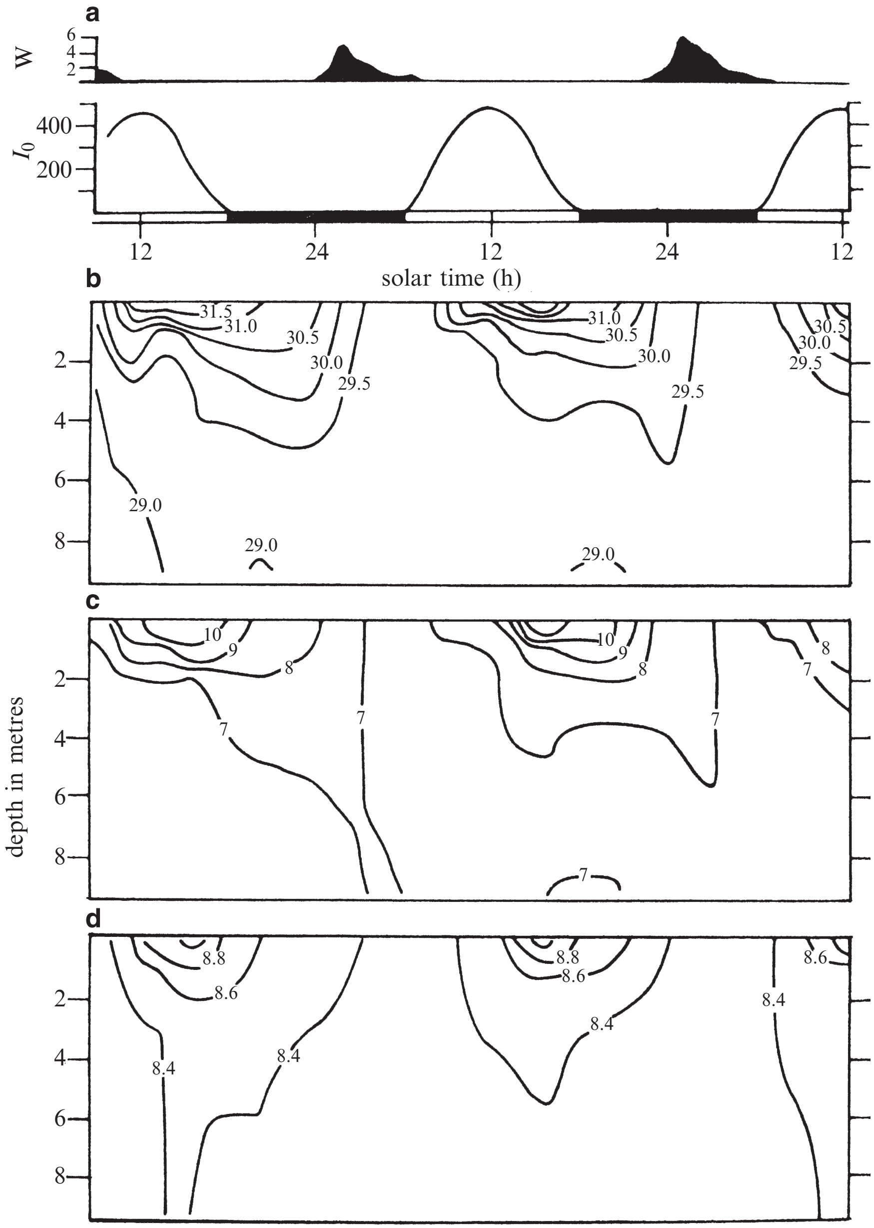

Fig. 1 Diurnal changes in the Gebel Aulia reservoir, 6–8 October 1955, of **(a)** wind strength *W* (as approximate force numbers, Beaufort scale) and incident solar irradiance I_o (in W m^{-2}, spectral region 400–700 nm), **(b)** temperature (isotherms in °C), **(c)** dissolved oxygen (isopleths in mg l^{-1}), and **(d)** pH (from Talling, 1957b)

and in Upper Egypt. As Entz (1976) notes, surface water temperatures are often considerably below mean air temperatures. The evaporation component has been evaluated by Gorgy (1959) for Lake Qarun (Fayum) from an estimated energy balance. Although the evaporation loss from Lake Nasser has engaged much attention (e.g. Omar & El-Bakry, 1970), published calculations of the energy balance and its components seem to be limited to the Gebel (or Jebel) Aulia reservoir (Talling, 1990). For the different circumstances of Lake Tana, Hutchinson (1957, p. 522) has used data of Morandini (1940) to estimate the various contributions to nocturnal heat loss, with evaporative cooling predominant.

Since the Nile flows through a wide belt of latitude, longitudinal (N–S) gradients of water temperature might be anticipated. These are best shown (Fig. 2) during the "winter" (Dec–Jan) season of the northern areas, when water temperatures from Khartoum (Prowse & Talling, 1958; Talling & Rzóska, 1967; Abu Gideiri, 1969) to Cairo (Abdin, 1948a; Ramadan, 1972 – Fig. 5) fall to about 17–19°C, in contrast to more maintained levels near 28°C in the southern Sudan (Talling, 1957a; Bishai, 1962). The headwaters are typically a little cooler, due to altitude and probably the reduction of insolation by cloud cover. Talling (1969) has compared the relatively constant surface temperatures of lakes Victoria (23.9–27.1°C), Edward, and Albert with the large seasonal range at Aswan (16–30°C: from Abdin, 1948b), as part of general seasonal trends in African freshwaters. The maximum temperatures in Lake Nubia-Nasser are among the highest in large African lakes.

3 Transparency and Light Penetration

As in many freshwaters, and probably most rivers, these related features are mainly controlled by the particulate content of the river water. The more numerous measurements of transparency denote the depth at which a Secchi disc disappears from view. This measure of turbidity is more strongly influenced by the scattering of light than is light penetration (or attenuation, or extinction) itself. The latter is best estimated, for specific spectral regions isolated by colour filters, from the response of a submerged photo-cell which – in homogeneous water – decreases exponentially with depth. The rate of decrease is measured by the vertical extinction (attenuation) coefficient (ε), which is expressed in ln units per meter and varies with wavelength. The depth with 1% of the surface response ($z_{1\%}$ in m) is related to ε by the relationship

$$z_{1\%} = \frac{4.6}{\varepsilon} \tag{1}$$

The minimum extinction coefficient over the visible spectrum, ε_{min}, usually dictates the depth of the euphotic zone (z_{eu}) and photosynthetic zone. An approximate relationship (Talling, 1965) is

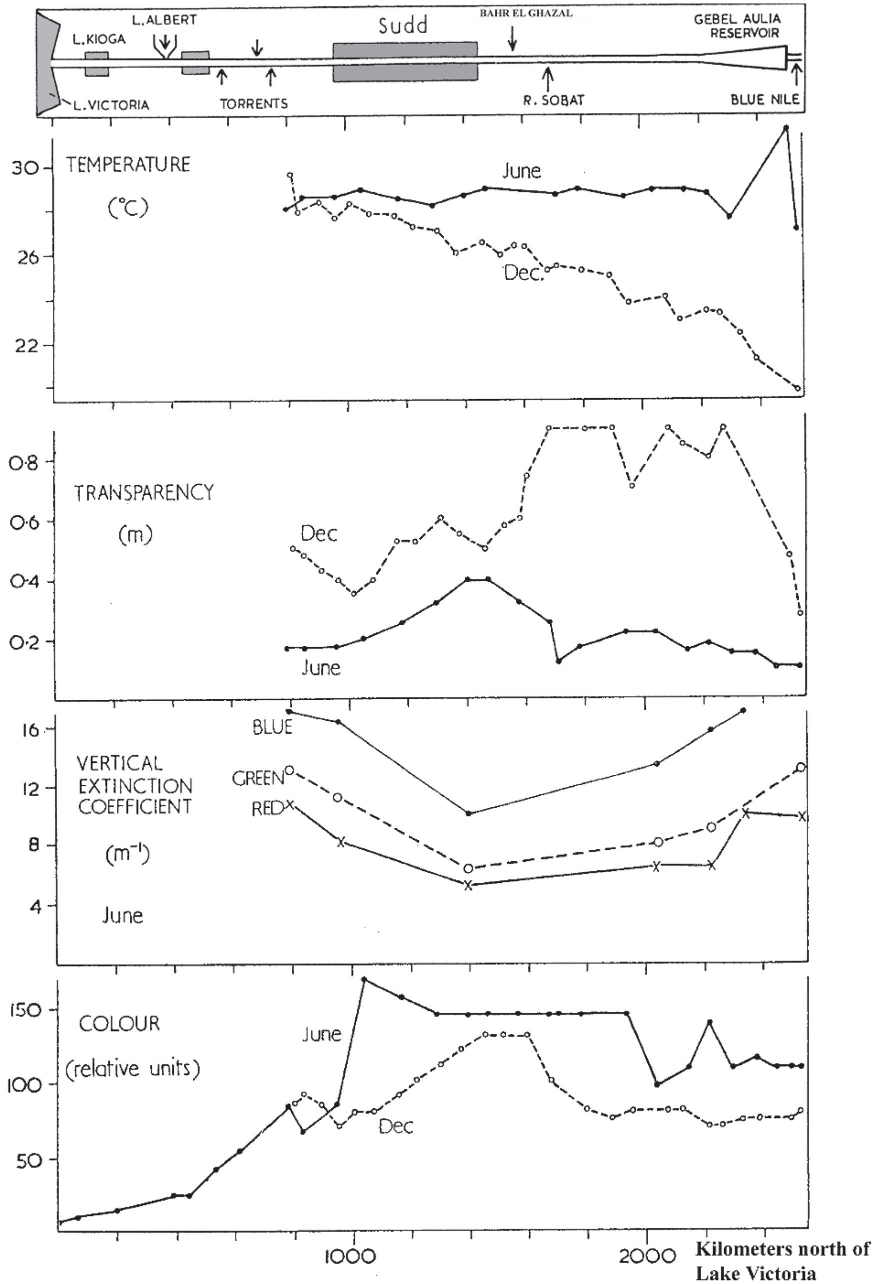

Fig. 2 The variation of some physical properties – temperature, transparency, light extinction, and colour – along the White Nile between Lake Victoria and Khartoum, in June and December 1954. See also map in Fig. 3 (from Talling, 1957a)

$$z_{eu} \cong \frac{3.7}{\varepsilon_{min}} \tag{2}$$

Many measurements of light penetration in the Nile have been made without colour filters, over a broad spectral region (Abdin, 1948a, b, c) and the corresponding extinction coefficients are slightly higher than ε_{min}. The latter can be used as a summarizing characteristic, as can $z_{1\%}$.

The clearest water investigated in the Nile system is that of offshore Lake Victoria (Levring & Fish, 1956; Fish, 1957; Talling, 1957c, 1965, 1966). The measured variation over a year of ε_{min} at one station was 0.16–0.31 ln units/m (z_{eu} = 12–21 m), with higher extinction at times of higher phytoplankton density (Talling, 1966) and in the recent period since eutrophication. Light penetration is much lower in the other headwater lakes (Albert, Edward, George, Tana); the most penetrating spectral region shifts from green, through orange, to red in the turbid waters of L. Tana and L. George. High extinction in the latter is chiefly governed by the dense phytoplankton which discolours the water (Ganf, 1974a, 1975). In lakes Edward and especially Albert (Levring & Fish, 1956; Talling, 1965) both phytoplankton and fine silt contribute to the extinction, and silt is probably dominant in L. Tana – for which a measurement near Bahar (or Bahir) Dar was made by Talling (unpublished) in March 1964: ε_{min} = 1.2 ln units/m, z_{eu} ~ 3 m). The Secchi transparency is usually about one-third to one-half of the euphotic depth.

In the following river water, more detritus is carried in suspension and light penetration is usually low. Thus a longitudinal section of the White Nile in June 1954 (Fig. 2) yielded ε_{min} coefficients of minimum extinction – displaced to the red spectral region – between 5 and 11 ln units m^{-1}, with transparency between 0.1 and 0.4 m. Higher values of transparency in the following December indicate considerable temporal variation, probably related to water level and the seasonal flow of some mountain torrents (Talling, 1957a). Seasonal changes are accentuated in the Blue Nile, with transparency reduced to virtually zero by the load of silt carried in the flood water (Fig. 10). This silt has produced a seasonal minimum of transparency and $z_{1\%}$ downstream, as at Aswan (Abdin, 1948b, 1949) and Cairo (Abdin, 1948a; Ramadan, 1972).

The storage of water in the Nile reservoirs involves two opposing influences on the particulate content, and so on light penetration and transparency. Larger particles will sediment out, but the enhanced growth of phytoplankton may reduce light penetration. Net clarification seems characteristic of the old Aswan reservoir (Abdin, 1948b; Elster & Vollenweider, 1961) and the later Lake Nasser (Entz, 1972, 1976), with Secchi transparency values often reaching several metres and exceptionally 6 m in upwelling situations. The new Roseires reservoir has also led to increased transparency in the lower Blue Nile as well as in the reservoir itself. However, phytoplankton can greatly reduce transparency in L. Nasser (Entz, 1976), and its effect appears dominant in most longitudinal sections of the filled Gebel Aulia reservoir (Brook & Rzóska, 1954; Figs. 2 and 8). A longitudinal section from Aswan to Cairo (Elster & Vollenweider, 1961) showed a decrease of transparency downstream, probably due to increase of silt and detritus in flowing water. In the Sudd swamp region, where many measurements have been made (see Rzóska, 1974), optical conditions in flowing and standing waters are not sharply contrasted; the former typically carry much detritus, and the latter abundant phytoplankton. Unusually high transparency exists in the Bahr el Ghazal tributary, reaching 2.5 m or more.

The increased transparency brought about downstream by the new Roseires dam has had an adverse effect upon a traditional style of fishing by cast-nets (Hammerton, 1972d). In the Gebel Aulia reservoir, no well-defined pattern of diurnal vertical migration by zooplankton could be demonstrated (Rzóska, 1968), possibly due in part to the shallow euphotic zone affected by wind-induced turbulence.

4 Salinity and Conductivity

As in most freshwaters, salinity and discharge tend to be inversely related. Their relationship also depends upon the balance between precipitation and evaporation, and the prevalence in the drainage basin of readily-eroded and weathered minerals and of exposed saline deposits (e.g. evaporites) from earlier geological periods. The Amazonian combination of high discharge and low salinity is unknown in the Nile system, where even the flood water of the Blue Nile has an ionic content greater than 1 meq l^{-1} of cations or anions and an electrical conductivity (20°C) above 100 μS cm^{-1}. However, the ionic content and conductivity fall appreciably in the seasons and reaches affected by flood water from the Blue Nile and River Atbara, as at Khartoum (Figs. 4 and 10). Lake Nasser (Entz, 1976; Elewa, 1985) and Cairo (Aladjem, 1926, 1928; Hurst, 1957; Ramadan, 1972: see Fig. 5). Entz (1976) and Elewa (1985) have shown that in Lake Nasser the conductivity differences can be used to identify water masses and trace their movement downstream. Analyses made before the High Dam showed that there was an appreciable increase in solutes between Aswan and Cairo (Aladjem, 1928; Elster & Vollenweider, 1961).

It is in the headwaters that the greatest variation of salt content occurs. The existence there of some relatively saline waters was established by early surveys (Hurst, 1925, 1957; Tottenham, 1926) with gravimetric analyses, but most results are based upon estimations of conductivity (see Talling & Talling, 1965). This increases ninefold along the lake series Victoria – Tana – Albert – Edward (Tables 1 and 2), and it is the lesser contribution of high conductivity water from L. Albert and the Western Rift which raises the conductivity of the White Nile from the low initial level of L. Victoria (Fig. 3). As the volume derived from L. Albert can vary over short periods (Tottenham, 1926), owing to wind action and the peculiar Nile inflow-outflow configuration, conductivity can fluctuate in the Albert Nile (Beauchamp, 1956) and pulses of higher conductivity water are probably still recognisable in the Sudan (Talling, 1957a). Further downstream, an increase can sometimes occur in the Sudd swamp region where much water is lost by evapo-transpiration. A diluting effect of the River Sobat is more consistently found (Fig. 3; see also Rzóska, 1957 and Bishai, 1962), and which will be greater during the seasonal high flows

Table 1 Water characteristics of the White and Main Niles

Characteristic	Lake Victoria 2.iii.61 (1)	Nr. Lado (S. Sudan) 25.xii.54 (2)	Khartoum 19.iii.63 (3)	Khartoum 1965–67 (4)	Wadi Halfa 15–20.iii.64 (5)	L. Nubia 23.ii.68 (5)	L. Nasser 23.iii.74 (6)	Cairo 29.iii.74 (6)
Conductivity (k_{20}, μS cm^{-1})	97	235	240	220–500	290	350	237	307
As meq l^{-1}:								
Na^+	0.45	–	1.26	1.09–1.78	–	–	0.85	1.20
K^+	0.10	–	0.18	0.18–0.24	–	–	0.16	0.17
Ca^{2+}	0.28	0.38	0.92	0.71–0.95	–	–	1.18	1.39
Mg^{2+}	0.21	–	0.65	0.62–0.96	–	–	0.62	0.82
$HCO_3^- + CO_3^{2-}$ (alky)	0.92	2.40	2.80	2.3–3.3	–	–	2.33	2.70
SO_4^{2-}	0.05	0.10	0.04	–	–	–	0.22	0.37
Cl^-	0.11	0.28	0.14	0.17–0.27	–	–	0.16	0.41
As μg l^{-1}:								
total P	47	–	–	–	–	–	90	49
PO_4-P	13	60	–	2–120	20	10	–	–
NO_3-N	11	30	–	10–90	‘0’	100	–	–
As mg l^{-1}:								
Si (x2.1 = SiO_2)	2.0	2.8	13.5	8.4–13	10	11	6.9	4.8
pH	8.0	7.9	–	8.0–8.9	8.1	8.4	–	–
Transparency (m)	–	0.50	–	–	0.20	0.98	–	–

(1) Talling (1966), Talling and Talling (1965); (2) Talling (1957a); (3) Talling and Rzóska (1967); (4) Hammerton (1972d); (5) Hammerton (1972b); (6) Talling and Heron, unpubl.

Table 2 Water characteristics of the Blue Nile

	Lake Tana				Khartoum		Roseires reservoir	
Characteristic	8.xii.65–18.iv.66 (1)	11–12.iii.64 (2)	Tissisat Falls 12.iii.64 (2)	Gorge, M. bridge 10.iii.64 (2)	10.iv.64 (2)	1965–67 (3)	xi.67 (4)	v.68 (4)
Conductivity (k_{20}, µS cm^{-1})	200–240	137	156	231	238	140–390	200	300
As meq l^{-1}:								
Na^+	0.31–0.41	0.24	0.26	0.57	0.47	0.20–0.39	0.19	0.36
K^+	0.03–0.05	0.04	0.05	0.07	0.06	0.04–0.07	0.04	0.06
Ca^{2+}	0.70–0.76	0.94	0.93	1.52	1.50	0.98–1.41	1.03	1.27
Mg^{2+}	0.50–0.70	0.45	0.52	0.80	0.72	0.41–0.54	0.42	0.56
$HCO_3^- + CO_3^{2-}$ (alky)	1.52–1.92	1.52	1.57	2.23	2.57	1.63–2.66	1.74	2.46
SO_4^{2-}	–	0.05	0.08	0.48	0.36	–	–	–
Cl^-	0.03–0.07	0.04	0.05	0.11	0.08	0.06–0.21	0.10	0.20
As µg l^{-1}:								
PO_4-P	15–20	30	24	24	–	2–120	35	<4
NO_3-N	0–80	–	–	–	–	1–100	55	2
As mg l^{-1}:								
Si (x2.1 = SiO_2)	8.4–9.4	6.8	6.8	8.9	8.7	7.5–11		9.4–11
pH	8.1–8.4	8.4	8.5	–	–	8.2–9.1	–	–
Transparency (m)	–	1.1	–	–	–	–	–	–

(1) Hammerton (1972b); (2) Talling unpublished, Talling and Rzóska (1967); (3) Hammerton (1972d); (4) Hammerton (1972b).

in this river. At a time of low levels here and at Khartoum, in March–April 1958, Gay (1958) found high conductivity values near 350 µS cm^{-1} (20°C) along a considerable length of the White Nile. As values in the same season of 1954–1956 and one later year were much lower (Talling, unpublished; Abu Gideiri, 1969), sporadic increases are suggested, possibly related to the saline discharge from Lake Albert. An exceptionally low conductivity of 40 µS cm^{-1} was encountered by Rzóska (1957, 1974) at Lake Ambadi on the Bahr el Ghazal, whose waters are distinctive in other respects.

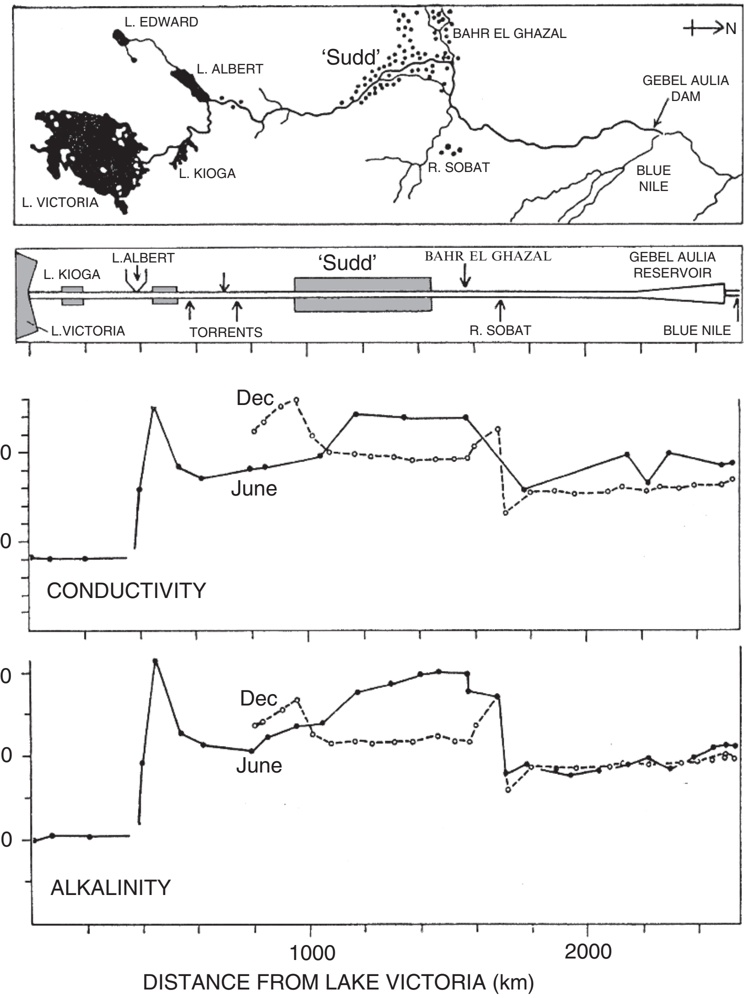

Fig. 3 The variation of conductivity (µS cm^{-1}, 20°C) and alkalinity (meq l^{-1} × 10) along the White Nile between Lake Victoria and Khartoum, in June and December 1954 (from Talling, 1957a)

On the Blue Nile, there is a net increase of conductivity in the Gorge region between Lake Tana and Roseires (Table 2). Little further change was found by Talling & Rzóska (1967) and Hammerton (1970) to Khartoum, where values are still lower than in the White Nile – and especially so in the flood season.

Within Egypt, some enclosed lateral water-bodies derived from the Nile have relatively high salinity. They include Khor Toshka off Lake Nasser (El-Shabrawy & Dumont, this volume), Lake Qarun in the Fayum depression, and the Wadi Natrun (Talling, 1992). In the Delta lakes, the salt content can be increased by penetration of sea-water as well as by evaporation and local pollution (Elster & Vollenweider, 1961; Aleem & Samaan, 1969; El-Wakeel & Wahby, 1970; Talling, 1992). Older values were usually in the range 0.5–5‰ Cl, but changes have occurred since the High Dam altered the hydrological and silting regimes. At the same time, the previously marked effects of the annual Nile flood water upon salinity (and fisheries) of the south-eastern Mediterranean (Hecht, 1964; Oren, 1969) have disappeared.

5 Major Ions

The bicarbonate plus carbonate ions strongly dominate the total anionic content in virtually all Nile waters (Delta lakes excluded). As their combined concentration is closely approximated by the titration alkalinity – the effects of H^+, OH^-, and $SiO(OH)_{3^-}$ – being generally negligible – alkalinity is closely correlated with total ionic concentration and so with conductivity. Approximate relationships, applicable to many other African freshwaters (Talling & Talling, 1965), are

$$\begin{aligned}\text{conductivity } (\mu\text{S cm}^{-1}, 20^\circ\text{C}) &\simeq 100 \times (\text{alkalinity, meq l}^{-1})\\ &\simeq 85 \times (\text{total cations or anions, meq l}^{-1}) \qquad (3)\end{aligned}$$

For examples, see Tables 1 and 2 and Figs. 3, 5, and 10. Numerous and relatively precise measurements of alkalinity are available for waters throughout the Nile system, and give useful indications of total ionic content. The general range for alkalinity is roughly 1–3 meq l^{-1} in the major stretches of the river, with an upper limit of 9 meq l^{-1} in L. Edward.

The remaining major anions, Cl^- and SO_4^{2-}, show different patterns of distribution. Concentrations of chloride are very low (~0.05–0.15 meq l^{-1}) in the major headwaters unaffected by the saline injection from the Western Rift, but are much increased below this in the White Nile (Talling, 1957a). Further downstream, the River Sobat has a strong diluting influence, as has the Blue Nile flood-water (Fig. 4) for the combined waters in the Main Nile below Khartoum. The extremely low concentrations described for the White Nile by Bishai (1962) are incompatible with all other analyses. Concentrations measured at Aswan and Cairo (Table 1, Fig. 5) indicate additional inputs to the river in Egypt, although a seasonal minimum existed during the flood-water of the pre-High Dam era (Fig. 5; Hurst, 1957 for 1933–1936 analyses).

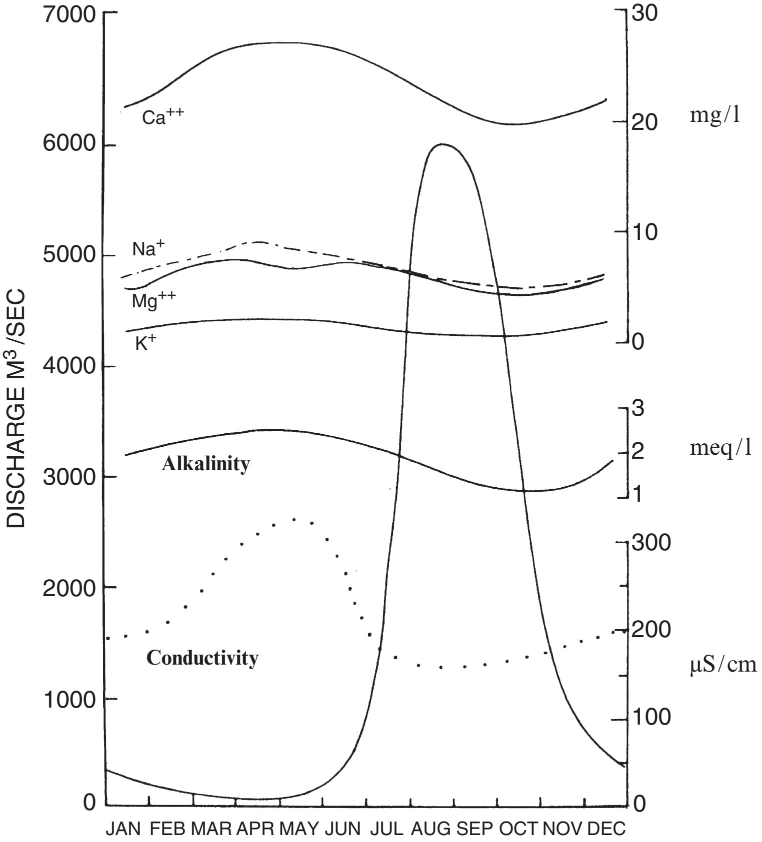

Fig. 4 Seasonal changes in concentrations of major cations, alkalinity, and conductivity (20°C) in the Blue Nile at Khartoum, shown in relation to discharge (from Hammerton, 1972d)

Sulphate is present in low concentration, at or below 0.05 meq l^{-1}, in the headwater lakes Victoria (Beauchamp, 1963; Lehman & Branstrator, 1994) and Tana. Considerable enrichments occur from the Western Rift (L. Albert) discharge to the White Nile, and in the Gorge region to the Blue Nile (Tables 1 and 2). Concentrations in the Blue Nile persist downstream in the Sudan plain, but in the White Nile a remarkable loss occurs as the water traverses the Sudd swamps (Talling, 1957a). First discovered by Beam (1906, 1908), the effect is presumably due to microbial reduction.

As regards the major cations, the chief interest lies in the widely varying ratio of the divalent (Ca^{2+}, Mg^{2+}) to the monovalent (Na^+, K^+) ions. The Blue and White Niles contrast in this respect: calcium is predominant in the former, and sodium in the latter. The ratio downstream is particularly influenced by flood water from the Blue Nile, as noted at Cairo by Abdin (1948a). The fewer analyses of potassium show a particularly high content in the White Nile, which is probably derived largely from

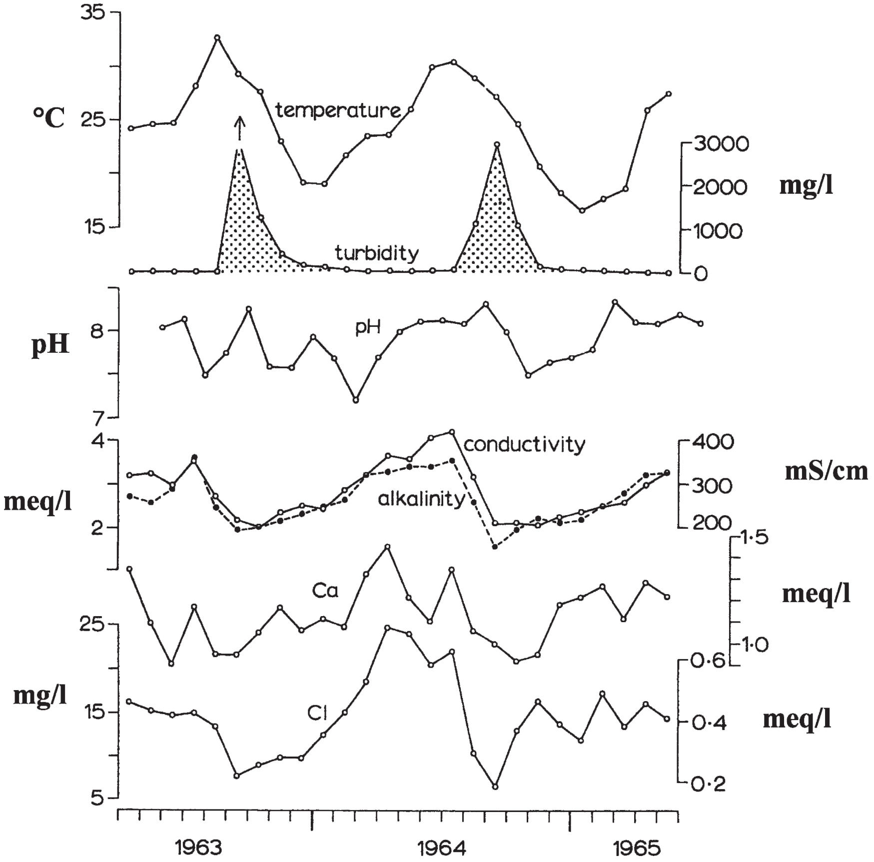

Fig. 5 Seasonal changes of seven physical and chemical characteristics of Nile water at Cairo, before the High Dam. Turbidity maxima indicate the annual flood water (adapted from Ramadan, 1972)

the potassium-rich waters of Lake Albert and the Western Rift drainage. Although the precipitation of $CaCO_3$ may well have influenced ionic proportions in the more saline headwater lakes of Edward and Albert (Talling & Talling, 1965), there is no evidence for present-day losses of calcium on a large scale in the river itself, or in Lake Nasser (Entz, 1976). However, Hammerton (1970) found examples of benthic calcium carbonate deposition on a small scale in the Blue Nile.

6 Dissolved Gases and pH

Despite possibilities for equilibration with the atmospheric reservoir, the content of *dissolved oxygen* and *carbon dioxide* may be altered by intense biological activity in several regions of the Nile system. Concentrations of the two gases are inversely correlated, if free rather than total carbon dioxide is considered, as is usual in natural waters. The total carbon dioxide content is dominated by the bicarbonate ion, which also accounts for the major part of the titration alkalinity, in turn cross-correlated with conductivity and salinity (see above).

Oxygen depletion is pronounced in two types of situation – swamp waters, and the deeper layers of stratified lakes and reservoirs. The first is illustrated by the passage of the Bahr el Jebel through the Sudd swamps (Talling, 1957a; Bishai, 1962; Kurdin, 1968; Rzóska, 1974), where a partial deoxygenation occurs (Fig. 6). Its extent appears to vary seasonally, as does the rapidity – and hence distance – of recovery downstream. Some important chemical consequences affecting SO_4^{2-}, Fe, and possibly PO_4-P are noted in this chapter. Although less studied, severe depletions probably occur from time to time in swamp-affected regions of the River Sobat and its tributaries, and perhaps lead to fish kills there (Bacon, 1918) as near Shambe on the Bahr et Jebel.

The second, deep water, situation occurs annually in the stratified waters of lakes Victoria (Fish, 1957; Talling, 1966; Hecky et al., 1994) and Nasser (Entz, 1976), for most of the year in Lake Edward (Beadle, 1981), and diurnally in Lake George (Ganf, 1974b). The examples of deoxygenation in Lake Albert probably occur irregularly in time; they appear to develop from profile-bound density currents (Talling, 1963), and may be responsible for the occasional kills of Nile perch (*Lates niloticus*) in this lake. In other Nile reservoirs, long periods of stratification with deep deoxygenation are lacking. However, short periods of variable deoxygenation have occurred in the Roseires reservoir, including an episode of complete deoxygenation soon after its first filling (Hammerton, 1972a, b). Extensive barriers to atmospheric exchange were introduced to parts of the White Nile by floating mats of the water hyacinth *Eichhornia*.

Oxygen supersaturation, due to photosynthetic activity, is often encountered in regions with abundant phytoplankton. It develops diurnally and interacts with the diurnal temperature (density) stratification, as shown by Talling (1957; Fig. 1) for the Gebel Aulia reservoir and by Hammerton (Fig. 7) for the White Nile at Khartoum. The latter involved a wide, slowly flowing water-mass which differentiated both vertically and horizontally. In the neighbouring Blue Nile, surface supersaturation during the annual phytoplankton maxima was also found (Talling & Rzóska, 1967). Further downstream, high levels of supersaturation have been recorded for some occasions and localities in Lake Nubia-Nasser (Entz, 1976). At Cairo, in the pre-High Dam period, slight supersaturation developed during the cooler winter season and values were above 70% saturation throughout the year (Ramadan, 1972).

Direct determinations of *carbon dioxide* content in the Nile system are few. They include swamp waters in Uganda (Carter, 1955; Milburn & Beadle, 1960) and Lake George (Ganf & Milburn, 1971); which are characterised respectively by strong enrichment and depletion by biological agencies. Most estimates, of free CO_2 are deduced from pH and alkalinity. Though these are approximate, the large variations involved should be reasonably well-established. The inverse relation with oxygen concentrations is well shown by longitudinal surveys along the White

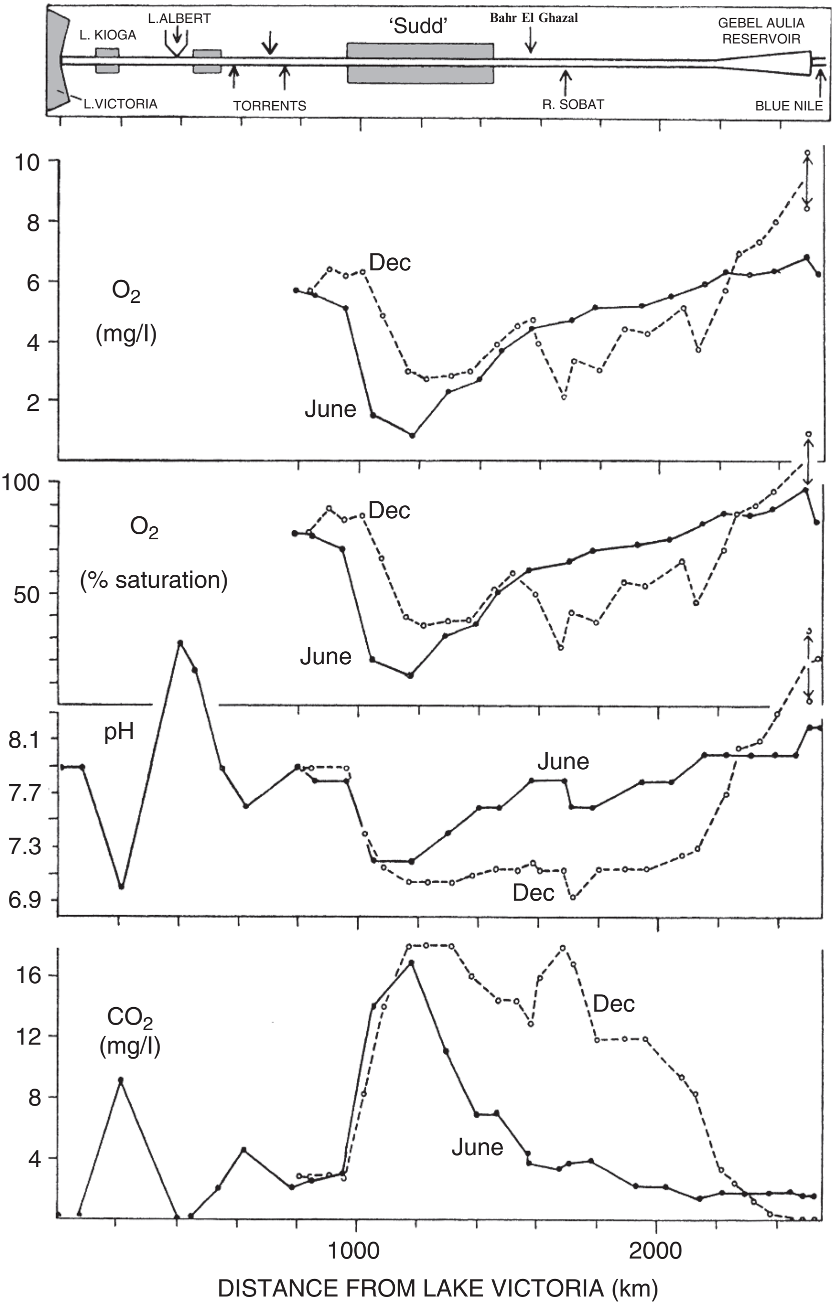

Fig. 6 The variation of dissolved oxygen, pH, and free carbon dioxide along the White Nile between Lake Victoria and Khartoum, in June and December 1954. See also map in Fig. 3 (from Talling, 1957a)

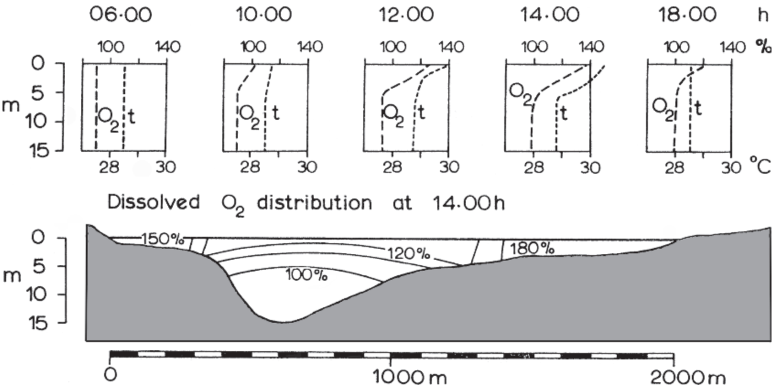

Fig. 7 Stratification in the White Nile near Khartoum. Above, diurnal changes of temperature and dissolved oxygen (as % saturation); below, cross-section of the river showing horizontal and vertical differences in dissolved oxygen (Hammerton, in Talling, 1976)

Nile (Talling, 1957a; Bishai, 1962; Kurdin, 1968), where CO_2 enrichment occurs in the swamp regions and is reduced rather slowly downstream (Fig. 6). It is also shown by a comparison of the seasonal changes in areal contents of oxygen and free carbon dioxide in Lake Victoria (Talling, 1966). Depletions of carbon dioxide, involving free CO_2 and bicarbonate, occur from algal photosynthesis in most waters with a rich phytoplankton. Owing to the limited rates of CO_2 diffusion across the air-water interface, the deficits persist through night-time more than does oxygen supersaturation.

Levels of *pH* are chiefly governed by the bicarbonate-carbonate alkalinity and the concentration (or tension) of free CO_2. When the latter is in equilibrium with the atmosphere, reference values of pH are obtained which change only slightly with temperature and increase approximately linearly with the logarithm of the alkalinity. This relationship, and the displacements of pH observed in some Nile waters due to CO_2 enrichment or depletion, are illustrated by Talling & Talling (1966). Thus, the air-equilibrium value is approximately pH 8.0 for Lake Victoria, pH 8.2 for the White Nile near Khartoum, and 8.9 for Lake Albert. The values of pH measured for Nile waters (see Tables 1 and 2 and Figs. 6, 9, and 10) rarely fall below 7; exceptions include Lake Ambadi and some swamp waters in the Sudd region (Rzóska, 1974), and the River Sobat (Talling, 1957a). In this respect there is a sharp contrast with many other large tropical rivers of lower alkalinity, such as the Amazon and Congo. The depression of pH in water of the White Nile (Bahr el Jebel) as it traverses the Sudd region is shown in Fig. 6 (Bishai, 1962; Kurdin, 1968; Rzóska, 1974). Conversely, the elevation of pH in regions of the White and Blue Niles with intense algal photosynthesis can be seen in Figs. 1, 8, 9, and 10. Other examples

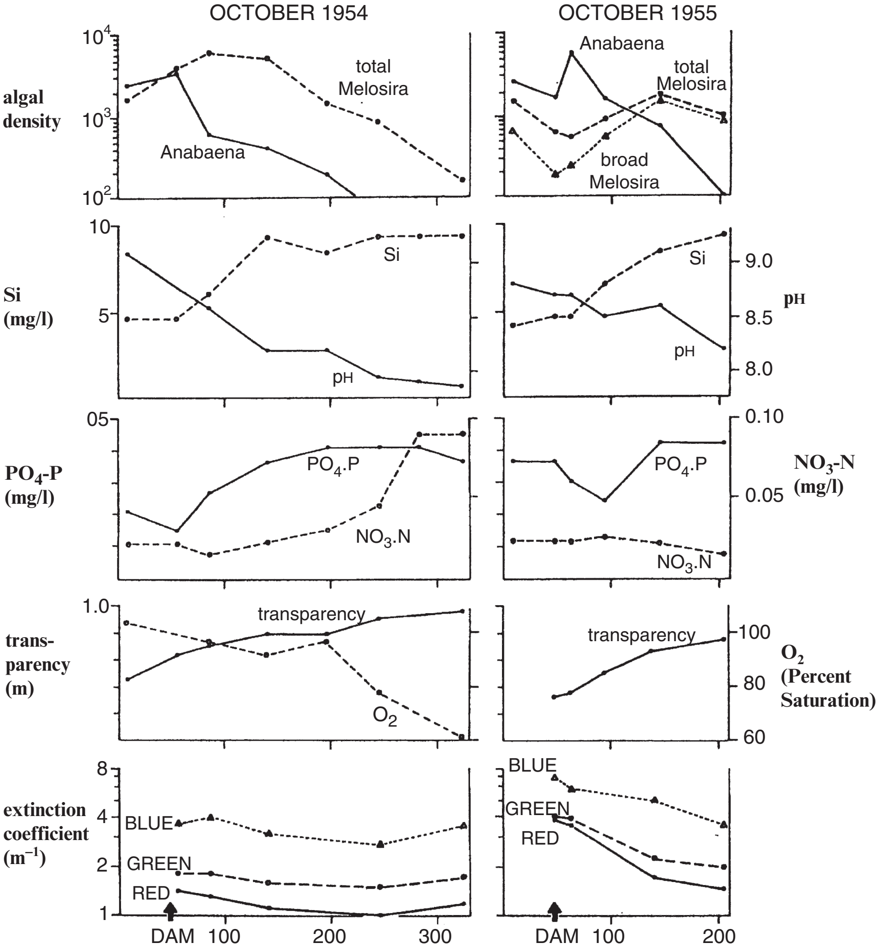

Fig. 8 Two longitudinal sections of the Gebel Aulia reservoir region of the lower White Nile, showing changes in major phytoplankton components and various physical and chemical characteristics influenced by phytoplankton development above the dam. Concentration units for *Aulacoseira granulata* are cells ml^{-1}, for *Anabaena flos-aquae* f. *spiroides* coil-turns ml^{-1} (from Prowse & Talling, 1958)

in Lake Nasser are noted by Entz. The higher values reached are 1 pH unit or more above the air-equilibrium values, as in the White Nile (pH 9.3) and the Blue Nile (pH 9.1–9.2) at Khartoum (Prowse & Talling, 1958; Talling & Rzóska, 1967; Hammerton, 1972d), Lake Nasser (pH 9.6: Entz, 1976) and Lake George (pH 10+: Viner, 1970). In comparison with these, the ranges of pH recorded by Abdin (1948a) and Ramadan (1972) at Cairo in the pre-High Dam period are relatively small (Fig. 5).

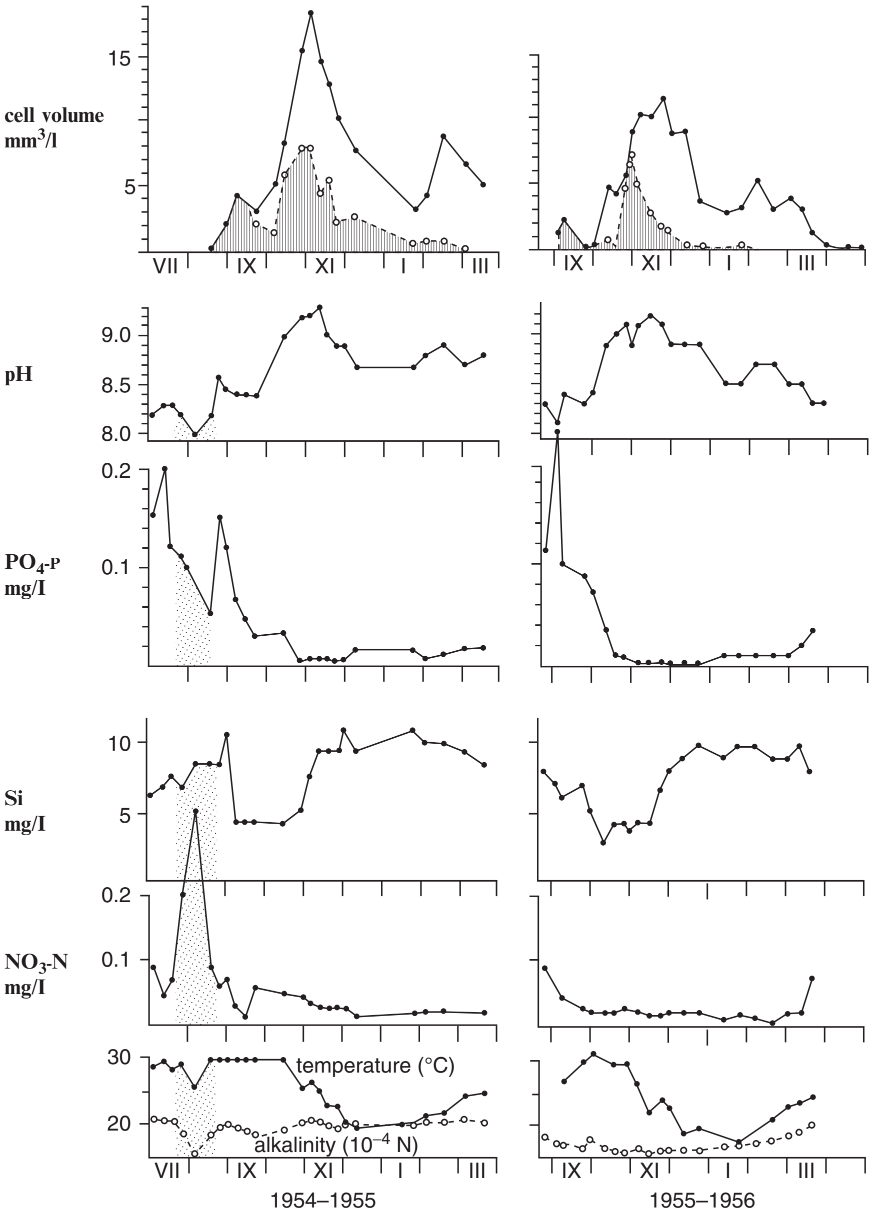

Fig. 9 Seasonal changes in the White Nile near Khartoum, of: phytoplankton crops (with the *Aulacoseira* component shaded), concentrations of some plant nutrients, pH, alkalinity, and temperature. Stippled areas indicate admixture with Blue Nile water (from Prowse & Talling, 1958)

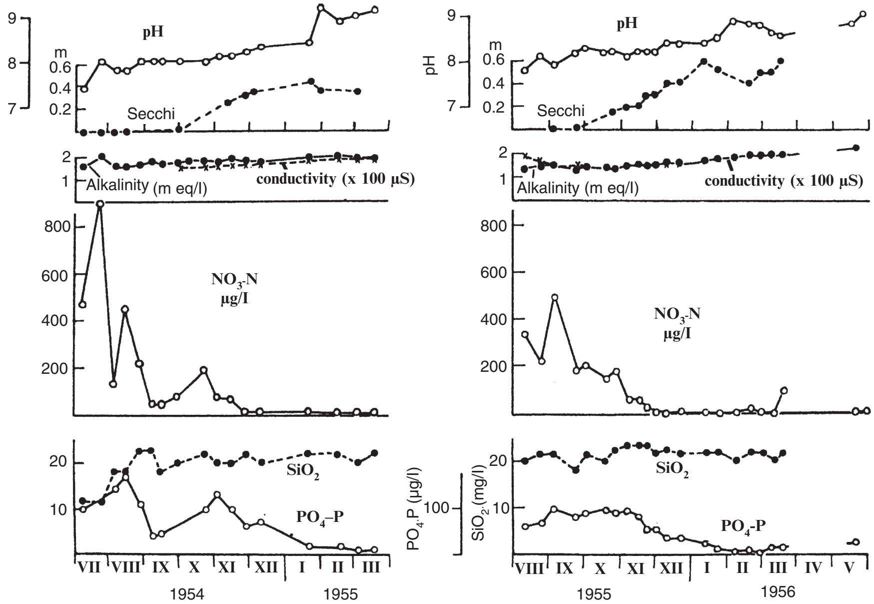

Fig. 10 Seasonal changes in the Blue Nile at Khartoum of transparency (Secchi disc), pH, conductivity (20°C), alkalinity, and three plant nutrients (from Talling & Rzóska, 1967)

7 Plant Nutrients

The nutrients considered below are often suspected of limiting algal production in freshwaters, and can be severely depleted during the growth of phytoplankton in parts of the Nile system. Although the major ions also include important nutrients, which may influence properties of the water as a growth medium, the quantities present are normally much in excess of the amounts incorporated in the algal crops and depletions are not significant. An exception is the requirement for relatively large amounts of carbon dioxide, which often involves appreciable depletions of bicarbonate.

Most analyses of nutrient elements in Nile waters have been confined to the soluble inorganic fraction, from which particulate material was excluded (e.g. by filtration). Some estimations exist of *total phosphorus*, involving a digestion procedure, mainly for the headwater lakes (Talling & Talling, 1965) and a few stations in the Sudan and Egypt (Table 3). However, as pointed out by Golterman (1975), nutrient transport by rivers will often be dominated by the neglected particulate fraction. Further, the suspended silt of the lower Nile has been shown by Elster and Gorgy (1959) to rapidly influence the concentrations of soluble phosphate and nitrate by adsorption and mineralization.

Phosphate is present in relatively considerable concentrations in much of the Nile, considering its status in most regions as an unpolluted river. A major source exists

Table 3 Water characteristics of Nile tributaries

	Lake Edward	Lake Albert	Bahr el Ghazal		← River Sobat →				R. Atbara
Characteristic	22.vi.61 (1)	xi.60–viii.61 (1)	30.xii.53 (2)	4.xii.60 (3)	xii.07–x.08 (4)	10.xii.54 (2)	1.i.61 (3)	2.v.64 (5)	vi.x.07 (6)
Conductivity (k_{20}, µS cm^{-1})	925	720–780	–	100	–	112	110	–	–
As meq l^{-1}:									
Na^+	4.78	3.96	–	–	0.01–0.31	–	–	–	–
K^+	2.30	1.66	–	–	<0.01–0.13	–	–	–	–
Ca^{2+}	0.62	0.45–0.54	–	–	0.36–0.59	0.44	–	–	–
Mg^{2+}	3.93	2.57–2.64	–	–	0.23–0.56	–	–	–	–
$HCO_3^- + CO_3^{2-}$ (alky)	9.85	7.27–7.33	2.14	1.06	0.47–1.01	1.52	1.00	1.15	2.0–2.8
SO_4^{2-}	0.65	0.56–0.94	–	–	'None'	<0.03	–	–	<0.02
Cl^-	1.01	0.93–1.08	<0.06	–	<0.03–0.05	<0.06	–	–	0.05–0.12
As µg l^{-1}:									
Total P	127	120–200	–	–	–	–	–	–	–
$PO_4 \cdot P$	18	120–170	20	25	–	45	63	4	–
$NO_3 \cdot N$	24	4–33	–	25	–	15	80	160	–
As mg l^{-1}:									
Si(x2.1 = SiO_2)	3.0	0.02–0.52	18	12	3.6–10.7	12	14	–	–
pH	9.1	8.9–9.0	7.8	7.4	–	6.8	7.8	7.15	–
Transparency (m)	–	–	1.2	1.6	–	0.35	0.45	0.30	–

(1) Talling (1963); (2) Talling (1957a); (3) Bishai (1962); (4) Beam (1911); (5) Kurdin (1968); (6) Beam (1908).

in the Western Rift near Lake Edward. Here a tributary stream rich in particulate phosphorus was found by Golterman (1973), and some others, analysed by Viner (1975a), contained >200 μg l^{-1} of soluble PO_4-P. The source leads, via the Semliki River (also analysed by Viner, 1975a), to concentrations around 150 μg l^{-1} of soluble inorganic, and total, P in Lake Albert (Talling, 1963; Table 3). Concentrations downstream are much increased from this supply (Talling, 1957a). Some further increase (June) or decrease (December) can occur seasonally in the Sudd swamps and in the Blue Nila at Khartoum, possibly by the control of adsorption equilibria by the level of deoxygenetion or by the control of swamp drainage patterns by changing water levels (Talling, 1957a; Bishai, 1958; Talling & Rzóska, 1967; Hammerton, 1972d), but declined thereafter to <10 μg PO_4-P l^{-1} (Figs. 9 and 10). The first part of this decline may be influenced by hydrological changes upstream, such as the continued decline of flood-water in the Blue Nile and the effects of the Sudd and Sobat discharge in the White Nile. This phase included the initial growth of the major diatom *Aulacoseira granulata* in both rivers, which occurred in a relatively phosphate-rich medium. A progressive decline in phosphate and nitrate in the Roseires reservoir was measured by Hammerton (1972b) for the 1967–1968 inter-flood season; these nutrients also decreased along a longitudinal section towards the dam. The later part of the phosphate decline observed by Talling at Khartoum was undoubtedly due to uptake associated with dense phytoplankton, which now included abundant blue-green algae – especially *Anabaena flos-aquae* f. *spiroides*. Supporting evidence from longitudinal sections upstream on the White Nile is shown in Fig. 8. Besides direct uptake of phosphate by the algae, some adsorption on other suspended particles will occur (Golterman, 1975) and may be affected by the higher pH associated with the algal maxima. Equally speculative is a possibly significant exchange of phosphate between water and bottom sediments, especially in such basins of standing water as the Gebel Aulia reservoir and Lake No, for which analyses of sediments show considerable quantities of phosphate-phosphorus (Drover & Bishai, 1962; Bishai, 1962). Sediment-water exchange in Lake George has been studied by Viner (1975b, c).

For the Main Nile below Khartoum, there appears to be only fragmentary published information on the spatial or seasonal changes in phosphate concentrations. As the dense phytoplankton passing Khartoum does not persist, its mineralization is likely to be an important source of phosphate. However, it may be eclipsed by the Blue Nile silt, especially in the main deposition zone now in upper Lake Nubia, where blooms of blue-green algae – especially *Microcystis* – seem to have been especially dense (Hammerton, 1972b; Entz, 1976). Entz notes some unpublished evidence for a decline in phosphate concentrations from south to north in Lake Nubia-Nasser. Analyses of two 1974 samples from Lake Nasser and Cairo (Table 1) indicate moderate concentrations of total phosphorus. Analyses of reactive inorganic phosphate at Cairo, from November 1941 to August 1942, were tabulated by Abdin (1948a). The range was 20–100 μg PO_4-P l^{-1}, with the lowest values found shortly before arrival of the flood water. Earlier seasonal analyses given by Lucas (1908) were of a similar magnitude, with the highest values from the flood-water period.

Inorganic Nitrogen is mainly made up of ammonium- and nitrate-nitrogen; analyses for nitrite have shown insignificant amounts (e.g. Prowse & Talling, 1958; Bishai, 1962). Concentrations are generally low, and may restrict the growth of some algae unable to fix atmospheric nitrogen (e.g. *Aulacoseira granulata*). The methods often used are likely to be inaccurate in the low concentration range (<100 μg N l^{-1}); thus nitrate was probably underestimated by the phenol disulphonic acid method. However, the following general features appear to be well-established.

Nitrate is an exceptional ionic constituent in that its concentration increases steeply with discharge. This feature is connected with its behaviour as a readily leached soil-constituent and probably its sharp pulse of concentration in many African soils after the onset of the rainy season (Viner, 1975a). Relatively high concentrations, up to 1000 μg NO_3-N l^{-1}, have been found in the flood water of the Blue Nile at Khartoum (Beam, 1906, 1908; Talling & Rzóska, 1967; Sinada & Abdel Karim, 1984a; Fig. 10). The River Sobat, which also carries seasonal flood water from Ethiopia, has been recorded as rich in nitrate by Kurdin (1968), though not by Talling (1957a) or Bishai (1962). Flood water in Egypt (pre-High Dam period) was also reported to be relatively rich in nitrate, as found at Cairo by Abdin (1948a). The decline in concentration at Khartoum after flood levels pass is probably accentuated by the growth of *Aulacoseira granulata*, which in both rivers may be ended by the depletion of nitrate (Prowse & Talling, 1958; Talling & Rzóska, 1967). A relationship between nitrate depletion and *Melosira* growth is also shown by a longitudinal section along the Gebel Aulia reservoir in October 1954 (Fig. 8). Hammerton (1972b) noted declines in both time and space for the Roseires reservoir in 1967–1968, and Entz (1976) refers to evidence for a decline in nitrate concentrations from south to north along Lake Nubia-Nasser.

In the headwaters, excluding the Blue Nile in flood, the measured concentrations of nitrate are generally low (<60 μg NO_3-N l^{-1}). Nitrogen-limitation of phytoplankton production may be widespread in the headwater lakes and elsewhere in African freshwaters (Talling & Talling, 1965; Moss, 1969; Viner, 1972). Under stratified lake conditions, higher concentrations of nitrate can appear in the deeper layers of lakes Victoria (Talling, 1966; Hecky, 1993) and Albert (Talling, 1963), provided that deoxygenation is not complete and persistent.

Ammonium-nitrogen has been generally recorded in concentrations below 100 μg l^{-1}, which are often comparable with the corresponding concentrations of nitrate-nitrogen. A product of organic decay, it is relatively abundant in swamp water as in the Sudd (Talling, 1957a; Bishai, 1962; Rzóska, 1974), where the main river channel is also enriched. Increases are also typically present in the deeper, less oxygenated layers of stratified lakes, such as Victoria (Talling, 1966) and Edward (Beadle, 1932; Damas, 1937). High concentrations may occasionally appear in surface waters from the decay of dense water-blooms of blue-green algae. One example, which also involved a pulse of nitrate, was observed in fishponds at Gordon's Tree near Khartoum which were filled with water from the nearby White Nile (Talling, unpublished). Metabolic exchanges of NH_4-N have been studied intensively in L. George, including rapid uptake by the dense phytoplankton (Viner, 1972) and diurnal patterns of excretion by zooplankton (Ganf & Blažka, 1974).

Silicon is present in dissolved form as silicic acid, $Si(OH)_4$ and (at higher pH) its derivative $SiO(OH)_3^-$. In many analyses it is expressed as the equivalent concentration of silica (SiO_2), the form in which it is incorporated into diatoms and constitutes the chief biological sink in the Nile system. Concentrations in the headwater lakes, except Lake George, are generally lower than those (typically 10–24 as mg SiO_2 l^{-1}) in the river stretches of the Sudan and Egypt. The difference results partly from depletion by planktonic diatoms in water-bodies of long retention time, and partly from the greater opportunities for dissolution and transfer of ubiquitous rock and soil silicates in running waters. The mobility of silica in tropical soils subject to laterization is well known, and it is perhaps significant that particularly high concentrations of silica are found in the Bahr et Ghazal tributary of the White Nile which drains a lateritic area (Table 3; Talling, 1957a). Because of such effects, a close parallelism between the contribution of silicon and phosphate-phosphorus as products of rock weathering – assumed by Golterman (1973, 1975) – seems improbable. A longitudinal section of the White Nile (Talling, 1957a) suggested a significant enrichment from the minor torrents which contribute to the Bahr et Gebel (Mountain Nile; written as Bahr el Jebel in Sudan) as it descends from the Uganda plateau to the Sudan plains. Enrichment must also occur to the Blue Nile from torrential tributaries in the Gorge region (Table 2).

Depletions of soluble Si induced by diatom growth are conspicuous in several headwater lakes where the prevailing concentrations are relatively low. The annual maximum of *Aulacoseira nyassensis* var. *victoriae* in the offshore waters of Lake Victoria produced an appreciable reduction, from about 4.5 to 3 mg SiO_2 l^{-1} in 1961 (Talling, 1966). Still lower concentrations were found in later years (Hecky, 1993) and are frequent in inshore channels and bays where planktonic diatoms (including *A. ambigua*) are abundant, but values below 1 mg SiO_2 l^{-1} – more likely to limit diatom growth – have been rarely recorded (Lungáyia et al., 2000). Such low values do appear typical of Lake Albert (Talling, 1963), where diatoms dominate the phytoplankton; an alternative abiogenic origin was also suggested by Talling. In this elongate lake, the concentrations tend to decrease along the axis away from the Semliki inflow. Downstream, in the Gebel Aulia reservoir, a longitudinal decline was found by Prowse and Talling (1958) during the development of large populations of *Aulacoseira granulata* (Fig. 8). A seasonal depletion occurred in the same month (October) at a station below the dam near Khartoum (Fig. 9), and was of roughly the same magnitude (10 to 5 mg Si l^{-1}, or approx. 20 to 10 mg SiO_2 l^{-1}). No such depletion, attributable to diatom growth, was recognisable at a corresponding station on the Blue Nile during 1953–1956, although some decline there was found by Sinada and Abdel Karim (1984a) in later years. At Cairo, Abdin (1948a) found that concentrations declined from 12 to 2.4 mg SiO_2 l^{-1} in the period of 1941–1942 between successive flood-waters, but the part played by diatoms is conjectural. Considerably higher concentrations (26 to 13 mg SiO_2 l^{-1}) are listed by Hurst (1957) for the years 1933–1936. Measurements made after the High Dam do not appear to be published (except here, Table 1).

Iron is present in considerable concentrations in waters of the White Nile in and below the Sudd swamps, where values (approximating total iron in filtered samples) increase sharply in the main river as well as in swamp waters (Talling, 1957a; Bishai,1962). The increase can be attributed to the release of ferrous iron under reducing conditions and supply of organic complexing substances, the latter probably correlated with an increase of colour.

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River Nile Pollutants and Their Effect on Life Forms and Water Quality

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Abstract Data on concentrations of toxic substances and their impact on aquatic organisms and water quality are summarized. Most information deals with Egypt; few studies have been done in Sudan, Ethiopia and Tanzania. Egypt is the most populous, agricultural and industrial country in the basin. Therefore, most sewage release to the river takes place in Lower Egypt. Lakes in northern Egypt are affected by drainage of polluted water and this affects the diversity of their fish, phytoplankton and other microorganisms. Nile pollutants are derived from sources such as industrial wastewater, oil pollution, municipal wastewater, agricultural drainage, and include natural cyanotoxins. In order to monitor pollutants, test organisms are needed in which these compounds can be traced at the tissue level. Various fish, shellfish, aquatic animals, aquatic plants and algae are used for this purpose.

1 Introduction

The ancient Egyptians laid down the foundations of conservation by protecting the three resources of the environment: water, soil and air. They paid special attention to preserving the River Nile. A doctrine still deeply rooted in every Egyptian is that he will not enter paradise if he polluted the Nile. This report deals with the identification and characterization of pollutants of River Nile water. The different sources of pollution that affect the water depend on human activities such as use pattern, population density, industry, sanitation systems, and on social and economic conditions in the countries of the basin. But even in the source lakes on the East African plateau, changes are taking place. Mwanuzi et al. (2003) stated that Lake Victoria has undergone substantial, mostly negative changes, especially over the last 30 years. One of the driving factors of these is nutrient enrichment from human activities, causing eutrophication. This has been associated with, among other things, a rapid proliferation of water hyacinth, algal blooms, and a general disruption of the ecosystem.

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2 Sources of Pollution

The Nile receives pollution from different sources in all countries along the river, but especially from industrialized areas. Industrial wastewater contributes most pollutants to the river. However, oil pollution, municipal wastewater and agricultural pollution also contribute heavy metals, pesticides, herbicides, and microbes to the water. The blooming of cyanobacteria, elicited by excess nutrients (eutrophication), leads to the production of cyanotoxins, which affect the health of fish and may poison humans.

2.1 Industrial Wastewater

The industrial sector is an important user of water and a contributor to pollution. Egypt is the most industrialized country of the Nile and faces rapidly increasing deterioration of its surface and groundwater due to increasing discharge of polluted domestic and industrial effluents. Egyptian industry uses 638×10^6 m^3 y^{-1} of water, of which 549×10^6 m^3 y^{-1} is discharged back to the river. Industrial activities are concentrated around big cities such as Cairo and Alexandria, which use 40% of the total water (Wahaab & Badawy, 2004), but agro-industrial and small private industry in Upper Egypt recently started to contribute to Nile pollution too. Sugar cane industries exert significant influence on water quality in the south of Upper Egypt, while hydrogenated oil and onion-drying factories affect water quality in the north of Upper Egypt (Wahaab & Badawy, 2004). Food processing industry is responsible for more than 50% of biological oxygen demand (BOD) while chemical industry is responsible for more than 60% of heavy metal discharges. The high BOD load from food processing is attributed to ten sugar factories between Aswan and Cairo, for which a total BOD load of 490 t day^{-1} was estimated in 1980.

2.1.1 Heavy Metals

During its transit of Egypt, the Nile receives numerous non-point and point source discharges. Lead and cadmium were detected in raw Nile and in finished drinking water of four treatment plants in greater Cairo between 1993 and 1994 (Mohamed et al., 1998). They found levels of 29.6 μg l^{-1} for lead and 4.15 μg l^{-1} for cadmium, but Gomaa (1995) found concentrations in Nile water 14 and 24 times greater than those obtained by Mohamed et al. (1998). Elsokkary and Müller (1990), Zayed et al. (1994), Gomaa (1995), Soltan and Awadalla (1995) and Mohamed et al. (1998) reported monitoring results from Greater Cairo; their data are summarized in Table 1.

The problem of wastewater disposal has tremendously increased since the expansion of industrialization in Egypt. The discharge of large quantities of wastewater without treatment affects the use of river water for both drinking and irrigation purposes, and has a damaging effect on aquatic life. Wastewater from electroplating industries in Helwan area (south Cairo) is characterized by a high content of Cr, Zn, Cu, Fe and Mn (El-Rafei et al., 1987). Fayed and Abd El-Shafy (1985) determined the levels of Cu, Zn, Cd, and Pb in water, sediment, and aquatic plants from the

Table 1 Range of lead and cadmium in River Nile water

	Concentration range (μg l^{-1})	
Source	Lead	Cadmium
Sherief et al. (1980)	ND–0.001	ND–12
Khallaf et al. (1994)	1.0–3.81	0.01–0.07
Elsokkary and Müller (1990)	14–327	0.09–11.8
Zayed et al. (1994)	4–20	0.2–0.4
Gomaa (1995)	ND–1100	ND–80
Soltan and Awadalla (1995)	16–40	1.0–4.0
Mohamed et al. (1998)	9.6–26	4.5–7.1
Ali and Soltan (1999)	0.003–0.018	0.001–0.003
Rashed (2001a)	ND–0.005	ND–10

ND: not detected

Nile and its branches at sites characterized by heavy industrialization and dense population. The results revealed that concentrations in sediments were, in most cases, much higher than in plants. Metal content in plants downstream of wastewater discharge points was usually higher than in plants upstream of these points. Dekov et al. (1997) collected samples from sediment, suspended matter, water and ground water at 12 sites in the Nile valley, around Sohag (Central Egypt) and close to Aswan High Dam. Dissolved transport is a major process for Ca, K, Sr, Zn, Cu, Ni and V. Mn, Fe and Cr are mainly carried by suspended matter.

In Lake Victoria too, concentrations of Pb and Cd were high at the majority of the sites of the lake (Ljung, 2002). This is alarming since these metals are among the most hazardous to humans and the environment. Mercury contamination from processing of gold ore on the southern shores is currently considered among the most emergent phenomena of chemical contamination (Focardi et al., 2006).

2.1.1.1 Effects of Heavy Metals on Phytoplankton

Heavy metal pollution affects water quality and the distribution and diversity of phytoplankton. Shehata and Bader (1985) studied the changes of phytoplankton density in relation to physicochemical characteristics along the Nile. They found three major phytoplankton groups: green algae, blue-green algae, and diatoms. Statistical analysis revealed significant positive correlations between chlorophyll-*a* content and concentrations of phosphorus and nitrate. Phytoplankton diversity, primary production, ammonia, and nitrite content revealed no pollution, however. Ali and Abdel-Salam (1999) described the use of algae as bioindicators of pollution by industrial metals in the Nile. Phytoplankton algae varied with waste type and with environmental and growth conditions. In samples containing ceramic waste, Euglenophyta and *Cyclotella* sp. (Bacillariophyta) were potential indicator species of pollution, while in samples containing metal waste, *Cyclotella* sp. was dominant. Under laboratory conditions, *Scenedesmus* sp., *Actinastrum hantzschi*i (Chlorophyta), *Oscillatoria limnetica* (Cyanophyta) and *Nitzschia linearis* (Bacillariophyta) were also potential indicators of pollution.

2.1.1.2 Effects of Heavy Metals on Fish

Fish may accumulate toxic metals, coming from such sources as accidental spillage of chemical wastes, precipitation contaminated with air-borne pollutants, discharge of industrial or sewerage effluents, agricultural drainage, domestic wastewater, and gasoline from fishery boots (Jent et al., 1998; Rashed, 2001a). In Lower Egypt, Morshdy et al. (1999) found that the concentrations of Hg, Cd and Pb in *Bagrus bayad* muscle ranged from 0.026 to 0.391, 0.028 to 0.053 and 0.022 to 0.654 μg g^{-1} wet wt., respectively. Up to 24% and 6% of all samples exceeded the permissible limit set by FAO/WHO for Cd and Pb, but none exceeded the limit for Hg. Pollution of water by heavy metals impairs growth and alters liver contents of glycogen and triglycerides as well as the activities of metabolic enzymes of the catfish, *Clarias gariepinus* (El-Ezabi & El-Naggar, 2004). In Lake Nasser, *Oreochromis niloticus* was used as a bioassay organism (Patin, 1984). The trace elements Co, Cr, Cu, Fe, Mn, Ni, Sr and Zn were determined in muscle, gills, stomach, intestine, liver, vertebral column and scales, as well as in the aquatic plant (*Najas armata*), sediment and lake water (Awadallah et al., 1985) (Table 2). In spite the presence of most of the heavy metals in the tissues of the fish, permissible levels for human uses were recorded (Rashed, 2001a).

2.2 Oil Pollution

The Nile is used for water supply and to transport different types of cargo, including oil and oil products. In addition, many factories and oil distribution centres are located along its shores. Oil pollution may also derive from barges, tankers and boats on river or canals, from industrial wastes, metallurgical industries, engineering work, garages, or any places using lubricating or fuel oils (El-Sheekh et al., 2000). Process and cooling water is pumped from the

Table 2 Heavy metal concentrations (μg l^{-1}) in fish from the River Nile

Fish	Cd	Cu	Hg	Ni	Pb	Zn	Reference
Bagrus bayad	0.028–0.053	–	0.026–0.391	–	0.022–0.654	–	Morshdy et al. (1999)
Karmout	0.02–0.14	0.61–2.1	–	0.92–2.69	0.17–0.28	0.46–2.09	Khallaf et al. (1994)
Oreochromis niloticus	–	0.099	–	–	0.095	–	Awadallah et al. (1985)
Oreochromis niloticus	0.03–0.12	0.34–2.49	–	1.04–4.04	0.046–0.05	0.39–5.08	Khallaf et al. (1994)
Oreochromis niloticus	0.088	–	–	0.25	0.95	–	Rashed (2001b)

Nile and returns to it after use (Moursy, 1983). Oil pollution may also take place through the discharge of sewage and some industrial wastewater (McGechan, 1973; Anderson et al., 1974; Simpson, 1973; Cross & Lawson, 1974; El-Sheekh et al., 2000). Oil compounds affect the taste and odour of drinking water and may be harmful to fish and human health (Mackie et al., 1972; Kleopfer & Fairless, 1972; Novak et al., 1973; Connell, 1974; Howgate et al., 1977; Moursy, 1983).

The toxicity of oils is caused by unsaturated hydrocarbons, naphthenic acids and other compounds containing aromatic groups and nitrogen (Baker, 1970). The actual toxic dose is related to the amount of dissolved non-volatile material (Ostgaard, 1994). Moursy (1983) surveyed the oil and grease along the River Nile and found that the top area was around Lake Nasser port at Aswan, followed by oil distribution centres and ship-waiting areas at Assiut, boat docks, shipyards, an electric power station at Cairo, and factories along Rosetta branch.

2.2.1 Effects of Oil Pollution on River Nile Organisms

Oil pollution affects the abundance, species composition, productivity and physiological condition of a variety of biota (Hao, 1996). El-Sheekh et al. (2000) studied the growth and metabolic activities of algae in the Nile. *Chlorella homosphaera* and *C. vulgaris* were affected differently by oil pollution. The first species was more tolerant, presumably because of previous acclimation to polluted locations, while *C. vulgaris* was hit severely and occurred only at non-polluted locations. The assemblage of different algae at two locations, one polluted and the other non-polluted with oil, indicated that Chlorophyta are more tolerant than Cyanophyta and Bacillariophyta. El-Sheekh et al. (2000) found that oil pollution decreased phytoplankton standing crop in polluted locations. El-Dib et al. (2001) found that total algal counts, growth rate and chlorophyll-*a* decreased under fuel oil treatment. The presence of crude oil or its refinery products (solar or lubricating) in the culture media of algae inhibited growth, proteins and nucleic acid content.

3 Municipal Wastewater

The population increase in countries along the Nile Rive, especially Egypt, results in more wastewater and this requires governments to increase the number of water treatment plants. The constituents of concern in domestic and municipal wastewater are: pathogens, parasites, nutrients, oxygen demanding compounds and suspended solids. Toxic substances such as heavy metals and organic micro-pollutants also occur, due to the mixing of domestic with industrial and commercial activities. The bulk of treated and untreated domestic wastewater is discharged into agricultural drains. All drains of Upper Egypt flow back to the Nile and many irrigation canals are contaminated with pollutants from domestic sources (APRP, 2002). For details on microbial pollution, see Rabeh (this volume).

4 Agricultural Drainage

Drainage water seeping from agriculture fields is a non-point source of pollution. Such non-point sources, however, collect and concentrate in agricultural drains to become point sources to the river, the northern lakes, and irrigation canals. Non-point sources may also influence ground water quality. Major pollutants in agricultural drains are salts, nutrients, pesticide residues, pathogens and toxic organic and inorganic pollutants (APRP, 2002). In Egypt only, the Nile from Aswan to the delta barrage receives wastewater from 124 point sources, of which 67 are agricultural drains; the remainder are industrial sources.

4.1 Organic Pollution

A number of studies assess Nile pollution by pesticides and heavy metals (Mohamed, 1998; El-Kabbany et al., 2000), and pollution by organic chemicals in delta lakes and sediments in Egypt (El Sabrouty et al., 1994). Drainage water was highly polluted and contained more pesticide residues than canal waters. El-Kabbany et al. (2000) confirmed the presence of 16 organochlorine pesticides in most of the water samples; the percent positive samples followed the order endrin > total BHC > total DDT (1,1,1-trichloro-2,2-bis(4-chlorophenyl)ethane) > endosulfan > heptachlor epoxid > heptachlor. These pesticide residues represent different chemical classes.

El-Gendy et al. (1991) analyzed residues of organochlorine insecticides and polychlorinated biphenyls (PCBs) in water from seven different locations along the Nile and its branches. The data showed high concentrations at Kafr El Zayat city and indicate that Rosetta branch was more polluted than the Damietta branch. *p,p′*-DDE (1,1-dichloro-2,2-bis(4-chlorophenyl)ethylene) and γ-HCH isomers dominated the DDTs and HCHs distributions at all locations.

Yamashita et al. (2000) reported that among different organochlorine pesticides analyzed, *p,p′*-DDE was the most predominant in fish (7.6 to 67 ng g^{-1} wet wt.), sediments (3.2 to 432 ng g^{-1} dry wt.) and suspended solids (5.3 to 138 pg l^{-1}). However, in the dissolved phase of water samples hexachlorocyclohexane (HCH) compounds predominated (α-HCH, 71 to 2,815 pg l^{-1}). Concentrations of organochlorine pesticides, except chlordane, were higher in Manzala Lake than in the River Nile. Concentrations of organochlorine pesticides in fish corresponded with those in sediments from each location. Comparison of organochlorine concentrations in Nile River water with those reported in earlier studies suggested a decrease in concentrations during the last decade. The distribution of HCHs in Lake Manzala was similar to the technical mixtures, suggesting recent use. The major environmental impacts on Lake Manzala are due to direct discharge of untreated wastewater, discharge of irrigation water from drainage canal and land reclamation. In general, levels of organochlorine insecticides in Nile water are within safety margins and compares to the permissible limits for drinking waters (Badawy, 1998).

Barakat (2004) reviewed the persistent toxic substances in the environment of Egypt, and stated that the data available represent limited studies or hot spot situations. Most data was obtained in the 1980s and levels usually show an extremely large span of concentrations. Apparently, data obtained is the result of individual research work rather than of the existence of monitoring networks. In most cases, it is not possible to assess the environmental significance of the reported values, as they do not correspond to standard sampling techniques. In addition, variable results as a function of analytical methods used make data difficult to compare and use in assessments. Nevertheless, compounds proven to be of concern are DDT, polychlorinated biphenyls (PCBs), γ-HCH, polycyclic aromatic hydrocarbons (PAHs), hexachlorobenzene (HCB) and organotin compounds. Other compounds are suspected to be ubiquitous but data are lacking. A number of reports have identified potential sources of pesticides to the Egyptian Mediterranean and possible locations for contamination by organochlorine pesticides, HCB, HCH and PAHs. Localized inputs of PTS have been identified from freshwater discharges in coastal areas (e.g. Nile estuary and coastal lakes) and near sewage outfalls of industrialized and populated cities. Based on the limited data available, present levels of organochlorine pesticides would not adversely affect marine and freshwater environments. Levels in fish were generally below the acceptable tolerance levels for human consumption (Yamashita et al., 2000). Osfor et al. (1998) found high significant differences in levels of lindan, heptachlor, endrin, dieldrin, *p*,*p*′-DDE and propoxur in River Nile water when compared with that of Manzala Lake. Levels of lindan, endrin, malathion and diazinon were significantly higher in soil sediment of Manzala Lake, while the levels of heptachlor, aldrine, *p*,*p*′-DDE, DDT, parathion, propoxur and zectran were significantly higher in soil sediment of River Nile.

5 Cyanotoxins

Cyanobacteria often show extraordinary development (blooms) in eutrophic and hypertrophic lakes and rivers. Increased eutrophication due to agricultural, municipal and industrial runoff contributes much to the growth of such species, many of which are toxin-producers. Intoxicated blooms degrade drinking or recreational water and increase the risk of poisoning to animals and humans (Carmichael, 2001 Carmichael et al., 2001). Toxic cyanobacteria include *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Microcystis*, *Nodularia*, *Nostoc* and *Oscillatoria* (Haider et al., 2003). Cyanotoxins exist in a wide diversity of chemical forms, and include cyclic peptides and alkaloids. Among the cyclic peptides are microcystins and nodularins. The alkaloids include anatoxin-a, anatoxin-a (S), cylindrospermopsin, saxitoxins (STXs), aplysiatoxins and lyngbyatoxin (van Abeldoorn et al., 2007). Cyanotoxins are divided into hepatotoxins (e.g. microcystins, nodularins, cylindrospermopsins), neurotoxins (e.g. anatoxin-a, homoanatoxin-a, saxitoxins) and dermatotoxins (e.g. lyngbyatoxins, aplysiatoxins). These toxins are found mainly in planktonic cyanobacteria, but some information is available about benthic species, capable of producing anatoxins, microcystins or saxitoxins (Hamill, 2001; Verschuren et al., 2002; Gugger et al., 2005).

Abdel-Rahman et al. (1993) first isolated and characterized microcystins (MCYSTs) from *Microcystis aeruginosa* in Egypt. Most studies on toxic Cyanobacteria in Egyptian freshwaters deal with planktonic species in the river (Brittain et al. 2000, Mohamed & Carmichael, 2000), but the toxicity of benthic mats of cyanobacteria formed on river and irrigation-canal sediments was studied by Mohamed et al. (2006). They described the species composition and toxicity of extracts of 19 species using an *Artemia salina* assay, mouse bioassay and enzyme linked immunosorbent assay (ELISA). They showed that all the 19 species were toxic. *Calothrix parietina* and *Phormidium tenue* caused toxicity to mice with neurotoxic signs appearing within 12 h after injection. Five species showed hepatotoxic effects to mice within 6 h. ELISA showed that all extracts with hepatotoxic effects to mice contained high levels of microcystins. HPLC analysis revealed that these extracts contained two peaks, corresponding to microcystin-YR and -LR. Benthic species should thus be considered side by side with planktonic species during monitoring of toxic cyanobacteria, particularly the River Nile which is the main source of drinking water in Egypt. Cyanotoxins can accumulate in different organisms in the aquatic habitat. Mohamed (2001) indicated that they may accumulate in primary consumers like *Daphnia* with a possible transfer to the top of the aquatic food web in irrigation canals.

6 Water Quality and Pollution of the River Nile

In spite of discharging of different kinds of wastes into the River Nile, the water quality does not yet exhibit pollution levels high enough to create health risks except locally, where the presence of Coli bacteria indicates unsafe levels for direct use of such water in irrigation and fisheries (APRP, 2002). The high dilution factor and the high self-assimilation capacity of Nile water makes that the pollution of the River Nile is only worrisome near to cities and industrial discharges.

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Bacteria and Viruses in the Nile

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Abstract Microbial water quality along the River Nile varies with location and depends on flow rate, water use, population density, sanitation systems, domestic and industrial discharges, demands for navigation, and agricultural runoff. In Lake Victoria, bacterial indicators of sewage pollution and bacteria, morphologically and functionally close to *Desulfovibrio*, *Desulfobacter* and *Desulfococcus* have been detected. The growing population of Bahir Dar Town increasingly pollutes Tana Lake. The microbial load of the Blue and White Niles increases steeply at Khartoum, Sudan. Microbial conditions in Egypt often meet established water quality standards, but some areas are polluted by ca 34 industrial facilities, discharging to the Nile between Aswan and Cairo. Enteroviruses were isolated with a high frequency and positive results were high along 300 km in the south of Egypt. Deterioration is rapid in front of Cairo and in the delta (Damietta and Rosetta Branches), especially during low flow, due to municipal and industrial effluents and agricultural drainage. Here, the bulk of treated and untreated domestic wastewater is discharged to agricultural drains. Total coliform (TC) bacteria reach 10^6 (most probable number, MPN 100 ml^{-1}) in many delta drains, 200 times the Egyptian standard of 5×10^3 MPN 100 ml^{-1}. The Damietta Branch receives nutrients (primarily ammonia) and organics from the Delta Company for Fertilizer and Chemical Industries in Talkha, and agricultural drainage water in the vicinity of the Faraskour Dam. Raw sewage from villages also drains to the Damietta Branch. At ca 120 km downstream from the Delta Barrage, the Rosetta Branch receives polluted inflows from five drains (El-Rahawy, Sobol, El-Tahreer, Zaweit El-Bahr and Tala) and from industry at Kafr El-Zayat.

Abbreviations CBVs: Coxsackie B viruses; Pfu: Plaque-forming unit; WTPs: Water treatment plants; WQI: Water quality index; NRI: Nile Research Institute; MPN: Most probable number; HD: High Dam; TC: Total coliforms; Cfu: Colony forming units; FC: Faecal coliforms; FS: Faecal streptococci; TCC: Chromocult Coliform Agar; SASF: Sulphite-reducing anaerobic spore formers; TBCs: Total

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Bacterial Counts; NBI: Nile Basin Initiative; AHD: Aswan High Dam; WHO: World Health Organization

1 Introduction

The aim of this chapter is to discuss bacteria and viruses in the Nile. Much more is known about the Nile in Egypt than upstream, but some information on Lake Victoria, Lake Tana, and the White and Blue Niles is available. Such information is needed to evolve methods for an effective management of the river. A major problem in Egypt is that, because population and industry are centered on the Nile valley, all surface waters continually receive domestic sewage, agricultural drainage and industrial effluents (Abdel-Gawad, 1995; Dewedar et al., 1995; Rabeh, 1999; Rabeh et al., 1999; El-Shenawy et al., 2000; Sabae & Rabeh, 2000; Rabeh, 2003; Rabeh & Azab, 2006; Amer, 2007; Rabeh et al., 2007; Sabae & Rabeh, 2007).

The Egyptian Nile and its two branches are divided into four segments as follows:

1. Upper Egypt Segment
2. Greater Cairo Segment
3. Damietta Branch Segment
4. Rosetta Branch Segment

Each segment will be treated separately. In addition, information on Lakes Tana and Victoria, the White and Blue Niles, and the High Dam Lake (Lake Nasser–Nubia) is given.

2 Lakes Tana and Victoria

Little information is available on the bacteriology of Tana Lake. Most of the lake still appears to be in a rather pristine condition, yet a threat is posed by the growth of social and economic activities in the region of Bahir Dar. Here, the current practice is one of discharging untreated industrial, municipal and domestic waste into the lake, with adverse effects of this on the sustainability of the use value of the lake and on the livelihood of traditional communities living around the lake (Teshale et al., 2002). The major point sources of contaminants are pit latrines and septic tankers at the level of households, hotels, hospitals, municipalities, and recreational sites. As a result, coliforms (more than 180 cfu $100\,\mathrm{ml}^{-1}$) and *Escherichia coli* have been confirmed at the periphery of the southeastern and southwestern parts of the lake, close to the sources of pollution (Adane, 2005).

Compared to Tana, more information is available on the bacteriology of Lake Victoria.

3 Lake Victoria

3.1 Bacterial Indicators of Sewage Pollution

Bacterial indicators near the shore of Lake Victoria at Port Bell range from 11 to 500 MPN 100 ml^{-1}, 0.3 × 10^3–8 × 10^3 MPN 100 ml^{-1}, 2 × 10^4–23 × 10^4 cfu 100 ml^{-1} and 0.4 × 10^2–13 × 10^2 MPN 100 ml^{-1} for faecal coliforms (FC), total coliforms determined with lauryl sulphate broth (TCM), total coliforms determined with Chromocult Coliform Agar (TCC), and sulphite-reducing anaerobic spore formers (SASF) (Byamukama et al., 2000). The concentration of FC at different fishing grounds of Lake Victoria ranges from <1 cfu 100 ml^{-1} water to >600 cfu 100 ml^{-1}. The maxima correspond with storm events and catchment-based activities such as urban discharge. FC bacteria concentrations, however, are lower than the US class A (WW) standard of 200 cfu 100 ml^{-1} water (Werimo, 2006).

3.2 Pathogenic Bacteria

Lake Victoria is used for bathing, washing, and watering livestock, leading to contamination with human and animal waste. However, *E. coli* contamination could not be detected near its shores at Port Bell from July to September 1998 (Byamukama et al., 2000). Investigation of a 1997 cholera outbreak in rural Western Kenya implicated water from Lake Victoria as a risk factor (Shapiro et al., 1999). From May 1997 through April 2001, drinking Lake Victoria water (the major source of water for all uses in rural Western Kenya) caused bloody diarrhea. The illness (27%) could have been averted by avoiding drinking lake water (Brooks et al., 2003).

3.3 Bacteria Involved in Biogeochemical Cycles

Sulphate-reducing bacteria (SRB) in water and sediment of Lake Victoria along the shores of Mwanza municipality resemble *Desulfovibrio*, *Desulfobacter* and *Desulfococcus* species. The MPNs for acetate-utilizing SRB were higher in sediments at water hyacinth-infested stations and at the Mirongo River mouth than in open water. Stations infested by aquatic weeds and the Mirongo River mouth had more formate-utilizing SRB than an offshore and open water station. Water hyacinth-infested stations had a slightly higher mean population, followed by the Mirongo River mouth. The offshore and open water stations had the lowest population of formate-utilizing SRB. Lactate-utilizers were the dominant SRB species in sediments at the water hyacinth-infested and Mirongo River mouth stations, while offshore, MPNs for lactate-utilizing SRB were much lower than those for acetate and formate-utilizing SRB. In addition, SRB densities correlated positively with nutrients in the sediments. The highest positive correlation was between

SRB and PO_4-P (r = 0.93) followed by SO_4-S (r = 0.83); the lowest was with NO_3-N (r = 0.17) (Muyodi et al., 2004).

4 White and Blue Niles

4.1 Total Bacterial Counts

Bacteriological examination of White Nile water at Melut, Upper Nile province, South Sudan during October–November 1983 showed high (10^7 cfu ml^{-1}) TBCs compared with the middle White Nile (Mascher, 1987). Bacteriological data at Khartoum in 1997–2003 (NBI, 2005) revealed higher TBCs (1.7×10^2–2.1×10^3 cfu 5 ml^{-1}) in the White than in the Blue (90–1.2×10^3 cfu 5 ml^{-1}) and main Nile (1.7×10^2–1.7×10^3 cfu 5 ml^{-1}).

4.2 Bacterial Indicators of Sewage Pollution

Bacteriological examination around Khartoum revealed contamination with TC and FC, with the White Nile as contaminated as the Blue Nile (Abdel-Magid et al., 1984). The White Nile at Melut, South Sudan, showed a high incidence of coliforms (92.8%) and of *E. coli* (31%), but the middle White Nile had a better bacteriological quality (Mascher, 1987). TC and FC of the Blue and White Niles at Khartoum in January–July 1984 was higher than upstream in the White Nile, while the east bank of the White Nile was more contaminated than the west bank. The microbial load of the rivers increases conspicuously as they pass through Khartoum (Mahgoub & Dirar, 1986). In the Blue, White and Main Nile, TC and FC peak during the flood, due to wash-in of faecal residues from fields, toilets and sewers (NBI, 2001). El-Hassan (2002) conducted a survey at Khartoum to identify sources of pollution. The highest value of coliforms in the Blue Nile (10×10^3 100 ml^{-1}) was at the confluence (17×100 ml^{-1}); bacteria in the White Nile were uncountable. Also, a survey at Khartoum detected colon bacteria (*E. coli*) in all White Nile samples, which were more polluted than the Blue Nile (Saeed, 2004). Data by the Khartoum State Water Corporation in 1997–2003 showed that the highest contamination (10–30 cfu 100 ml^{-1}) was in the White and main Nile (0.0–20 cfu 100 ml^{-1} TC); lowest values occurred in the Blue Nile (0.0–10 cfu 100 ml^{-1} TC). The reasons for this are that the White Nile is wide, and its speed and discharge lower than that of the Blue Nile. Furthermore, the presence of weeds, organic and colloidal material facilitate the growth of bacteria. Nine sampling sites in the Blue and White Niles and their confluence during 2002 and 2004 again showed the White Nile as more polluted than the Blue Nile (NBI, 2005). FC in northern Sudan ranged from 100 to 200×100 ml^{-1} during May, the hottest month, and from 210 to 625×100 ml^{-1} during October, the end of the rainy season. The higher counts in the wet season reflect the 'flushing' effect of the rains. The FC counts are not just from the local environment and rainfall, but are derived from the wider catchment and from tributaries (Musa et al., 1999).

5 The High Dam Lake

5.1 Total Bacterial Counts

During June–July 1975, TBCs of Lake Nubia in Sudan were surveyed from Wadi Halfa to Songa, 470 km south of the High Dam (HD). Samples from five stations (Table 1) showed that the south of Lake Nubia had lower TBCs than the north. In most cases, TBCs increased with depth. This aspect was also clear in Lake Nasser. Moreover, mean TBCs in Lake Nubia were higher than in Lake Nasser, either because more nutrients are carried by the Nile from Sudan or because recently drowned vegetation, provides bacteria with organic matter, encouraging their reproduction (Saleh, 1976).

From the main axis of Lake Nasser between Aswan High Dam (AHD) and Abu-Simbel, two sets of samples were taken; the first was collected from winter to autumn 1974, the second from winter to autumn 1984. The lowest TBC at 22°C (saprophytic bacteria) and 37°C (parasitic bacteria) was detected in winter. The highest was in summer (Table 2), and counts tended to increase by early spring. In summer, a renewal of nutrients carried by the flood provides bacteria with extra organic matter. There also was a decrease in TBC from south to north, but they increased again near the High Dam, where decaying material from fisheries activities abounds. The ratios of TBCs at 22°C and 37°C were over 1.0 and were narrow in summer and autumn, but wider in winter and spring (Elewa & Azazy, 1986). Twelve years later, TBCs in Lake Nasser ranged between 4×10^3 and 187×10^6 and between 3×10^3 and 52×10^3 cfu ml^{-1} at 22°C and 37°C. The highest counts were during spring, at high temperatures and abundant organic matter (Rabeh et al., 1999). TBCs at 22°C in subsurface water were from 0.12×10^5 cfu ml^{-1} at Khor Korosko during autumn to 933×10^5 cfu ml^{-1} during spring at Khor El-Allaqui. Those at 37°C varied from 0.06×10^5 to 650×10^5 cfu ml^{-1} at Khor El-Allaqi during autumn and spring. Similar results were obtained by Saleh (1976), Elewa

Table 1 Total bacteria Counts (TBCs ml^{-1}) and sulphate-reducing bacteria (SRB) (MPNs 100 ml^{-1}) at different depths and in bottom water of Lake Nubia during 1975

Bacteria	TBCs ml^{-1}			SRB 100 ml^{-1}		
Layers stations	0.0	10 m	Bottom	0.0	10 m	Bottom
Songa	370	780	75×10^4	93	93	2.4×10^6
Aterry	260	440	1.6×10^6	3.6	3.6	1.1×10^6
Section 6	700	580	1.4×10^6	21	93	2.4×10^6
Sections 3	870	900	1.6×10^6	7.3	240	2.4×10^6
Halfa	470	1,070	1.0×10^6	21	240	2.4×10^6

Table 2 Changes in total bacteria Counts (TBCs) and specific groups of bacteria in the northern part of Lake Nasser during 1974/1984 (counts ml^{-1})

Seasons	Bacteria years	Total bacterial counts 22°C	Total bacterial counts 37°C	*Azotobacter*	N_2-fixing Clostridia	Nitrifying bacteria	Aerobic cellulose decomposing bacteria
Winter	1974	187	73	24	26	6	66
	1984	340	290	17	14	22	110
Spring	1974	414	188	170	58	8	130
	1984	750	360	110	46	39	330
Summer	1974	3,730	2,520	260	170	14	1,700
	1984	5,100	4,400	140	64	120	2,200
Autumn	1974	743	673	320	33	12	320
	1984	1,800	1,200	64	17	84	450

and Azazy (1986) and Rabeh et al. (1999). The increase in heterotrophic bacteria in the Khors during spring may also relate to development of phytoplankton: the lowest Secchi disc reading (1.54 m) was during spring, the highest during winter (Anon., 1996). In bottom waters, the bacteria counted at 22°C fluctuated from 0.06×10^5 cells ml^{-1} at Khor El-Ramla during autumn to 961×10^5 cfu ml^{-1} at Khor El-Allaqui during spring. The number of bacteria at 37°C fluctuated from 0.1×10^5 cfu ml^{-1} during autumn at Khor El-Ramla and Kalabsha, to 680×10^5 cfu ml^{-1} at El-Allaqi during spring. Khor El-Ramla showed the lowest average TBCs at 22°C and 37°C in subsurface and bottom waters (Rabeh, 2001), in harmony with a high transparency (2.5 m on average) and high dissolved oxygen (11.03 mg l^{-1} on average). Such a negative relationship between TBCs and transparency had previously been reported by Saleh (1976), Elewa & Azazy (1986) and Rabeh et al. (1999). These authors also found an inverse relationship between TBCs and DO, as bacteria consume considerable quantities of DO. Also, TBCs at both 22°C and 37°C were higher in bottom than in subsurface water. The ratio at 22°C to that at 37°C was low, slightly above or below unity. The lowest TBCs at 22°C and 37°C occur in winter, with a sharp increase during summer, reflecting the development of phytoplankton. Thus, lower transparency was recorded during summer than in winter (Rabeh, 2003). High bacterial density during summer might also explain the drop in dissolved oxygen near the bottom. Bacteria use DO in biological oxidations, and this oxygen is not compensated as long as thermal stratification lasts (Rabeh, 2003). The highest TBC were during autumn (flood), when new nutrients arrive, the lake level rises, and shore-land is flooded. The coastal zone contributes minerals to the lake, *inter alia* from drowned vegetation that provides fresh organic matter. Moreover, the flood carries an allochthonous microflora to the lake. In Lake Nasser, TBCs at 22°C and 37°C were higher in bottom than in subsurface water (Saleh, 1976; Rabeh, 2001). Changes in TBC at 22°C were associated with a similar change at 37°C (ratio slightly higher than 1). In non-polluted waters, the ratio of 22°C: 37°C counts is usually 10 or more; in polluted waters it is usually below 10 (APHA, 1980; Rabeh, 2000, 2003). Accordingly, subsurface and bottom waters of the lake are polluted (Rabeh, 2003). Similar low ratios were previously recorded for Lake Nasser by Elewa and Azazy (1986) and Rabeh (2001). However, it is not convenient to rely on this ratio only to get an accurate assessment of water pollution, especially in warm water (Hosny, 1966; Rabeh, 1993, 2001).

5.2 Bacterial Indicators of Sewage Pollution

During 1996, the MPN of TC and FC along the main channel of Lake Nasser ranged between 0.0 and 54 × 10^4 and between 0.0 and 33 × 10^4 100 ml^{-1} for TC and FC. The highest counts of indicator bacteria were recorded during winter. This may be due to tourism between the High Dam and Abu-Simbel, but other human activities add to the pollution, problem, such as the Aswan fish factory (Rabeh et al., 1999).

TC varied from 0.002 × 10^3 cells 100 ml^{-1} in subsurface water of Khors El-Ramla. Kalabsha, El-Allaqui and Korosko during autumn, to 50 × 10^3 cells ml^{-1} at Khor El-Ramla during winter. Absence of FC was recorded during autumn at Khors El-Ramla, Kalabsha and Korosko; highest values (3.2 × 10^3 cells 100 ml^{-1}) fell during winter at Khor Kalabsha. The high coliforms during winter may be caused by intense fishing and tourism during winter, and/or high pH values (Rabeh, 2001), with a peak of pH 8.61 during winter (Anon., 1996). In bottom waters, TC were absent during autumn, to reach 90 × 10^3 cells 100 ml^{-1} at Khor Kalabsha during winter. FC fluctuated from a complete absence at Khors Kalabsha and Korosko during autumn to 9 × 10^3 cells 100 ml^{-1} at Khor Kalabsha during winter. With respect to spot-wise variations, Khor Toushka had the lowest average TC in subsurface and bottom waters, while Khor El-Ramla and Khor Kalabsha had the highest. Again, such variation was in harmony with average pH, with Khor Toshka showing the lowest average (8.17) and Khor El-Ramla and Kalabsha the highest (8.29 and 8.37) (Anon., 1996). Khor Korosko had the lowest average FC, while the highest was in Khor Kalabsha. The high TC and FC at Khors El-Ramla and Kalabsha is attributed to the activities of fishermen. El-Shahat (2000) reported 1,997and 6,841 fishing boats and fishermen in Lake Nasser during 1997. The high numbers of coliforms in Khor El-Ramla, against low numbers in Khor Tushka, is paralleled by a high concentration of ammonia nitrogen in the former (26.94 $\mu g\ l^{-1}$) (Anon., 1996). Indeed, Hosny (1966) and Rabeh (1993) found ammonia nitrogen to be necessary for the multiplication of coliforms.

TC and FC were higher in bottom than in subsurface waters, concordant with Rabeh (1996, 2000). Also, the highest bacterial indictors (TC and FC) occurred at the High Dam. The lowest TC and a complete absence of FC were noted in the south of the lake during the flood. This might be due to dilution by the flood, although the flood water is an important source of bacteria. Conversely, high TC and FC during winter might reflect the polluting effect of cruise boats (which are really floating hotels) between the High Dam and Abu-Simbel. Another indicator is the high concentration of ammonia nitrogen during this season (3–171.36 and

24.05–345.74 μg l^{-1}) in subsurface and bottom water. As well, TC and FC were high in bottom waters. This relates to either lower bactericidal effects of solar ultraviolet rays on bottom water, sedimentation of suspensions containing adsorbed cells, higher bottom concentrations of ammonia nitrogen, or higher contamination with sediment bacteria (Rabeh, 2003). Indeed, Van Donsel and Geldreich (1971) found that the density of FC in sediments may amount to 100–1,000 times those in the overlying water.

Again, high TC and FC in the khors reflect fishing activities (Rabeh, 2001). FS in the main channel ranged from 1 to 1,900 and from 6 to 2,100 org. 100 ml^{-1} in subsurface and bottom waters, while counts in subsurface water of the khors were 2–2,100 org. 100 ml^{-1}. In the White Nile, the Sobat, the Blue Nile, the Atbara and the Main Nile, bottom water reached 3–3,900 org. 100 ml^{-1}. In the main channel, TC/FC ratios varied from 0.0 to 0.845 and from 0.025 to 0.791 in subsurface and near-bottom water. In the khors, this ratio was 0.25–0.77 in subsurface water and 0.25–0.68 in bottom water. At the mouth of El-Sheikh Zayed canal, TC an FC were 3–460 org. 100 ml^{-1}, 0.0–21 org. 100 ml^{-1}, and 23–9,300 org. 100 ml^{-1}, and 9–900 org. 100 ml^{-1} in subsurface and bottom water. Here, the ratios were from 0.0 to 0.18 and from 0.016 to 0.39 in subsurface and bottom water. The FC/FS ratio in the khors ranged from 1.4 to 2.25 and from 1.8 to 3 for subsurface and bottom waters, suggesting fishing activities and grazing cattle (about 20,000 heads) around the lake (Rabeh, 2003).

5.3 Bacteria Involved in Biogeochemical Cycles

In Lake Nubia, the MPNs of SRB were lower than in the north of the lake, and bottom water had higher numbers than upper layers (Table 1). In most cases, SRB increased with depth. This was not the case in samples from Lake Nasser. Moreover, MPNs in Lake Nubia were higher than in Lake Nasser (Saleh, 1976).

During the hot months (summer and autumn), a problem of odor may arise in some areas of Lake Nasser due to H_2S produced by sulphate-reducing, anaerobic bacteria (SRB). These bacteria are exceptionally high in anaerobic bottoms, after the consumption of oxygen by aerobic bacteria in the presence of organic matter (Saleh, 1976). SRB were completely absent along the main channel and in selected khors during winter. Low water temperature and aerobic conditions prevailing during this season inhibit these strict anaerobic bacteria. In contrast, the number of SRB in the main channel ranged from 0.21 to 0.64 org. ml^{-1} and from 1.2 to 450 org. cm^{-3} in bottom water and sediment. Khor Kalabsha showed higher counts than Khor El-Ramla. However, the lowest counts were at the source point station, and the highest at E1-Madiq station, in line with high organic matter (2.56–3.27%) and a high concentration of SO_4 (34.5 mg l^{-1}) (El-Shabrawy & Abdel-Regal, 1999). The situation reverses at Abu Simbel where low organic matter (1.53–2.6%, average 1.29%), low SO_4 (0.0–1.65, 1.09 mg l^{-1}on average) and, accordingly, the lowest counts of SRB occur.

The lake thermally stratifies during summer. Thus, the highest concentration of H_2S (6.56 mg l^{-1}) falls during summer, when anaerobic conditions prevail and stagnation prevents sulphide, from being oxidized (Rabeh, 2003). *Azotobacter chrococcum*, the predominant soil species, is also present in considerable numbers in High Dam lake water. *Azotobacter*, like TBCs, increases significantly in summer and autumn, while clostridial spore counts are lower in water than *Azotobacter*, in contrast to soils. These bacteria are unable to survive in the oxygenated water found in winter and spring. These findings are in harmony with data on dissolved oxygen and temperature.

Nitrifying bacteria (Table 1) are low. Aerobic cellulose decomposers evolve in parallel with organic carbon content: counts increase markedly in summer and autumn. As a drought period had begun in 1980 and water level fell from 178 to 158 m, changes in microbiological and chemical characteristics of Lake Nasser occurred. TBCs at 22°C and 37°C increased in comparison to 10 years earlier (Table 1). The activity of phyto and zooplankton and/or relative bacterial densities also responded to less water flowing from in the south, a result paralleled by organic carbon content, and confirming a result of Schmidt (1969). Nitrogen fixers (the aerobic *Azotobacter* and the anaerobic *Clostridia*) tended to decrease, perhaps due to less suspended material in flood water. Nitrifying bacteria (Table 1) increased in comparison to 10 years earlier, suggesting a rise in nitrifying activity related to a higher activity of total bacteria and confirmed by increased nitrate in the lake after the period of drought. Aerobic cellulose decomposers increased in summer, in parallel with TBCs and organic carbon (Elewa & Azazy, 1986).

6 Viruses

Little virological information is available on River Nile water. South and north of Abu-Simbel, enteroviruses ranged from 0 to 42 plaque-forming units (pfu) mg l^{-1}. Just south of the High Dam (1.5 km), enteroviruses were either completely absent or scored up to 7.2 pfu l^{-1} (Ali et al., 1996).

7 Upper Egypt

7.1 *Total Bacterial Counts*

Bacteria developing at 22°C in subsurface bank water ranged from 4.8×10^5 cfu ml^{-1} at Edfo during winter, to 22×10^6 cfu ml^{-1} at Luxor during summer. Those developing at 37°C varied between 3.75×10^5 and 68×10^5 cfu ml^{-1} l at the same sites during winter and spring. In mid-Nile, bacteria developing at 22°C and 37°C in subsurface water reached 1.2×10^5–31×10^5 and 0.06×10^5–48×10^5 cfu ml^{-1}.

In near-bottom water in mid Nile, they ranged from 2×10^5 to 30.2×10^5 and from 1.8×10^5 to 47.8×10^5 cfu ml^{-1}. In sediment in mid-River both cultures reached from 12×10^6 to 36×10^8 cfu g^{-1} and from 15×10^6 to 4.18×10^8 cfu g^{-1} (Sabae, 2004).

7.2 Bacterial Indicators of Sewage Pollution

TC in Upper Egypt fluctuated between 76 MPN 100 ml^{-1} at Aswan and 3.3×10^3 MPN 100 ml^{-1} at Nagaa Hammadi (El-Sherbini et al., 1991); FC ranged from 7.3×10^2 cfu 100 ml^{-1} at Assuit (544 km below High Dam) to 1.02×10^3 100 ml^{-1} 610 km below the High Dam. These values parallel those at drains in this area (Mahrous, 1997). The water quality index (WQI) derived from two campaigns conducted by the Nile Research Institute (NRI) during February and September 2000 showed that 71% of all sampling sites had a good quality during winter; the remaining sites had a medium quality. During summer, 43% of the sites maintained a good quality, the rest dropping to a medium quality. FC from the bank at a site where water was pumped, were much higher. This indicates the presence of untreated human waste *(*Ezzat et al., 2002). Similarly, MPN of bacterial indicators in subsurface water near the bank were $93–46 \times 10^2$, $23–14 \times 10^2$ and $40–15 \times 10^2$ 100 ml^{-1} for TC, FC and FS, while their MPN in mid-Nile ranged from 23 to 20×10^2, 0.0 to 2.4×10^2, 0.0 to 16×10^2 100 ml^{-1}. In mid-Nile sediment, they varied from 9×10^2 to 21×10^4, 0.0 to 12×10^3 and 0.0 to 36×10^3 100 ml^{-1} (Sabae, 2004).

7.3 Complementary Bacterial Indicators

Water treatment plants at Beni-Suif governorate receive water from the main river. The density of bacterial indicators in Nile water at the intake of these plants ranged from 0.3 to 8.9×10^3 and from 1 to 7.4×10^3 cfu 100 ml^{-1} for *Aeromonas hydrophila* and total staphylococci. Their average ranged from 7.4×10^2 to 1.6×10^3 and from 3.7×10^2 to 4.5×10^2 cfu 100 ml^{-1} for both bacteria (Shaban & El-Taweel, 2002).

7.4 Pathogenic Bacteria

Pathogenic bacteria in Nile water at the source points of water treatment plants at Beni-Suif ranged from 0.6 to 4.8×10^2, 0.2 to 2.3×10^3 and 1 to 8.8×10^2 cfu 100 ml^{-1} for *Salmonella*, *Vibrio* and *Listeria*. The average ranged from 95 to 3.5×10^2, 4.4×10^2 to 1.8×10^3 and 5×10^2 to 6.2×10^2 cfu 100 ml^{-1} for all three groups (Shaban & El-Taweel, 2002).

7.5 Viruses

Behind Aswan Dam (AD), enteroviruses amounted from 0 to 28.8 pfu l^{-1}. In front of Aswan city they were absent, reaching 10 pfu l^{-1} near the east bank of the river (Ali et al., 1996).

8 Greater Cairo

Monitoring of microbiological characteristics of the Nile prior to and after the High Dam construction, especially at Cairo, has been in progress since 1963.

8.1 Total Bacterial Counts

During 1963, TBCs at 22°C at Giza ranged from 15×10^2 cfu ml^{-1} in January to 955×10^2 cfu ml^{-1} in October; at 37°C they varied from 7×10^2 cfu ml^{-1} in February to 975×10^2 cfu ml^{-1} in October. In the next year, they fluctuated from 50×10^2 cfu ml^{-1} during May to 900×10^2 cfu ml^{-1} during October and from 17×10^2 cfu ml^{-1} during January to 2815×10^2 cfu ml^{-1} during September, at 22°C and 37°C. TBCs at 20°C and at 37°C markedly increased during the flood, when organic matter reached a maximum. Except during the flood, bacteria in Nile water during this 2-year period were relatively low: the ratio of counts at 22°C: 37°C ranged from 0.5 during September to 4.6 during June 1963, and from 0.17 during September to 3.2 during January 1964 (Hosny, 1966). The picture during 1964–1965 revealed that the rise and fall in bacteria followed seasonal changes, with highest counts (10^5–10^7 ml^{-1}) during the flood. Thereafter, a phase of decline (10^3–10^5 ml^{-1}) prevailed (Saleh, 1980a). But between June 1965 and August 1966, monthly average TBC rose to 10^3–10^6 100 ml^{-1}, and in October 1965, bacterial numbers were at their highest. TBCs during summer1965 were markedly higher than in the next year. No significant differences existed between the two incubation temperatures (El-Abagy, 1971).

After the filling of the High Dam, a cessation of the seasonal floods occurred, as well as a drop in bacterial counts at 22°C and 37°C (10^3–10^5 ml^{-1}) (Saleh, 1980b). About 10 years later, in 1984, TBCs at both temperatures had risen to 10^5–10^7 cfu ml^{-1} at El-Gezira (El-Deeb, 1986). During summer 1994–spring 1996, TBCs at 22°C and 37°C ranged from 1.0×10^3 to 7.8×10^5 and from 5.0×10^2 to 6.4×10^5 cfu ml^{-1} (El-Taweel, 1998). Similarly, the lowest TBCs at 22°C (7×10^4 ml^{-1}) and 37°C (6×10^4 ml^{-1}) were in subsurface water at El-Maadi, the highest at 22°C (214×10^5 ml^{-1} l) and at 37°C (187×10^5 ml^{-1} l) at Warraq El-Hadar, August 1997 to July 1998. Growth at 22°C and 37°C did not differ significantly (Sabae, 1998). Bacteria developing at 22°C and 37°C in subsurface water near the bank at Shoubra El-Kheima region ranged from 10×10^4 to 144×10^4 and 5.9×10^4 to 142.6×10^4, while in mid-Nile they ranged from 4×10^4 to 136×10^4 and from 3.1×10^4 to 170×10^4. Their densities decreased away from the bank and were higher in near-bottom than in subsurface water. Bank sediment TBCs ranged from 14×10^6 to 190×10^6 g^{-1} and from 10.3×10^6 to 189.1×10^6 g^{-1} at 22°C and 37°C. In mid-Nile, they varied from 4×10^6 to 180×10^6 g^{-1} and from 2.1×10^6 to 178.2×10^6 g^{-1} (Rabeh, 2000). TBCs at 22°C ranged from 1.3×10^2 to 4.2×10^5, while at 37°C they ranged between 1×10^2 and 3×10^5 ml^{-1} (February 2000–March 2001) (El-Taweel & Shaban, 2003).

8.2 Bacterial Indicators of Sewage Pollution

Before the filling of the High Dam, TC ranged between 13 ml^{-1} in July 1963 and 165 ml^{-1} in April, while they ranged from 13 ml^{-1} in July and September to 260 ml^{-1} during March 1964. In 1963, FC ranged from 1 ml^{-1} l in June to 26 ml^{-1} in March and from 1 ml^{-1} in June to 157 ml^{-1} in April (Hosny, 1966). Saleh (1968) showed that the middle of the river (subsurface, 5 and 10 m) contained faecal streptococci between June 1965 and August 1966. The old MPN-index of Nile water fell between 4.8×10^1 and 8.17×10^2 100 ml^{-1}. The new MPN readings were 1.19×10^3 (September 1965) when a rise in turbidity and C: N ratio occurred. During 1966, there was a decline in FS during February, with the MPN-index always below 10^2. Between March and August 1966, there was a fluctuation between log 1 and log 2, with occasional rise to log 3 at the 10 m level. Apart from a casual drop to a density below 10^2, uncharacteristic of Nile water, the MPN of coliforms fluctuated between 10^2 and 10^3 (1965–1966) with variations at different depths. Of subsurface samples, the majority gave coliform densities between 10^2 and 10^3 (El-Abagy, 1977).

After 1973, the complete filling of the High Dam Lake, a rise in coliforms and FS, and a higher incidence of untyped forms marked the river water. During 1975–1978, FS readings of 100–1,000 ml^{-1} were recorded in the Cairo segment (Saleh, 1980a). From October 1986 to November 1987, the densities of TC were 6×10^2–3.16×10^4, 3.5×10^3–$3.9\ 10^4$ and 1.02×10^3–10.01×10^4 at El-Tebbin, Giza and Rod El-Farag. FC reached 3–3.16×10^4; 1.3×10^3–3.7×10^4 and 7.6×10^2–1.8×10^4 at the same sites (El-Marazky, 1988). Moreover, TC along the Cairo segment was from 1.2×10^3 at El-Tebbin to 6.6×10^3 cfu 100 ml^{-1} at El- Maadi, while FC ranged from 5×10^3 to 5.8×10^3 cfu 100 ml^{-1} at both sites. The mean TC and FC increased from the entrance of Cairo to El-Qanater, reaching maxima of 3.8×10^3 and 2.8×10^3, 4.7×10^3 and 3.7×10^3 for TC and FC at El-Badrashin and El-Maadi (Table 3). Six drains (Ghamaza El-Kobra, El-Tebbin, Khour El-Sail Badrashin, El-Hawamdia sugar, Khour El-Sail Maasera, and Kotsica Starch) represent point sources of pollution in this area. The highest TC and FC were in the drains of El-Hawamdia Sugar, khour El-Sail Maasera, and kotsica Starch between El-Badrashin and El-Maadi. El-Hawamdia Sugar and kotsica Starch Drains are industrial in nature, and dense TC and FC (2.7×10^4 and 1.9×10^4 cfu 100 ml^{-1}) were recorded here. In contrast to coliforms, FS showed a decrease from Cairo to El-Qanater. The ratio of FC to FS was 1.1–1.9 at the entrance of Cairo, against 6.7–7.2 at El–Maadi (Abu-Shady, 1996). The range of TC, FC and FS at five sites of

Table 3 Classical and complementary bacterial indicators ($\times 10^3$ 100 ml^{-1}) of River Nile along Greater Cairo segment

Stations	Total coliform	Faecal coliform	Faecal streptococci	*Staphylococcus aureus*	*Aeromonas hydrophila*
El-Ekhssas	3.1	2.1	1.2	4.4	3.4
El-Tebbin	2.9	1.8	0.86	3.7	2.8
El-Badrashin	3.8	2.8	0.94	4.8	3.5
El-Maadi	4.7	3.7	0.53	5.2	4.4
El-Qanater	3.3	2	1.1	3.4	3.4

Greater Cairo were 3.6×10^3–5.1×10^3, 2.0×10^3–5×10^3 and 2.2×10^2–2.6×10^3 cfu 100 ml^{-1} (Haeikal, 1994). El-Taweel (1998) found similar densities during summer 1994–spring 1996: 49×10^4–1.6×10^4, 2×10^3–5.2×10^3 and 20×10^3–1.4×10^3 MPN 100 ml^{-1} for TC, FC and FS. Compared with standards for drinking water (>50 and <5,000 for TC; >20 and <2,000 for FC and >20 and <1,000 for FS), the Nile is locally polluted (El-Taweel, 1998).

MPN of bacterial indicators in subsurface water near the bank ranged from 110×10^2 to $1{,}600 \times 10^2$, 35×10^2 to 900×10^2 and 23 to 175 100 ml^{-1} for TC, FC and FS, while MPN in mid-stream ranged from 3.4×10^2 to 350×10^2, 1.1×10^2 to 150×10^2, and 9 to 36 100 ml^{-1}. Bacterial indicators in near-bottom water were 15×10^3 –650×10^3, 8×10^3 –350×10^3 and 35–500 100 ml^{-1} for TC, FC and FS, while counts in mid Nile ranged from 4×10^2 to 425×10^3, 2×10^2 to 75×10^3 and 20 to 250 100 m^{-1} (Rabeh, 2000). Such findings confirm Fayez et al. (1987) who found similar TC near the bank and in mid-stream. Bacteria in near-bank sediment amounted to 110×10^3 –$1{,}600 \times 10^3$, 64×10^3 –850×10^3 and 28×10^3–350×10^2 100 ml^{-1} for TC, FC and FS. MPN in mid-Nile were 110×10^3–1500×10^3, 42×10^3–650×10^3 and 23×10^2–250×10^2 100 ml^{-1}, higher than in water (Rabeh, 2000). In February 2001, FC fluctuated between 1.2×10^2 100 ml^{-1} at Maadi and 1×10^3 100 ml^{-1} at Shoubra El-Kheima (upstream of Ismailia Canal intake) (Ezzat et al., 2002), while El-Taweel and Shaban (2003) recorded MPNs of TC of up to 80×10^3 100 ml^{-1} at Branching Point, and FC's of up to 16×10^3 100 ml^{-1} at Branching Point. FS ranged between 40 100 ml^{-1} and 8×10^3 100 ml^{-1} at El-Gezira and Branching Point.

8.3 Complementary Bacterial Indicators

During summer 1994–spring 1996, the count of *Aeromonas hydrophila* at Cairo changed. *A. hydrophila* showed values from 1.0×10^3 to 2.4×10^5 cfu 100 ml^{-1}, higher in spring (1.5×10^5) than in other seasons (between 1.1×10^4 and 6.4×10^4 cfu 100 ml^{-1}) (El-Taweel, 1998). In contrast, *A. hydrophila* ranged from 2×10^3 100 ml^{-1} at El-Tebbin to 6.7×10^3 100 ml^{-1} at El-Maadi (Abu-Shady et al., 1996). It comprised 0.01–2.1% of TBCs and had no significant correlation with TC, FC, FS (El-Taweel, 2003). *Staphylococcus aureus* ranged from 1.5×10^3 100 ml^{-1} at El-Qanater to 6.7×10^3 100 ml^{-1} at El-Badrashin (Abu-Shady et al., 1996). Finally, total staphylococci around Greater Cairo occurred at mean values between 6.4 × 10^2 and 1.9 × 10^3 100 ml^{-1} (El-Taweel, 1998).

All along the Greater Cairo segment of the Nile, the mean counts of *S. aureus* and *A. hydrophila* exceeded permissible values.

8.4 Pathogenic Bacteria

Salmonella was detected in 25 out of 32 samples in summer 1994–spring 1996. Higher counts during summer and winter (1.6 × 10^3 and 1.4 × 10^3 cfu 100 ml^{-1}), contrasted with lower counts during autumn and spring (2.5 × 10^2 and 5.0 × 10^2 cfu 100 ml^{-1}). All reflect municipal and food processing discharges at Cairo (El-Taweel, 1998). Later, *Salmonella* were detected in 23 out of 28 samples collected from Cairo (from 18 cfu 100 ml^{-1} to 6.4 × 10^2 cfu 100 ml^{-1}with annual average 1.2 × 10^2–1.9 × 10^2) (El-Taweel & Shaban, 2003).

Vibrio's were present at Cairo during summer 1994–spring 1996. The highest value was detected during winter (1.6 × 10^4 cfu 100 ml^{-1}). During other seasons, it sunk to 1.1 × 10^3–5.7 × 10^3 cfu 100 ml^{-1}. According to a biochemical identification, *V. cholerae* represented 30–62% of total vibrios (El-Taweel & Shaban, 2003).

The *Listeria* group was also detected at Cairo, with *Listeria monocytogenes* representing up to 60% of the total. Higher counts, during summer and winter, were 2.5 × 10^4 and 3.2 × 10^4 cfu 100 ml^{-1}. During autumn and spring, values declined to 2.0 × 10^2–2.6 × 10^2 cfu 100 ml^{-1} (El-Taweel, 1998). Luppi et al. (1988) isolated *Listeria* spp. in 22% of river samples, whereas Bernagozzi et al. (1994) isolated *Listeria* spp. in 59% of surface waters from Italy; 72% were identified as *L. monocytogenes*.

The decrease in various microbial parameters in Nile water upstream of Cairo and at El-Qanater after leaving Cairo suggests that the river has an ability to purify itself, especially at high flow rates (ca 175 M m^3 day^{-1}).

8.5 Bacteria Involved in Biogeochemical Cycles

Before AHD, large numbers of *Azotobacter* (up to 11,000 ml^{-1}, average 2004) were found during the flood with TBCs and suspended matter content at their maximum; conversely, counts were low, ca 400 ml^{-1}, during low water. Clostridial spore counts ranged from 3 to 220 spores ml^{-1}, average ca 45 spores ml^{-1} (Hosny, 1966). MPNs of sulphate-reducing bacteria (SRB) were low at the industrial region of Shoubra El-Kheima. The highest counts were at the discharge point of Shoubra El-Kheima Electric Power Station, a site of thermal pollution enhancing bacterial multiplication. In addition, leaching of SRB from pipes of the cooling system may have occurred, since these bacteria may develop and cause corrosion to iron pipes. MPNs of SRB were much higher in sediment (20–1,600 g^{-1}) than in water (Sabae, 2000).

8.6 Viruses

Two strains of *E. coli* (ATCC No. 13706 and the local No. 3) were used as hosts for phages, applying the APHA and Kott-MPN procedures to raw River Nile water at El-Tebbin, Giza and Rod El-Farag during 1986 and 1987. The local isolate No. 3 had the highest susceptibility to phages, with plaque forming units 10^2 and 10^5 100 ml^{-1} of Nile water. The counts obtained by Kott-MPN ranged between 6 and 81 cfu 100 ml^{-1} at El-Tebbin, using the ATCC strain. With APHA, the same host and the same site, counts ranged between 66 and 1,130 pfu 100 ml^{-1}. When strain *E. coli* No. 3 (more sensitive to phage lysis) was used as host for the phage, the counts of coliphages were about similar to those obtained with the ATCC-host (47–1,470 pfu 100 ml^{-1}). In Nile water at Giza, coliphages with ATCC strain No. 13706 ranged from 102 to 3,890 and 9 to 275 pfu 100 ml^{-1} l, while coliphage counts with the local host ranged from 74 to 3,630 and 3 to 178 pfu 100 ml^{-1} using APHA and Kott techniques, respectively. Nile water at Rod El-Farag had a relatively high phage density (4,786 pfu 100 ml^{-1}), while El-Tebbin water yielded the lowest density (1,470 pfu 100 ml^{-1}). Comparing the two techniques, APHA gave higher counts than the Kott-technique. A similar trend was observed with ATCC No. 13706 as a host compared with local strain No. 3. The plaque-forming unit (pfu) using local *E. coli* No. 3 and ATCC No. 13706 as hosts was 10^2 100 ml^{-1} of Nile water. The mean counts of coliphages by APHA ranged between 63 and 4677 using ATCC No. 13706 whereas the Kott-MPN technique suggested 6–478 pfu 100 ml^{-1} (El-Marazky, 1988).

Enteroviruses, especially Coxsackie B viruses (CBVs) have been detected in water and wastewater by many investigators (Montserrat et al., 1994; Wyn-Jones et al., 1995). In the Nile, enteroviruses were studied monthly from November 1999 to October 2000 by RT-PCR (Ali et al., 2002). Enterovirus-positive samples represented 11/12 (91.6%), 8/12 (66.6%) and 4/12 (33.3%) at the intakes of El-Giza, El-Maadi and Mostorod water treatment plants (WTPs). Moreover, Coxsackievirus CB2 was present in 3/23 (14.2%) of enterovirus-positive samples (Table 4).

Table 4 Enteroviruses and Coxsackie viruses type B in Nile water at the intake of three water treatment plants (WTPs)

	Positive RT-PCR samples	
Stations	No.	Percent
El-Giza	11/12	91.6
El-Maadi	8/12	66.6
Mostorod	4/12	33.3
Total	23/36	63.8
No. of CB	3/23	14.2

9 Damietta Branch

9.1 Total Bacterial Counts

During 1977, TBCs at 22°C ranged from 1.3×10^3 cfu ml^{-1} at the intake of the water treatment plant of El-Mansoura to 5.15×10^4 cfu ml^{-1} in south El-Mansoura during April and September, while at 37°C they varied between 3.2×10^3 cfu ml^{-1} at Talkha Fertilizer Factory during January 1978 and 1.8×10^5 cfu ml^{-1} at the south El-Mansoura city during April 1977. No significant differences existed between 22°C and 37°C (El-Mongy, 1978). TBCs at 22°C at upper Damietta Branch during summer 1994–spring 1996 varied from 2.1×10^3 to 6.3×10^5, while at 37°C they ranged from 5.0×10^2 to 5.1×10^5 (El-Taweel, 1998). WQI during 2000 showed that water entering the branch in winter is of good quality; it deteriorates downstream but later regains a medium condition. Low flow during winter, in addition to pollution sources along the branch, explain the changes in WQI. Recently, TBCs have ranged from 10.8×10^7 to 150×10^7 cfu ml^{-1} and from 8.8×10^7 to 152×10^7 cfu ml^{-1} at 22°C and 37°C. The highest number occurs in summer, the lowest in winter. Site-wise there is an increase in bacteria from El-Qanater to Damietta, attributable to domestic, sewage and agricultural effluents. Statistically, TBCs at 22°C and 37°C correlate positively ($r = 0.82$) (Sabae & Rabeh, 2007).

9.2 Bacterial Indicators of Sewage Pollution

During January 1978, TC and FC was lowest (23 and 13 MPN index 100 ml^{-1}, respectively) at south El-Mansoura, with highest TC (9.2×10^2 100 ml^{-1}) at El-Khiyariya village (5 km north El- Mansoura) during October 1977 and of FC (3.5×10^2 100 ml^{-1}), at Talkha Fertilizer Factory during August 1977. During summer 1994–spring 1996, TC at the beginning of Damietta Branch was 49×10^4–1.6×10^4 MPN 100 ml^{-1}, with annual average 5.6×10^3 MPN 100 ml^{-1}, while FC varied from 8.0×10^3 to 2.3×10^3 MPN 100 ml^{-1}, with annual average 6.2×10^2 MPN 100 ml^{-1}. FS fluctuated between 20 and 4.1×10^2 MPN 100 $ml^{-1}$with annual average 1.2×10^2 MPN 100 ml^{-1} (El-Taweel, 1998). A monitoring trip in February 2001 indicated that FC ranged from 9×10^2 100 ml^{-1} at Zefta (upstream of irrigation intakes at Zefta Barrage, 1,058 km from AHD) to 3.5×10^3 100 ml^{-1} at 1,025 km from AHD. Except at Zefta Barrage, FC counts exceeded WHO (1989) guidelines for unrestricted irrigation (1,000 100 ml^{-1}) at all sampling sites. Discharge of human wastes in Damietta Branch is responsible for this (Ezzat et al., 2002). MPN of TC during 2005–2006 varied from 240 to 16×10^4 100 ml^{-1} and from 40 to 75×10^2 100 ml^{-1} for FC. FS fluctuated between 4×10^2 and 21×10^2 100 ml^{-1} at Damietta Branch and was highest at Damietta City. Highest TC, FC and FS occurred in spring and summer (Table 5). A positive correlation ($r = 0.74$) was found between TBCs and bacterial indicators. FC/

Table 5 Most probable number (MPN) of total coliforms (TC), faecal coliforms (FC) and faecal streptococci (FS) × 10^3 100 ml^{-1} at Damietta Branch

Seasons Bacteria	Autumn			Winter			Spring			Summer		
Stations	TC	FC	FS	TC	FC	FS	TC	FC	FS	TC	FC	FS
El-Qanater	0.24	0.021	0.012	0.43	0.04	0.004	0.900	0.400	0.093	0.270	0.070	0.075
Benha	0.44	0.090	0.46	0.46	0.043	0.026	2.400	0.930	0.210	1.500	0.390	0.400
Zefta	1.90	0.400	0.15	1.10	0.044	0.040	11.00	1.500	1.500	7.500	0.400	0.390
Talkha	2.00	0.700	0.24	2.10	0.44	0.040	15.00	2.100	1.600	21.00	2.000	0.440
El-Serw	9.30	2.100	0.24	1.50	0.36	0.040	15.00	2.100	0.430	39.00	2.300	0.460
Faraskour	11.0	0.700	0.46	4.00	0.46	0.150	46.00	2.400	1.500	110.0	7.000	1.100
Damietta	46.0	2.300	1.10	16.0	2.30	0.390	110.0	6.400	1.500	160.0	7.500	2.100

FS ratios were in the range 0.19–11, consistent with faecal pollution. (Sabae & Rabeh, 2007).

9.3 Pathogenic Bacteria

E. coli, the main indicator of faecal pollution, constituted 16% of gram-negative bacteria in Damietta water from autumn 2005 to summer 2006. Clearly, the water was subject to sewage pollution. *P. aeruginosa* was common (12%). Among gram-negatives, *K. pneumoniae* represented 14%, *Salmonella cholerasuis* 11%, *Shigella* spp. 9%, *Serratia liquefaciens* and *Proteus vulgaris* each 8%, *Acinetobacter* sp. 7%, and *Brenneria nigrifluens* 5%. Six other isolates were identified as *Flavimonas oryzihabitans and Chryseomonas luteola* (three isolates each) (Sabae & Rabeh, 2007).

10 Rosetta (Rashid) Branch

10.1 Total Bacterial Counts

In summer 1994–spring 1996, TBCs at 22°C at upper Rosetta Branch totaled 2.1×10^3–7.2×10^5 cfu ml^{-1}; at 37°C they varied from 7.0×10^2 to 5.2×10^5 cfu ml^{-1} (annual average 1.5×10^5) (El-Taweel, 1998). El-Rahawy Drain, receiving agricultural drainage and sewage from Giza Governorate, is one of the main wastewater discharges to the Rosetta Nile. The highest TBCs (28×10^8 and 40.1×10^8 cfu ml^{-1} at 22°C and 37°C) are found at this point. Bacteria increased more downstream (5×10^5–15×10^7 and 8×10^5–17×10^7 cfu ml^{-1}, at 22°C and 37°C) than upstream of the discharge (2×10^4–16×10^5 cfu ml^{-1} at 22°C and 3×10^4–21×10^5 cfu ml^{-1} at 37°C). One important factor in Nile water is suspended matter, due to bacterial adherence to particles. Thus, there is a negative correlation ($r = -0.84$) between TBCs and transparency. The ratio of 22°C: 37°C counts ranges between 0.2 and 12.83 (Sabae, 1999).

10.2 Bacterial Indicators of Sewage Pollution

TC density at Kafr El-Zayat district fluctuated between 10^2 and 10^4 MPN-index 100 ml^{-1}, except at industries which discharge wastewater continuously, and where average density increased to $10^5 \times 100\,\text{ml}^{-1}$ (El-Abagy & Kamel, 1992). During summer 1994–spring 1996 TC was 1.3×10^2–1.6×10^4 MPN 100 ml^{-1} at the beginning of Rosetta Branch (annual average 5.5×10^3 MPN 100 ml^{-1}). FC was 11–3.3×10^3 MPN 100 ml^{-1}, with annual average 7.6×10^2 MPN 100 ml^{-1}; FS was 40–1.2×10^3 MPN 100 ml^{-1} (annual average 3.2×10^2 MPN 100 ml^{-1}) (El-Taweel, 1998). Rosetta Branch is polluted at the discharge of El-Rahawey Drain, where MPN of TC, FC and FS reach 90×10^6, 25×10^5 and 45×10^4 100 ml^{-1} (Sabae, 1999). The drain discharges ca 28×10^4 m^3 day^{-1}, of which 193×10^2 m^3 to Rosetta Nile. Water opposite Rashid city is higher in TC, FC and FS than near the sea. During February 2001, FC ranged from 1.7×10^2 100 ml^{-1} (upstream of Edfina Barrage, 1,156.5 km from AHD) to 1.3×10^3 100 ml^{-1} at Kafr El-Zayat (1,075 km from AHD). The highest counts were at Kafr El-Zayat, after which the water complied with WHO Guidelines for irrigation (Ezzat et al., 2002). In Rosetta as in Damietta, a trend occurs whereby water quality deteriorates downstream to reach its worst condition ca 120 km downstream.

10.3 Pathogenic Bacteria

Pseudomonas aeruginosa was not detected in Rashid estuary, suggesting sensitivity of these bacteria to high salinity (23.48–30.08&permile;) (Mostafa et al., 2001).

11 Conclusions

Microbial information provides evidence for pollution levels that create health risks at specific locations where pathogens as well as viruses reach unsafe levels for use in drinking, irrigation and fisheries. Human contact degrades water quality; people use the Nile for swimming, bathing, and washing, all of which may cause bacteriological pollution. Lake Victoria is also used for bathing, washing clothes, and watering livestock, and is similarly contaminated with human and animal wastes. A 1997 cholera outbreak in rural Western Kenya implicated water from Lake Victoria as a possible cause.

The counts of bacteria and pathogens in drains are even higher. Untreated human waste in these drains reaches dangerous levels. The bacterial indicators of pollution depend on the quality and quantity of waste discharged. Self-purification and competition for nutrients play a role in determining the value of such bacterial indicators.

The major sources of pollution of the White and Blue Niles are:

1. Urban centers adjacent to the Nile (e.g. Khartoum). The following adversely affect the quality of water: inputs from industry (sugar factories which dispose highly enriched organic waste), agricultural and domestic sewage sources, and drinking water for a growing population.
2. Some recently established hotels dispose sewage directly into the Nile.
3. Recreational sites on the banks of the Blue and White Niles threaten the microbial quality of Nile water.
4. Burri power station on the Blue Nile uses water for cooling and releases exhaust oil and cooling water to the Nile.
5. Raw domestic and industrial sewage in rainy season finds access to the river. With the increasing population of Khartoum, the Nile should receive only treated sewage.

The water quality of Lake Nasser is good. However, some settlements around the lake and upstream do not take precautions about water pollution. Therefore, protection of water quality should not be restricted to the river downstream of the Aswan High Dam. SRB can be a nuisance and may release H_2S under conditions present in the bottom of Lake Nasser during the hot season. Fishing in the lake ensures a gradual decrease in the organic and inorganic load leading to a lower microbiological oxygen consumption and better aeration. Enteroviruses were isolated with a frequency of 60% and positive results were unexpectedly high along 300 km of river in the south of Egypt.

The microbial load in Nile water along Egypt is due to:

1. The River having become a sink of domestic waste: 98.5% of the Egyptian population in the valley and delta lives on 1.3% of the area of the country.
2. An increasing number of boats and floating houses discharging to the river.

The major source points of pollution in Upper Egypt are nine drains, viz. Khour El-Sail Aswan, Main Draw, El-Berba, Kom Ombo, Houd El-Sebaia, Mataana, El-Ballas, Bany Shaker, and Etsa; as well as sugar factories, oil and soap factories in Sohag and a touristic galleon parking.

The water quality index (WQI) resulting from two monitoring campaigns conducted during winter (February 2000) and summer (September 2000) proved that about 71% of the sampling sites during winter show good quality of water, while the remaining sites offer a medium quality water. WQI during summer shows that only 43% of the sampling sites has good water quality; the rest is medium.

In Greater Cairo, the major source points of pollution are six drains: Ghamaza El-Kobra, El-Tebbin, Khour El-Sail Badrashin, El-Hawamdia sugar, Khour El-Sail Maasera, and Kotsica starch in addition to El-Hawamdia sugar factory

Damietta Branch is adversely affected by Talkha fertilizers and High Serw power station. The WQI for Damietta Branch during 2000 shows that during winter, water enters the branch with good quality, deteriorates downstream, then regains a medium condition. The low flow during winter, in addition to wastes from different pollution sources along the branch explain these changes.

Major source points of pollution of Rosetta Branch are five drains: El-Rahawy Drain in the south, Sobol Drain, El-Tahrrer Drain, Zawiet El-Bahr Drain and Tala Drain, in addition to industry at Kafr El-Zayat.

- The same trend of WQI occurs along the Rosetta Branch where the water reaches its worst condition 120 km downstream. The branch receives pollutants from five drains: El-Rahawy, Sobol, El-Tahreer, Zaweit El-Bahr and Tala, as well as from industrial effluents. The extremely low flow during winter, in addition to wastes from different sources explains the changes in WQI along its course.
- In spite of the high dilution factor and the high self-purification capacity of the Nile, the impact of discharges on microbial quality of the water is significant, especially during low flow years.

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Phytoplankton: Composition, Development and Productivity

Jack F. Talling, Faisal Sinada, Ola E. Taha, and Emad M.H. Sobhy

Abstract Phytoplankton is widely but unevenly developed in regions of the Nile system. These are successively examined here with regard to community composition and abundance, interpreted in relation to upstream–downstream changes, time-sequences, and probable limiting factors.

Features in the headwater lakes are largely distinct from those in subsequent flowing sections of the river and in its reservoirs with seasonal or long-term retention. Regions with such retention are generally those with greatest, usually seasonal, plankton development, although some exceptions exist. Community composition is mostly dominated by diatoms (e.g. *Aulacoseira granulata*) or Cyanobacteria (e.g. *Anabaena flos-aquae* f. *spiroides*), but there are many species of green algae and some flagellates (e.g. *Pediastrum*, *Volvox*).

A remarkable desmid association has been described from the small Lake Ambadi of the *Sudd* region.

Diatoms are generally the pioneers in seasonal sequences or successions, which are often ended by the influx of relatively turbid though nutrient-rich floodwater. Sequences of species of estimated abundance have been studied intensively in relation to environmental factors in some reservoir-influenced regions. In the Blue Nile there is now a cascade system of two reservoirs linked by conditions of free-flow but subject to strong annual floodwater from Ethiopia. Events in the upper and more recent reservoir have brought about changes in those observed downstream. At Lake

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Nasser there is a community-differentiation between the main lake and its lateral arms or khors (e.g. Khor el Ramla). Here, and further downstream in Egypt, there have been maintained assessments of total abundance by chlorophyll-*a* estimation. In these, and in species biodiversity, there is evidence for some long-term changes.

Nutrient-phytoplankton relationships include possible limitation by low concentrations of inorganic nitrogen and – for a common diatom – by those of carbon dioxide associated with pH levels above 9.0. Light-limitation is also expressed in determinations of photosynthetic productivity, available from several upstream and downstream regions. This productivity can be high, conditioned by community abundance, vertical light penetration, and a frequently high specific activity per unit measure of biomass.

1 Introduction

Several reasons may lead to vigorous and varied developments of planktonic algae in regions of the Nile system. First, there are large headwater lakes in which lacustrine phytoplankton can develop, and possibly travel down their outflows as potential 'inocula' for renewed growth downstream. Second, the retention of water in the reservoirs within the Sudan and in Egypt provides the additional time favourable for phytoplankton development to which marginal retentions also contribute. Third, the great length of the river and its component stretches increase the time of travel of any water-mass, and so the opportunities for planktonic growth.

In this article, an outline is given of the phytoplankton found in various regions of the Nile system. Although some description of species-composition of these communities is provided, the main emphasis is upon the patterns of development in space and time. Where available, estimates of primary production rates are also discussed. Following headwaters in Ethiopia and Uganda, the Nile is divided into three rivers traversing the Sudan plain, namely the Blue Nile, the White Nile, and their union in the Main Nile, which finds its way northwards to Egypt.

2 The Blue Nile

The Blue Nile flows out of Lake Tana over a series of rapids and quickly descends into a deep gorge until it enters the Sudan plain south of Roseires at latitude 12° N. Between Lake Tana and the Sudan plain the Blue Nile receives many torrential tributaries which supply most of the river water. The annual discharge from Lake Tana is only 7% of the corresponding water reaching Khartoum. The flood occurring annually at Khartoum is mainly due to the torrential rains on the Ethiopian Plateau. The river is not navigable, except for short stretches, until well within the Sudanese border. In the lower part of its course in the Sudan, the Blue Nile receives two tributaries: the Dinder and the Rahad Rivers, both flowing down from the Ethiopian Plateau. The contribution of these two tributaries-only noticeable during the rainy season on the Ethiopian Plateau-is small, their combined annual discharge barely exceeding 8% of that of the main river. No other tributary drains into the river until it joins the White Nile at Khartoum.

2.1 Headwaters on the Ethiopian Plateau

2.1.1 Lake Tana

During much of the last century, little became known about the phytoplankton of this large, oligo-mesotrophic relatively shallow lake on the headwaters of the Blue Nile, but recently research became quite active (Wondie et al., 2007; Vijverberg et al., 2009). Brunelli & Cannicci (1940) gave a brief list of species and photomicrographs; additional (partly unpublished) observations were made later by Talling (Talling & Rzóska, 1967), Gasse et al. (1983), and Gasse (1986). Seasonal and quantitative records were formerly lacking, except for a single estimate by Talling of chlorophyll-*a* content (3.7 mg m^{-3}) from near Bahir Dar in March 1964.

Brunelli & Cannicci found a scanty development of blue-green algae (Cyanobacteria), chiefly of the genera *Anabaena* and *Microcystis*, but more considerable numbers of diatoms, especially species of *Aulacoseira* (formerly named *Melosira*) and *Surirella*. In samples collected by Talling in March 1964 from near the south shore, a diatom resembling *Aulacoseira granulata* var. *jonensis* f. *procera* (Talling & Rzóska, 1967) or other *Aulacoseira* spp. (Gasse et al., 1983; Gasse, 1986) were strongly dominant, although a spirally coiled *Anabaena* sp. was common. Some desmids (esp. *Staurastrum leptocladum*), *Pediastrum clathratum*, and *Surirella* spp. were well represented, as in some other large African lakes including L. Victoria. Detached littoral diatoms were also common, at least in inshore areas, as might be expected in this shallow and often turbulent lake.

Wondie et al. (2007) collected much quantitative data on primary production rates, chlorophyll-*a* content and biomass of phytoplankton of the lake from April 2003 to November 2004. Lake Tana was still characterized by low nutrient concentrations, and a low water transparency due to high silt load of the inflowing rivers during the rainy season (May–November) and daily resuspension of sediments in the inshore zone. The mean chlorophyll-*a* concentration varied seasonally and ranged from 2.6 to 8.5 mg m^{-3} in the offshore zone. Gross primary production in the open water ranged between 0.03 and 10.2 g O_2 m^{-2} day^{-1}. The highest production rates observed in the post-rainy season (October–November) coincided with a bloom of *Microcystis*. The phytoplankton is dominated by Cyanobacteria in the post-rainy season whereas diatoms are dominant during the dry (December–April) and the pre-rainy season (May–June). Cyanobacteria are dominated by two *Microcystis* species of which *M. flos-aquae* is the most abundant. Diatoms are dominated by five species of *Aulacoseira*: *A. agassizii*, *A. ambigua*, *A. granulata*, *A. muzzanensis* and *A. distans*, of which *A. granulata* is the most dominant (>50% of *Aulacoseira* spp. combined). *Melosira varians* occurs in significant numbers. Chlorophyta are less abundant: *Pediastrum* and *Staurastrum* species are usually the most frequent, though *Volvox* sometimes abounds (Dumont, 1986).

2.2 Lower Stretches

Due to the topography and nature of the river on the Ethiopian Plateau, the Ethiopian headwaters are not expected to contribute significantly to the plankton of the Blue Nile. Qualitatively most of the dominant species of Lake Tana do not reappear conspicuously in the lower stretches within Ethiopia. Quantitatively, the concentrations of cells counted in samples from the points of entry to the Sudan plain near Roseires (before construction of the Roseires dam) were low. In 1964, plankton was scantily represented at the Tissisat Falls, and not seen at all at stations further down the Blue Nile Gorge (Talling & Rzóska, 1967).

3 The White Nile Subbasin

3.1 Lake Victoria

The phytoplankton of Lake Victoria is varied and rich in species. This diversity was recognized early in the hydrobiological exploration of the Nile system: it is illustrated in the systematic account and lists of species published by Schmidle (1899, 1902), West (1907), Ostenfeld (1908, 1909), Virieux (1913), Woloszynska (1914), Hustedt (1922), Bachmann (1933), Thomasson (1955), Talling (1957c, 1966, 1987), Richardson (1968), Lung'ayia et al. (2000) and Kling et al. (2001). Most of the earlier descriptions were based on preserved samples obtained as isolated collections by plankton nets, liable to selective over-representation of some components and the loss of some fragile or very small species. Quantitative estimation over prolonged periods before 1962 were initiated by Fish (1957), and extended by Talling (1957, 1966, 1987) and Evans (1962). They were based on northern areas of the lake near the Nile outflow at Jinja, and showed large differences – qualitative and quantitative – between the more offshore 'open' lake and the inshore waters of the numerous gulfs and bays.

Diatoms and blue-green algae made up the greater part of the phytoplankton in both offshore and inshore waters. Green algae were also well represented offshore by numerous species of Chlorococcales (esp. *Pediastrum clathratum, Coelastrum reticulatum*, *C cambricum*, *Sorastrum americanum*, *Tetraedron arthrodesmiforme*) and desmids (esp. *Staurastrum leptocladum* f. *africanum*, *S. limneticum*, *S. anatinum*, *S. gracile* var. *nyansae*, *S. muticum*, *Cosmarium moniliforme*), although their contribution to total biomass was usually minor. Species of the diatom genus *Aulacoseira* were often dominant in both inshore and offshore regions. The cosmopolitan *A. ambigua* was typical of inshore bays, but *A. nyassensis* var. *victoriae* was the major form in the main lake, where it showed large seasonal changes of population density related to the annual cycle of stratification (Fish, 1957; Talling, 1966).

Offshore, low densities during the warmest and most stratified phase were also shared by many species in the phytoplankton, reflected in the seasonal minimum of chlorophyll-*a* content. This condition was ended by the cooler and windy phase of June–August, when near isothermal mixing returned to most of the lake, filaments of *Aulacoseira* were returned to the surface layers, and deep accumulations of nutrients were dispersed. In 1961, population increases were then exhibited by most planktonic algae, and most conspicuously by the principal diatoms (*Aulacoseira nyassensis* var. *victoriae*, *A. agassizii*, *Nitzschia acicularis*, *Surirella nyassae*, *Stephanodiscus astraea*). A different type of population cycle was followed by the Cyanobacteria *Anabaena flos-aquae* and *Anabaenopsis tanganyikae*, which declined over the isothermal period and increased strongly during the following phase of superficial stratification. Over the year as a whole, however, the predominant Cyanobacteria were small-celled colonial forms, tentatively identified as *Aphanocapsa elachista* and *A. delicatissima* West & West (Talling, 1966).

The total concentration of phytoplankton in the offshore surface waters was not large. Expressed as chlorophyll-*a* content, Talling (1966) obtained values of 1.2–5.5 mg chl-*a* m^{-3}. Much larger concentrations occurred in shallow inshore bays and gulfs; the large Nyanza (Kavirondo) Gulf was particularly rich, with 20 mg chl-*a* m^{-3} recorded in December 1960 (Talling, 1965).

Such was the situation until the 1970s. By the mid 1980s, clear signs of eutrophication were present (Hecky, 1993), with increasing blue-green dominated algal blooms and often a prominence of *Anabaenopsis raciborskii* (Kling et al., 2001). There was enhanced deep deoxygenation, and increase in some nutrient levels. A rapidly growing human population on the lake shores, altering land use and disposing of its raw sewage into the lake, is in part to blame for this (Lipiatou et al., 1996). By 1990, primary production had doubled, chlorophyll-*a* in offshore water was about four times the values measured by Talling (1965, 1966) and, among nutrients, nitrate had increased strongly but silicate–silicon was decreased. Currently, it has been suggested that the lake is approaching a situation of nutrient saturation and is light- rather than N or P-limited. For details, consult Lehman (2009).

3.2 Lake Kyoga

Traversed by the Victoria Nile this lake (also written as Kioga) is extremely shallow, dendritic in outline, and surrounded by areas of swamps (Green, 2009). A general survey and description was made by Worthington (1929a, b), and accounts of the phytoplankton were given by Bachmann (1933) and Evans (1962). Evans showed that horizontal gradients could occur within the lake, between areas more and less affected by the inflowing Nile, involving dissolved substances and algal abundance. Thus, in one section, passing from the inflowing Nile to the north-east arm, the electrical conductivity increased threefold and silicate tenfold; the concentrations of *Aulacoseira* spp. declined strongly, giving place to high numbers of the filamentous cyanobacterium *Planktolyngbya* (formerly *Lyngbya*) *limnetica*. The available information does not permit generalization for the lake as a whole. However, the transition from an *Aulacoseira* to a *Planktolyngbya* or *Planktolyngbya-Anabaena* dominated plankton is probably frequent in sections from flowing river to standing waters in other swampy regions of the White Nile, including the Sudd swamps downstream (Talling, 1957b).

From the brief accounts available, it appears that the phytoplankton of L. Kyoga shares a number of species characteristic of L. Victoria and less often encountered in lower reaches of the Nile. Examples include the diatom *Aulacoseira nyassensis* var. *victoriae*; the green algae *Coelastrum reticulum*, *C. cambricum*, *C. microsporum*, *Sorastrum hathoris* (possibly conspecific with *S. americanum*: cf. Talling 1966), *Tetraedron trigonum* and the desmid *Staurastrum leptocladum*; and the Cyanobacteria *Planktolyngbya circumcreta* and *Aphanocapsa elachista*. It seems clear, however, that this lake does not contain the wide variety of species characteristic of L. Victoria. There is no information on seasonal changes.

3.3 Lake Albert

This typical Rift lake is contacted by the White (Victoria) Nile only at its extreme north-east end, and its main water-mass maintains physical, chemical and biological conditions very different from those in the river (Talling, 1957a). It constitutes the junction between the White Nile proper and the drainage from the West Rift Valley and is typically dominated by small diatoms, identified by Talling (1963) as *Stephanodiscus astraea* with its var. *minutula* and *Nitzschia bacata*. The former was also noted by Bachmann (1933) as the dominant component in the net collections from 1927–1928. Talling also encountered occasional water-blooms of *Anabaena flos-aquae*, and from sampling in the early 1960s, provided information on the vertical, horizontal and seasonal distribution of these three species (Fig. 1), as did Evans (1997) later. These observations, and those of Hecky and Kling (1987), show that the phytoplankton appears lacking in variety of species, and differs considerably from that of any other water on the Nile system. Some species typical of L. Victoria (e.g. *Aulacoseira nyassensis*, *Staurastrum leptocladum* f. *africanum*) have been recorded from net samples by West (1909) and Bachmann (1933), but were not found by Talling or later observers.

A few records were made by Prowse and Talling (unpublished) and Evans (1997) on the phytoplankton in the inflowing and outflowing White Nile. Little was found in the inflow, below the Murchison Falls, but the two characteristic diatoms of L. Albert were present along a considerable stretch of the outflowing White (Albert) Nile.

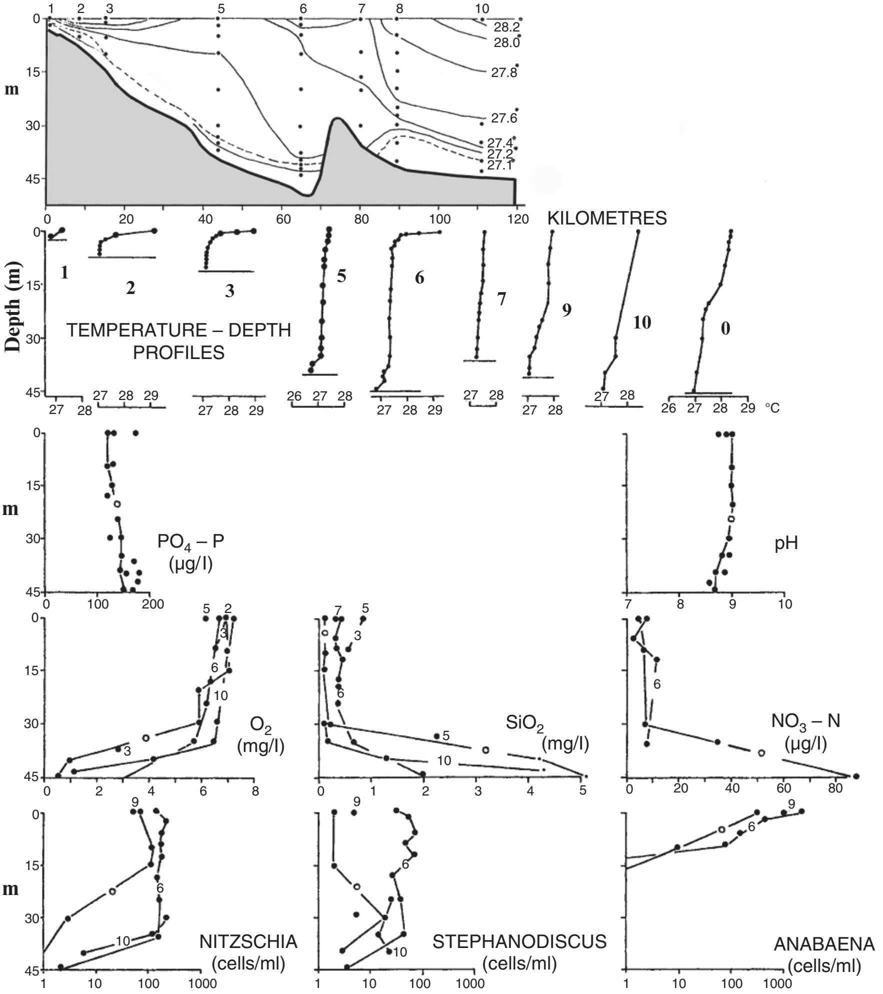

Fig. 1 Lake Albert: stratification patterns of temperature, some chemical components, and three species of planktonic algae, at numbered stations on a longitudinal section during 24–27 November 1960 (from Talling, 1963)

4 The Sudan Plain

4.1 The Blue Nile

For the purpose of this section, the Blue Nile within the Sudan plain is divided into six zones as shown in Table 1.

The natural flow of the Blue Nile has been altered by artificial hydrological regimes within the Sudan. Two dams have been built across the Blue Nile: Sennar

Table 1 Blue Nile zones within the Sudan Plain

Zone	Description	Comments
I	From Sudanese–Ethiopian border to tail of Roseires reservoir	About 100 km of free river flow not affected by the backwater of Roseires dam
II	Roseires reservoir	Backwater effect extending ca 100 km upstream
III	From Roseires dam to Sennar reservoir	Zone of free river flow not affected by backwater of Sennar dam
IV	Sennar reservoir	Backwater effect extending 140 km upstream
V	From Sennar dam to few kilometers south of Khartoum	Zone of free river flow receiving two seasonal tributaries: the Dinder and the Rahad
VI	Vicinity of Khartoum	Five kilometre river length east of confluence with the White Nile

dam and Roseires dam. Hydrobiological investigations of the Nile within the Sudan began with casual observations over 150 years ago. For the purpose of the present description, this period is divided into three stretches of time. Since dams have profound influence upon productivity and ecology of rivers, the three periods of time are marked by the construction of the two dams. Thus:

(i) First period: ends in 1925, before the completion of Sennar dam.
(ii) Second period: begins with the formation of Sennar reservoir in 1925 and ends in 1966, before the completion of Roseires dam.
(iii) Third period: from the formation of Roseires reservoir in 1966 to the present.

4.1.1 Description of the Phytoplankton During the First Period (1831–1925)

Prior to the construction of the Sennar dam in 1925 limnological research was largely neglected in the Sudan; hydrobiological data on the Blue Nile were scanty. The only material pertaining to the Nile consisted of some occasional notes compiled by passing biologists. These include notes on algae by Grunow (1870) and Gurney (1911).

4.1.2 Second Period (1925–1966)

High quality limnological work which has contributed to our knowledge of the biology of the Nile within the Sudan has been carried out by the Hydrobiological Research Unit, established in the Faculty of Science, University College of

Khartoum in 1953 long after the construction of the Sennar dam. Most of the work, however, was carried out within the vicinity of Khartoum.

4.1.2.1 Zones I–III

Observations on the Blue Nile indicate that little of the headwater lacustrine phytoplankton survives and prospers after the descent to the Sudan plain. Qualitatively, most of the dominant species of Lake Tana do not reappear conspicuously in the lower stretches. Quantitatively, the concentrations of cells counted in samples from the points of entry to the Sudan plain near Roseires were low. In 1964, the Tana plankton was scantily represented at the Tissisat Falls, and not seen at all at a station further down the Blue Nile Gorge.

Hammerton (1970a, b, 1971a), in three surveys carried out during February 1964–1966, found a sparse plankton in the 400 km section of the river upstream of Sennar reservoir. The diatom *Aulacoseira granulata* (formerly *Melosira granulata*) and the cyanobacterium *Anabaena flos-aquae* – two principal components of the Blue Nile plankton below Sennar reservoir – were present in very small numbers (around 20 cells ml^{-1}). All samples collected during 1964–1966 contained visible quantities of silt, fine sand and organic detritus with a Secchi disc visibility less than 50 cm. Poor light penetration, coupled with high current velocity, might be the sole factor checking the development of phytoplankton within this stretch before construction of the Roseires dam.

4.1.2.2 Zone IV (Sennar Reservoir)

As already mentioned, no hydrobiological studies were carried out within this zone prior to the construction of the Sennar dam. Hammerton (1970a, b, 1971a), confirming the 1955 findings of Talling & Rzóska (1967), found that as the water enters the dam basin most of the silt settled out. The Secchi disc visibility increased considerably resulting in a dense phytoplankton development. *Aulacoseira granulata* increased from around 20 cells ml^{-1} to 2.1×10^3 cells ml^{-1} in the reservoir. There was a similar increase in numbers of *Anabaena flos-aquae*. Unfortunately, no work on the phytoplankton along this zone was carried out from the 1960s to the present date.

4.1.2.3 Zone V (from Sennar to South of Khartoum)

Talling & Rzóska (1967) made the first longitudinal survey of its kind along this stretch of the Blue Nile during December 1955. They observed that densities of *Aulacoseira* increased appreciably in the first 150 km stretch below the dam but not further downstream. Increase in the *Anabaena* population was much more pronounced in the lower stretch below the dam. Talling & Rzóska concluded that most of the phytoplankton biomass reaching Khartoum is produced in true river conditions below Sennar reservoir. Hammerton (1970a, b, 1971a), in his different longitudinal surveys, also concluded that the plankton population which was brought to full development in Sennar dam basin persisted as a true river plankton throughout Zone V for over 360 km downstream, but with little of the gain in numbers downstream of the reservoir that was described by Talling & Rzóska. Possibly a variable gain is introduced near Khartoum by a seasonal 'stowing-up' of water due to the level in the adjacent White Nile.

4.1.2.4 Zone VI (Khartoum)

This zone has probably been better studied than other stretches. Brook (1954), in his systematic account of the phytoplankton of the Blue Nile from samples collected at Khartoum between 1949 and 1952, identified over 90 algal taxa. His detailed study was not repeated until after the completion of Roseires dam when Sinada (1972) presented a similar account. Of the 90 taxa reported by Brook (1954), only a few contributed significantly to total phytoplankton biomass. Rzóska et al. (1955) and Talling & Rzóska (1967), from records made during 1951–1953 and 1954–1956, have shown that the dominant species in the Blue Nile were *Aulacoseira* (formerly *Melosira) granulata* and its variety *angustissima*, *Anabaena flos-aquae* f. *spiroides* and *Planktolyngbya* (formerly *Lyngbya) limnetica*. Their findings are summarized below.

The concentration of plankton was low during the flood period of July–October when adverse conditions of rapid flow and high turbidity were prevalent. As the current subsided in November, diatoms were the first to appear in numbers, particularly *Aulacoseira granulata*, which was favoured by the post-flood relatively high concentrations of nitrate-nitrogen and phosphate-phosphorus (Fig. 2). The reduction of the former nutrient to concentrations in the range of 10–20 $\mu g\ l^{-1}$ was probably responsible for limiting further growth of *Aulacoseira. Anabaena flos-aquae* produced high population densities during January–February and was probably responsible for the depletion of phosphorus. The phytoplankton concentration declined during March–April, but a second maximum developed during May/early June before the entire plankton was washed out in late June by early flood water. The components of the second maximum were: *Aulacoseira granulata*, *Anabaenopsis cunningtonii*, *A. tanganyikae*, *Anabaena flos-aquae* f. *spiroides*, *A. scheremetievii*, *Raphidiopsis curvata* and *Ulnaria Synedra) acus. Planktolyngbya limnetica* was a minor component of the maximum of May–June 1956 (Talling & Rzóska, 1967) although a major one in 1953 (Rzóska et al., 1955).

No further seasonal studies on the phytoplankton of the Blue Nile were carried out between 1956 and 1962. The Hydrobiological Research Unit, University of Khartoum launched a long term study in 1963 to document the impact of the Roseires dam on the biological conditions of the Blue Nile. Hammerton (1970a, b, 1971a), and Hammerton (1972b), in contributions which include pre- and post-reservoir data,

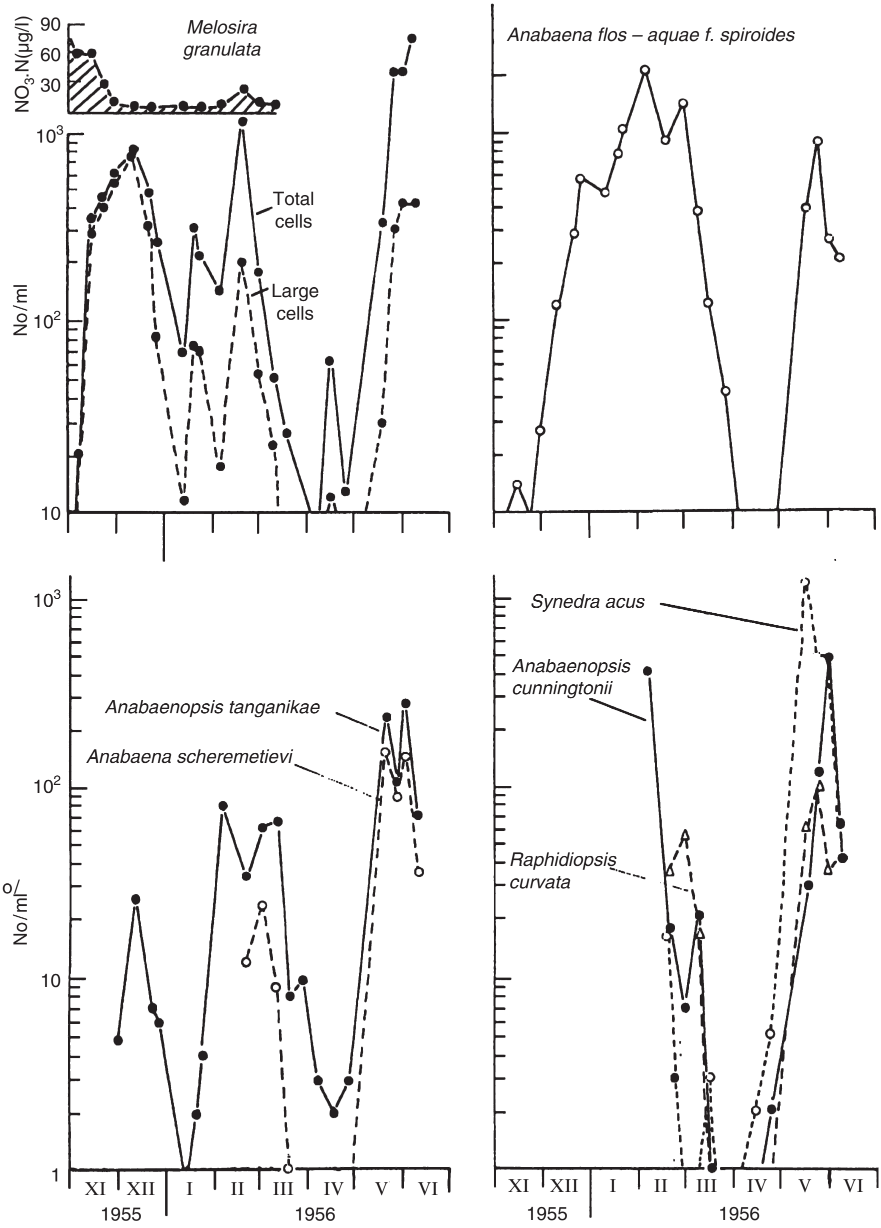

Fig. 2 Seasonal changes in the densities of phytoplankton species of the Blue Nile at Khartoum, 1955–1956. Units of population are cells (*Melosira*, *Synedra*, *Anabaena scheremetievi*), filaments (*Anabaenopsis*, *Raphidiopsis*), or coil turns of about 20 cells (*Anabaena flos-aquae* f. *spiroides*). An inset (*shaded*) shows some concurrent variation of nitrate-nitrogen (from Talling & Rzóska, 1967)

sampled the Blue Nile at Khartoum during 1963–1966 and observed seasonal cycles and succession of phytoplankton which were remarkably predictable and similar to those recorded by previous workers.

4.1.3 Third Period (1966–2004)

Man-made lakes have profound influence on the biological productivity and ecology of rivers. With this in mind in 1963, 3 years before the completion of Roseires dam, a long-term study of the whole 740 length of the Blue Nile within the Sudan was launched to determine the impact of Roseires dam on the biological conditions of the river. A survey carried out on conditions before and after the dam was put into use. The valuable earlier studies carried out by Brook (1954), Rzóska et al. (1955), Talling & Rzóska (1967) and Hammerton (1970a, b, 1971a) have provided baseline data for comparison with conditions in the newly formed reservoir and in the river after the filling of the reservoir.

4.1.3.1 Zone I

This zone was not affected by the formation of Roseires reservoir. Within this zone normal river conditions existed with much detritus suspension and few adventitious organisms (El-Moghraby, 1972).

4.1.3.2 Zone II (Roseires Reservoir)

The Reservoir was first filled in October 1966. Shortly after that Hammerton (1971b, 1972b) observed the development of a moderately rich plankton, with *Microcystis flos-aquae* and *Phormidium mucicola* as important components. *M. flos-aquae* rapidly dominated in December 1966 when the surface of the lake was bright green. It was remarkable that *Microcystis* had never previously been a major component of the Blue Nile (Brook, 1954; Talling & Rzóska, 1967). *Aulacoseira granulata*, always an important component of the plankton of the Blue Nile at Khartoum, was present throughout the sampling season with peak growths in November 1966, March and May 1967. The other important component of the plankton of the Blue Nile, i.e. *Anabaena flos-aquae*, did not appear in detectable numbers until January 1967 and reached a peak in February 1967.

During the second season, November 1967–May 1968, the phytoplankton showed heavier growth than during the first season, with the dominant algae being the same, *Aulacoseira granulata*, *Microcystis flos-aquae* and *Anabaena flos-aquae* (Hammerton, 1971c, 1972b). Several other algae were present, including *Pediastrum* spp. *Aulacoseira granulata* was already abundant in November 1967 and increased through December to a peak of 4.1×10^3 cells ml^{-1} in January 1968. During February 1968 there was a sharp increase, recording only 4.4×10^3 cells ml^{-1} in March but

5.2×10^3 cells ml^{-1} in May 1968. *Microcystis flos-aquae* and *Anabaena flos-aquae* were present in November 1967 but formed dense blooms during December 1967–February 1968. In March 1968 *Pediastrum* spp. became dominant whereas *Microcystis* reappeared in enormous numbers in May 1968. During 1969–1970, the Roseires reservoir showed further deviation from the usual seasonal cycle except for *Aulacoseira granulata*, which produced a heavy growth in November (Hammerton, 1972a, b). Unexpectedly, *Volvox aureus* dominated the plankton in December 1969 but disappeared in January 1970 to be replaced by *Pediastrum simplex* var. *duodenarium*, which continued to dominate throughout February 1970. Only traces of *Anabaena flos-aquae* and *Microcystis flos-aquae* were present during that season – the first time that Cyanobacteria failed to be a major component of the phytoplankton of the Blue Nile.

It is apparent that the reservoir during the first 3 years of its filling (1966–1970) had not stabilized biologically. The seasonal cycles and succession of the phytoplankton as described above differed from year to year during the first 3 years of its filling. Unfortunately no further studies were undertaken subsequently and therefore it is not possible to point out when the biological regime of the reservoir had thoroughly stabilized. But it can be safely stated that the formation of Roseires reservoir had brought about changes in the species composition and seasonal cycle of the plankton in the Blue Nile.

4.1.3.3 Zone III

It is unfortunate that the phytoplankton within this stretch of the river has not been studied. The only available information is that reported by Hammerton (1971c) that the phytoplankton densities along this stretch of the river were reduced to 40% of that of the Roseires reservoir.

4.1.3.4 Zone IV (Sennar Reservoir)

Phytoplankton in the Sennar reservoir was not studied on a seasonal basis before the construction of Roseires dam in 1966. Hammerton (1971c, d, 1972a, b), however, followed the seasonal cycles of the phytoplankton in the Sennar reservoir for three later consecutive seasons: November 1967–May 1968, November 1968–May 1969 and November 1969–May 1970. His findings are summarized below.

Aulacoseira granulata was dominant throughout 1967–1968, increasing from 3.1×10^3 cells ml^{-1} in November 1967 to 1.2×10^4 cells ml^{-1} in January 1968, then decreasing to 1.5×10^3 cells ml^{-1} in March before rising to a second smaller peak of 5.0×10^3 cells ml^{-1} in May 1968. *Anabaena flos-aquae*, co-dominant throughout much of the season, also showed peaks in January and May 1968 of 4.9 and 3.6×10^3 coil-turns ml^{-1} respectively. The total population densities in the Sennar reservoir were higher than those in the Roseires reservoir or indeed than any previous records in the Blue Nile. Hammerton (1971c) did not mention *Microcystis* *flos-aquae* in the Sennar reservoir during 1968 although it was a co-dominant member of the phytoplankton of the Roseires reservoir.

During 1968–1969 two periods of phytoplankton growth were observed in Sennar reservoir. The first started in October 1968 and ended in February 1969 with *Aulacoseira granulata* dominant; the second extended from April to June 1969 with *Microcystis flos-aquae* being the dominant alga and *A. granulata* co-dominant. However, similar to Roseires reservoir, *Anabaena flos-aquae* was not reported in the plankton of Sennar reservoir during that season.

During 1969–1970, two periods of maximum phytoplankton growth were observed: a shorter period during October–December 1969 with a dense growth of *Aulacoseira* during November, and a second period from March to June 1970. During the latter period *Aulacoseira* peaked in April, to be followed by *Microcystis* which dominated the plankton in May 1970.

Anabaena flos-aquae, a cyanobacterium prominent for so many years in the Blue Nile, became less important during November 1968–May 1970. It is unfortunate that no further studies were carried out after 1970 to ascertain the role played by *Anabaena flos-aquae* in the Sennar reservoir after the construction of the Roseires dam. The fluctuations in the densities of *Aulacoseira*, *Microcystis* and *Anabaena* within the Sennar reservoir during 1969–1970 closely reflected the seasonal changes of the numbers of these organisms in the Roseires reservoir. Thus it is not unreasonable to assume that the upstream Roseires reservoir greatly influenced the phytoplankton composition and density within the Sennar reservoir.

4.1.3.5 Zone V

The only available longitudinal survey carried out along this stretch of the Blue Nile during the third period indicated seasonal variations in species composition and densities of the phytoplankton that are reminiscent of the changes in Sennar reservoir (Hammerton, 1971d). However, there was a decrease in the densities of the major components of the phytoplankton downstream of Sennar dam, with a slight increase near Khartoum. The populations near Khartoum were less healthy than at Sennar (Hammerton, 1971d).

4.1.3.6 Zone VI (Khartoum)

Sinada (1972) studied the phytoplankton of the Blue Nile at fortnightly intervals uninterruptedly for 29 consecutive months from August 1968 to December 1970. The principal components of the phytoplankton during this period were *Aulacoseira granulata*, *A. distans*, *A.* sp. (*A. ambigua*?), *Ulnaria acus*, *Microcystis flos-aquae*, and *Anabaena flos-aquae*.

Aulacoseira granulata in Zone VI showed a regular seasonal cycle (Sinada & Abdel Karim, 1984a). It appears at the end of the flood season in September/October and quickly establishes a peak in November–December before it decreases sharply to minimum numbers which are maintained until May. In late May/early June a sudden summer peak occurs before being washed out in late June by early flood water (Sinada & Abdel Karim, 1984a). This seasonal cycle of *Aulacoseira* reported during 1968–1970 is reminiscent of that reported by Rzóska et al. (1955) and Talling & Rzóska (1967) in the same Zone VI 14 years earlier. Yousif (2004) when studying the Blue Nile at Khartoum 30 years later, from May 2001 till February 2002, documented a seasonal cycle of *Aulacoseira* similar to that found by previous workers.

Aulacoseira distans was first reported in the Blue Nile in 1968 (Sinada, 1972). It continues to be an important component of the phytoplankton to the present date (Yousif, 2004; Sinada, unpublished). The maximum development of *A. distans* at Khartoum during 1968–1970, 1986–1988 and 2001–2003 always occurred in November–December although this period might extend until February (Sinada & Abdel Karim, 1984a; Yousif, 2004: Sinada, unpublished).

Ulnaria acus showed definite recurrent peaks during November–December and May–early June as reported by Sinada (1972) and Yousif (2004). *Anabaena flos-aquae* was prominent only during January–February 1969 (8.0×10^2–2.8×10^3 coils ml^{-1}). It was striking that this cyanobacterium maintained very low numbers during the rest of the period of the above-mentioned study, similar to conditions in Roseires reservoir as reported by Hammerton (1971c, d, 1972a, b). The cyanobacterium *Microcystis flos-aquae* attained maximum development during February–May 1969 but maintained much lower numbers during the following season. Yousif (2004) reported recurrent peaks of this cyanobacterium during December–January and April–May.

As observed by the pioneers in the early 1950s, Sinada (1972) and Sinada & Abdel Karim (1984a) supported by Yousif (2004) 30 years later reiterated that the annual flood of the Blue Nile is the most important factor limiting the growth of the phytoplankton. The scarcity of planktonic algae during the flood, despite high nutrient concentrations, is attributable to the high silt content ($>4\,g\ l^{-1}$ suspended matter). The Secchi disc visibility during the flood season is in the very low range of <1–5 cm. In addition, the current velocity may be as high as $1.8\,m\ s^{-1}$ compared to $0.09\,m\ s^{-1}$ during May/early June when the second maximum of algal growth occurs. The increase in algal densities begins in late October/early November when the current subsides (velocity $<0.35\,m\ s^{-1}$) and most of the silt settles out (Secchi visibility around 20 cm). It is obvious that poor light penetration coupled with high current velocity is the sole factor checking the development of phytoplankton in the Blue Nile during the flood season. These conditions reported in the Blue Nile during the annual phase of the flood period during 1968–2002 by Sinada & Abdel Karim (1984a) and Yousif (2004) were no different from those reported before the construction of Roseires dam by Rzóska et al. (1955), Talling & Rzóska (1967) and Hammerton (1970a, b).

Sinada (1972) listed over 150 algal species belonging to 74 genera of various algal classes. Yousif (2004) listed about 125 algal taxa belonging to 80 genera in the Blue Nile at Khartoum. Comparing these two lists with that of Brook (1954) compiled in early 1950s, it is obvious that there was an increase in diversity of species.

Many algae appeared though in small numbers and a few others disappeared. Among the important species which were first reported during the 1968–1970 (study were *Aulacoseira distans* and *Acanthoceras* formerly *Attheya zachariasi*. These two diatoms contributed appreciably to the total phytoplankton biomass of the Blue Nile at one time or another. Of the important species which appeared during the 2000–2003 study were *Aulacoseira nyassensis* (large and small forms) and *A. ambigua*, which contributed appreciably to the total phytoplankton biomass of the Blue Nile at one time or another. Likewise the colonial cyanobacterium *Microcystis flos-aquae* which had been reported by Brook (1954) in 1951–1953 as being an unimportant component of the phytoplankton of the Blue Nile, preponderated shortly after the filling of Roseires reservoir and spread downstream (Hammerton, 1972b). It continued to constitute an important phase in the phytoplankton of the Blue Nile at Khartoum throughout 1968–1970 and during 2001–2002 (Sinada, 1972; Yousif, 2004). Occasional samples from the Blue Nile at Khartoum during 1977–1983 have shown that *Microcystis flos-aquae* as well as *Aulacoseira distans* have established themselves (Sinada, unpublished) with recurrent peaks during the same months of the year in different years, although the magnitude of the peak differed from year to year. *Anabaenopsis cunningtonii* and *A. tanganyikae*, recorded by Rzóska et al. (1955) and Talling & Rzóska (1967) as important members of the plankton of the Blue Nile during 1951–1956, were rarely observed during 1968–1970 or during 2000–2002 (Sinada, 1972; Yousif, 2004). Similarly, *Planktolyngbya limnetica* – which constituted an important component of the phytoplankton of the Blue Nile in the early 1950s – was not seen in the Blue Nile during 1968–1970 or thereafter (Sinada, 1972; Yousif, 2004).

It is obvious that the algal flora of the Blue Nile has undergone a considerable change within a short period of time between 1956 and 1968. This change may be attributed to the construction of the Roseires dam in 1966.

4.2 The White Nile

For the purpose of this section, the White Nile within the Sudan plain is divided into five zones, shown in Table 2.

4.2.1 The Phytoplankton in Zone I (from the Sudanese–Ugandan Border to Bor)

Little is known of the phytoplankton of the upper reaches of the White Nile within the Sudan plain. After entering the plain, the White Nile flows over shallow gradients for about 1,400 km before it is seasonally impounded in the Gebel (= Jebel) Aulia reservoir near Khartoum. The Gebel Aulia dam on the White Nile, 45 km upstream of the confluence with the Blue Nile, creates favourable conditions for the development of a pure phytoplankton. Similar to conditions in the Blue Nile,

Table 2 White Nile zones within the Sudan Plain

Zone	Description	Comments
I	From Sudanese–Ugandan border to Bor (Bahr El Jebel River)	About 100 km zone of free river flow
II	Sudd region: from Bor to Lake No/Malakal (Bahr El Jebel and Bahr El Zeraf River)	The two main tributaries twine through the Sudd swamps for 540 km
III	From Malakal to Gebel Aulia reservoir	Zone of free river flow, not affected by the backwater of Gebel Aulia dam
IV	Jebel Aulia reservoir	Backwater effect extending 260 km upstream
V	From Gebel Aulia dam to Khartoum	Forty-five kilometre of free river flow to confluence with the Blue Nile

the White Nile waters indicate that little of the headwater lacustrine phytoplankton survives and prospers after the descent to the Sudan plain. Qualitatively, most of the dominant species of lakes Victoria and Albert do not reappear conspicuously in this stretch of the White Nile. Quantitatively, the concentrations of cells in samples from the point of entry to the Sudan plain near Juba were low.

4.2.2 Zone II: Sudd Region

These two courses of the White Nile flow through the swamps of the Sudd Region (for details, see Green & El-Moghraby, 2009) in southern Sudan for 540 km. They carry a rudimentary impure plankton and rich detritus suspension (Rzóska et al., 1955; Sinada, unpublished). In this reach, scattered observations have shown phytoplankton to be present in low densities, near or below the limits of quantitative estimation. It is composed predominantly of the diatom *Aulacoseira granulata* and its elongate variety *angustissima*, with smaller numbers of the cyanobacterium *Planktolyngbya limnetica* (Brook & Rzóska, 1954; Prowse, 1954 and unpublished; Rzóska, 1974; Talling, unpublished; Sinada, unpublished). In the region of the *Sudd* swamps, adjacent bodies of standing water are frequent and often bear rich populations of *P. limnetica*, sometimes accompanied by *Anabaena flos-aquae* f. *spiroides* (e.g. Prowse, 1954; Talling, 1957b). These will contribute some cells to the main river. A more remarkable and completely different development of phytoplankton exists in one such water, Lake Ambadi, on a tributary system (Bahr el Ghazal) with distinctive water chemistry (Green & El Moghraby, 2009). There Prowse (in Grönblad et al., 1958) found several species – *Dinobryon sertularia*, *Botrycoccus braunii*, *Asterococcus limneticus* – rarely or never recorded elsewhere from the Sudanese Nile, whereas the more common species of the main river and lagoon – *Aulacoseira granulata*, *Planktolyngbya limnetica*, *Anabaena flos-aquae* f. *spiroides* – were not seen. Still more distinctive of L. Ambadi, and adjacent parts of the Bahr el Ghazal, is the exceptional diversity of desmids (chiefly non-planktonic), some not recorded elsewhere (Grönblad et al., 1958; Grönblad, 1962).

4.2.3 Zone III: Malakal to Gebel Aulia

A zone of free river flow not affected by the backwater of Gebel Aulia dam. The White Nile flowing out of the *Sudd* region still carries a rudimentary impure plankton and rich detritus suspension until it enters the Gebel Aulia reservoir.

4.2.4 Zone IV: Gebel Aulia Reservoir

On entering the large lake-like storage basin of the Gebel Aulia reservoir, whose influence extends for 400 km upstream, the current slackens and detritus and adventitious non-planktonic forms settle out. A pure plankton formation develops, increasing in density towards the dam (Brook & Rzóska, 1954; Rzóska et al., 1955).

Here, near the end of the White Nile, a dense phytoplankton develops each year in the annually impounded water of the reservoir. It has been studied extensively by hydrobiologists at Khartoum, both for the seasonal aspects deduced mainly from sampling downstream of the dam (Rzóska et al., 1955; Prowse & Talling, 1958) and for the longitudinal development along the river (Brook & Rzóska, 1954; Prowse & Talling, 1958). Both approaches show that the first alga to produce dense populations was the predominant species of the upstream 'inoculum' – *Aulacoseira granulata*. Later in time (Fig. 3) and space it was succeeded by Cyanobacteria – especially *Anabaena flos-aqua*e (Lyngb.) Bréb. f. *spiroides* (Woron.) Elenk (= *A. flos-aquae* var. *intermedia* Woron. f. *spiroides* Woron.) and *Planktolyngbya limnetica*, with *Anabaenopsis tanganyikae*, *A. cunningtonii* and the diatom *Ulnaria acus* forming lesser maxima. The total densities reached were sufficient to discolour the water and reduce transparency to less than 1 m; they were estimated by Prowse & Talling (1958) to be in volume between 10 and 30 $\mathrm{mm}^3\ \mathrm{l}^{-1}$. Although rather few species make large contributions to the total biomass, a considerable number of minor constituents occur.

4.2.5 Zone V: From Gebel Aulia Dam to Khartoum

With 45 km of free river flow to the confluence with the Blue Nile, this zone has been studied extensively. It is not unreasonable to assume that the river water passing through the zone, only 45 km downstream Gebel Aulia Dam, carries a true picture of the plankton in the reservoir behind the dam. Few species make large contributions to total biomass, and a considerable number of minor constituents occur. The overall algal flora of the White Nile is rich and diverse. Over 150 taxa were identified by Brook (1954), Sinada (1972), and Abdelrahman (2004).

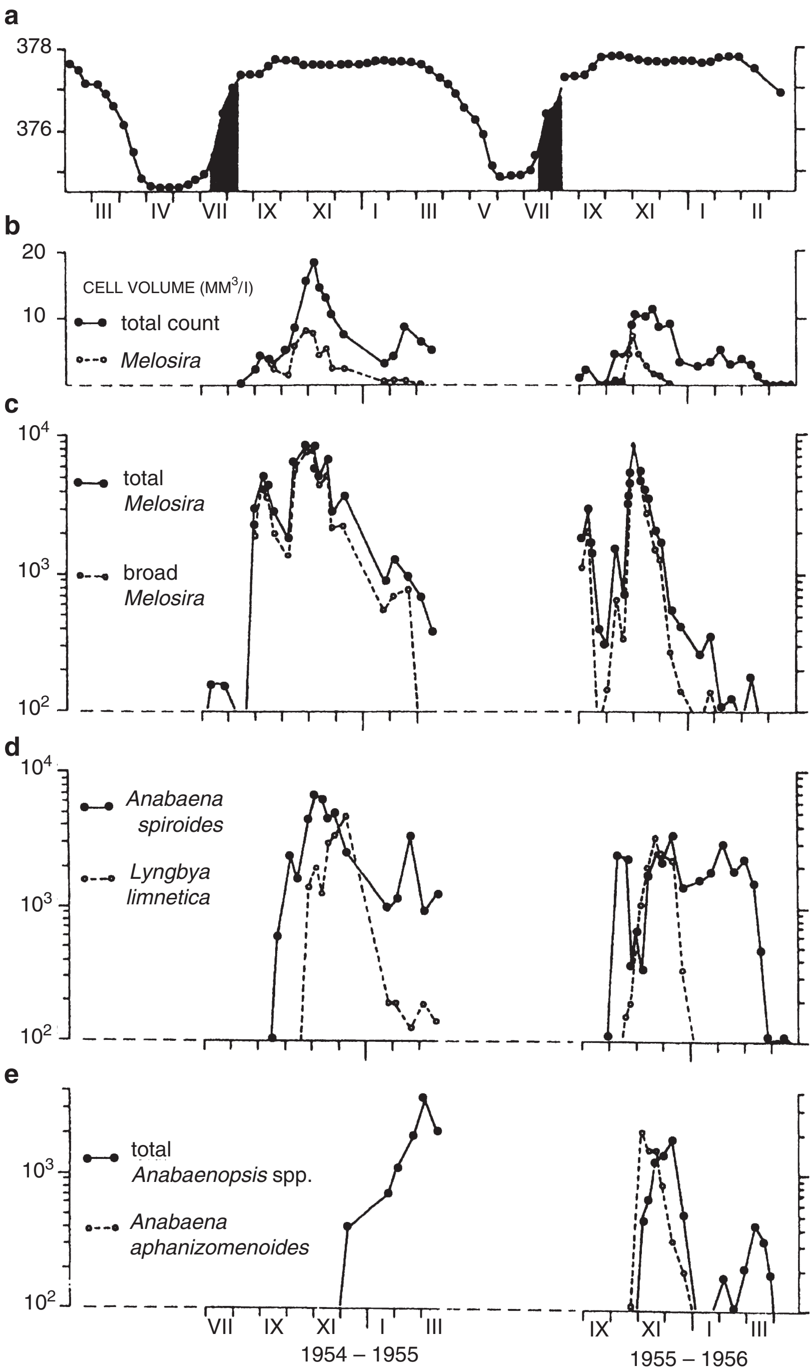

Fig. 3 Seasonal changes in the densities of phytoplankton species of the White Nile near Khartoum, 1954–1956 (**b**–**e**), shown in relation to water level in m (**a**) in the Gebel Aulia reservoir 40 km upstream. Full closure of the reservoir-dam is indicated by black columns. Units for *Aulacoseira* (*A. granulata*) are cells ml^{-1}, for '*Anabaena spiroides*' (*A. flos-aquae* f. *spiroides*) coil-turns ml^{-1}, and for *Planktolyngbya* formerly *Lyngbya Anabaenopsis*, and *Anabaena aphanizomenoides*, filaments ml^{-1} (from Prowse & Talling, 1958)

Comparing the lists of algae recorded in the White Nile near Khartoum by Sinada (1972) during 1968–1970 and by Abdelrahman (2004) in early 2000s with those recorded by Brook (1954) during 1949–1952, appreciable changes in composition of species are noted. *Planktolyngbya limnetica*, *Anabaenopsis cunningtonii* and *A. tanganyikae*, important components in the early 1950s (Brook, 1954; Prowse & Talling, 1958; Talling & Rzóska, 1967), maintained themselves in reduced numbers during the next 40 years.

Diatoms were then prominent in the White Nile at Khartoum, being the most dominant algal group throughout the years. Species that contributed appreciably to total algal biomass were: *Aulacoseira granulata* and its var. *angustissima* (?), *A. nyassensis*, *A. distans*, *Navicula* spp., *Fragilaria* spp., *Cocconceis placentula* and its var. *lineata* and *Synedra* spp. The concentration of chlorophyll-*a* in surface water of the White Nile showed a peak of 8.9 mg m^{-3}, with diatoms dominating the phytoplankton (Abdelrahman, 2004). Cyanobacteria were the second major group. The prominence and bulk of biomass of this group was due to the filamentous form *Anabaena flos-aquae* which had been reported by all workers throughout the decades. However, *Planktolyngbya limnetica*, *Anabaenopsis cunningtonii* and *A. tanganyikae*, which were sometimes dominant in the 1950s, were replaced by *Oscillatoria* spp. (Abdelrahman, 2004).

Green algae were less numerous and represented by Chlorococcales. Although Grönblad et al. (1958) and Grönblad (1962) observed a rich and diverse desmid flora in L. Ambadi and adjacent parts of Bahr el Ghazal in the Sudd Region, desmids were poorly represented in the White Nile.

4.3 The Main Nile Within Sudan

From Khartoum to Lake Nubia we have scanty knowledge of the phytoplankton and its development. It seems likely that the seasonally rich plankton that passes downstream from Khartoum is largely lost in the upper cataract stretch. A few samples collected by Rzóska (1958) and Hammerton (1970) showed that *Aulacoseira granulata* was still the dominant species in the Dongola region. Further downstream at Wadi Halfa, at the head of the newly formed Lake Nasser–Nubia, Hammerton (1972b) found a more mixed phytoplankton with abundant *Microcystis aeruginosa*. The recent creation of a new reservoir (Meroë or Merowe) by a dam above Dongola can be expected to lead to more phytoplankton development.

5 The Main Nile Within Egypt: Lake Nasser–Nubia

The present Lake Nasser–Nubia was preceded by the smaller Aswan Reservoir with seasonal rather than over-year retention. Its phytoplankton was studied in 1942 by Abdin (1948c, 1949). Seasonal development was interrupted by silt-laden floodwaters. Once again the diatom *Aulacoseira granulata* was the preponderant species and increased soon after the annual storage of water began. Population maxima of green algae, especially species of *Volvox*, *Eudorina*, and *Pediastrum* followed. A final maximum of *Melosira varians* was recorded before the return of the flood water in July. Although not quantitative, the records were notable for the minor representation of blue-greens (Cyanobacteria). In a later sample collected in April 1957 (Elster & Vollenweider, 1961), the dominant species were *Melosira varians* and *Volvox globator*, although several blue-greens were common.

Investigations of phytoplankton in Lake Nasser were initiated in the early 1970s by UNDP, FAO and the Egyptian government. In the late 1970s and the early 1980s, some fragmentary work devoted to the lake phytoplankton was carried out, summarized by Bishai et al. (2000) (see also El-Shabrawy, 2009).

The phytoplankton standing crop varies between stations and periods. Taha and Mageed (2002) and Ibrahim & Mageed (2005) reported peaks of phytoplankton at Korosko, where a Great Bend in the lake occurs. This forms a kind of threshold for phytoplankton distribution (Habib et al., 1990). The lowest crop was observed at the southern end of the lake where flood water, loaded with silt, enters the lake (Latif, 1981).

The number of phytoplankton species increased with reservoir age (Abd El-Karim, 2005). Lists of those observed are given by Samaan (1971) (27 species), Latif (1974) (20). Zaghloul (1985) (43), El-Otify (1985) (59), Mohamed et al. (1989) (50), Abdel-Monem (1995) (84) and Ibrahim & Mageed (2005) (94). The dominant diatoms were *Cyclotella* spp. and *Aulacoseira & Melosira* spp., while blue-greens were dominated by *Lyngbya* spp., *Oscillatoria* spp. and *Anabaenopsis cunningtonii*. Green algae were dominated by *Ankistrodesmus* spp. and *Closterium* spp. (Taha & Mageed, 2002). Blooms of *Microcystis aeruginosa* were recorded by Habib et al. (1990), Mohamed & Loriya (2000) and Ibrahim & Mageed (2005). Mohamed & Loriya (2000) recorded blooms from 1987 to 1994. They reported blooms of *Microcystis aeruginosa* only in the upper region between Wadi Halfa and Abu Simbel. Recently, blooms have also been observed in the central area of the lake. Occasionally, they are even seen at Korosko. Formerly, *Microcystis aeruginosa* blooms occurred before the flood, but now they tend to occur around the year (Mohamed & Loriya, 2000). Most investigators (Samaan & Gaber, 1976; Gaber, 1982; El-Otify, 1985; Zaghloul, 1985; Taha & Mageed, 2002; Ibrahim & Mageed, 2005) have found diatoms and Cyanobacteria to be the most common groups, although their relative dominance varied with time and place. El-Otify (1985, 2002) found that Bacillariophyceae dominated from March 1982 to May 1982, from November 1982 to February 1983, from April 1983 to June 1983 and from November 1983 to February 1984. Cyanophyta ranked second, Chlorophyta third and Pyrrophyta fourth. Ibrahim & Mageed (2005) detected six classes: Bacillariophyceae, Cyanobacteria, Chlorophyceae, Chrysophyceae, Dinophyceae and Cryptophyceae.

Many investigators have studied chlorophyll-*a* – a measure of total phytoplankton abundance – along the main channel of the lake as well as in khors since the early stages of filling (Habib, 1984, 1992, Habib & Aruga, 1987; Habib et al., 1987; Abdel-Monem, 1995; Taha & Mageed, 2002; Ibrahim & Mageed, 2005). The results indicate that chlorophyll *a* concentration in the 0–8 m layer is high in the southern region compared with the north. High chlorophyll-*a* concentrations occur in the upper 8 m layer from March–April to October–November (Abd El-Karim, 2005).

Annual average values of chlorophyll-*a* (µg l^{-1} = mg m^{-3}) at six stations in the main channel of Lake Nasser from 1986 to 1997 are given by Mohammed (2000). He found a maximum annual average of about 10.5 µg l^{-1} in 1990, while the average minimum, ca 6.2 µg l^{-1}, was recorded in 1997. High concentrations usually occurred in the euphotic zone. A stratified vertical distribution was noted from April to September, while the distribution was homogeneous from November to February. He recorded a maximum average value of 13.1 µg l^{-1} at El-Allaqi in 1990, and a minimum value of 1.8 µg l^{-1} at El-Ramla in 1994. Taha & Mageed (2002) stated that the lowest chlorophyll-*a* value, 0.6 µg l^{-1}, was recorded at the eastern side of Toshka. In contrast, near the western bank of Korosko, the maximum was 15 µg l^{-1}. In the Khors, they found a maximum of 7.4 µg l^{-1} at Khor Allaqui, and a minimum of 0.90 µg l^{-1} in Khor Toshka.

Habib et al. (1987) and Habib (1992) discussed the monthly distribution of chlorophyll-*a* along one large khor near Aswan, the Khor El Ramla, from October 1982 to April 1983. Highest average values occurred inside the Khor, except in January and February 1983. The highest value, 16.4 µg l^{-1}, was recorded in April 1983, the lowest, 4.7 µg l^{-1}, in October 1982. Mean average chlorophyll-*a* showed a maximum of 10.8 µg l^{-1} inside and a minimum of 9 µg l^{-1} outside the Khor.

6 The Main Nile Within Egypt: Aswan to Delta

Phytoplankton studies began in the 1930s (Bachmann, 1936) and 1940s (Abdin, 1948a, b), followed by Elster & Jensen (1961), Elster & Vollenweider (1961), Ibrahim (1978), El-Ayouti & Ibrahim (1980), Shehata & Bader (1985), Abdel-Hamid (1991), Touliabah (1996), Abd El-Karim (1999) and Sobhy (1999, 2008).

The standing crop of phytoplankton shows a gradual increase over time, from 10×10^6 (Shehata & Bader, 1985) to 39×10^6 cells l^{-1} (Abd El-Karim, 1999). This increase may be due to enrichment with nutrients, particularly after the High Dam (HD) construction. According to NWRC (2000), the Nile receives wastewater from about 124 point sources (67 agricultural drains; the remainder industrial sources) between Aswan and El-Kanater Barrage. The impact of these discharges on the quality of the Nile water (Abdel-Satar, 2005) is only locally significant due to the high self-purification capacity of the Nile water (El Sheekh, 2009).

Elster & Jensen (1961) found that *Melosira varians* and *Volvox globator* were dominant between Aswan and Cairo. Shehata (1968) found that among 16 species identified, the diatoms *Aulacoseira granulata* and *Melosira varians* were ubiquitous; other important species were *Pediastrum* sp. and various Cyanobacteria, especially in spring and summer (*Microcystis* sp., *Anabaena flos-aquae* and *A. constricta*, less predominant were *Oscillatoria*, *Lyngbya* and *Nodularia spumigena*). El-Ayouty

(1976) stated that species of genera *Synedra*, *Nitzschia*, *Bacillaria*, *Biddulphia*, *Amphora*, *Cocconeis*, *Cyclotella*, *Navicula*, *Neidium*, *Cymatopleura*, and *Melosira (*now *Aulacoseira)* were dominant at Cairo. Zidan (1983) pointed out that although diatoms represented the highest standing crop, Chlorophyta contributed more genera to the community. Abdel-Hamid (1991) recorded 314 taxa between 1987 and 1988 from south Cairo to Damietta and Rosetta. *Scenedesmus quadricauda*, *Synedra ulna*, *Chroococcus limneticus*, *Cryptomonas marssonii*, and *Gymnodinium* sp. were the abundant species. *Cocconeis placentula*, *Cyclotella* spp., *Aulacoseira granulata* and *Ulnaria* (formerly *Synedra*) *ulna* (diatoms), *Ankistrodesmus falcatus*, *Botryococcus braunii*, and *Kirchneriella* spp. (Chlorophyceae), *Anabaenopsis raciborskii*, *Gomphosphaeria lacustris*, *Merismopedia tenuissima* and *Microcystis aeruginosa* (Cyanophyceae) were dominant among 82 species from River Nile and irrigation canals at Qalubia governorate (Hamed, 1993). Abd El-Karim (1999) and Sobhy (1999) found that *Cyclotella*, *Synedra*, *Aulacoseira* (diatoms), *Scenedesmus*, *Crucigenia*, *Ankistrodesmus*, *Oocystis* (green algae), *Microcystis*, *Chroococcus*, *Merismopedia* (blue-green algae) were abundant among 254 and 302 taxa recorded at Damietta Nile branch and River Nile at Helwan. Sobhy (2008) mentioned that *Cyclotella ocellata*, *Melosira* (= *Aulacoseira) granulata*, *Nitzschia palea*, *Nitzschia paleacea*, *Aulacoseira granulata* var. *angustissma* (diatoms), and *Microcystis aeruginosa*, *M. flos-aquae*, *Chroococcus minutus* and *C. dispersus* (Cyanobacteria) tolerate many types of pollution.

Volvox, a dominant species in the past (Abdin, 1948a, b; Elster & Jensen, 1961; Elster & Vollenweider, 1961), has now disappeared from the river, whereas species newly recorded include the Cryptophyceae *Chroomonas acuta* and *Chroomonas nordstedii*, the Chrysophyceae *Bitrichia ollula* and *Dinobryon sertularia*, and some diatoms such as *Acanthoceras zachariasii* (Abd El-Karim, 1999; Sobhy, 1999).

Among researchers working on single groups of phytoplankton, El-Shimi (1984) studied the distribution of diatoms (planktonic and benthic) at seven stations (Aswan, Qena, Suhag, Asyut, El-Minya, Beni-Suef and Cairo region). She recorded 277 taxa, with *Aulacoseira granulata* var. *granulata*, *Cyclotella kuetzingiana* var. *planetophora*, *Fragilaria* spp., and *Synedra* spp. dominant. Hamed (2005) provided a list of 290 taxa of blue-green algae inhabiting Egypt (River Nile, Nile Delta, Nile Valley, Cairo, Southern Sinai, Isthmic Desert and Mareotic sector). The main element of this flora – much non-planktonic – was formed by the Oscillatoriaceae, with 61 species and varieties of *Oscillatoria* on record.

Chlorophyll-*a* concentrations parallel standing crops and increase from Aswan to Cairo and the Delta branches (Ibrahim, 1978; Shehata & Bader, 1985; Abdel-Hamid, 1991; Touliabah, 1996; Abd El-Karim, 1999; Sobhy, 1999, 2008), reflecting enrichment with nutrients via agricultural drains (Fayed & Shehata, 1976; Kobbia et al., 1991). Chlorophyll-*a* also varies with time, from 5 to 37 $\mu g\ l^{-1}$ (Shehata & Bader, 1985), with average 22.4 $\mu g\ l^{-1}$ (Abdel-Hamid, 1991). The highest values, 41–108 $\mu g\ l^{-1}$, were recorded by Sobhy (1999) at Helwan region. During recent years (up to 2005), the Nile floods have been high. Therefore, the irrigation ministry in Egypt has released more water from the High Dam to clean the river, causing a drop in standing crop and chlorophyll-*a* concentrations.

7 Limiting Factors

From the previous account, it appears that dense and varied developments of phytoplankton are typical of the standing waters, either in the headwater lakes or downstream reservoirs. The deduction might be made that this feature expresses a requirement for sufficient retention time, as contrasted with times of travel in free-flowing river conditions. However, such conditions may be unfavourable in other physical respects. Light penetration must be so low in such silt laden flood waters as to interrupt plankton development in the Blue Nile (Talling & Rzóska, 1967). The high extinction coefficients reported by Talling (1957) also imply unfavourable light conditions in reaches of the upper White Nile. Further, the rather rapid loss of lake plankton below the headwater lakes suggests that mechanical factors, including severe turbulence, may be destructive. Much further down the Nile, in Nubia and in Egypt, there are instances of considerable phytoplankton development in flowing water conditions.

In the physically more favourable environments of the lakes and reservoirs, nutrient limitations are likely to loom larger. Both Bini (1940) and Talling (1966) were impressed by the low concentrations of inorganic nitrogen which they measured in lakes Tana and Victoria respectively, and suggested that these might play a large part in the regulation of planktonic populations. However, support from detailed population estimates and correlative analysis is only available from Lake Victoria amongst the headwater lakes, and from the lowermost stretches of the White and Blue Niles near Khartoum. In the latter, the initial seasonal growth of *Aulacoseira granulata* was observed to end when measured nitrate concentrations were depleted to low values ($<20\,\mu g\ l^{-1}\ NO_3$-N: Prowse & Talling, 1958; Talling & Rzóska, 1967; see Fig. 3). This check did not affect the increase of the second principal component, *Anabaena flos-aquae* f. *spiroides*, which would be likely to fix atmospheric nitrogen – and which might be recycled to the advantage of later species in the seasonal succession. Depletions of dissolved phosphorus and (in the White Nile) silicon also accompanied the seasonal algal increases. Phosphorus limitations are possible but conjectural. Silicon limitation is unlikely because of relatively high residual concentrations, even though the predominant diatom of the Nile – *Aulacoseira granulata* – is generally associated with considerable concentrations (Kilham, 1971). Its peaks resulted in a reduction of concentrations of dissolved silicon (Sinada & Abdel Karim, 1984a).

From these and other African inland waters, there is evidence that strongly alkaline conditions (near or above pH 9.0) are unfavourable for *Aulacoseira*–plankton (Talling & Talling, 1965; Talling & Rzóska, 1967). Such conditions are reached as the result of photosynthesis during the seasonal maxima of blue-green algae in the White and Blue Niles near Khartoum. It is possible, but not proven, that they may limit the *Aulacoseira* component (a supposition supported by experimental work elsewhere: Talling, 1976), although vigorous photosynthesis by the Cyanobacteria continues (Prowse & Talling, 1958).

8 Rates of Photosynthetic Production

The photosynthetic activity of phytoplankton may alter the content of dissolved oxygen, carbon dioxide, and hence pH. These changes have a strong diurnal component, related to daily irradiation, which was traced as early as 1927 in the Nyanza (Kavirondo) Gulf of Lake Victoria (Worthington, 1930). Following observations by Pyle (1950) on standing waters in the Sudd region, Talling (1957b) extended them for a lagoon and other productive water-bodies of the White Nile system, and derived estimates of the daily gross photosynthetic production per unit area. The latter lay between 4 and 11 g O_2 m^{-2} day^{-1}, approximately equivalent to between 1.5 and 4 g C m^{-2} day^{-1}, and were compared with independent estimates from water samples exposed in light and dark bottles.

The light and dark bottle (oxygen) method was used by Talling (1957, 1966) to examine the headwater lakes, including Victoria, Albert, Edward, and George. Work on L. George is described by Ganf (1975) and Ganf & Horne (1975). In all these lakes, estimates of maximum daily gross production were high, between 10 and 16 g O_2 m^{-3} day^{-1}; net photosynthesis was difficult to estimate, but was probably much lower (cf. Ganf, 1974 for L. George). As noted earlier, later measurements of photosynthetic production were made on Lake Tana (Wondie et al., 2007); others are available from Lake Victoria (Mugidde, 1993; Silsbe et al., 2006). Talling (1966) showed that the photosynthetic rates per unit area can be relatively insensitive to the wide variation in phytoplankton density (per unit volume) mainly because of self-shading effects on light penetration. However, the maximum (light-saturated) rates of photosynthesis per unit water volume were closely correlated with population density. The connecting factor, the maximum specific activity per unit population, was notably high compared to general experience with phytoplankton.

Further down the White Nile, in and below the Gebel Aulia reservoir near Khartoum, intense photosynthetic activity during phytoplankton maxima was studied by Talling (1957b), Prowse & Talling (1958), Hammerton (1972a), and Sinada & Abdel Karim (1984b). Some of the resulting depth profiles of activity, with related factors, are shown in Figs. 4 and 5. The photosynthetic zone is typically compressed into a layer 1–2 m deep, partly due to self-shading behaviour but mainly to the fine suspended material characteristic of the White Nile. As in the headwater lakes, the maximum specific activity (per unit of population) was usually very high; the rates calculated per unit cell volume agreed broadly with later measurements from the lakes based upon chlorophyll-*a* content. The gross production rates per unit area were moderately high, often exceeding 0.5 g O_2 m^{-2} h^{-1} or an estimated 5 g O_2 m^{-2} day^{-1}. For example, over a period of 30 days during the 1953 population maximum illustrated in Fig. 5, the estimated areal rates were 0.77 ± 0.07 g O_2 m^{-2} h^{-1} or 2.4 ± 0.2 g C m^{-2} day^{-1}. Later work in 1965, by Hammerton and collaborators, yielded estimates of similar magnitude (Hammerton, 1972a).

Hammerton (1972a, b, c) has also measured photosynthetic production at various points, and in various seasons, on the Blue Nile. The maximum rates per unit area

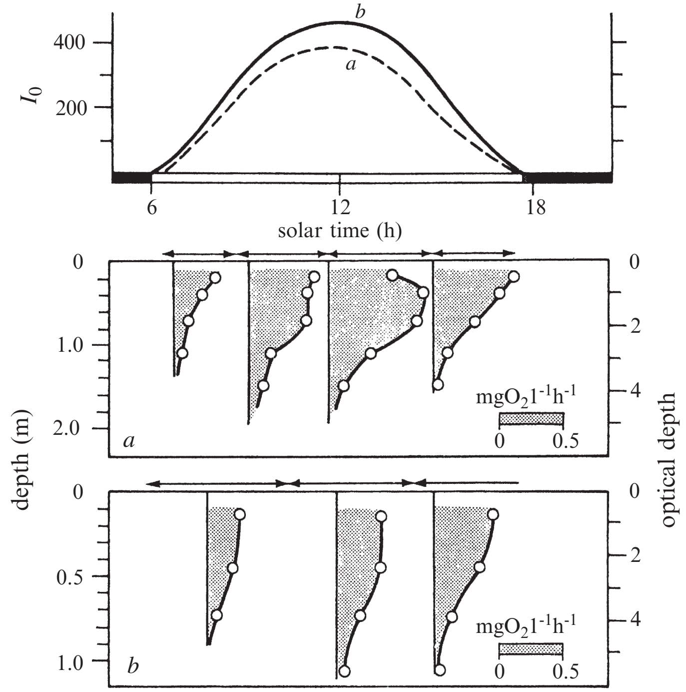

Fig. 4 Depth profiles of photosynthetic rate (*stippled areas*) in the Gebel Aulia reservoir for various periods during the day, during (**a**) 12 December 1954 and (**b**) 7 October 1955. The diurnal variation of incident solar irradiance I_o (in kerg cm^{-2} s^{-1} = W m^{-2}) is shown above (from Talling, 1957b)

are even higher than in the White Nile, possibly due to the reduced silt content and greater light transmission. Sinada & Abdel Karim (1984b) found that the maximum daily gross production was higher in the White Nile than in the Blue Nile, 10 and 6 g O_2 m^{-2} day^{-1}, respectively, when *Aulacoseira* preponderated during November.

Few measurements have been published for regions of the Nile below Aswan. Elster and Vollenweider (1961) list a series of seven stations (^{14}C exposures) from the (old) Aswan reservoir to Cairo, with the maximum areal rate (1.06 g C m^{-2} 6 h^{-1}) and deepest photosynthetic zone (5 m) in the Aswan reservoir. Corresponding values at Cairo were 0.358 g C m^{-2} 6 h^{-1} and 2 m. More work was carried out by Vollenweider (1960), Elster & Vollenweider (1961) and Aleem & Samaan (1969) on Lake Mariut, an extremely productive and polluted delta lake near Alexandria. Here, the dense phytoplankton could reduce the photosynthetic zone to as little as 0.35 m; estimates of daily production >4 g C m^{-2} day^{-1} were obtained.

Under present-day conditions on the Main Nile proper, the highest areal rates of photosynthetic production are to be expected from Lake Nubia–Nasser, where dense phytoplankton may occur with low background turbidity. Few measurements are published, but Entz (1972) refers to one high estimate of 15.5 g O_2 m^{-3} day^{-1} (or ~5.8 g C m^{-2} day^{-1}).

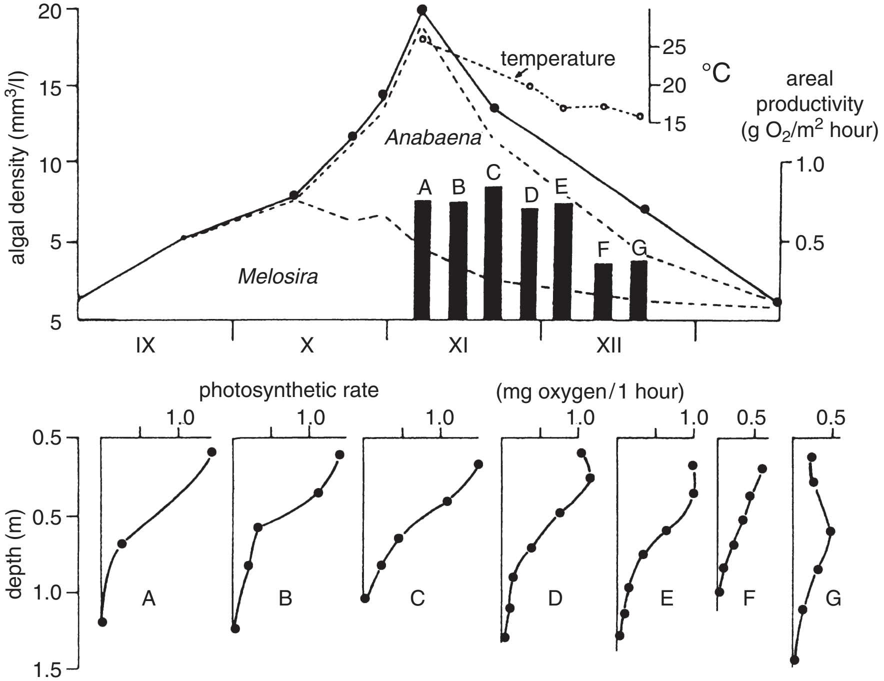

Fig. 5 Growth and decline of the 1953–1954 phytoplankton community in the White Nile at Gordon's Tree near Khartoum. Densities (in mm^3 cell volume l^{-1}) of two major components are shown, and associated rates of photosynthetic production per unit area (*histograms*). The latter are calculated from depth profiles of photosynthetic rate shown below (from Prowse & Talling, 1958)

In a more general setting, the production rates measured in the Nile system are notable for the high values per unit area often reached, and high specific rates per unit of population seem widespread. Although the depth of the photosynthetic zone varies over a wide range, self-shading effects of the phytoplankton appear less influential than the often high 'background' light absorption. High specific rates of population growth are indicated by some seasonal observations, especially during the first phase of annual water storage in reservoirs on the Blue and White Niles. Further evidence can be obtained from spatial increases downstream (Talling & Rzóska, 1967), which involve the interrelationship between events in time and space – probably the most fundamental issue of river biology.

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Hydrophytes of the Nile in Egypt

Mahmoud A. Zahran

Abstract The vascular freshwater weeds of the River Nile in Egypt comprises 87 species of flowering plants, belonging to 45 genera and 25 families. Out of these, 12 are dicots and 13 are monocots. In addition there are 3 pteridophytes, viz. *Azolla filiculoides*, *Marsilea aegyptiaca* and *M. capensis*. Cyperaceae is represented by 19 species followed by Gramineae (15 species), Lemnaceae and Potamogetonaceae (6 species each), Najadaceae (4 species), 3 species belong to each of 6 families and 2 species belonging to each of 3 families. The other families are represented by only one species.

Habitat wise, submerged hydrophytes are represented by 21 species (11 genera and 9 families), free floating hydrophytes by 9 species (6 genera and 4 families), fixed floating by 5 species (4 genera and 4 families) whereas emergent hydrophytes are represented by the highest number of species (54), in 28 genera and 13 families.

The aquatic vegetation of the Nile in Egypt is classified under 36 communities dominated by 8 submerged, 9 floating and 19 emergent species. The distribution of these communities and their floristic composition as well as the impact of the establishment of Aswan High Dam (1965) is discussed.

1 Introduction

The present article is a discussion of the aquatic plants (hydrophytes, macrophytes) growing in the Egyptian Nile, whether submerged, floating or emergent. Of the River Nile, the terminal 1,530 km lie within Egypt (see map in Dumont, 2009). Its basin includes the Fayum Province, a depression in the Western Desert connected with the river by a semi-natural irrigation canal (Bahr Yusuf) and occupied by saline Lake (=Birket) Qarun (see El-Shabrawy & Dumont, 2009).

Recently (1997), the Egyptian Government established two new canals to expand the amount of cultivable land irrigated by the Nile: Sheikh Zaied canal

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and El-Salam canal. The first takes water from Aswan High Dam Lake to the Toshka Depression of the Western Desert (El-Shabrawy & Dumont, 2009). El-Salam Canal, on the other hand, takes water from the Damietta Branch of the Nile to irrigate land in the north of the Sinai Peninsula. This means that two man-made sub-regions can be added to the present sub-regions: the Nile Valley, the Nile Delta, the Nile Fayum (three natural sub-regions), and Toshka and Sinai (two man-made sub-regions) (Zahran et al., 2003).

The Nile water in Egypt flows through a network of irrigation and drainage canals over the broad alluvial expanses of the valley, delta and Fayum. Khattab (1992) estimated the total length of the irrigation and drainage system at about 48,000 km, distributed according to the width of the bases of irrigation and drainage canals respectively as follows: 3,260 and 850 km for >10 m base width; 2,880 and 1,440 km for 5–10 m base width and 25,500 and 14,100 km for <5 m base width.

The description given hereafter deals with the Nile basin as it appears today. However, deep changes occurred over time, and those that took shape during the last four or five millennia were almost entirely due to man. The Nile valley during the Neolithic must indeed have looked quite different from today; in particular, the expanses of temporary and permanent marshlands were far more extensive than at present and large areas of Lower Egypt may have looked like miniature Sudd – swamps (Rzóska, 1976).

2 Diversity of the Hydrophytes in the River Nile in Egypt

According to Hassib (1951), the flora of the Nile in Egypt contains ca 534 species (algae excluded), ca 25% of the flora of the country. During the last 30 years, studies of the flora of the Nile, particularly after the establishment of Aswan High Dam (1965), have been carried out by Tackholm (1974), El-Hadidi (1971), Moursi (1976), Batanouny & El-Fiky (1983), Springuel & Murphy (1990, 1991), El-Kholi (1989), Khedr (1989), Murphy et al. (1989), Serag (1991, 1996, 2000), Shaltout et al. (1994), Zahran et al. (1998, 2003), Khedr (1998), Khedr & Zahran (1999), Hussein (2000) El-Bana et al. (2000), Bishai et al. (2000), Zahran (2003), Shaltout & Khalil (2005) & Khalil & Shaltout (2006). These studies reveal that the vascular freshwater weed flora of Egypt includes 87 species of flowering plants, in 45 genera representing 25 families (Table 1). Twelve are Dicotyledoneae, and 13 are Monocotyledoneae. In addition, the flora includes 3 Pteridophytes, namely: *Azolla filiculoides* of Azollaceae and 2 species (*Marsilea aegyptiaca* and *M. capensis*) of the Marsileaceae (Table 2). Nineteen families are represented by one genus; two (Alismataceae and Onagraceae) by two genera and two (Hydrocharitaceae and Lemnaceae) by three genera. Cyperaceae is represented by six and Gramineae by ten genera. The highest number of species (19) belong to Cyperaceae, followed by Gramineae (15 species). Lemnaceae is represented by six species, Potamogetonaceae by six, four Najadaceae, three species in each of Alismataceae, Ceratophyllaceae, Hydrocharitaceae, Juncaceae, Onagraceae, Polygonaceae and Ranunculaceae, and two species in Nymphaeaceae, Amaranthaceae and Marsileaceae. The other

Table 1 List of the macroaquatic flora of the River Nile system, Egypt (Täckholm, 1974; Boulos, 1995; Zahran et al., 2003)

		Distribution				
Family	Species	Nd	Nv	Nf	H	AB
I. Submerged						
Ceratophyllaceae	*Ceratophyllum demersum*	+	+	+	p	dN
	C. muricatum	+	–	–	p	rr
	C. submersum	+	–	–	p	rr
Haloragaceae	*Myriophyllum spicatum*	+	+	+	p	dN
Hydrocharitaceae	*Elodea canadensis*	+	–	–	p	dNd
	Otellia alismoides	+	+	+	p	c
	Vallisneria spiralis	–	+	–	p	rr
Lentibulariaceae	*Utricularia inflexa*	+	–	–	p	r
Najadaceae	*Najas graminea*	+	+	–	a	r
	N. horrida	+	+	–	a	dNv
	N. marina subsp. *Armata*	+	+	–	a	dN
	N. minor	+	–	–	a	r
Podostemaceae (incl. Tristicheae)	*Tristicha trifaria*	+	–	–	p	rr (Aswan cataract)
Potamogetonaceae	*Potamogeton crispus*	+	+	+	p	dN
	P. pectinatus	+	+	+	p	dNd
	P. perfoliatus	–	+	–	p	rr
	P. trichoides	–	+	–	p	rr
	P. lucens	+	–	–	p	r
	P. panormitanus	–	+	–	p	c
Ruppiaceae	*Ruppia maritima var. rostrata*	+	+	+	p	dN
Zannichelliaceae	*Zannichellia palustris*	+	+	+	p	cc
II. Floating						
(a) Free floating						
Araceae	*Pistia stratiotes*	+	–	–	p	dNd
Azollaceae (Pteridophyta)	*Azolla filiculoides*	+	+	+	p	dNd
Lemnaceae	*Lemna gibba*	+	+	+	p	dNd
	L. minor	+	–	–	p	rr
	L. perpusilla	+	–	–	p	rr
	Spirodela polyrhiza	+	+	+	p	cc
	S. punctata	+	–	–	p	r
	Pseudowolffia hyalina	+	+	+	p	c
Pontederiaceae	*Eichhornia crassipes*	+	+	+	p	dN

(continued)

Table 1 (continued)

Family	Species	Distribution Nd	Nv	Nf	H	AB
(b) Fixed floating						
Nymphaeaceae	*Nymphaea caerulea*	+	–	+	p	dNd
	N. lotus	+	–	+	p	dNd
Onagraceae	*Ludwigia stolonifera*	+	+	+	p	dNd
Potamogetonaceae	*Potamogeton nodosus*	+	+	+	p	dN
Gramineae (Poaceae)	*Vossia cuspidata**	+	+	+	p	dNd + near Cairo
III. Emergent						
Alismataceae	*Alisma plantago–aquatica*	+	–	–	p	r
	A. gramineum	+	+	–	p	r
	Damasonium alisma	+	+	+	p	r
Amaranthaceae	*Alternanthera nodiflora*	+	+	–	a,p	c
	A. sessiles	+	+	–	a,p	c
Cruciferae (Brassicaceae)	*Rorippa palustris*	+	+	–	Bi	c
Cyperaceae	*Carex divisa*	+	+	+	p	c
	Cyperus alopecuroides	+	+	+	p	dNd
	C. articulatus	+	–	–	p	dNd
	C. difformis	+	+	+	p	dNd
	C. digitatus subsp. *Auricomus*	+	–	–	p	rr
	C. fuscus	+	–	–	a	rr
	C. papyrus	+	–	–	p	dNd + dNv (cultivated)
	C. schimperianus	+	–	–	p	Nd
	Eleocharis capitata	+	–	–	a,p	rr
	E. granulata	+	–	–	a,p	r
	E. palustris	+	+	+	p	cc
	E. parvula	+	–	–	p	rr
	Fuirena ciliaris	+	–	–	p	rr
	Pycreus mundtii	+	–	+	p	dNf
	P. polystachyos	+	–	–	p	r
	Scirpus articulatus	+	–	+	p	rr
	S. litoralis	+	+	+	p	dNd
	S. maritimus	+	–	–	p	dNd
	S. triqueter	+	+	+	p	dNd
Elatinaceae	*Bergia capensis*	+	–	–	p	c

(continued)

Table 1 (continued)

Family	Species	Distribution			H	AB
		Nd	Nv	Nf		
Gramineae (Poaceae)	Echinochloa colona	+	+	+	a	cc
	E. crusgalli	+	+	−	a	cc
	E. pyramidalis	Unknown	locality			rr
	E. stagnina	+	+	+	p	dNd
	Hermarthria altissima	+	−	−	p	r
	Leersia hexandra	+	−	−	p	dNd
	Leptochloa fusca	+	+	+	p	dNd
	Panicum repens	+	+	+	p	cc
	Paspalidium geminatum	+	+	+	p	c
	P. obtusifolium	+	−	−	p	rr
	Paspalum distichum	+	−	−	p	dNd
	Phragmites australis	+	+	+	p	dN
	P. mauritanus	+	−	−	p	rr
	Saccharum spontaneum subsp. *Aegyptiacum*	+	+	+	p	dNd
Juncaceae	*Juncus bufonius*	+	+	+	a	c
	J. fontanesii subsp. *Pyramidatus*	+	−	−	p	r
	J. subulatus	+	+	+	p	dNd
	Marsilea capensis	+	−	−	p	rr
Marsileaceae (Pteridophyta)	*M. strigosa*	Unknown	locality		p	rr
Onagraceae	*Epilobium hirsutum*	+	+	+	p	c
	Ludwigia erecta	−	+	−	a	rr
Polygonaceae	*Persicaria lanigera*	+	−	−	p	rr
	P. salicifolia	+	+	+	p	dNd
	P. senegalensis	+	+	+	p	dN
Ranunculaceae	*Ranunculus rionii*	+	−	−	a	r
	R. sceleratus	+	+	+	a	rr
	R. trichophyllum	+	−	−	a,p	rr
Scrophulariaceae	*Veronica anagallis – aquatica*	+	+	+	p	cc
Typhaceae	*Typha domingensis*	+	+	+	p	dN

Nd = Nile Delta (including the northern lakes), Nv = Nile Valley (including the southern reservoirs), Nf = Nile Fayum, N = Nile system, H = habit of plant (a = annual, bi = biennial, p = perennial), AB = abundance (rr = very rare, r = rare, c = common, cc = very common, d = dominant), + = present, − = absent.

Table 2 Dominant aquatic macrophytes in the River Nile system of Egypt (after Zahran et al., 2005)

Dominant species	A	B
I. Submerged species		
1. *Ceratophyllum demersum*	+	+
2. *Elodea Canadensis*	−	+
3. *Myriophyllum spicatum*	+	+
4. *Najas horrida*	+	−
5. *N. marina* subsp. *Armata*	+	−
6. *Potamogeton crispus*	+	+
7. *P. pectinatus*	−	+
8. *Ruppia maritima*	−	+
II. Floating species		
1. *Azolla filiculoides*	−	+
2. *Eichhornia crassipes*	+	+
3. *Lemna gibba*	−	+
4. *Ludwigia stolonifera*	−	+
5. *Nymphaea caerulea*	−	+
6. *N. lotus*	−	+
7. *Pistia stratiotes*	−	+
8. *Potamogeton nodosus*	+	+
9. *Vossia cuspidata*	−	+
III. Emergent species		
1. *Cyperus alopecuroides*	−	+
2. *C. articulatus*	−	+
3. *C. difformis*	−	+
4. *C. papyrus*	−	+
5. *C. schimperianus*	−	+
6. *Echinochloa stagnina*	−	+
7. *Juncus subulatus*	−	+
8. *Leersia hexandra*	−	+
9. *Leptochloa fusca*	−	+
10. *Paspalum distichum*	−	+
11. *Persicaria salicifolia*	−	+
12. *P. senagalensis*	+	+
13. *Phragmites australis*	+	+
14. *Pycreus mundtii*	−	+
15. *Saccharum spontaneum* subsp. *aegyptiacum*	−	+
16. *Scirpus litoralis*	−	+
17. *S. maritimus*	−	+
18. *S. triqueter*	−	+
19. *Typha domingensis*	+	+

A = recorded in the Aswan area only (River Nile section at Aswan + Aswan Reservoirs), B = recorded in the other parts of the River Nile system northwards including northern lakes, + = occurs as dominant, − = does not occur as dominant but may occur otherwise.

families are represented by a single species. According to habitat, submerged, floating or emergent, the distribution is as follows: submerged hydrophytes are represented by 9 families, 11 genera and 21 species, free floating hydrophytes by four families, six genera and nine species, fixed-floating hydrophytes by four families (Potamogetonaceae is represented also by submerged plants and Onagraceae also by emergent plants), four genera and five species and emergent hydrophytes are represented by 13 families, 28 genera (*Ludwigia* occurs also in the fixed floating group) and 54 species. Potamogetonaceae is represented by six submerged and one floating species whereas Onagraceae is represented by one floating and two emergent species.

The diversity of the aquatic plants of Egypt attracted the attention of Kassas (1971), who stated that the building of dams and barrages across the Nile and its tributaries, particularly Aswan High Dam, had segmented the natural hydrobiological system, with undoubted impact on water quality and biota. The low species diversity of the aquatic vegetation types of the irrigation and drainage canals in the Nile Delta is considered by Shaltout et al. (1995) to be related to the high disturbance of these habitats caused by the repeated removal of the silt and weeds during maintenance.

The emergent and floating macrophyte groups were reported by Khedr and El-Demerdash (1997) to have high species richness. The highest mean value was recorded in the group dominated by *Azolla filiculoides* (6.1 species per stand); the lowest (4.5 species per stand) in the group dominated by *Ceratophyllum demersum*.

Khedr (1999c) reported that the Shannon Diversity Index (H′) was highest in emergent macrophytes (H′ = 1.26), followed by free-floating species (H′ = 1.07) and fixed-floating species (H′ = 0.87). He noted that the Shannon Diversity Index positively correlated with species richness ($r = 0616$, $P < 0.0001$) and evenness ($r = 0.433$, $P < 0.0001$). The vegetation group with the dominant species *Potamogeton crispus* and *P. nodosus* in the irrigation canals showed the highest Shannon mean evenness value ($E_s = 0.77$). The lowest mean evenness value ($E_s = 0.53$) was recorded in the vegetation group dominated by *Eichhornia crassipes* and *Echinochloa stagnina*. The Simpson Index was highest (S = 0.55) in this vegetation group, and lowest (S = 0.31) for submerged species.

3 Hydrophyte Communities

The aquatic vegetation may be classified into 36 communities dominated by 8 submerged, 9 floating and 19 emergent species, as shown in Table 2. The submerged communities are dominated by: *Ceratophyllum demersum*, *Elodea Canadensis*, *Myriophyllum spicatum*, *Najas horrida*, *N.marina armata*, *Potamogeton crispus*, *P. pectinatus and Ruppia maritima*. The free-floating dominants are *Azolla filiculoides*, *Eichhornia crassipes*, *Lemna gibba and Pistia stratiotes* whereas *Ludwigia stolonifera*, *Nymphaea caerulea*, *N. lotus*, *Potamogeton nodosus* and *Vossia cuspidata* are the dominant fixed-floating species. Boulos (1995) reported that *V. cuspidata* may also grow as a submerged hydrophyte. The emergent communities are dominated by: *Cyperus alopecuroides*,

Table 3 Distribution of the communities of the hydrophyte vegetation of the River Nile system in Egypt

Group	Communities in A + B	Communities in A only	Communities in B only	Total
I. Submerged	3	2	3	8
II. Floating	2	0	7	9
III. Emergents	3	0	16	19
Total	8	2	26	36

A = recorded in the Aswan Area only, including Aswan Reservoirs, B = recorded in the Nile system northwards, A + B = recorded in the whole Nile system of Egypt.

Table 4 Occurrence (%) of the freshwater dominant macrophytes in the three subregions of the River Nile system in Egypt

Subregion	Nd (%)	Nv (%)	Nf (%)
I. Submerged (22%)	45	36	19
II. Floating (25%)	46	23	31
III. Emergents (53%)	50	26	24

Nd = Nile Delta, Nv = Nile Valley, Nf = Nile Fayum.

C. articulatus, *C. difformis*, *C. schimperianus*, *Echinochloa stagnina*, *Eleocharis capitata*, *Juncus subulatus*, *Leersia hexandra*, *Leptochloa fusca*, *Paspalum distichum*, *Persicaria salicifolia*, *P. senegalensis*, *Phragmites australis*, *Pycreus mundtii*, *Saccharum spontaneum* subsp. *aegyptiacum*, *Scirpus litoralis*, *S. maritimus S. triqueter* and *Typha domingensis*. The distribution of the 36 communities in the three subregions, Nile Valley, Delta and Fayum (Table 3), reveals that *Najas horrida* and *N. marina* subsp. *armata* are dominants in the Aswan area only. Both may occur as associate species northwards. On the other hand, there are 26 communities, dominated by 3 submerged, 7 floating and 16 emergent species characteristic of the main river north of Aswan area. These dominant hydrophytes may occur as associate species in the Aswan area. Eight species (three submerged, two floating and three emergent) are dominants in all parts of the River Nile.

Table 4 shows the occurrence (%) of the freshwater dominant macrophytes, in the three subregions of the Nile in Egypt: 53% of the dominant hydrophytes are emergent, 25% are floating and 22% are submerged dominant species. The Nile Delta subregion contains the highest number: 45% of the submerged, 46% of the floating and 50% of the emergent species. The Nile Valley subregion contains the lowest number (23%) whereas the Fayum subregion contains 31% of dominant floating hydrophytes.

4 Two Important Plants: Papyrus and Water Hyacinth

4.1 Cyperus papyrus (Fig. 1)

C. papyrus is a tall, robust, leafless sedge that can grow 4–5 m high. It features a grass-like clump of triangular green stems that rise up from thick, woody rhizomes. Each stem is topped by a dense clusters of thin, bright green, thread-like rays

Fig. 1 Dense growth of *Cyperus papyrus* on the bank of Damietta Branch, River Nile, Egypt (*see Color Plates)*

around 10–30 cm in length. Greenish-brown flower clusters appear at the end of the rays. The flowers give way to brown, nut-like fruits.

Papyrus forms vast stands in swamps and along stream banks throughout eastern Africa. In Egypt, where papyrus is entwined with cultural history, Tackholm and Drar (1950) thought it had became extinct 150 years earlier. In July 1968, however, discovered a stand of about 20 plants among other reeds in a freshwater swamp of the Wadi El-Natrun Depression. Also, Hussein (2000) recorded papyrus in some islands of the River Nile in the area of Cairo, and Serag (2000) found it in the wetlands associated with the downstream section of the Damietta Branch of the River Nile. In ancient Egypt, as far back as 4,400 BP, it was used for food, fiber, shelter, formal bouquets, funeral garlands, boats, fans, sandals, matting corkage, boxes and paper. Its pith was recommended for food, while the starchy rhizomes and lowermost parts of them were cutoff and consumed raw, boiled, or roasted papyrus was also a favorite ornament in ancient art and craft (N.A.S., 1976). Papyrus swamps provide hypoxic and structural refugia for cichlids from predatory fish Nile Perch and are an important habitat for endangered bird species. Galen, Dioscoroides and later Islamic pharmacologists, e.g. Ibn Gulgul and El-Ghafigi, included papyrus among medicinal plants. The pith was recommended for widening and drying a fistula. The main use, anyhow, seems to have been confined to burnt papyrus sheets, the ash of which was reputed to have the action of pulverized charcoal and used for certain diseases.

Also, the little boat (or box) in which the mother of the Prophet Moses or Musa (1350–1340 BC) released her son to the Nile was made of papyrus.

Embarking upon his Ph. D. thesis on papyrus, Ragab (1980) faced the difficulty that this plant had become extremely rare in Egypt. In 1960, he travelled to the Sudan where *C. papyrus* grows abundantly in the Sudd, brought back a few rhizomes, and planted them on the bank of the Nile at Giza. One year later, he had enough shoots to establish a plantation and start experiments on papyrus sheet making. He succeeded in producing paper from the culms of papyrus using drawings of ancient pharaonic paintings and created a new touristic industry in Egypt. During the 30 subsequent years, Ragab produced and exported more than 10 million papyrus paper sheets to different parts of the world.

4.2 Water Hyacinth

E. crassipes (water hyacinth), is a perennial, surface free-floating, mat-forming aquatic plant of wide distribution in South America. In Egypt, *E. crassipes* was introduced as an ornamental plant during the rule of Khedive Tawfiq (1879–1892) and has, for many years, been grown in gardens of Cairo and Alexandria (Zahran, 1976). Percheron (1903) warned about the dangers of its spread in the Egyptian canals and drew attention to the problems that would occur if it would grow freely. Indeed, few decades later, Simpson (1932) reported *E. crassipes* to be widely distributed in freshwater channels of the Nile Delta and near Cairo and Alexandria. In the brackish water of the delta lakes, it is limited by its lack of tolerance to saline water. Zahran (1976) stated that it is difficult to find a canal, stream or drain not infested by water hyacinth particularly in the Fayum and Nile Delta.

E. crassipes has many uses, e.g. as soil fertilizer, raw material for paper making, biogas production and fodder for livestock and fish as well as cleaner for chemical pollutants of the water (Baruah, 1984). In Egypt, mechanical, manual, chemical and biological (herbivorous fish) control measures have been tried. Biological control by a fungal pathogen using pure powder of the fungal pathogen has been attempted, but large-scale application needs further tests.

5 Impact of the Aswan High Dam

Rorslett (1988) stated that building a dam across a river, and impounding water behind it, causes profound changes in limnological regime. These include chemical and physical changes, in turn affecting flora and fauna. The establishment of the Aswan High Dam (1964) brought the River Nile under full control, with great effects on the plant life associated with the river (Nd, Nv, Nf), and its artificial reservoirs, natural lakes, and irrigation and drainage systems. Two examples are presented to show the impact of the High Dam; the first describes the status of the aquatic weeds in the extreme south (Aswan area), the second in Lake Manzala (Delta).

5.1 Aswan Area

The extreme south of the Nile in Egypt is occupied by three water bodies: Lake Nasser (High Dam Reservoir), Aswan Reservoir, and the River Nile north of Aswan Reservoir. Ali et al. (1995) noted that Lake Nasser water level is strongly dependent on the flood pattern. A high range of water level fluctuation was recorded in 1988 after a series of low-flood years. First, a continuous low water level exposed littoral shallow water habitats, and submerged macrophytes became exposed and desiccated. Following this, a period of continuous high water level caused low-light conditions.

These two events caused substantial loss of submerged aquatic plants in Lake Nasser during 1988. The initial community had *Najas horrida*, not recorded by Tackholm (1974) or by Boulos (1995), as the dominant species with six others. Following the destruction of this community, *Najas marina armata* became dominant, with four other taxa present (*Najas horrida*, *Potamogeton schweinfurthii*, *Vallisneria spiralis* and *Zannichellia palustris*). In Aswan Reservoir, however, the water level regime follows a fixed pattern in which each day a certain amount of water is released. Usually, water is stored overnight and released during the day. A severe physical disturbance results from this daily range of ca 3 m level fluctuation (Ali, 1987). In this reservoir *Ceratophyllum demersum* was the dominant macrophyte, with *Najas horrida*, *Potamogeton crispus* and *Zannichellia palustris*. In the river, the water level is regulated to meet Egypt's demands for cultivation. This results in a gradual increase in water level, followed by a gradual decrease and creates a favourable habitat in which more species became established than before regulation. Submerged species that thus became established include *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Najas horrida*, *Potamogeton pectinatus* and *Vallisneria spiralis*, in addition to the alga *Chara globularis* var. *globularis* (Ali, 1987).

According to Springuel and Murphy (1990) and Ali et al. (1995), data collected prior to 1988, on the frequency and standing crop of macrophytes of the littoral zone (0–3 m depth) of Lake Nasser, Aswan Reservoir and River Nile at Aswan show that aquatic plant growth differs significantly ($P < 0.05$), with a downstream trend of increasing production from Lake Nasser through Aswan Reservoir to the river channel below the dam. There were major differences in community dominance in the three systems during 1988–1989. *Najas marina armata* dominated the disturbed zone of Lake Nasser, making up nearly 40% of total standing crop. Other species present were *Chara globularis* var. *globularis*, *Najas horrida* and *Vallisneria spiralis*. In contrast, in both the Aswan Reservoir and River Nile, the dominant species were *Ceratophyllum demersum* (comprising 59–78% of total standing crop) and *Potamogeton crispus* (comprising 15–20% of total standing crop). In the River approximately 25% of total submerged standing crop was of other species, notably *Myriophyllum spicatum* and *Potamogeton perfoliatus*. Ali and Soltan (2006) stated that *M. spicatum* replaced the originally dominant *Najas marina armata* in Lake Nasser.

In the River Nile, there was a seasonal shift in dominance of the submerged community from *Ceratophyllum demersum* during autumn and winter, through *Potamogeton crispus* in early summer, to *P. perfoliatus* in late summer and early autumn. In Aswan Reservoir *Ceratophyllum demersum* showed continuous dominance, reaching its peak standing crop during winter when water levels are lowest. In Lake Nasser, a different community was present, co-dominated by *Najas horrida* and *N. marina armata* (Ali et al., 1995). The altered water regime of the Nile also favours the upstream spread of *Eichhornia crassipes*. In January 1986, two plants found in the River just north of Aswan were removed. No subsequent occurrences have been recorded since (Springuel & Murphy, 1990).

5.2 Lake Manzala

Lake Manzala (31°–31° 30′ N, 31° 50′–32° 15′ E), the largest of the delta lakes of Egypt (Khedr, 1989) opens to the Mediterranean Sea. Its northern section is consequently characterized by saline water. The south has many inlets through which water drains from the surrounding provinces (Port Said, Ismailia, Damietta, Sharkiya and Dakahliya). Also, sewage from Cairo reaches Lake Manzala through Bahr El-Baqar Drain, while freshwater reaches the lake from Damietta branch. Thus, Manzala Lake receives three types of water: freshwater, sea water and drainage water. Abu Al-Izz (1971) states that the flow of drainage water rate to the lake diminishes its salinity to 0.8–1.0%. Manzala Lake was even used for drinking during times of flood. However, since the establishment of the Aswan High Dam (1965) no more floods occur and the regime of the four lakes has changed. In general, they have become fresher, but with a horizontal saline gradient. However, huge amounts of drainage and sewage waters reach the lakes daily, in addition to a small amount of Nile water, with considerable effects on their chemical, physical and biological characteristics.

The vegetation of Lake Manzala has been discussed by Montasir (1937) who recognizes three vegetation types: hydrophytic, halophytic and helophytic. The dominant helophytes were *Cyperus* spp., *Juncus* spp., *Phragmites australis* and *Typha domingensis* and the dominant hydrophytes were *Ceratophyllum demersum*, *Eichhornia crassipes*, *Lemna* spp. and *Potamogeton crispus*. Khedr (1989) reported that, apart from the dominant reeds (*Phragmites australis* and *Typha domingensis*), Lake Manzala is characterized by five dominant hydrophytes: *Eichhornia crassipes*, *Ludwigia stolonifera*, *Najas marina armata*, *Potamogeton pectinatus* and *Ruppia maritima*. Other species include *Alternanthera sessilis*, *Ceratophyllum demersum*, *Cyperus articulatus*, *Echinochloa stagnina*, *Epilobium hirsutum*, *Juncus subulatus*, *Leersia hexandra*, *Lemna gibba*, *L. minor*, *Leptochloa fusca*, *Nymphaea caerulea*, *Panicum repens*, *Paspalidium geminatum*, *Paspalum distichum*, *Persicaria salicifolia*, *P. senegalensis*, *Pistia stratiotes*, *Scirpus litoralis* and *S. maritimus*. Khedr (1997) recognized eleven aquatic communities in Lake Manzala dominated by *Ceratophyllum demersum*, *Najas marina armata*, *Potamogeton crispus* and *Ruppia maritima* (submerged), *Eichhornia crassipes*, *Ludwigia stolonifera*, the fern *Azolla filiculoides* (floating), *Echinochloa stagnina*, *Phragmites australis*, *Scirpus maritimus*, and *Typha domingensis* (emergent).

The associate species, in addition to those recorded by Khedr (1989), include *Nymphaea lotus* and *Spirodela polyrhiza* (floating) and *Marsilea aegyptiaca*, *Rorippa palustris* and *Veronica anagallis-aquatica* (emergent). At that time, *Myriophyllum spicatum* had not yet reached Lake Manzala. Nowadays, this submerged plant occasionally grows in the lake (Khedr & Zahran, 1999; Zahran, 2003).

Khedr (1997) obtained a TWINSPAN dendrogram from 100 stands studied, which he split into eight ecologically meaningful groups. In terms of their indicator species, these are:

Group A. Indicated by *Ludwigia stolonifera* and *Azolla filiculoides* characteristic of stagnant freshwater in the western and southern parts of the lake.

Group B. Indicated by *Eichhornia crassipes*, *Echinochloa stagnina* and *Azolla filiculoides*, characteristic of the polluted parts of the lake at the mouth of the drains in the south-west.

Group C. With *Potamogeton pectinatus* as indicator species, more abundant than floating emergent species in all parts of the lake.

Group D. With *Najas marina armata* and *Ceratophyllum demersum* as indicator species. Both are dominant in the west and middle parts of the lake, forming dense monospecific stands that hinder navigation.

Group E. Indicated by *Typha domingensis*, variably distributed but with low abundance close to the sea because, unlike *Phragmites australis*, this species is not highly salt-tolerant.

Group F. With *Scirpus maritimus* as indicator species. In swamps and around islands, particularly in shallow parts.

Group G. Indicated by *Phragmites australis*, the most frequent species in the lake; it occurs in all parts, even if saline and polluted.

Group H. Indicated by *Ruppia maritima*, dominant in the shallow parts and lagoons of the section near the Mediterranean Sea, where salinity is relatively high.

Variations in characteristics within each group are often large. Groups A and B, dominated by floating hydrophytes, occur in areas having the lowest EC values (1.77 and 1.37 mS cm^{-1}, respectively). Groups C and D, dominated by submerged species, are significantly different from most others with respect to depth and dissolved oxygen. Group H, indicated by *Ruppia maritima*, differs from others with respect to EC, CI, pH and PO4-P. It has the highest mean values of these variables: 21.05 mS cm^{-1}, 13.4 g l^{-1}, 9.05 and 3.25 µg l^{-1}, respectively. Group F, indicated by *Scirpus maritimus*, differs from all except Group A with respect to nitrate concentration.

Of all environmental factors, EC seems to control the distribution of aquatic plant communities best. *Ruppia maritima* is restricted to the saline section, whereas

Eichhornia crassipes, *Ludwigia stolonifera*, *Azolla filiculoides* and *Echinochloa stagnina* are dominant in fresh or slightly saline waters. *Phragmites australis*, *Potamogeton pectinatus* and *Scirpus maritimus* are of wide ecological amplitude; they occur in all parts of the lake.

There is evidence for change in the macrophyte communities in recent times. During a 1989 survey, *Ceratophyllum demersum*, *Echinochloa stagnina* and *Scirpus maritimus* were considered as associate species but now they are dominants. *Azolla filiculoides*, formerly absent from the lake (Khedr, 1989), now dominates a well-established community (Khedr, 1997). This fern, introduced to Egypt as a biofertilizer in rice fields, successfully invaded the Nile Delta drainage and irrigation canals (Khedr & EI-Demerdash, 1995). Other recently recorded species are *Marsilea aegyptiaca*, *Rorippa palustris* and *Veronica anagallis-aquatica*.

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Aquatic Plants of the Sudan

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Abstract The hydrophytes of the Sudan range from small floating plants to the tall reeds of the Sudd. They inhabit a diversity of habitats, and show remarkable vertical and longitudinal zonation, phyletism, growth forms and ecology. Ninety-five species belonging to 33 families are on record. One taxon (*Suddia*) is endemic. Their status reveals a disheartening situation. Negligence is reflected in meager studies, no attempts to utilize and no policy to conserve.

To conserve the diversity of the hydrophytes of the Sudan, a delicate balance between utilization, conservation and control is required. The fact that the Sudd has recently been declared a Ramsar site raises hopes that these objectives may be reached in a near future.

1 Introduction

The aquatic vegetation of the Sudan has not been well studied. This is reflected in meager knowledge, almost no attempts to utilize these plants, and a complete absence of a policy to conserve them. This chapter endeavours to highlight the diversity in Sudanese aquatic plants in habitats, distribution, phyletism, growth forms and ecological niches. The term “aquatic plants” is used to designate those macrophytes that are truly aquatic, including the bank trees but excluding the microphytes (algae).

2 Aquatic Habitats of the Sudan

2.1 Running Waters

The main Nile runs for more than 3,000 km within the confines of Sudan. The Blue Nile, the 2,000 km of the tributaries of the White Nile, and the seasonal rivers Atbara, Dinder and Rahad together add up to over 6,000 km (Beshir & El-Moghrabi,

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H.J. Dumont (ed.), *The Nile: Origin, Environments, Limnology and Human Use*,

1980). All four main rivers (White Nile, Sobat, Blue Nile and Atbara) in addition to many seasonal khors, discharge into the Main Nile within Sudan. The five subbasins of the Nile are all represented within the Sudan (Fig. 1). As described by Ali (1990), the Sudan Nile is a mosaic of contrasting combinations: long and short, fast and slow, permanent and seasonal, silty and clear, infested and weed-free, dammed and free-flowing. One of its salient characteristics is the swamps of its upper reaches, which include the famous "Sudd", the most extensive wetland in the world (Thompson, 1985; Green & El-Moghraby, 2009) (Fig. 3). The Sudd has witnessed remarkable events during the 1960s–1980s, caused by unprecedented rise in the level of Lake Victoria between 1961 and 1964 (Beadle, 1974), which nearly doubled the area of swamp (El-Moghraby & El Sammani, 1985; Howell et al., 1988) and the low discharge of the Blue Nile in the early 1980s. These were natural phenomena, while the advent of the water hyacinth (*Eichhornia crassipes*) in 1958 (Gay, 1958) and its proliferation in the White Nile, the construction of Roseires and the Aswan high Dams were anthropogenic events. Both had equally profound impacts (Ali, 1990).

In addition to the "Sudd", the Machar and the Bahr al Ghazal Swamps should be mentioned (Fig. 2). The first is a triangle north of the River Sobat and east of the White Nile taking its name from Khor Machar. The swamps are fed by local precipitation and by numerous small torrents rising in the Ethiopian foothills over c. 200 km from south to north. The area also receives spill water through various channels from the Sobat (JIT, 1954). Though there are at times measurable discharges to the White Nile from Khors Adar and Wol, this amount is small. The area of seasonally flooded marchland and swamp is estimated at c. 6,500 km^2 (Howell et al., 1988).

The other wetland, the Bahr al Ghazal swamp, is fed by local precipitation and rivers descending from near the Sudan-Congo-Chad divide. The combined annual discharge of the main Bahr el Ghazal tributaries is ca 13.5 km^2. Most of this water eventually evaporates or transpires in seasonally inundated floodplains and permanent swamps. It never reaches the Nile.

2.2 Natural Lakes

Among freshwater lakes in western Sudan, Lake Kundi lies in southern Darfur, close to the seasonal Bahr el Arab. Lake Keilak is situated in South Kordofan, about 200 km north of the junction of Bahr el Arab and Bahr el Ghazal (Fig. 1). The drainage system of the two lakes, their bathymetric features, their physical–chemical properties and their biota are discussed by Green et al. (1984). Lake Kundi has a vegetation dominated by *Ceratophyllum demersum* and *Nymphaea lotus*, while Lake Keilak is rich in *Ceratophyllum demersum*, *Najas pectinata and Nymphaea lotus*. Beside these, there are two crater lakes in Darfur: the Dariba lakes in the volcanic caldera of Jebel Marra (Green et al., 1979) and the Malha salt lake in the Meidob Hills.

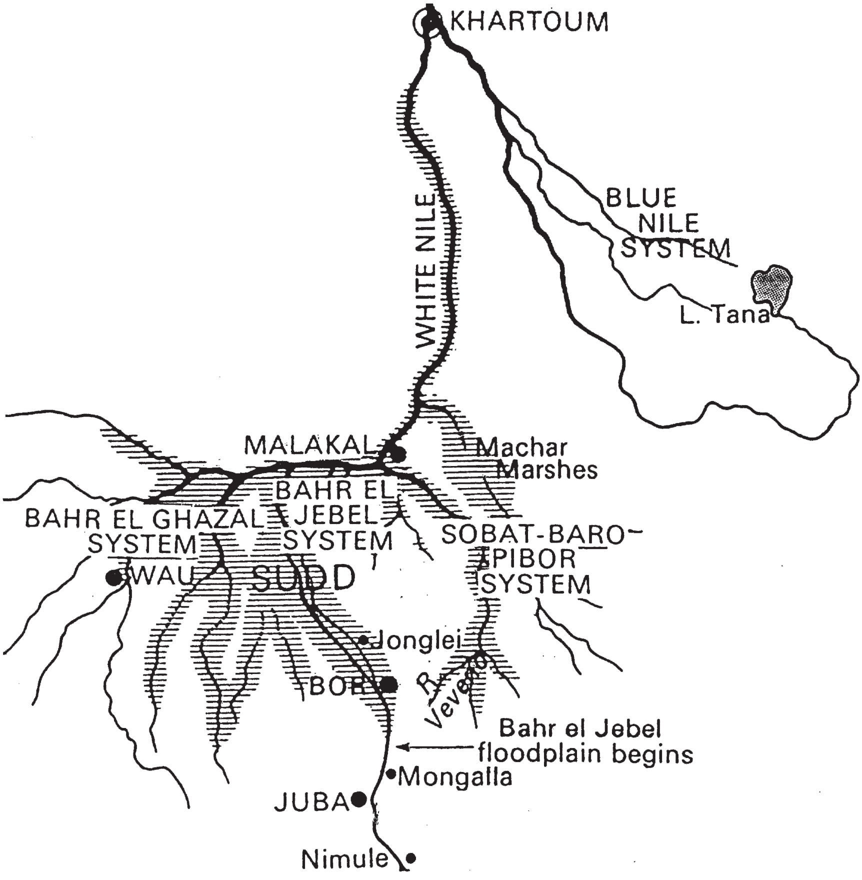

Fig. 1 The part of the Nile basin in Sudan and adjacent countries

2.3 Man-Made Lakes

The construction of a number of dams has resulted in the creation of large impoundments. These include Sennar and Roseires on the Blue Nile, Khashm el Girba on the River Atbara and Lake Nubia on the main Nile (Fig. 1). A new large lake has already formed by the impoundment of Merowe Reservoir in 2008.

3 The Diversity of Aquatic Plants

Although Dandy (1937) reported seven *Potamogeton* species, no study was dedicated to aquatic plants before 1948, although aquatic plants were mentioned sporadically by travelers and bird watchers. Paradoxically, the "Sudd", considered as a

Fig. 2 (**a**) and (**b**) Two typical aerial views of the Sudd, with the Bahr El Jebel meandering through several swampy Lakes. The reeds *Typha*, Papyrus and *Phragmites* occupy the wetlands. The big lake is inhabited by floating, submerged and floating-leaved hydrophytes. In the foreground of Fig. 3b, woody trees occupy the relatively higher ground (*see Color Plates)*

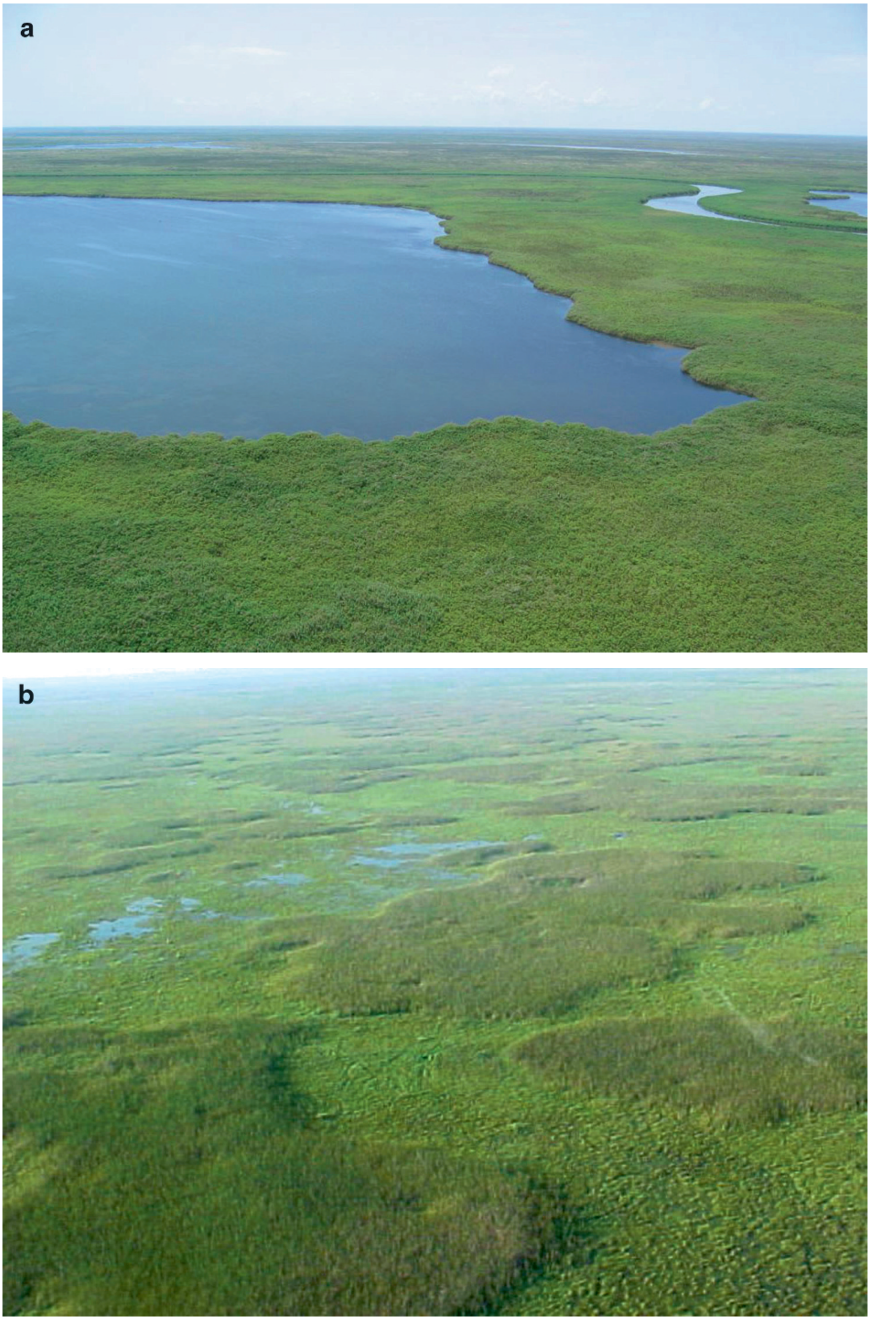

Fig. 3 (**a**) and (**b**) Vast swamps in the Sudd region occupied by *Typha domingensis* (*dark patches*) and *Cyperus papyrus* (*lighter green patches*). (**a**) Shows a large Sudd lake with the Bahr El Jebel in the background (*see Color Plates)*

political and a geographical blockage, drew the attention of scientists to the aquatic plants that constituted this natural barrier (Migahid, 1947, 1948; Dirar, 1951; Talling, 1957). The seminal paper by Migahid (1948) was the only in-depth attempt to describe its vegetation, even though interest in the Sudd vegetation was also spurred by plans to utilize the water lost in the swamps (Equatorial Investigation Team, Jonglei Investigation Team, 1954).

Attention to aquatic plants in Central Sudan was stimulated by problems with aquatic weeds in the Gezira irrigation scheme. Weeds started to grow few years after gravity irrigation started to operate and a rapid build-up took place (Andrews, 1945). The minor canals of the agricultural schemes provided excellent conditions for weed growth because of their design and sluggish flow (Beshir, 1978). As soon as a policy of intensification and diversification of cropping was adopted, aquatic plants became a serious problem (Hamdoun & Desougi, 1979). The work of Andrews (1945) was solely dedicated to aquatic macrophytes. Their taxonomy, morphology and distribution were dealt with in Andrews' three volumes on the flowering plants of Sudan (1950, 1952 and 1956).

The appearance of *Eichhornia crassipes* in the Nile in Sudan in 1958 was another landmark. By its adverse impact on evapotranspiration rates, navigation, irrigation pumps, water supply, and fisheries, the water hyacinth engendered research into aquatic weeds in general.

4 Habitat Diversity

Aquatic plants occupy all habitats described earlier. The geographical zonation in the distribution and diversity of aquatic plants follows a N-S gradient, linked with the southward increase in rain intensity and duration. The diversity is in the density of plants as well as in their types. The diversity of aquatic vegetation is also a reflection of the different aquatic habitats and their water characteristics. Thus, the vegetation of crater lakes is distinct from that in fresh waters. Only salt-tolerant *Scirpus* grow in the vicinity of some springs that feed the hypersaline Malha lake, Meidob Crater (pers. obs., 1985), but *Ceratophyllum demersum* and *Nymphaea lotus* abound in Lake Kundi and *Ceratophyllum demersum*, *Nymphaea lotus*, *N. coerulea* and *Najas pectinata* in Lake Keilak (Green et al., 1984). Within freshwater, plants in the main river axis are different from those in natural and man-made lakes. In the swampy region of the southern Sudan, aquatic macrophytes exhibit a horizontal zonation from the main river to the higher land (Fig. 4).

5 Phyletic Diversity

The aquatic plants of the Sudan belong to Charophyta (macro-algae), (Pteridophyta, Gymnosperms, and Angiosperms) (Table 1). The only wetland gymnosperm in Africa is *Podocarpus* (Denny, 1985), of which Andrews (1950) cited two species in

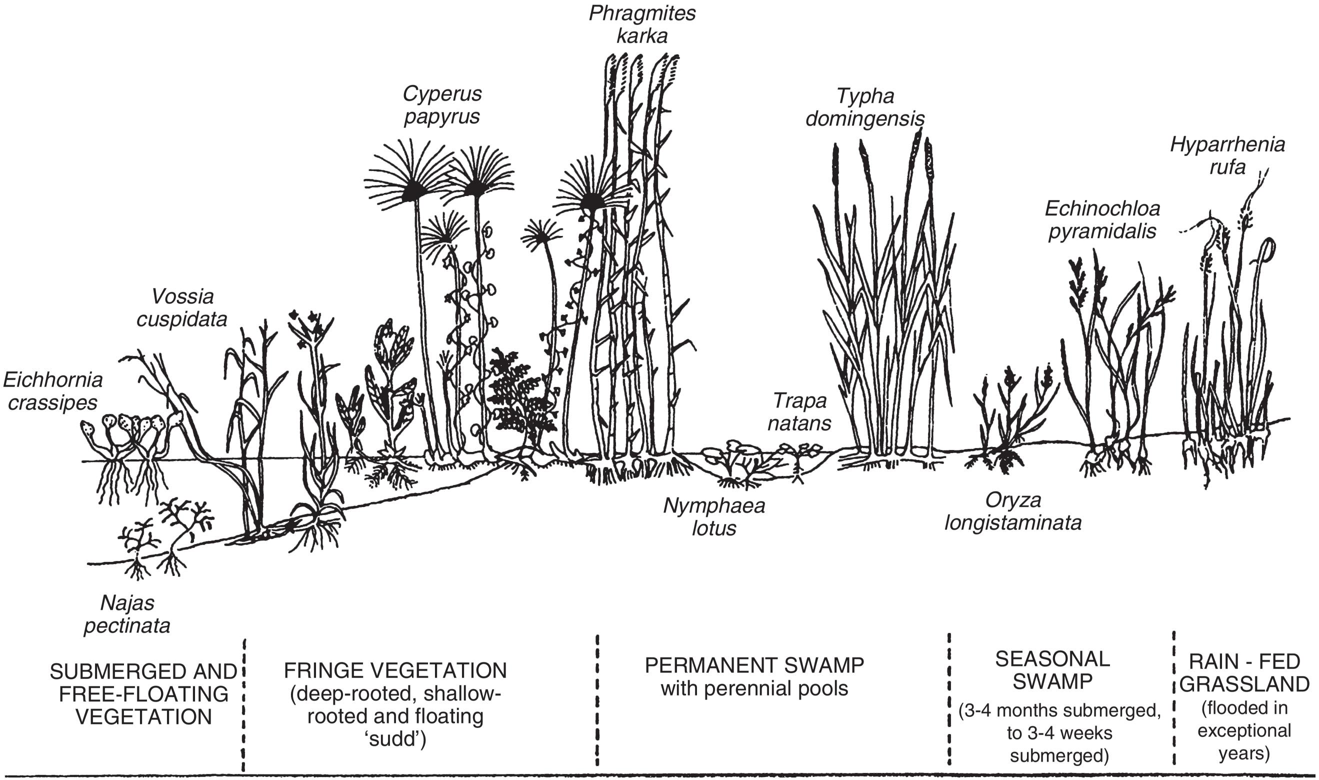

Fig. 4 A typical hydrosphere in the upper Nile Swamps of southern Sudan, showing river and wetland zonation (after Denny, 1985)

Fig. 5 *Suddia sagitifolia*, the single higher plant presumed endemic of the Sudd swamps (*see Color Plates)*

Table 1 Hydrophytes in Sudanese waters (from various sources)

No.	Family	Latin name	Distribution
1	Characaeae	*Chara globularis* (A. Br. Ex Kutz.)	CS, SS
		Nitella sp.	CS, SS
2	Azollaceae	*Azolla nilotica* Decne ex Mett.	SS
3	Isoetaceae	*Isoetes schweinfurthii*	SS
		Cyclosorus interruptus (Willd.) H.	SS
4	Marsileaceae	*Marsilea nilotica* L.	WN, SS
		M. gibba	SS
5	Parkeriaceae	*Ceratopters cornuta* (Beauv.) Lepr.	SS
6	Podocarpaceae	*Podocarpus spp*. (L'Herit) Pers.	SS
7	Alismataceae	*Alisma plantago-aquatica* L.	KF
		Limnophyton obtusifolium (L.) Miq.	CC, SS
		Burnatia enneandra M. Mitch.	CC, SS
		Caldesia reniformis (D. Don) Kakino.	EQ
		Laphotocarpus guayanensis (Kunth)	KF
		Ranalisma humile (Kunth) Hutch.	KF
		Wiesneria schweinfurthii Hook. F.	EQ
8	Aponogetonaceae	*Aponogeton subconjugatus* Schumach.	SS
		A. vallisnerioides Bak.	EQ
9	Amaranthaceae	*Alternanthera nodiflora* R. Br.	CS, SS
		A. sessilis (L.) R. Br.	WS
10	Araceae	*Pistia stratiotes* L.	SS
11	Asteraceae	*Melanthera scandens* (Schumach.)	SS
12	Ceratophyllaceae	*Ceratophyllum demersum* L.	WS

(continued)

Table 1 (continued)

No.	Family	Latin name	Distribution
13	Commelinaceae	*Commelina diffusa* Burm. F.	CC, SS
		C. benghlensis L.	RS, CS, SS
14	Convolvulaceae	*Ipomoea aquatica* Forsk.	CS, SS
		I. cairica (L.) Sweet.	CS, SS
		I. rubens (Choisy).	CS, SS
15	Cucurbitaceae	*Lufa cylindrical* (L.) M.J. Roem.	SS
16	Cyperaceae	*Cyperus alopecuroides* Rottb.	CS, SS
		C. albomarginatus	SS
		C. munditi (Nees) Kunth	CS, SS
		C. papyrus L.	SS
		Frimbristylis subaphylla Boeck.	EQ
		Scirpus cubensis Poepp. & Kunth.	CS, SS
17	Droseraceae	*Aldrovonada vesiculosa* L.	SS
18	Fabaceae	*Aeschynomene indica* L.	CS, SS
		Desmodium hirtum	SS
		Sesbania rostrata pubescens DC	SS
		Mimosa pigra L.	WS
19	Hydrocharitaceae	*Lagarosiphon schweinfurthii* Casp.	EQ
		L. cordofanus (Hochst.) Casp.	CS
		Nechamandra alternifloia (Roxb.)	WN
		Ottelia alismoides (L.) Pers.	CS
		O. ulvifolia (Planch.) Walp.	CS, SS
		O. brachyphylla (Gurke) Dandy	EQ
		O. scabra Bak.	CC, SS
		Vallisneria spiralis Fenzl.	CC, SS
20	Lentibulariaceae	*Utricularia thonningii* Schumach.	CS, SS
		U. stellaris L.	CS, SS
		U. exoleta R. Br.	CC, SS
		U. reflexa Oliv.	EQ
21	Lemnaceae	*Lemna perpusilla* Torr.	CC, SS
		L. polyriza L.	EQ
		L. aequinoctialis Welw.	EQ
		Spirodela polyrrhiza L. (Scheild).	SS
		Wolffiella hyalina (Del.) Hegelm.	DF, KF, SS
		Wolffiopsis sp. Den Hartog & Vd Plas.	SS
22	Najadaceae	*Najas pectinata* (Parl.) Magnus.	CS, SS
		N. graminea Del.	CS, EQ
		N. schweinfurthii Magnus.	EQ
23	Nymphaeaceae	*Nymphaea lotus* L.	CS, SS
		N. caerulea Sav.	CS, SS
		N. micrantha Guillem & Perrott.	CS, SS
24	Onagraceae	*Jussiaea diffusa* Forsk.	CS, SS
		Ludwigia stolonifera (Guill & Perr.)	SS
		L. leptocarpa Nutt.	CS, SS
		L. suffruticosa L.	CS, SS
25	Palmae	*Borassus aethiopicum* Mart.	CS, SS
		Hyphaene thebaica (L.)	NS, CS

(continued)

Table 1 (continued)

No.	Family	Latin name	Distribution
26	Poaceae	*Echinochloa stagnina* (Retz.) Beauv.	WS
		E. haploclada (Stapf.)	SS
		E. pyramidalis (Lam.).	CS, SS
		Phragmites karka (Retz.).	CS, SS
		Oryza brachyntha Chev. & Roehr.	EQ
		O. barthii A. Chev.	EQ
		O. longistaminata A. Chev. & Rochr.	SS
		O. punctata Kotschy ex Steud.	CS
		Panicum repens L.	CSIC, SS
		Paspalum polystachyum R. Br.	EQ
		Vossia cuspidata (Roxb.) W. Griff.	CSIC, SS
		Sporobolus pyramidalis Beauv.	CS, SS
		Hyparrhenia rufa (Nees) Stapf.	CS, SS
		Digitaria debilis (Desf.) Willd.	KF, SS
		Suddia sagitifolia Renvoize	SS
27	Polygonaceae	*Polygonum glabrum* Willd.	WS
		P. tomentosum Wild.	CS, SS
		P. limbatum Meisn.	CS, SS
		P. lanigerum R. Br.	SS
		P. senegalense Meisn.	DF, EQ
28	Pontederiaceae	*Eichhornia crassipes* (Mart.)	CS, SS
29	Potamogetonaceae	*Potamogeton crispus* L.	CS
		P. bunyonyiensis Denny & Lye	SS
		P. nodosus Poir.	CSIC
		P. pectinatus L.	CSIC
		P. perfoliatus L.	CSIC
		P. schweinfurthii A. Benn.	SS
		P. octandrus Poir.	CS, SS
		P. pubillus L.	DF
30	Scrophulariaceae	*Limnophila indica* (L.)	CS, SS
31	Trapaceae	*Trapa natans* var. *bispinosa* Roxb.	SS
32	Typhaceae	*T. angustata* Bory Chaub.	WS
		T. domingensis Pers.	SS
33	Verbenaceae	*Phyla nodiflora* (L.) Greene.	NS, SS
34	Vitiaceae	*Cayratia ibuensis* (Hook) Suessseng.	SS
35	Zannichelliaceae	*Zannichellia palustris* L.	CSIC

CS, Central Sudan; DF, Darfur; KF, Kordofan; CSIC, Central Sudan in irrigation canals; SS, South Sudan; NS, North Sudan; WS, Widespread; EQ, Equatoria.

the Imatong Mountains, South Sudan at altitudes of 2,000–3,000 m. *Chara globularis* and *Nitella* sp. are the only macroalgae present. Pteridophytes are represented by *Isoetes schweinfurthii, Marsilea* sp., *M. nubica, Ceratopters cornuta* and *Azolla nilotica* (Mackleay, 1953).

6 Life Form Diversity

Aquatic plants include both woody and herbaceous forms. Among the woody species, growing on the banks along rivers, *Acacia nilotica* (Sunut) is found on partially flooded areas. *Tamarix nilotica* is a pioneer on new-formed sandbanks. *Hyphaene thebaica* and *Faidherbia albida* (formerly *Acacia albida*) grow on riverbanks with groundwater within reach (Van Noordwijk, 1984). The only woody macrophyte found in permanent water is *Herminaria elaphroxylon* (Ambatch). The palms *Hyphaene thebaica* and *Borassus aethiopum* are distributed in grasslands which are regularly waterlogged or seasonally flooded. Denny (personal communication, 2002) also expects swamp palms such as *Phoenix* and *Raphia,* and *Ficus* spp. in the southern swamps.

The various aquatic macrophytes in the Sudan manifest five types of growth forms viz. free-floating (*Pistia stratiotes*), rootless submersed (*Ceratophyllum demersum*), rooted submersed (*Vallisneria* sp.), floating-leaved submersed (*Nymphaea lotus*), emergent (*Vossia cuspidata, Utricularia* spp.) and trailing on the water surface from the bank (*Ipomoea aquatica*). Beside these, and associated with emergent plants, are certain twiners and climbers such as *Ipomoea cairica, Luffa cylindrica* and *Cayratia ibuensis*.

7 Uses of Macrophytes

Macrophytes are used locally for food, fodder and as building materials. Denny (1985) gave a summary of the use of *E. crassipes* in Sudan: it is grazed fresh by cattle during the dry season, and serves as a mulch and fertilizer. When used as a mulch, it suppresses the growth of the major weed, *Cyperus rotundus,* and conserves soil moisture. GTZ conducted trials in Sudan to generate biogas from water hyacinth in the White Nile (Philip et al., 1983). Table 2 summarizes the uses of some aquatic plants. Emergent plants such as *Phragmites* sp. *and Typha* sp. have been used in phytoremediation, to remove dissolved solids and oil from the huge amounts of water extracted with crude oil. Aquatic macrophytes also provide shelter, food, hatching and nesting sites for other organisms. They play an important role in the gaseous balance in both the atmosphere and hydrosphere. Certain species are bio-indicators of pollution though such a claim has not been substantiated and documented in Sudan.

Denny (pers. com.) draws attention to the possible positive and important role of water hyacinth and wetland vegetation in general for the water cycle and in the rainfall pattern in Southern Sudan.

At a global level, aquatic plants are important to alleviate climate change caused by the emanation of greenhouse gases (GHGs). Aquatic plants can absorb and sequester considerable amounts of the GHGs. Within such a context, and considering the expansive wetlands in the Sudan, attention should be paid to study and quantify the contribution of Sudanese hydrophytes to reduce global warming.

Table 2 Some uses of aquatic plants in Sudan

Plant	Uses
Cyperus papyrus	Local inhabitants cut the tall stems for use as mats and roofing material. Animals graze on its umbels
Phragmites karika	Culms are used as building material and in mat making
Phragmites sp. *and Typha* sp.	Major components in phytoremediation, to purify oil-produced water
Azolla nilotica	Usually hosts the blue-green, N-fixing Anabaena azolli
Borassus aethiopium	Fishing boats are made from the tree timber. Fruits are edible.
Hyphaene thebaica	Trunks are used as building material. Fruits are edible.
Eichhornia crassipes	Grazed by animals, used as mulch and fertilizer and for the generation of biogas.
Trapa natans	The fruit is rich in starch and fat. Used as food.
Nymphaea spp.	Rhizomes and fruits are used as food by Nilotic tribes
Aeschynomene indica	Raft making
Oryza spp.	Potential rice crop

8 The Dilemma of Aquatic Plants

Diversity of aquatic macrophytes in Sudan is also manifested in the problems they face. Aquatic macrophytes have traditionally been regarded as a nuisance; in the best of cases, they have been neglected. This attitude is reflected in the fact that Sudanese aquatic macrophytes have received little scientific attention. One cannot but wonder at the absence of aquatic plants among the cash crops in a country endowed with such diverse aquatic habitats and plants. Although many records of aquatic weeds are available (Andrews, 1945; Ali, 1977; Hamdoun & Desougi, 1979; Desougi, 1980; Denny, 1984), there is no complete record of the aquatic flora of the country. Their classification is neither accurate nor complete, a problem exacerbated by the fact that local aquatic botanists are rare and there are no research programmes on aquatic ecosystems. The discovery in 1979 of the so far only endemic aquatic plant of the Sudan, the swamp grass *Suddia sagitifolia* (Renvoize et al., 1984), sharply precipitates this situation. The distribution of this remarkable monospecific genus is still imperfectly unknown. It is rhizomatous, with nodal rooting, reaches a height of 2.5 m and grows within papyrus swamp. Its enormous, 12 cm wide leaves are well adapted to function in the shade of reed swamps (Thomson, 1985) (Fig. 6).

9 Exotic Species

The most profound ecological changes in the aquatic ecosystems of the Sudan can be illustrated by the case of the Nile cabbage (*Pistia stratiotes*). Up to 1957, this species was the largest free-floater in the country. In 1957, the water hyacinth (*Eichhornia crassipes*) reached southern Sudan (Gay, 1958). By 1960, the whole White Nile from Juba to Jebel Aulia dam as well as its tributaries over a distance of 3,270 km were infested (Obeid, 1975). The native free-floating water cabbage had been pushed out and had become confined to temporary pools and small khors.

10 The Jonglei Canal

The Jonglei canal, designed to bypass the "Sudd", to conserve part of the water now lost to evapo-transpiration and seepage (see Fig. 1 and Dumont, 2009), is alleged to have significant impacts on the wetlands of southern Sudan, including their flora. Once completed and operated, it is expected to reduce the seasonally flooded grasslands. The most prone to change are the emergents. *Vossia* and *Cyperus* will retreat downstream, while a substantial reduction may be expected in the zone currently occupied by *Typha*. The seasonally flooded grasslands dominated by *Oryza longistaminata* and by *Echinochloa pyramidalis* will decrease in area by between 10% and 23% (Howell et al., 1988). The canal itself, with its regulated flow regime, would mostly encourage the spread of free-floating plants (Ali, 1977).

11 Civil Strife in the South

Civil war in the south of Sudan raged from 1956 to 1972 and broke out again in 1983. It was terminated by the signing of the Comprehensive Peace Accord in 2005. Though there is no as yet a proper assessment of the effect of war on the wetland ecosystems, one could envisage certain scenarios. The cutting of forests, inevitable as a direct action in war or as a side activity by armed troops, could have lead to serious soil erosion. This could increase sedimentation of the waterbodies, in particular lentic ones, and may cause a shift in the aquatic communities at the expense of floating and submerged species. Burning and cutting of *Papyrus*, *Phragmites* and *Typha* for access adversely affects not only these species, but also climbers and twiners associated with them.

12 Pollution

During three decades (1960–1980), a campaign to control water hyacinth with the herbicide 2, 4-D was carried out (Philip et al., 1983). Unfortunately, there was no evaluation of its impact on the aquatic ecosystem while we expect that such a practice would have also affected non-target floating *Pistia*, *Lemna*, *Wolffia* and *Spirodella*. Plants with floating leaves such as *Nymphaea* and *Limnophyton* could also be under threat. Furthermore, pesticides are generously applied annually on all irrigated agricultural schemes in the Sudan. With wind drift and excess water from the cultivated fields, pesticide residues find their way to the main Nile. Sadly, no research has been conducted on their impact on the aquatic flora.

For countless years, the wetlands of Southern Sudan have enjoyed stable conditions, with no significant anthropogenic interference. The term “stable” here has a special context. Odum (1967), cited in Denny (1984), describes wetlands as “pulse stable” ecosystems. Their stability relies on alternating “pulses” of environmental variables (in this case wet and dry phases). The communities of pulse-stable systems are characteristically resilient to change. However, recent anthropogenic activities could destabilize these systems. One serious threat is the oil extraction activities now overwhelming the Sudd region. Exploration, transportation and exportation of oil threaten the diversity of the wildlife, aquatic macrophytes and forests, as well as the hydrology of this intricate ecosystem (Springuel & Ali, 2005).

13 Conclusion

The Nile system in Sudan is rich in aquatic macrophytes. These communities exhibit remarkable diversity in phyletic constitution, range, horizontal zonation, life forms and uses. Endemism is low, with only one apparently endemic species, but studies are fragmented, and taxonomy is based on old sources. There is a need for a modern survey to document taxonomy, distribution, morphology, life forms, ecological niches, chemical composition, uses and threats. And inasmuch as global warming is now a reality, the role played by the hydrophytes of Sudan in alleviating global impacts through their ability to sequester carbon dioxide needs to be qualified and quantified. Particular emphasis is required for the Sudd region because of its high density and diversity of aquatic plants and because this pristine, pulse-stable ecosystem is under threat from oil exploitation. Now that a Comprehensive Peace Agreement, signed in 2005, has ended 22 years of civil war, and that in 2006 the Sudd has been given the status of a Ramsar site, this chapter raises an urgent plea to preserve the biodiversity of the swamp flora of southern Sudan.

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The Cnidaria of the Nile Basin

Henri J. Dumont

Abstract At least half of the cnidarian fauna of the Nile basin (7+ species) is suspected of being of allochtonous origin. In addition, species that are native (*Limnocnida* sp., *Hydra* spp.) have been poorly studied and seem to lack basin endemism. The introduced species (two of Pontocaspian and two of marine origin) are either salt-loving or tolerant of broad fluctuations in salinity. Yet, rapid changes in the lower Nile area in recent decades have secondarily eliminated three of them.

1 Introduction

The phylum Cnidaria is composed of predominantly marine animals. Several of these (including some sea anemones) occasionally enter the Nile delta lakes, but fail to establish populations there, and are thus not strictly Nilotic. Hydra's and several medusa-forming taxa of fresh and brackish water, solitary or colonial have, however, consistently been recorded from the Nile basin, even if some are suspected of being alien invaders. In Birket Qarun, three taxa (one brackish and two marine) seem to have been introduced yet again disappeared in recent times, due to an excessive salinisation of the environment. For details on the taxonomy of the "nilotic" taxa, consult Jankowski et al. (2008) and Dumont (2009).

2 List of Species Recorded

Protohydra leuckarti: delta lakes (supposition)

Hydra spp. (s.l.): Lake Borullus (El-Shabrawy, pers. com.), lakes Kundi and Keilak (Green et al., 1984).

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Limnocnida sp. (presumably *tanganjicae*): Lake Tana (sub *L. indica*) (Thiel, 1973), Lake Victoria (sub *L. victoriae*) (Kramp, 1964), Nile near Khartoum (Dumont, 1994), Nozha Hydrodrome (supposition) (Elster & Vollenweider, 1961).

Moerisia lyonsi: Birket Qarun in first half of twentieth century (Boulenger, 1908b).

Obelia sp.: Birket Qarun in 1970–1980s (Abdel-Malek & Ishak, 1980).

Cordylophora caspia: Nile delta, Birket Qarun in Fayum, Nile up to Sudd swamps (Boulenger, 1908a; Rzóska, 1949).

Apitasiogeton pellucidus: Birket Qarun during the 1990s.

3 Discussion: Nature and Distribution of the Nile Cnidaria

The only cnidarians that are with certainty native of the Nile basin are the Hydra's and the medusa *Limnocnida*. Yet, and remarkably, not a single full identification of a Hydra has become available to date. Possibly three to four species may be expected, but all remain to be confirmed, as well as their distribution across the basin. The brackish water *Protohydra leuckarti*, widely distributed around the Mediterranean Sea, almost certainly occurs in the brackish zones of the delta lakes, but have been overlooked to date.

As to the Limnomedusae, taxonomic confusion has so far handicapped the establishment of the nature of the Nile species. A *Limnocnida* cited from Lake Tana has been identified as *L. indica* by Thiel (1973) but without any illustrations. If *L. indica*, the "asiatic form" of the genus, indeed occurs in Africa, this might mean that only a single variable taxon exists, which appears unlikely. On the other hand, medusae from Lake Victoria were originally described as *L. victoriae* (Gunther, 1893), and may be conspecific with the widespread African *L. tanganjicae* (see also Gunther, 1907; Goy, 1977; Rayner & Appleton, 1989). Occasional specimens observed in the Nile near Khartoum (Dumont, 1994) have not been identified, and the same applies to a brief mass occurrence of medusae in the Nozha hydrodrome, an artificially isolated freshwater part of Lake Manzala (Elster & Vollenweider, 1961). The latter record was tentatively ascribed to *Limnocnida* by Dumont & Verheye (1984) and Dumont (1994), but it remains possible that it was the invasive *Craspedacusta sowerbyi*, an Asian species that has conquered all continents save Antarctica in the course of the twentieth century.

Moerisia lyonsi, a brackish water taxon first described (polyps and medusa) from Birket Qarun in the beginning of the twentieth century (Boulenger, 1908b) was long considered an endemic of the Fayum lakes. However, there are reasons to doubt that assumption. Birket Qarun was indeed a fresh, not a brackish water lake for most of its existence (El-Shabrawy & Dumont, 2009). It was artificially flooded with Nile water during pharaonic times and only turned brackish when the free flow of Nile water to the lake was impeded in Ptolemaic times. Salinisation remained modest, however, and a mesohaline state was only reached at the beginning of the twentieth century. Therefore, no favourable conditions for a local endemic species adapted to brackish water conditions existed in the lake until very recently and briefly. Furthermore, the mesohaline window of opportunity for the species was extremely brief: the lake salinity now exceeds that of seawater, and *Moerisia* is no longer found there. For a brief while, it was replaced by the marine hydroid *Obelia* sp. (Abdel-Malek & Ishak, 1980), and by the sea anemone *Apitasiogeton pellucidus*, but both have now vanished in their turn. It follows that *Moerisia lyonsi* is likely a synonym of *Moerisia maeotica* or *M. pallasi* from the Ponto-Caspian basin. This is corroborated by the appearance, probably synchronous with that of *Moerisia*, of another Ponto-Caspian invading hydroid in the Nile system: *Cordylophora caspia*. This colonial polyp was also first discovered in Birket Qarun, and again by Boulenger (1908a). Boulenger explained its presence by a hypothetical Pliocene connection between the Fayum depression and the Mediterranean. Later, however, it was shown that *Cordylophora* has an extraordinary salt tolerance, and occurs from pure freshwater to almost seawater, allowing it to invade the whole of Europe in the course of the nineteenth to twentieth centuries. In the Nile too, it soon became widespread, occurring as far south as Malakal in South Sudan, and in the Bahr el Zeraf and Bahr el Gebel (Rzóska, 1949).

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The Oligochaeta of the Nile Basin Revisited

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Abstract A hypothesis on the origin and migration routes of the oligochaetes of the Nile Basin is presented. Five routes (but probably more than five waves) are recognized. Species found far from their origin (e.g. *Gordiodrilus* from the Upper Nile, found in Selima Oasis and Tripolitania) may represent an earlier wave than those that live closer to their source (e.g. *Alma nilotica* in the Delta and at Bahariya Oasis). The occurrence of egg cases of *Alma nilotica* in Bahariya Oasis suggests that once a surface water connection between the Nile and that Oasis existed. Such migrations occurred when rainfall was 500 mm y^{-1} or higher. Introduced species (probably in the nineteenth century), such as *Allolobophora caliginosa*, *Pheretima* spp., *Branchiura sowerbyi*, are excluded from this discussion. Moreover, millenia of basin irrigation in Egypt and northern Sudan have caused a drastic impoverishment of the original fauna. The oligochaetes of the Northern Nile are therefore a mix of species from different sources. The fauna of the Upper Nile (the Sudd region) is Afrotropical, with the Ugandan, Ethiopian and Kenyan faunas distinct from each other. There is no relation with the fauna of Cyprus, the island nearest to the Nile Delta. There is also little relation between the Chad and Nile basins. The Nile fauna is distinct from that of adjacent West African countries (Central African Republic, Congo, DR Congo), and from that of Southern Africa.

Threats to the oligochaetes of the Nile include land reclamation, desertification, urban sprawl, soil and water pollution. There is a need for exploration in west and south Sudan, Ethiopia, Chad and the Central African Republic, before their oligochaetes become obliterated by environmental degradation.

1 Introduction

The oligochaetes comprise aquatic species, plus the familiar earthworms, which live in damp soil. Since the publication of a paper on the oligochaetes of the Nile Basin more than 30 years ago (Ghabbour, 1976), an update on this group has become necessary.

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Studies in Egypt started with Napoleon's expedition of 1798 and his attempts to record Egypt's natural history. The (few) worms collected were described by Savigny in the 1809 edition of the *Description de l'Egypte*, but these descriptions do not fit any identifiable species. European scientists and tourists, collecting in the mid-nineteenth century, discovered the unusual *Alma nilotica* Grube 1855, a 25–40 cm long worm that lives in near-shore Nile mud, hidden within the roots of plants. The illustrious W. Michaelsen collected from Egypt and published in 1897 a list of new and little known oligochaetes. He discovered an interesting species, called *Nannodrilus staudei* in honour of a German pharmacist in Cairo. British oligochaetologists also made collections, particularly from Lake Qarun in the Fayum Province. These efforts, though significant in establishing lists of Egyptian species, had to be consolidated by resident scientists able to visit several places in several seasons. This started with A. Khalaf El-Duweini in the 1930s, followed by the present writer in the late 1950s, covering the Sudan in the 1960s and Egypt in the 1970s (Khalaf El-Duweini & Ghabbour, 1968; Ghabbour, 1976; El-Kifl & Ghabbour, 1984; Ghabbour, 1996).

2 Composition of the Fauna of the Nile Basin

The origin and affinities of the species were discussed by Ghabbour (1998). Here, we add new data about their occurrence in the Nile Basin and adjacent territories, that may test previous hypotheses about the zoogeography of the oligochaetes of the region. When tackling the oligochaete fauna of the Nile Basin, we have to look into the fauna of (1) the Mediterranean Islands of Sardinia, Sicily, Crete, and Cyprus in the north, (2) the Levant in the east, and (3) western North Africa in the west.

Extra-Basin Countries

2.1 The Mediterranean Islands

The Cretan fauna is related to that of Greece, while that of Cyprus, the island nearest to the Nile Delta, has affinities with Anatolia and the Levant. Pavlíček and Csuzdi (2006) found two earthworm families in Cyprus: Lumbricidae (15 species) and Acanthodrilidae (one species). The majority are autochthonous (57–64%); 36–44% are introductions. The autochthonous species are (i) endemic of the Levant (*Dendrobaena semitica*), (ii) distributed in Anatolia and the Caucasus (*D. pentheri*), (iii) distributed from Europe to Anatolia (*Allolobophora nematogena*, *D. pantaleonis*, *Proctodrilus tuberculatus*), (iv) distributed from Europe to the Levant (*Murchieona minuscula*), (v) distributed in the Transcaucasian region and in the East Mediterranean (*Helodrilus patriarchalis*), or (vi) widely distributed in the Mediterranean basin (*D. byblica*, *Eiseniella neapolitana*, and *Octodrilus complanatus*). The Cypriot fauna is significantly richer than previously thought; it has more affinities with Anatolia than with the Levant, and none with Egypt.

Ghabbour (1996) reported the aquatic *Eiseniella tetraedra* at Burg El-Arab on the Egyptian Mediterranean coast, west of Alexandria. This species probably came from Sardinia and Sicily, via Tunisia and Libya.

2.2 The Levant

Pavlíček et al. (2003) list 31 earthworm species, in five families (Acanthodrilidae, Criodrilidae, Lumbricidae, Ocnerodrilidae and Megascolecidae). *Aporrectodea caliginosa* is represented by two subspecies. Out of all species, 39–42% (12–13 species) have been introduced and 58–61% (18–19 species) seem autochthonous. Eight to 11 species (42–61%) of the lumbricid genera *Dendrobaena*, *Bimastos* and *Allolobophora s.l.* are endemic. The autochthonous Levantine earthworms show affinities with Anatolia, Europe, the Caucasus, Iran, and North Africa, but their taxonomy needs revision. The authors conclude that the earthworm fauna of the Levant does not show a transitory character between the Afrotropical and Eurasian fauna. They later (2006) added that it is exclusively Palaearctic, and mainly related to the faunas of Anatolia-Caucasus and Europe. No observed earthworm endemism above the species level corresponds to the expected origin of earthworm fauna in the Levant between the Rupelian (30–28 My) and Tortonian (11.5–6 My) (Oligocene–Miocene). In spite of the fact that speciation in earthworms may take millions of years, the observed new species isolated in the desert oases and along the Negev and Sinai borders might change this perception if we could differentiate relicts surviving the expansion of the Arabo-Syrian desert belt from subsequent speciation. Recently, Pavlíček (2007), listed 34 species from the Levant, including six new to science: *Bimastos jordanis* Csuzdi & Pavlíček, 1999, *Dendrobaena negevis* Csuzdi & Pavlíček, 1999, *D. nevoi* Csuzdi & Pavlíček, 1999, *D. rothschildae* Csuzdi et Pavlíček 1999, *Perelia galileana* Csuzdi & Pavlíček, 2005 and *P. shamsi* Csuzdi & Pavlíček, 2005.

2.3 Western North Africa

In the last two decades, the earthworm fauna of western North Africa, poorly known previously, received more attention (Omodeo et al., 2003). These new data (including five new regional records) make it possible to outline ecological and biogeographical traits. In the Maghreb, cultivated fields can host dense earthworm assemblages. Some species have narrow habitat preferences: *Allolobophoridella eiseni* is corticicolous; *Eisenia xylophila* lives in decaying logs of *Quercus suber*, protected by the cork sleeve; *Octodrilus complanatus* does not occur in forests but dwells in pastures and grassland with sparse trees, *O. maghrebinus* is only found in oak forests. Litter-dwelling species are few: *A. eiseni*, *Dendrobaena lusitana*, *D. byblica* and *Dendrodrilus rubidus*, the last two being rare and probably of recent introduction. None of the autochthonus species is adapted to arid soils, except for *Hormogaster redii* which, by its ability to aestivate, can tolerate areas where the rainy season is restricted to a few weeks per year. In contrast, the diversity of the aquatic forms is remarkable: *Criodrilus lacuum*, *Eiseniella neapolitana*, *E. tetraedra*, *Allolobophora molleri* complex, *Helodrilus* cf. *oculatus*, *H. rifensis*, and *Nicodrilus* sp. The list of taxa recorded (38), though shorter than that of other Palaearctic territories of similar size, comprises some narrow-range and broad-range endemics that strongly characterise it. Its affinities are with the Iberian (and Macharonesian) fauna: the *A. molleri* complex, *D. lusitana*, *Allolobophora borellii* and *Lumbricus friendi*. A comparable relationship is seen in the Franco-Iberian genus *Prosellodrilus*, represented in the Maghreb by *P. doumandjii* and *P. festai*. In contrast, the two endemic species of *Octodrilus* (*O. maghrebinus* and *O. kabylianus*) and *E. xylophila* suggest a relationship with the Balkan fauna. This fauna is, again, unrelated to that of the Nile.

2.3.1 Mauritania

De Henau and Dumont (1976) collected five species of aquatic oligochaetes from the Western Sahara (Saguiat Al-Hamra and Guelta Zemmour): *Tubifex tubifex*, *Potamothrix hammoniensis* (of Holarctic distribution), *Nais raviensis* (possibly Palaeotropical), *Aeolosoma hyalinum* (separated from *A. niveum*, and hence its distribution could not be defined), and *A. hemprichi*. *Tubifex* and *Aelosoma* are cosmopolitan. Small and limited as this collection could be, it shows that the Atlantic border of the Sahara has an oligochaete faunule of a particular character, in part Holarctic and in part Tropical, but distinct from the Holarctic-Tropical mixture of North-East Africa.

2.3.2 Libya

Bennour and Nair (1997) mentioned that *Aporrectodea caliginosa* (Savigny, 1826) coexists in Benghazi, Cyrenaica, with *Aporrectodea rosea*, *Allolobophora chlorotica*, and *Aporrectodea culpifera* (?). Nair et al. (2005) collected earthworms from the Benghazi area and found three peregrine species: *Allolobophora caliginosa trapezoides*, *Allolobophora rosea* (= *Ap. rosea*), and *Microscolex dubius* (Family: Microscolecidae), in addition to those mentioned. These are mostly species from Europe (*Aporrectodea*) or from the Far East (*Microscolex dubius*) without biogeographical significance. They simply invaded an empty space. Only *A. rosea* is worthy of mention as a link with the same species in the Nile Delta.

2.3.3 Chad

Lauzanne (1968) published a preliminary list of Oligochaeta of Lake Chad: *Aulodrilus tchadensis* nov. sp., *Aulodrilus remex*, *Pristina synclitis*, *Alluroides tanganikae*, *Branchiodrilus cleistochaeta*, *Dero digitata*, *Aulophorus furcatus*, *Allonais* *paraguayensis ghanensis* (different from *A. p. equatorialis*), *Haemonais waldvogeli* (= *H. laurentis*), and *Euilyodrilus* sp. Again, there is almost no relationship with the Nile Basin fauna. An investigation in the area of Gebel Marra in Darfur would clarify the relationship of the oligochaete faunas of the Nile and Chad Basins.

Countries within the Nile Basin

Ghabbour (1976) subdivided the Nile Basin into three oligochaete subregions: the Main (Lower) Nile, from the Delta to Khartoum (characterized by *Alma nilotica* and *A. stuhlmanni*), the Upper Nile from Khartoum to the sources in Central and East Africa (characterized by *A. emini*), and the Ethiopian subregion (characterized by *Eudrilus eugeniae*).

2.4.1 Egypt

Species and locations newly investigated in Egypt (Pavlícek et al., 1997) include *Allolobophora* (*Aporrectodea*) *caliginosa*, associated with the aquatic *Eiseniella tetraedra* (Savigny, 1826) in a spring near the St. Catherine Monastery in South Sinaï (1,900 masl), and *Allolobophora* (*Aporrectodea*) *rosea* (= *Eisenia rosea*) on the slopes of the Mountain of Moses (2,470 masl), and near the Monastery at ca 1,670 masl. Bishai et al. (2000) recorded *Limnodrilus hoffmeisteri* Claparède 1862, *L. udekemianus* Claparède 1862, and *Pristina* sp. in Lake Nasser (see El-Shabrawy, 2009). Ibrahim (2007) found *Chaetogaster limnaei*, a fish parasite, in Al-Salam Canal, northern Sinaï. Moursi and Dekinesh (1984) found *Allolobophora* (*Aporrectodea*) *jassyensis* var. *orientalis* in the vicinity of Alexandria, showing that its range covers both sides of the Delta. A *Gordiodrilus* found by Khalaf El-Duweini and Ghabbour (1965) at Dahshur, 20 km south of Cairo, turned out to be *Chuniodrilus ghabbouri*.

2.4.2 Sudan

Oligochaete faunas in the two subregions of the Lower (Egypt and northern Sudan), and Upper Nile (Sudan White Nile and further south), though distinct, are related to each other by the occurrence of the genus *Alma*. The faunule of the Ethiopian highlands, however, is unrelated to that of the first two subregions.

2.5 The Blue Nile

The name Blue Nile in the Sudanese dialect (*Nil Azrag*) means Black Nile, because of the colour of the sediments carried by the floods. When the Egyptians and British heard the word "*azrag*", which means blue elsewhere in the Arab World, it was incorrectly translated into English as "blue". The intense black colour of the Blue

Nile floods provides a spectacular scene in Khartoum, as its waters push aside the clear waters of the White Nile at the confluence of the two rivers.

The explanation given by Ghabbour (1976) for the dissimilarity of the oligochaete fauna of the Main and Blue Niles was that the powerful Blue Nile floods destroy any oligochaetes on their course (Figs. 1–3). Dejen et al. (2004) suppose that the altitudinal Blue Nile was vigorous as far back as 29 million years ago, but with water temperatures low for the tropics. Gani et al. (2007) add that in its third phase, from 6 My ago to the present, it was characterized by incision rates that increased from 120 to 320 m My^{-1}, or 0.12–0.32 m My^{-1}. Moreover, according to Lamb et al. (2006), Lake Tana, the source of the Blue Nile, went through a period of desiccation, with an abrupt return to freshwater conditions at 14,750 BP, when the lake overflowed to the Blue Nile. This must have washed everything in its course into the Main Nile. The annual rainfall over the basin decreases from the south-west (>2,000 mm) to the north-east (ca 1,000 mm), with ca 70% occurring between June and September (see Camberlin, 2009 and Sutcliffe, 2009). Discharge amounts to 45.9 km^3. Between 1900 and 1997 annual river flow has ranged from 20.6 km^3 in 1913, to 79 km^3 in 1909 (Conway, 2000).

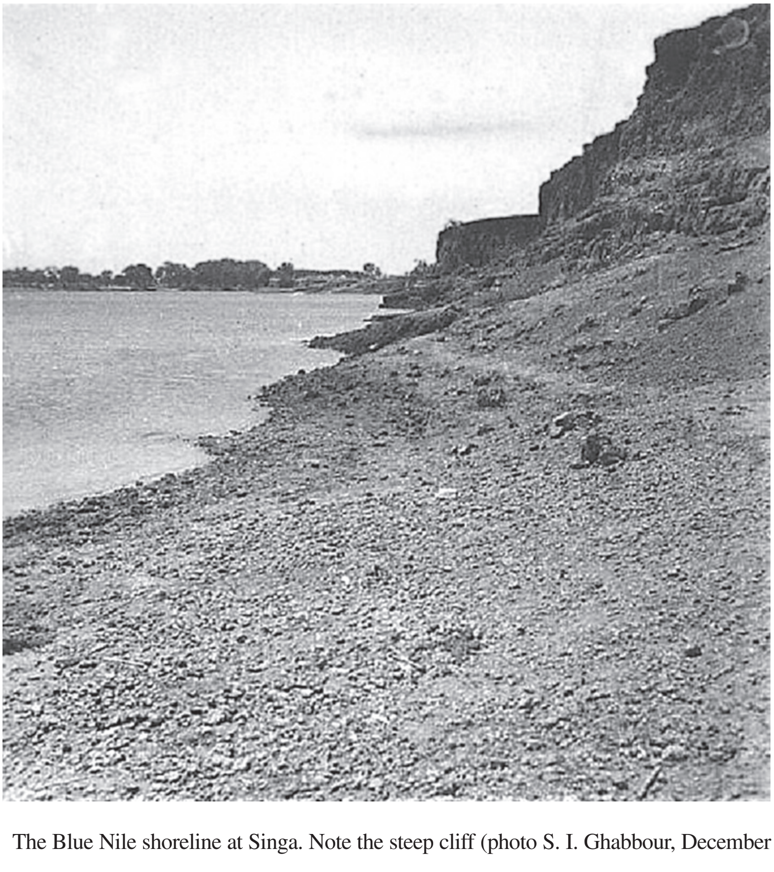

Fig. 1 The Blue Nile shoreline at Singa. Note the steep cliff (photo S. I. Ghabbour, December 1967)

Fig. 2 The surface of the cliffs bordering the shoreline of the Blue Nile at Singa. Note the deep erosion channels (photo S. I. Ghabbour, December 1967)

The Blue Nile floods excavate its banks every year, leaving steep cliffs on both sides. Dry season evaporation results in the precipitation of insoluble "kankar" (calcium carbonate nodules) in the soils of these banks. Terraces of the Blue Nile above Roseires, are 6 m above the present flood-level, and consist of clays, sands and "kankar" (Williams & Adamson, 1973). Aquatic oligochaetes, even if temporarily present, would be washed away again and again, explaining the dissimilarity of Ethiopian and Sudanese oligochaetes.

2.6 The White Nile

According to Williams et al. (2003), lake shorelines in the White Nile valley as far south as 10°N are revealed by remote-sensing imagery. The highest shoreline is at 386 m elevation and was eroded when the White Nile formed a lake as wide as 70 km and >500 km long. This palaeolake may have formed around 400 ka,

Fig. 3 Panoramic view of the Blue Nile at Roseires, showing the erosion of the shoreline (photo S. I. Ghabbour, February 1968)

during the exceptionally long “stage 11” interglacial, an ideal environment for the speciation of *Alma*.

2.7 Ethiopia

Jamieson et al. (2002) proposed a division of the Crassiclitellata on morpho-cladistic evidence, into two groups: the Aquamegadrili Jamieson, 1988 and the Terrimegadrili Jamieson, 1988 (all oligochaete families with multilayered clitella form a single clade, Crassiclitellata Jamieson, 1988). Aquamegadrili have an aquatic or semi-aquatic mode of life, and consist of the families Sparganophilidae (Holarctic), Biwadrilidae Jamieson, 1971 (Japan), Almidae (mostly warm tropics, including *Alma*, but also *Criodrilus* Hoffmeister, 1845, in the Mediterranean region), and Lutodrilidae (Southern Neartic). It is not unlikely that the aquamegadrile families, irrespective of mono- or polyphyly of the group, have always had an aquatic or amphibious existence. The remainder of the Crassiclitellata are predominantly terrestrial, hence the term Terrimegadrili. These consist of the superfamilies Ocnerodriloidea Beddard, 1891, Eudriloidea Claus, 1880, Lumbricoidea Claus, 1876, and Megascolecoidea Rosa, 1891. Erséus and Källersjö (2004) support the group Crassiclitellata, comprising the aquatic oligochaetes and the terrestrial earthworms, when extending their 18S rDNA phylogenetic analysis to all Clitellata (Annelida).

The classification by Jamieson et al. (2002), in which the superfamilies Ocnerodriloidea Beddard, 1891, Eudriloidea Claus, 1880, Lumbricoidea Claus, 1876, and Megascolecoidea Rosa, 1891, are grouped together under Terrimegadrili, raises the possibility that the Ethiopian faunule is of Palaearctic-Oriental origin, given the presence of *Eudrilus eugeniae* (Terrimegadrili) and the absence of *Alma* (belonging to Aquamegadrili). Sporka (1994) reported *Potamothrix tudoranceai* sp. n. (Tubificidae, Oligochaeta) in the Ethiopian Rift Valley Lake Zwai (alt. 1,640 masl). This genus is Palaearctic, and its discovery strengthens the probability of a Palaearctic-Oriental origin of the Ethiopian oligochaete faunule.

2.8 Lake Victoria

The cichlid fauna of Lake Victoria has intrigued the scientific community for a long time. Verheyen et al. (2003) argue that this superflock is derived from the geologically older Lake Kivu while Gross (2006) suspects that Lake Victoria cichlids are millions of years younger than their counterparts in Lake Malawi. The dominant oligochaete species in Lake Victoria and many other water bodies in the region, including southern Sudan (Equatoria Province) is the African swamp worm *Alma emini*. This species breathes air using the postero-dorsal part of the body, which is well supplied with blood, as a ‘lung’ across which gases are exchanged at the surface or under water. Worthy of mention is that its congeners *A. nilotica* (found from Khartoum to the Delta), uses 'gills', while *A. stuhlmanni* (found in the vicinity of Cairo), lacks external breathing organs.

There is, unfortunately, no census of the oligochaete fauna of Lake Victoria comparable to its cichlids. Muli and Mavuti (2001) found that the dominant oligochaetes are *Alma emini* Michaelsen and the cosmopolitan *Branchiura sowerbyi* Beddard, abundant in soft mud on the Kenyan side of the Lake.

2.9 Kenya

Adams et al. (2002) reported *Alma emini* as common in Lake Naivasha. Raburu et al. (2002) found that *Branchiura sowerbyi* and *Limnodrilus hoffmeisteri* dominate the benthic invertebrate community in that same lake. Mathooko et al. (2005) recorded *Limnodrilus* in the Njoro River.

2.10 Tanzania

Salt (1954) reported *Pygmaeodrilus montanus* Mich., Megascolecidae, and *Fridericia exserta* Bretscher (Enchytraeidae) from the Upper Kilimanjaro. Both species have not been recorded from other Nile Basin countries.

2.11 Lake Tanganyika

Martin (1996) observed that the Eudrilidae and Ocnerodrilidae (megadriles) of Lake Tanganyika are restricted to that lake. Compared to Lake Baikal (20–25 Ma), the oligochaete fauna of Lake Tanganyika is scarce. In Martin's opinion, this is due to a lack of studies, but it might also be the result of a lacustrine environment less favourable to oligochaetes. A better study of this fauna is still badly needed.

3 Adjacent Basins

3.1 Central and West Africa

In Lamto savannah in Côte d'Ivoire, Fragoso and Lavelle (1992) discovered *Dichogaster bolaui*, *D. saliens*, *D. baeri*, *D. arboricola* and *Chuniodrilus wattouxi*, living in litter accumulated in the crowns of palms, and another *Dichogaster*, found also in Mexico. Mainoo et al. (2008) published a list of Oligochaeta of sub-Saharan African countries (Table 1), which shows that Central Africa has a species of

Table 1 Earthworms commonly found in sub-Saharan Africa (after Mainoo et al., 2008)

Species	Country/Region
Agastrodrilus opisthogynus	Côte d'Ivoire
Amynthas minimus	Côte d'Ivoire
Amynthas rodericensis	Côte d'Ivoire
Chuniodrilus palustris	Côte d'Ivoire
Chuniodrilus zielae	Côte d'Ivoire
Dichogaster affinnis	West Africa
Dichogaster agilis	Côte d'Ivoire
Dichogaster annae	West Africa
Dichogaster bolaui	West Africa
Dichogaster gracilis	West Africa
Dichogaster grafii	Congo
Dichogaster itolienses	Rwanda
Dichogaster Modigliani	West Africa
Dichogaster saliens	West Africa
Eminoscolex lavellei	Rwanda
Eudrilus eugeniae	Ghana, Côte d'Ivoire, Nigeria, West Africa
Gordiodrilus peguanus	Central Africa
Hyperiodrilus africanus	Ghana, Côte d'Ivoire Nigeria, West Africa
Millsonia anomala	Côte d'Ivoire
Millsonia ghanensis	Côte d'Ivoire
Millsonia inermis	Burkina Faso
Millsonia lamtoiana	Côte d'Ivoire
Millsonia schlegeli	Côte d'Ivoire
Nemoatogenia lacuum	Congo
Pontoscolex corethrurus	South Africa, South America
Stuhlmania variabilis	Rwanda

Gordiodrilus but other countries mentioned do not have it, at least not as a common species. The common species of Rwanda, *Dichogaster itolienses*, *Eminoscolex lavellei*, and *Stuhlmania variabilis* are related to no other neighbouring region. The two *Chuniodrilus* species of Côte d'Ivoire (the other one is *Chuniodrilus zielae)* are not common elsewhere in West Africa. In Cote d'Ivoire, Csuzdi and Tondoh (2007) found four species of Eudrilidae and nine Acanthodrilidae, among which two *Dichogaster* new to science. The collection also included *Chuniodrilus vuattouxi* (*sic*). The genus *Chuniodrilus* Michaelsen, 1913, erected for *C. schomburgki* from West Liberia, remained monotypic until 1958, when Omodeo described *C. zielæ* from Côte d'Ivoire (Jamieson, 1969).

These findings mean that the oligochaete fauna of the Nile Basin is not related to that of neighbouring basins, and that the fauna of its high altitude sources (Ethiopia, Rwanda) is related to the Palaearctic-Oriental-Neotropical Terrimegadrilae (Eudrilidae, Ocnerodrilidae), different from that of its middle and lower reaches, which relate to the Mediterranean-Tropical Aquamegadrilae (Almidae).

According to Jamieson et al. (2002) the most speciose earthworm family, the Megascolecidae has a Pangean origin. It is native to the Nearctic, Ethiopian, Oriental, Australian, eastern Palaearctic (China, Japan, Korea) and southern Neotropical regions, including Central America. In South America, megascolecids are replaced by Glossoscolecidae. In the Ethiopian region, particularly in Tropical West and East Africa, the Eudrilidae greatly outnumber it in genera. Currently recognized subfamilies of the Megascolecidae are the Acanthodrilinae Vejdowsky, 1884 and Megascolecinae Rosa, 1891, with or without the Ocnerodrilinae Beddard, 1891. Indigenous acanthodriles dominate the faunas of south and east North America, Mexico, Guatemala, southern South America, South Africa, New Zealand, New Caledonia, and parts of Australia.

The native range of the Ocnerodrilidae includes the warmer parts of North and South America, the Dominican Republic, Africa, India and Burma. *Hyperiodrilus africanus* (Eudrilidae), is widespread in West Africa (Benin, Togo, Nigeria, Côte d'Ivoire) and in Central Africa (Congo, Congo Democratic Republic). The species first appeared in the 1980s in Lamto Reserve (Côte d'Ivoire), which is protected from fire. It rapidly became a key species of the earthworm community in that area, thanks to its high fecundity (Tondoh, 1998). Other earthworm species in Côte d'Ivoire include *Millsonia omodeoi* Sims 1986, *Dichogaster baeri* Sciacchitano 1952, *Dichogaster ehrhardti* Michaelsen 1898, *Agastrodrilus* sp., and *Stuhlmannia palustris* Omodeo and Vaillaud 1967 (Tondoh et al., 2007).

4 Discussion

Three decades after the publication of the list of oligochaetes of the Nile Basin (Ghabbour, 1976), little has been added to our knowledge of this fauna and its biogeography. The oligochaete fauna of many countries in the region remains unknown (e.g. the Arabian Peninsula, Central African Republic, Eritrea, Djibouti, Somalia, the Sudan, Chad, Ethiopia, Uganda, Kenya, Tanzania, Rwanda, Burundi). In contrast, more research was carried out in Africa than before, mostly for the role of Oligochaeta in biological soil fertility (the terrestrial species), or in fisheries (the aquatic species).

4.1 The Mediterranean

On the basis of the material collected in Morocco, Algeria, Tunisia, Lebanon, Syria and Turkey, and data on Israel and Egypt, we now attempt a synthesis of the biogeography of the oligochaetes of the South and Eastern Mediterranean basin. Martinez-Ansemil and Giani (1987) show that the fauna is characterized by species with a wide distribution (cosmopolitan, holarctic, palaearctic…) and therefore, with great affinities with the European fauna. Nevertheless, three communities can be distinguished:

- The south-west (North Africa; Morocco, Algeria, Tunisia), where the community is poor and allied with that of southern Europe, not with the Ethiopian region

- The south-east (Egypt), with some species of African origin
- The east (mainly Lebanon and Israel) with a diverse community that includes species with eastern affinities (East Siberian), but none typically Ethiopian or Sino-Indian

4.2 The Mediterranean Islands

There is no relation between the fauna of the Nile Delta and that of Cyprus. but there are connections between the Delta and Sardinia-Sicily, situated further away. The fauna of Crete and Cyprus is akin to the Balkans and Anatolia, and to some degree to the Levant, but not to that of the Delta. The reason perhaps is that the Sicily-Tunisia strait is only ca 150 m deep (Béranger et al., 2004) and periodically acted as a land bridge (see map in Meijer & Krijgsman, 2005). Crete and Cyprus, in contrast, are permanently separated from Africa by water more than 1,000 m deep.

Each glaciation during the last 800 ky lasted for about 100 ky, and locked up about 50 10^6 km^3 of water in continental ice, causing global sea level to fall over a range of ca 130 m (Flemming et al., 2003). Prior to 1 million years ago, the cycles were smaller.

4.3 The Great Lakes Plateau

The palaeo-geology of the Great Lakes Plateau, the Rift Valley lakes, and the speciation of cichlids in these lakes, may help us understand the movements of aquatic oligochaetes in Central and East Africa. One problem is how aquatic oligochaetes, such as *Alma emini*, could extend from the Lake Plateau, across the ridges of the Rift Valley,

Table 2 Altitude of some Nile Basin lakes (after several authors)

Lake	Altitude masl
Lake Victoria Basin, Great Lakes Plateau	1,780–2,225
Lake Kyoga, Great Lakes Plateau	1,100
Lake Albert, Western Rift	619
Lake Edward, Western Rift	913
Lake George, Western Rift	914
Lake Kivu, Western Rift	1,425–1,463
Lake Tana, Ethiopian Plateau	1,829
Lake Zwai (Ziwai), Eastern Rift	1,640
Lake Naivasha, Eastern Rift	1,890
Lake Tanganyika, Southern Rift	765
Lake Malawi, Southern Rift	500

to reach high altitude lakes such as Lake Naivasha. A comparison of the altitude of the lakes mentioned above, from north to south, may give an idea of the difficulty of solving this question.

We may ask not only how this happened, but also when. Perhaps lakes were originally situated at low altitudes, and later uplifted to their present altitude. According to Trauth et al. (2005), lake sediments in the Ethiopian, Kenyan, and Tanzanian rift basins suggest three humid periods, at 2.7–2.5 million years ago (Ma), 1.9–1.7 Ma, and 1.1–0.9 Ma, superimposed on a long-term aridification of East Africa.

The humid periods correlate with increased aridity in northwest and northeast Africa and with substantial global climate transitions. They had important impacts on the speciation and dispersal of mammals and hominins: the genus *Homo* arose in this region during that time. The latter part of the last glaciation, 50,000–12,000 years ago (kya), was characterised by a rapidly changing climate, cold conditions and corresponding vegetation and faunal turnover (Finlayson & Carrion, 2007). It is clear that the same could apply to other species, especially those whose survival is dependent on water, such as the fish fauna (Stewart, 2009). The Nile and two of its large basins now have a fish fauna with a primarily ‘nilotic’ distribution, while three other basins whose faunas were isolated in the Holocene have largely endemic faunas.

The patterns of oligochaete distribution and migration in the Nile and adjacent territories clearly show that transportation by birds or humans did not play a significant role. They follow the same natural drivers of climatic, geological events and soil conditions as other groups.

Research on the history of oligochaete species, compared to Mollusca, is handicapped by the lack of a fossil record. If any, they are usually cocoons, juveniles, burrows, or aestivation chambers which rarely reveal the identity of the concerned species. How the present-day distribution of oligochaete species came into being is therefore conjectural. There are, however, certain guidelines, such as the knowledge that terrestrial species can tolerate desiccation for a few hours, while aquatic species survive for only a few minutes (Ghabbour, 1975). Migrations are therefore impossible without soil moist enough to allow terrestrial species to move around (as in Europe after rain), or connected water-courses allowing aquatic species to move from one water body to another.

4.4 Chad

The Nile Basin oligochaetes are distinct from the West African Logone-Chari and Congo basins (Central African Republic, Congo, DR Congo), which are related to eastern South America.

Studies on fish, mollusks, and planktonic crustaceans have shown a close affinity between the Nile and Logone-Chad Basins, and no relationship with the Congo basin, but this is not supported by the oligochaetes. Dumont (1992) proposed that as *Cyperus papyrus*, widespread throughout the Eastern half of Africa, is still common in Lake Chad, it may have reached there from the Nile Basin during a Holocene connection between the Nile and Chad basins. In the light of this hypothesis, and although the aquatic species of Lake Chad appear largely unrelated to the Nile, an investigation of the species of Gebel Marra in Darfur (the Chad-Nile watershed) is highly desirable.

4.5 The Rift Valley Lakes

According to Di Paula (1972), the Ethiopian Rift Valley, which cuts through the Ethiopian-Somalian Plateau from north to south, is marked by a set of NNE-SSW faults. Knowledge on oligochaete speciation in this region must await three developments: (1) a reliability check on the identity of species reported in the literature, (2) a thorough investigation of the regional oligochaete fauna, and (3) decisive knowledge on the palaeo-geology of the region.

Such a thorough investigation becomes all the more urgent in light of the environmental degradation of waters and soils in many parts of the Nile Basin. Its oligochaete fauna faces several threats: land reclamation, desertification, urban sprawl, soil and water pollution. Hence, priority should be given to explore earthworms in countries such as western and southern Sudan, Ethiopia, Chad and the Central African Republic, before they are obliterated by environmental degradation and human encroachment. As a vivid example, the type locality of *Chuniodrilus ghabbouri* at Dahshur, originally a wetland, has been drained and is now a football field.

Muli (1996) reports that also Lake Victoria has recently undergone immense biological changes. These have led indigenous ecosystems and biota to extinction, such as haplochromine cichlids and benthic insects. There has been a shift from an oligochaete and insect-dominated community in 1984, to a community dominated by Mollusca and Oligochaeta. Such degradation is widespread in almost all Nile Basin lakes. Another factor are invasive species: Adams et al. (2004) report that *Salvinia molesta* invaded Lake Naivasha in the early 1960s and *Eichhornia crassipes* (the water hyacinth), since 1988. These mat-forming floating plants favour some oligochaete species (e.g. *Alma emini*) though probably at the expense of others.

4.6 The Nile Basin: An Overview

Much about the oligochaete fauna of the Nile remains unknown. Spots crucial for discerning ancient relationships occur at the divides between the Nile and neighbouring basins, e.g. the Chad-Nile, the Congo-Nile, and the East African rivers. They have not been well surveyed. At best, the present contribution may therefore indicate what are the questions to be addressed.

With species shared by the Nile and adjacent basins, we cannot know for sure when the basins were connected and allowed a migration. All we can do is suppose that migration occurred during a pluvial (wet period), and probably during the last one if we encounter populations of the same species. The deeper they are separated taxonomically, the more ancient the pluvial that allowed their migration. Such is the case of *Gordiodrilus*, with *G. zanzibaricus* in Selima Oasis and *G. siwaensis* in Siwa Oasis. Also, the wider they are separated geographically, the older their migration. And if a local endemic occurs in *cul-de-sac* localities, like *Nannodrilus* in Kharga Oasis and the Western Delta, we can assume a longer period of isolation.

In the case of *Eiseniella tetraedra*, that spread from the Italian islands to the Western Desert of Egypt, as well as the genera *Pygmaeodrilus* and *Allonais*, supposed to have migrated from East Africa to Siwa Oasis, and *Gordiodrilus*, extending step-by-step from Central Africa to Selima and Siwa Oasis, and Tripolitania, we assume older migrations than those of *Alma nilotica*, from the Nile to only as far as Bahariya Oasis. In the case of *Chuniodrilus*, whose bulk of species live in Côte d'Ivoire with an isolated endemic near Cairo, *C. ghabbouri*, migration must have taken place during a long period of favourable conditions, allowing speciation along the way. This species adds Eudrilidae to the list of oligochaete families in Egypt, outside their Central African range. This may well be the oldest migration in the region. It is also a salient example of the need for investigation of the oligochaete fauna in the gaps in between.

The movement of *Alma emini* from Lake Victoria to the high altitude Eastern Rift lakes may cast some light on the historical zoogeography of that part of the Nile Basin. Genner et al. (2007) claim that Lake Victoria cichlids are millions of years younger than their counterparts in Lake Malawi. Their results, based on genetics, contrast with the theory that diversification into major lineages took place within the Tanganyika basin. For Genner et al. (2007), ancient lake habitats played a key role in generating and maintaining diversity within radiating lineages, and lakes may have captured pre-existing cichlid diversity from multiple sources, from which adaptive radiations evolved. One could be tempted to duplicate this conclusion for East African oligochaetes.

4.7 Origins and Routes of Oligochaetes into Egypt

Recent data, enumerated in this paper, on the oligochaetes of the Nile Basin do not invalidate the hypothesis by Ghabbour (1996, 1998) on the origins and routes of migration of the species involved, as shown in Fig. 4. We trace five routes but perhaps more than five waves, as follows:

1. From the Balkans through the Levant, across Sinaï, to the Nile Delta. This is the case of *Allolobophora jassyensis* in the Delta and *Eiseniella tetraedra* in Sinaï.
2. From Italy, Tunisia and Libya, to Siwa Oasis in Western Egypt (*Eisenia rosea* var?), Burg El-Arab, west of Alexandria (*Eiseniella tetraedra*) and to the western Delta (*Eisenia rosea* var. *bimastoides*).

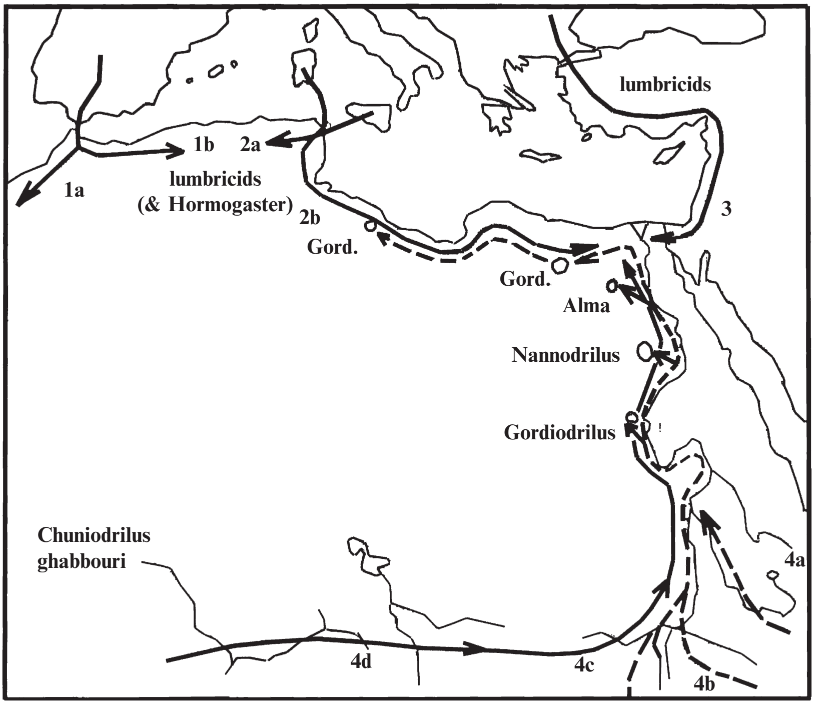

Fig. 4 Probable routes of entry of oligochaetes into the Nile Basin: (1) from the Iberian Peninsula to Morocco, (2) from the Italian Islands to the Delta, (3) from the Balkans and the Levant to the Delta, (4) a – from Ethiopia to the upper reaches of the Blue Nile, and b – from Kenya, c – from Uganda, d – from West Africa, along the Nile, to as far as Tripolitania (after Ghabbour, 1996)

3. From Kenya along the Nile to Selima Oasis (northern Sudan), to the Fayum Depression, the Oases of the Egyptian Western Desert, and along the Mediterranean coast to Tripolitania (*Allonais*, *Nannodrilus*, *Gordiodrilus*, *Pygmaeodrilus*, *Alma nilotica*).
4. From the Albertine Rift along the White Nile (*Alma stuhlmanni* and an unknown species associated with the tropical moss *Philonotis*), to Fayum and the Western Delta.
5. From West Africa (Mount Nimba) where the main stock of the genus *Chuniodrilus* occurs (*C. ghabbouri*).

Recently (nineteenth century) introduced species such as *Allolobophora caliginosa*, *Branchiura sowerbyi*, and *Pheretima* spp., perhaps represent a sixth (anthropogenic) route. Moreover, several thousand years of basin irrigation in the Nile Valley in Egypt and in northern Sudan have caused a drastic impoverishment (or rather wiping out) of the original earthworm fauna. The scarcity of earthworms in Egyptian soils is mostly attributable to the aridity of the climate and to the fact that the majority of cultivated land is under the plough (Khalaf El-Duweini &

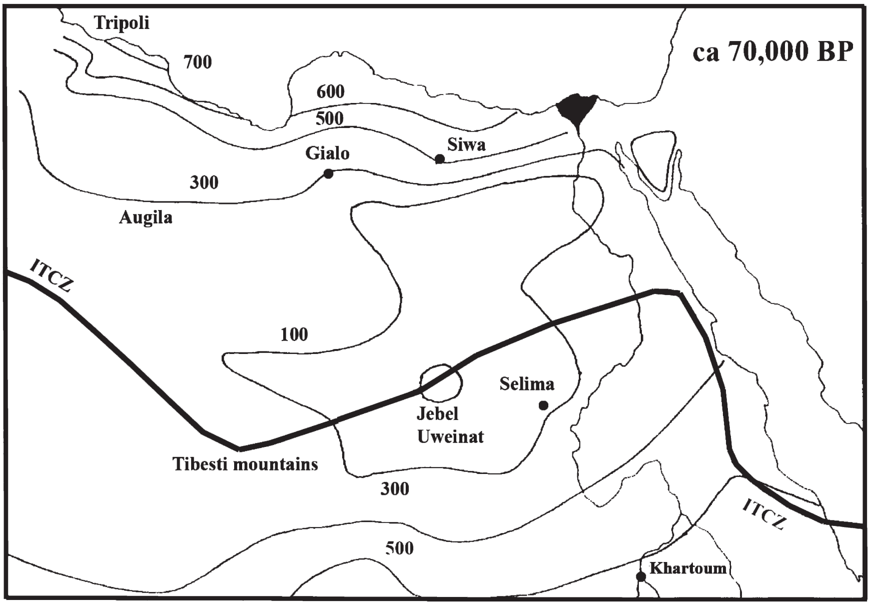

Fig. 5 Probable rainfall isohyets during the last effective Pluvial Period (ca 140,000–70,000 years ago), in eastern North Africa, that allowed oligochaete migrations as shown by their present distribution in Nile Basin countries, also showing the probable position of the ITCZ (the Inter-Tropical Convergence Zone). The Delta was submerged during that period (after Ghabbour, 1996)

Ghabbour, 1965). Basin irrigation in the Delta was progressively converted into perennial irrigation in the nineteenth century, after construction of the Delta Barrages, and in Upper Egypt in the twentieth century, after the construction of the Aswan High Dam in 1960. This explains the presence of native species outside the Nile Valley and not in the Valley itself, except in a few marginal neglected areas, which are all exploited now.

The oligochaete fauna of the northern Nile is therefore a mix of species from different sources, not a biogeographic region in its own right. The fauna of the Upper Nile (the Sudd region) is Afrotropical, with the Ugandan, Ethiopian and Kenyan faunas distinct from each other.

A number of species have been found only once: *Dendrobaena* sp., *Aelosoma hedleyi*, *A.* sp., *Paranais* sp., and *Eisenia fetida*. The records of *Limnodrilus hoffmeisteri*, *L. udekemianus*, and *Pristina* sp. in Lake Nasser are probably of no zoogeographic significance, as is the case of *Allolobophora caliginosa*. Only a few species show intra- and interbasin distribution patterns, such as *Alma* and *Gordiodrilus*.

The pluvial period that allowed *Alma nilotica* (known from the discovery of its of egg cases in 1971), to reach Bahariya Oasis, must have been during a major and effective pluvial period, probably the one that occurred 140,000–70,000 years ago. The presence of *Alma nilotica* in Bahariya Oasis, means that not only rainfall was favourable, but that there also existed a water connection between the Nile and the

Oasis. Pickford (1937) calculated that migrations of earthworms across dry land were only possible when rainfall was 500 mm y^{-1} or higher. Hence, one may draw – on the basis of these Saharan migrations – a map of isohyets of northeast Africa, at the time of these migrations. Such a map for that pluvial period (related to – but not necessarily identical with the Würm Glacial), is given in Fig. 5. More recent pluvials include the one suggested by Kuper & Kröpelin (2006) around 8,500–5,300 BP, humid enough to support a dry savanna vegetation (Sahelian trees and grassland cover) (Kröpelin et al., 2008). However, the wet period in southwest Egypt beginning around 9,000 BC allowed a rather dry environment only, with an annual rainfall of no more than 100–150 mm (Malville et al., 2008). Rain was unpredictable and the climate punctuated with droughts. Such conditions, in our opinion, were insufficient to allow earthworms to cross from the Nile to the Oases.

5 Conclusion

The oligochaete fauna of the northern Nile Basin is a mixture of species from different sources and cannot be considered a biogeographic region in its own right. The fauna of the Upper Nile (the Sudd region) is Afrotropical, while the Ugandan, the Ethiopian and the Kenyan faunas are distinct from each other, and unrelated to the fauna of Cyprus (the Mediterranean island nearest to the Nile Delta).

To sum up, the oligochaete fauna of the Nile Basin in its northern part shows a poor species richness, but the species that could traverse time and distances in as harsh an environment as the Sahara are certainly adapted to high temperatures. They are a mix of relicts coming from Europe and from Central Africa. They met and co-inhabit the Nile Valley, the Delta and the Oases. There is a certain degree of endemism (as for *Gordiodrilus*, *Nannodrilus*, *Chuniodrilus*, and *Alma*), and the endemics live side by side with cosmopolitan species.

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The Crustacean Zooplankton (Copepoda, Branchiopoda), Atyid Decapoda, and Syncarida of the Nile Basin

Henri J. Dumont

Abstract The about 17 spp. of calanoid copepods of the Nile basin are dominated by East African species, but in the lower Nile, several Mediterranean species are found. Some species are endemic to the basin and Lake Chad. Endemic species also occur in some of the East African plateau lakes. Two ecological groups are present: species typical of permanent, and species typical of ephemeral waters. Among Cyclopoida, the dominant genera are *Mesocyclops* and *Thermocyclops*, together about 20 species with African, Afro-Asian, and (few) with Mediterranean affinities. An invasive cyclopoid, *Acanthocyclops trajani*, has become dominant in the eutrophic delta lakes.

Among anomopods, about ten species of *Daphnia* with different ecological and geographic ranges have been found. Some 75 species of cladocerans are now on record, a number that is expected to increase in future years. Anostracans are represented by about six species of *Streptocephalus*, some of which are Mediterranean, other East African, and at least one restricted to the Ethiopian plateau. Syncarida (Bathynellacea) have been little studied, with three African species on record. Among decapods, *Caridina nilotica* occurs basin-wide and is partly planktonic, partly benthic.

By analogy with Lake Chad and Lake George, zooplankton production is estimated at roughly 40 t per km^2 for the East African plateau lakes. Production further north, in Lake Nasser and the Delta lakes, with a yearly biomass variation of a factor 3 (Nasser) to 10 (delta), and concomitant variations in water temperature, may not be fully compensated by higher biomasses and may be lower.

1 Introduction

The first studies on Nile zooplankton were conducted in the course of the nineteenth century (see Talling, 2009), and were linked to the early exploration of the African continent and the quest for the sources of the Nile (Schmarda, 1854;

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Richard, 1883, 1894, 1896; Stuhlmann, 1891; Barrois, 1891; Weltner, 1897, 1898; Ekman, 1904; Daday, 1910a, b; Gurney, 1911; Van Douwe, 1912a, b), or slightly later (Cunnington, 1915, 1920; Delachaux, 1917; Chappuis, 1922; Lowndes, 1936; Worthington, 1929; Steuer, 1942; Brunelli & Cannicci, 1940). Among more recent papers, Abu Gideiri (1969a, b), El-Moghraby (1972, 1977), Elster & Vollenweider (1961), Green (1971, 1984), Kiefer (1939, 1978), Löffler (1963) Monakov (1969), Ocioszynska-Wolska (1935), Steuer (1942), and Thomas (1961) should be cited.

Julian Rzóska (1976), having spent many years at Khartoum University, devoted much of his research to the equatorial Nile and its lakes (Rzóska, 1952, 1957a, b, 1968, 1974, 1976; Rzóska et al., 1955; Brook & Rzóska, 1954; Talling & Rzóska, 1967). In 1976, he attempted the first synthesis on the nature and composition of Nile zooplankton. He inventoried the copepods and cladocerans, but his lists are incomplete and contain spelling and taxonomic errors.

About a decade later, Dumont (1986a) again summarized the available knowledge in a book on comparative river ecology (Davies & Walker, 1986), but that synthesis lacked information on the Nile delta lakes. One conclusion stressed the homogeneity of the assemblage, from the lakes sources to the delta, with comparatively few endemics for the basin as a whole. A limitation of this analysis was the lack of studies dealing with the Congo basin, so that comparisons between the Nile and its big neighbour, the Congo, were handicapped. This continues to be the case today. To the West, the faunas of the Chad and Niger basins had been better documented (Rey & Saint Jean, 1968, 1969; Dussart & Gras, 1966; Dumont & Maas, 1987).

Since the 1980s, there has not been much progress in the faunal study of specific components of the Nile basin, with the exception of Lake Tana (Vijverberg et al., 2009), Lake Turkana (Maas et al., 1995) and the Kyoga swamps (Green, 2009a). Some significant new data relate to work done by local researchers in Lower Egypt, viz. the Fayum depression and the Nile delta lakes (Dumont & El Shabrawy, 2008, and references therein).

In order to facilitate further discussion we present an overview of the fauna in three tables: one for the calanoid copepods, one for cyclopoids, and one for the cladocerans (Tables 1–3).

2 Calanoids (Table 1, Figs 1 and 2)

This group of exclusively pelagic species contains a number of species of biogeographic interest. Calanoids are bisexual copepods, in which one male antenna is modified for amplexus. Most taxonomically diagnostic characters are found on the males. Ignoring the delta lakes, Verheye & Dumont (1984), listed 12 species from the basin, pertaining to subfamilies Diaptominae and Paradiaptominae. Including the delta lakes and the saline Birket Qarun, and some smaller lakes and temporary waters in the Albertine Rift and on the Ethiopian plateau, that list has now expanded to (possibly) about 20 species. A couple of these are marine and are normally limited to the mouth areas of the delta lakes. Diagnostic features of the males of the

Table 1 The main Calanoida of the Nile Basin (basin-wide species in bold)

	Nile Delta + Fayum	Lower Nile + L. Nasser–Nubia	White Nile + Reserv-oirs	Blue Nile + Reserv-oirs	Equatorial swamps (Sudd)	Lake Tana basin	L. Victoria	L. Turkana	Kyoga swamps	Lakes Albert–Edward	Small western rift lakes (Mutanda, Bunyoni)	Perma-nent waters	Tempo-rary waters	Lake Chad
1. *Arctodiaptomus salinus*[a]	x	–	–	–	–	–	–	–	–	–	–	x	–	–
2. *Metadiaptomus aethiopicus*	–	–	–	–	–	–	–	–	–	–	x	x	x	–
3. *Metadiaptomus mauretanicus*	x	x	x	–	–	–	–	–	–	–	–	–	x	?
Lovenula africana				?		?								
Lovenula falcifera				?		?								
4. *Neolovenula alluaudi*	x	–	–	–	–	–	–	–	–	–	–	–	x	–
5. *Paradiaptomus schultzei*	–	–	–	?	–	x	–	–	–	x	–	–	x	–
6. ***Thermodiaptomus galebi***	x	x	x	x	x	spp. *lacustris*	x	x	x	x	–	x	–	x
7. *Thermodiaptomus galeboides*	–	–	–	–	–	–	xE	–	–	–	–	x	–	–
8. *Thermodiaptomus mixtus*	–	x	x	x	?	–	–	–	–	–	–	–	x	–
9. ***Tropodiaptomus asimi***	–	x	x	x	x	–	–	–	–	–	–	x	–	–
10. *Tropodiaptomus kraepelini*		x	x	x	x	–	–	–	x	–	–	–	x	–
11. *Tropodiaptomus neumanni*	–	–	–	–	–	–	–	–	–	x	?	–	x	x

(continued)

Table 1 (continued)

	Nile Delta + Fayum	Lower Nile + L. Nasser–Nubia	White Nile + Reservoirs	Blue Nile + Reservoirs	Equatorial swamps (Sudd)	Lake Tana basin	L. Victoria	L. Turkana	Kyoga swamps	Lakes Albert–Edward	Small western rift lakes (Mutanda, Bunyoni)	Permanent waters	Temporary waters	Lake Chad
12. *Tropodiaptomus processifer*	–	x	–	x	x	ssp. *friedae*	–	–	–	–	–	–	x	x
13. *Tropodiaptomus stuhlmanni*	–	–	–	–	–	–	xE	–	–	–	–	x	–	–
14. *Tropodiaptomus turkanae*	–	–	–	–	–	–	–	xE				x	–	–
15. *Tropodiaptomus worthingtoni*	–	–	–	–	–	–	–	–	–	xE	–	x	–	–
Main marine species														
16. *Paracalanus parvus*	x													
17. *Paracartia latisetosa*	x													

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[a] *Arctodiaptomus brevirostris* Dussart occurs on the Ethiopian plateau, but seems restricted to the Balé mountains, which drain to the Indian Ocean via the Uebi Scebeli and Giuba; the two *Lovenula*'s in the table have, with certainty, only been found in the basins of the same two rivers plus the Awash.

Table 2 Pelagic Cyclopoids from the Nile Basin and their distribution, as currently known

Fresh-water species	Nile Delta + Fayum	Lower Nile + L. Nasser– Nubia	White Nile + Reserv- oirs	Blue Nile + Reserv- oirs	Equatorial swamps (Sudd)	Ethiopian Plateau Lakes	Lake Tana basin	L. Victoria	L. Turkana	Kyoga swamps	Lakes Albert– Edward	Small western rift lakes (Mutanda, Bunyoni)	Chad basin
1. *Acanthocyclops trajani*	x												
2. *Afrocyclops gibsoni*	x	x	x		x	x	x	x		x	x		x
3. *Diacyclops odessanus*	x												
4. *Mesocyclops aequatorialis*								x					?
5. *Mesocyclops aspericornis*		x	x	x		x							?
6. *Mesocyclops major*			x	x	x								
7. *Mesocyclops ogunnus*	x	x	x	x	x	x	?	?	x	x			x
8. *Mesocyclops paludosus*											x		
9. *Mesocyclops rarus*					x				x		x	x	
10. *Mesocyclops salinus*					x	x			x				
11. *Thermocyclops consimilis*	x	x											x
12. *Thermocyclops crassus*	x	x	x	x	x	x	x	x	?	x	x	x	x
13. *Thermocyclops decipiens*					?			?		?	x		
14. *Thermocyclops dybowskii*	x												
15. *Thermocyclops emini*	x	x	x	x	x			x					x
16. *Thermocyclops ethiopiensis*						x	x						
17. *Thermocyclops hooki*											Rwenzori Lakes only		
18. *Thermocyclops neglectus*	x	x	x	x	x	x	x	x	x	x	x	x	x
19. *Thermocyclops oblongatus*	x	x	x	x	x	x	x	x		x	x	x	x
20. *Thermocyclops schmeili*											x		
Marine species													
21. *Oithona nana*	x												

(?) Occurrence of species probable, but not confirmed.

Table 3 Predominantly Pelagic Cladocerans (Anomopods and Ctenopods)

	Nile Delta + Fayum	Lower Nile + L. Nasser–Nubia	White Nile + Reservoirs	Blue Nile + Reservoirs	Equatorial swamps (e.g. Sudd)	Ethiopian Plateau lakes and ponds	Lake Tana basin	L. Victoria	L. Turkana	Kyoga swamps	Lakes Albert–Edward	Small western rift lakes (Mutanda, etc.)	Permanent waters	Temporary waters	Lake Chad basin
Ctenopoda:Sididae															
Diaphanosoma excisum	x	x	x	x	x	x	x	x		x	x	x	x		x
D. mongolianum	x	x				?	?	x					x		?
D. sarsi					x			x		x	x		x		x
Anomopoda: Daphnioidea															
Ceriodaphnia cornuta		x	x	x	x	x	x	x		x	x	x	x		x
C. dubia	x	x								x			x		x
C. quadrangula	x	x		x	x	x	x			x		x	x		x
C. reticulata	x														x
Daphnia barbata			x	x	x	x	x	x		x	x		x		
D. curvirostris[a]												x	x		
D. laevis										x	x	x	x		
D. longispina[b]	x	x	x	x									x		x
D. lumholtzi			x	x	x										x
D. magna	x							x					x	x	x
D. obtusa[a]						x					Rwenzori lakes				
D. pulex[a]	x												x		
D. similis	x													x	X
Moina brachiata	x														X
M. micrura	x	x	x	x	x	x	x	x		x	x	x	x	x	X

M. salina	x								x				x	x
Scapholeberis kingi													x	x
Simocephalus vetulus	x	x	x	x	x	x	x						x	x
Anomopoda: Bosminidae														
Bosmina longirostris	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bosminopsis deitersi					x			x		x	x	x	x	x
Anomopoda: chydoridae														
Chydorus sphaericus	x	x	x	x	x	x	x	x	?	x	x	x	x	x

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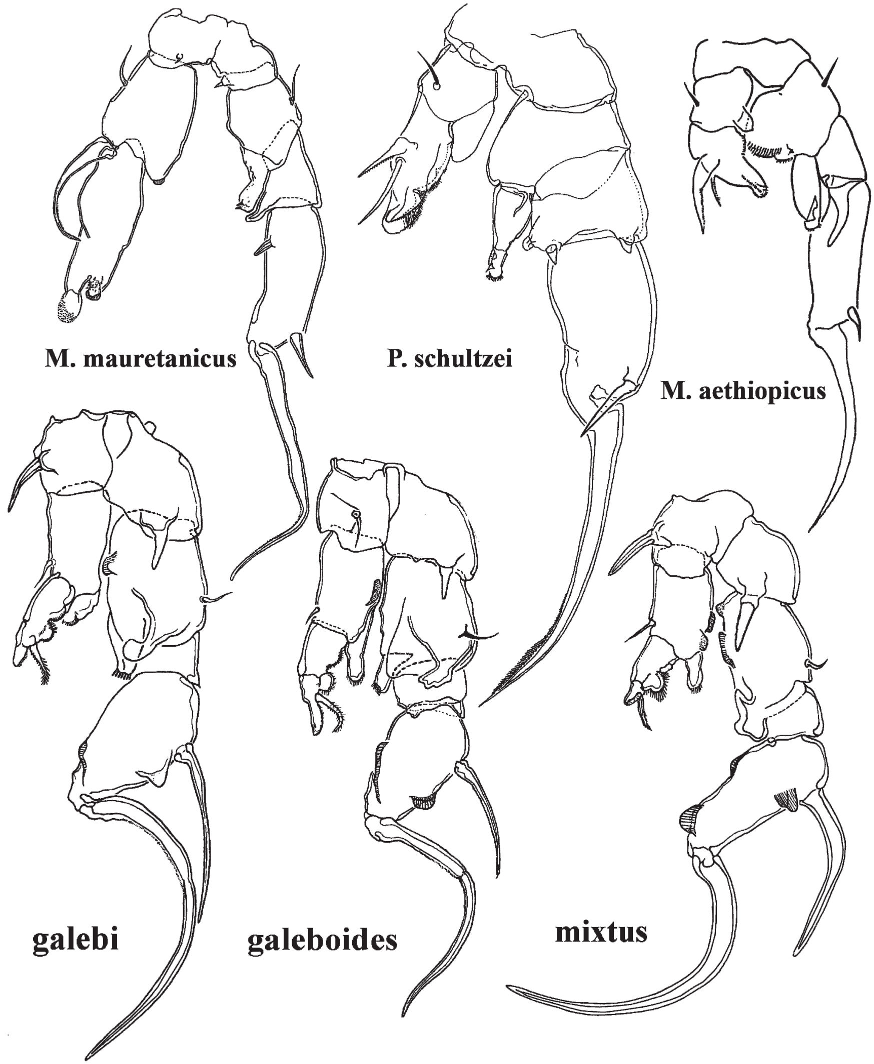
[a] These three species have often been confused, and cited sub *D. pulex*. More cryptic species may actually exist under the name *D. pulex*.

[b] In some cases, this species has been misidentified, and is really Daphnia hyalina (see Vijuerberg et al., 2009).



THERMODIAPTOMUS

Fig. 1 Calanoid copepods can best be identified from the structure of the asymmetric fifth pair of trunk limbs in males. Shown above are the limbs of the species of the subfamily Paradiaptominae (*Metadiaptomus* and *Paradiaptomus*) that occur in the Nile basin. Below are three species of *Thermodiaptomus* (subfamily Diaptominae). *Thermodiaptomus galebi* and *T. galeboides* are so closely related that their specific status is in doubt (orig.)

most prominent taxa are shown in Figs 1 and 2. *Thermodiaptomus galebi* would be a perfect indicator species for the Nile basin, if it did not extend westward to Lake Chad (Dussart & Gras, 1966). This fact is, however, interesting *per se*, since it testifies to a comparative ease of faunal exchange between the two basins in the

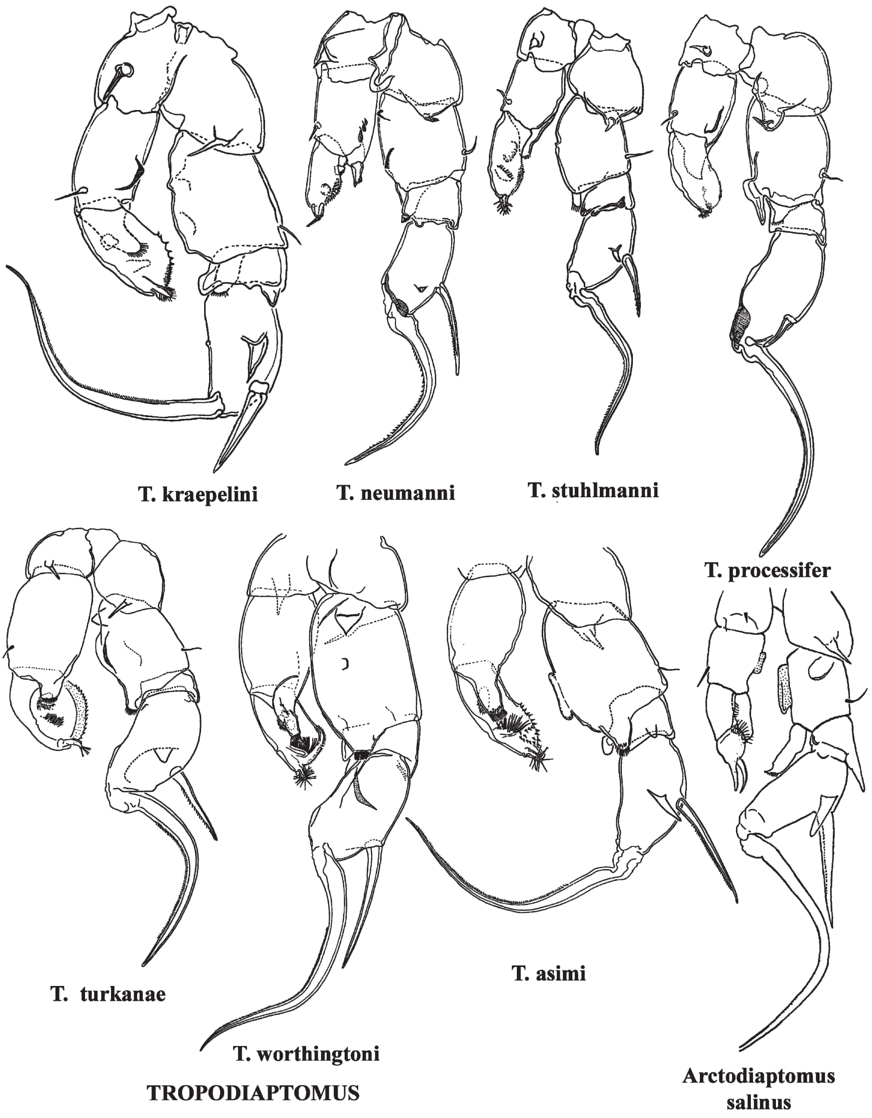


Fig. 2 The second important subfamily of calanoids is the Diaptominae. Most Nile representatives pertain to the large genus *Tropodiaptomus*; only in the delta, and on the Ethiopian plateau a few *Arctodiaptomus* species occur (orig.)

past. There is no indication of structural differences between Chadian and Nilotic populations, suggesting exchange has been operative until the Pleistocene and even Holocene. In contrast, there is a subspecific differentiation between Nilotic and Lake Tana populations, and the latter was recently described as a separate subspecies (*T. galebi lacustris*) by Defaye (1988). The Tana basin has a second endemic subspecies, *Tropodiaptomus processifer friedae* (Verheye & Dumont, 1984). The *processifer*-species complex is widely distributed across the Nile basin, but does not appear in the source lakes. Towards the West, it extends to Lake Chad, and further into the Niger basin (Dumont et al., 1981). In Lake Victoria, *Thermodiaptomus galebi* is replaced by *T. galeboides*. The relationship between both is so close (Fig. 2) that their specific status is in doubt, however. A third *Thermodiaptomus, T. mixtus*, also occurs in the Nile basin, but became common ("visible") only in the reservoirs created by the damming of the Blue Nile reservoirs upwards of Khartoum (Rzóska, 1957; Talling & Rzóska, 1967; Abu Gideiri, 1969a, b).

Several calanoids are endemic to the source lakes of the river. Two species may be endemic to L. Victoria: the aforementioned *Thermodiaptomus galeboides*, and *Tropodiaptomus stuhlmanni* (Dumont & Maas, 1988). Curiously, calanoids may periodically be undetectable from Lakes Albert and Edward, although *T. worthingtoni* was originally described from Lake George (Lowndes, 1936) and was later found in Lake Albert too (Kiefer, 1952). Their disappearance might be related to anthropogenic changes in the lakes (Green, 2009b). Recently, Lehman et al. (1998a) reported *Thermodiaptomus galebi* from lakes Albert-Edward. I examined some specimens and found that they have characters of both *galebi* and of *galeboides*, reinforcing the idea that both should be merged to only one species.

On the other hand, Lake Turkana, currently severed from the Nile and becoming progressive more saline (Johnson, 2009), is home to the morphologically well-defined *Tropodiaptomus turkanae* (Maas et al., 1995), previously confused with *T. banforanus*, a species from West Africa.

In lakes situated within the Congo basin, Lake Kivu definitely has no calanoid, but this is believed to be for the same reason as the current absence of native pelagic fish there, viz. a holocene poisoning of the ecosystem by volcanism, and no immigration afterwards (Dumont, 1986a). Lake Tanganyika has one endemic, *Tropodiaptomus simplex*, and several species are restricted to the Congo basin (*T. ricardoae, T. femineus*), yet probably many species and even genera remain to be discovered here. In high-altitude lakes situated on or close to the divide between Nile and Congo (the Rwenzori range), no calanoids have been found (Eggermont et al., 2009). These young, fishless lakes have an impoverished zooplankton fauna. This raises a biogeographic problem, because elsewhere in Africa, including the Ethiopian highlands, Mount Kilimanjaro and Mount Elgon, similar lakes have one or two species of *Lovenula* (Rayner, 1999).

Some *Tropodiaptomus* species found in the Nile are not shared with the Sahel to the west, but with East Africa, and may extend as far south as South Africa. This is the case of *T. asimi,* recently separated from the oriental *T. orientalis*, and its relative, the wide-ranging East African *T. kraepelini* (Dumont & Maas, 1989).

Thermodiaptomus and *Tropodiaptomus* predominantly live a pelagic life in permanent water bodies, and are adapted to coexisting with predatory fish. There are, however, exceptions. *Tropodiaptomus neumanni*, for example, lives preferentially or exclusively in temporary waters, shielded from vertebrate (fish) predation. It occurs on the East African plateau and in the Lake Chad depression but not in the lake itself. In 1985, it was discovered in rain-pools in Darfur, about halfway between the Lake Chad and the Nile, though still in the Nile basin (Dumont & Maas, 1989). It is the third species shared by the Nile and Chad basins.

Most species living in temporary or closed high-mountain waters (e.g. crater lakes), devoid of (pelagic) fish, pertain to the subfamily Paradiaptominae. These are generally bigger than typical Diaptominae, and often conspicuously red or purplish. The most widespread in the Nile valley is *Metadiaptomus mauretanicus*. It occurs in ephemeral ponds between the Atlantic and the Arabian peninsula, but was considered a rarity south of Egypt until Dumont and Maas (1989) found it west of the River Nile, in Kordofan and Darfur (Sudan). In the equatorial Nile zone (Blue Nile and East African Plateau), it is replaced by *Paradiaptomus schultzei*, which is shared between the Nile and Lake Chad (Verheye & Dumont, 1984).

In the lower Nile and the delta, *Neolovenula alluaudi* is found. This, again, is a large species that used to live in shallow depressions flooded at the beginning of the annual floods (Gurney, 1911). How far south this species extended is unknown, but its predominantly Mediterranean range suggests it was limited to the lower Nile. It disappeared, presumably around the mid-twentieth century, as a consequence of drainage of temporary ponds and, after the commissioning of the Aswan high dam, of river regulation. The large-bodied *Lovenula africana* and *L. falcifera* are restricted to the Ethiopian plateau, mostly in fishless waters, temporary or semi-permanent (Defaye, 1988). *Metadiaptomus colonialis* also occurs here, in similar environmental conditions, but all three have so far been recorded only from sites that are part of the Awash basin. Whether they also live in aquatic environments that water down to the Blue Nile is possible but remains to be shown. This doubt does not weigh on *Metadiaptomus aethiopicus*, that used to be common in some upland lakes of the Albertine Rift (e.g. Lake Bunyonyi) but disappeared there after the 1930s, after some limnetic fish species had been introduced (Green, 2009b).

Arctodiaptomus salinus is a rare representative in the Nile valley of a big temperate Eurasian genus (Ranga Reddy, 1994). It also used to be limited to the delta and Birket Qarun. It is a brackish-water species that occurs widely in North Africa and the Iberian Peninsula and was rather common in the Fayum until the first decades of the twentieth century, where it was eliminated by increasing salinity (Dumont & El-Shabrawy, 2008). In the wake of this salinisation, marine calanoids began to appear. They had, at times of low Nile flows, temporarily invaded the delta lakes, but as Birket Qarun began to reach salinities close to or even in excess of marine values, *Paracartia latisetosa*, in particular, became a dominant element of the plankton of the Birket (El-Shabrawy & Dumont, 2009). *Arctodiaptomus brevirostris* from Ethiopia is endemic to the Balé mountains (Löffler, 1978; Dussart, 1974). It has palaearctic affinities, and lives in isolation in some high mountain lakes that do not belong to the Nile catchment but drain to the Indian Ocean.

Summing up, the Nile basin is home to two types of calanoids: most species live in permanent waters, but a few prefer ephemeral pools. *Thermodiaptomus galebi* and perhaps *Tropodiaptomus asimi* occur basin-wide. Up to four species and two subspecies may be endemic to the source lakes. Most Nile calanoids have Afrotropical affinities, even those found in the delta, but at least two “northern” species used to occupy the Mediterranean Nile until they went extinct by environmental change.

Salinity is still on the increase in Birket Qarun, where marine taxa now replace pre-existing brackish-water species.

3 Cyclopoids (Table 2)

Cyclopoids are a varied order of pelagic and littoral, bisexual copepods, in which male antennae are modified for amplexing the female. However, taxonomically diagnostic characters are, for unknown reasons, mainly limited to females. Numerous genera of Cyclopidae occur worldwide; other families occur in the sea (e.g. the Oithonidae). The taxonomy of freshwater cyclopoids has improved much in the past few decades, yet quite a few genera require revision, and older papers cannot be trusted as far as specific identifications go. The main pelagic genera in Africa are *Mesocyclops* and *Thermocyclops*, and several species of each occur in the Nile basin. Before the 1980s, all *Mesocyclops* were called *M. leuckarti*, until Kiefer (1981) showed that this species is restricted to temperate and continental Eurasia, and Van de Velde (1984) clarified the taxonomy of African species. However, there have been few follow-up studies after these seminal papers, such that we still do not know for sure which of the numerous *Mesocyclops* of Africa are restricted to particular geographic ranges. At least seven species have been recorded from the Nile. Of these, the most widespread are *M. ogunnus, major*, and *equatorialis*. Two appear to be restricted to the Lake Victoria–Kyoga zone (*M. paludosus* and *M. rarus*). *M. salinus*, in spite of its name, is not limited to saline waters, although it resists salinity better than many of its congeners, and is common in Lake Turkana. The only species that has so far been reliably identified from the delta lakes is *M. ogunnus*. Most others are wide-ranging, but largely restricted to the African continent. *M. aspericornis* is shared between the Afrotropical and the Oriental regions.

A similar situation exists in *Thermocyclops*, although the work of Baribwegure (2003) should now make it possible to identify all species correctly. With up to ten species they are the most successful copepod genus in the basin. They are largely tropical, and the majority is African. One (*T. hooki*) is restricted to the high mountains of East Africa (Löffler, 1968; Eggermont et al., 2009). One species of Eurasian affinity (*T. dybowskyi*) was identified from the Cairo environs (Gurney, 1911). This record is plausible, since other species of "European" origin have been found in the delta and there exist certified records of *dybowskii* from the Maghreb and from the Levant. Interestingly, the related East African *T. schmeili* has been found in lakes Victoria and Edward (Baribwegure & Dumont, 2003). *T. crassus* and *T. decipiens* are two widespread species, with tropicopolitan or sub-cosmopolitan ranges.

Together, by numbers and biomass, *Mesocyclops* and *Thermocylops* make up the bulk of the copepod biomass in the river and its lakes. In Lakes Edward–Albert, they are overwhelmingly dominant.

In other large genera, like *Eucyclops*, *Ectocyclops*, *Tropocyclops*, and *Paracyclops* there is still much confusion and/or a dearth of reliable data. *Eucyclops serrulatus* and *Tropocyclops confinis* and *prasinus* have been cited many times and may indeed populate the Nile basin, but other species may hide under these names as well. In West Africa (the Niger basin: Dumont, 1986c) these genera have a number of endemic species, so more research in the Nilotic zone is desirable.

Afrocyclops gibsoni occurs in the whole of Africa, and extends to the Nile Delta. Three other species and subspecies occur in the East African axis and in Ethiopia (Defaye, 1988) but have not been found in the Nile valley proper.

In the delta lakes, representatives of additional genera, typical for brackish-water conditions in temperate climate zones occur, viz. *Apocyclops panamensis* (possibly an alien invader), *Diacyclops odessanus,* and *Halicyclops neglectus*. Further, *Acanthocyclops trajani,* not cited by Elster & Vollenweider in the 1950s, today is the dominant pelagic cyclopoid of the delta lakes, suggesting but not proving that this species, well adapted to eutrophic conditions, invaded the lakes in the course of the second half of the twentieth century. *Acanthocyclops* species typically live in the temperate parts of the Holarctic. Considerable taxonomic confusion surrounds this animal's name. It has variously been cited as *A. vernalis, robustus,* or *americanus*. I here use *A. trajani* to unambiguously indicate a species that is widespread in Europe, and thus a northern element in the fauna of the delta lakes. With *Diacyclops odessanus*, possibly *Thermocyclops dybowskii*, and the calanoids *Arctodiaptomus salinus* and *Neolovenula alluaudi*, these represent a significant "non-African" element in the crustacean zooplankton of the lower Nile.

The delta lakes, finally, witness periodic incursions of marine species. Not less than four species of *Oithona* have so far been identified; *Oithona nana* is the most common.

On the third group of copepods, the Harpacticoida, only scattered information is available, although this is a speciose group. Some species may turn out to be restricted to the lower Nile, while groundwater forms may show considerable local endemism, and largely undescribed faunas exist in high mountain zones (e.g. the Rwenzori, Eggermont et al., 2009). No meaningful analysis is feasible at this time.

4 Cladocera (Table 3)

The Cladocera are cyclic parthenogens that are part of the Class Branchiopoda. They fall into four orders, three of which are represented in the Nile basin, although the order Anomopoda is by far the commonest and most abundant. Of the so-called "predatory Cladocera" or Onychopoda (Rivier, 1998), species of *Evadne* and *Podon polyphemoides* occasionally enter the delta lakes. These are predominantly marine-littoral or brackish water animals that penetrate brackish lagoons along the delta coast as salinity permits. Of the Order Ctenopoda, comprised of numerous species of *Diaphanosoma*, at least three species, and possibly more occur in the Nile basin. They are strictly limnetic, and may occur at great abundances. One, *Diaphanosoma mongolianum*, is mostly temperate Eurasian, and is rather common in the delta. In the past, it was frequently confused with *D. brachyurum*. It is yet another temperate species in the Nile fauna, but has also been recorded from Lake Nasser–Nubia

(El-Shabrawy & Dumont, 2003) and from Lakes Victoria, Albert and Edward (Lehman et al., 1998b). The commonest nilotic ctenopod is *D. excisum*. It occurs basin-wide, and is also widespread in Asia. *D. sarsi* has about the same range as *D. excisum*, but is distinctly less common. With its large eye, filling up about the entire head, it is more visible than *D. excisum*, and therefore frequently falls prey to visual predators.

Of the anomopods or true water-fleas the Nile basin inventory is likely not yet complete. Ecologically, the anomopods fall into a pelagic group, predominantly composed of rather large species of the family Daphniidae (plus Moinidae), and of smaller species of Bosminidae, and in a second group of largely littoral-benthic species, mainly composed of Chydoridae and Macrothrichidae. The Chydoridae are the most species-rich family. The biogeography of the anomopoda used to be simple: most species were "cosmopolitan". However, upon closer analysis, it turned out that most of these "species" are really genera, or groups of genera. The taxonomy of these genera requires considerable expertise, and their status and composition has been in a state of flux for a number of years. This certainly applies to *Alona,* the largest genus of all. *Alona* s.l. is a polyphyletic group that is currently being divided into a number of monophyletic genera and species that may be amenable to a biogeographic analysis. Unfortunately, of many species recorded earlier from the Nile basin, we cannot presently define the identity. Thus, although we can update the treatments by Rzóska (1976) and Dumont (1986), it is almost certain that a discussion of the Nile anomopods 10 years from now will again look different from today's.

A paradigm of contemporary zooplankton ecology is that large species, like *Daphnia*, are more vulnerable to (visual) predation than small species (Dodson, 1974a, b). An important and abundant class of predators is fish, and in Africa, omnivores and planktivores are especially numerous among the ichthyofauna (Witte, 2009). Paradoxically, most large zooplankton species are pelagic, and exposed to predation more than species that burrow into the benthos (the large larvae of the dipteran *Chaoborus* are the classical example of this – see Lehman, 2009), or hide in littoral vegetation. Since about 1980, it became clear that *Daphnia* cannot hold out in the plankton of tropical lowland lakes of Africa (Dumont, 1980) or Asia (Fernando, 1980), but for reasons that are not yet fully clear, they may still occur in winter if the yearly temperature amplitude is more than 12°C, or if the water is turbid, or if they live at an altitude of above 1,000 m, or a combination of these. Further, deep lakes offer hypolimnetic refuges to diurnal migrants (Worthington, 1931; Zaret & Suffern, 1976). The acquisition of drought-resistant stages in the life cycle is also helpful: many large species, copepods and cladocerans alike, preferentially occur in temporary pools (Rzóska, 1961). For large crustaceans, like the fairy shrimp (Anostraca), this is the only type of environment where they are able to survive. Some minor adaptations useful to facilitate survival include a transparent body that predators may not be able to see in turbid water, small eyes (the pigment spot of the eye may be a clue to predators) (Zaret, 1980), or the development of morphological defenses, like a smaller or bigger body size, and long tail-spines and helmets (Dodson, 1989). Green (1967) described an elegant

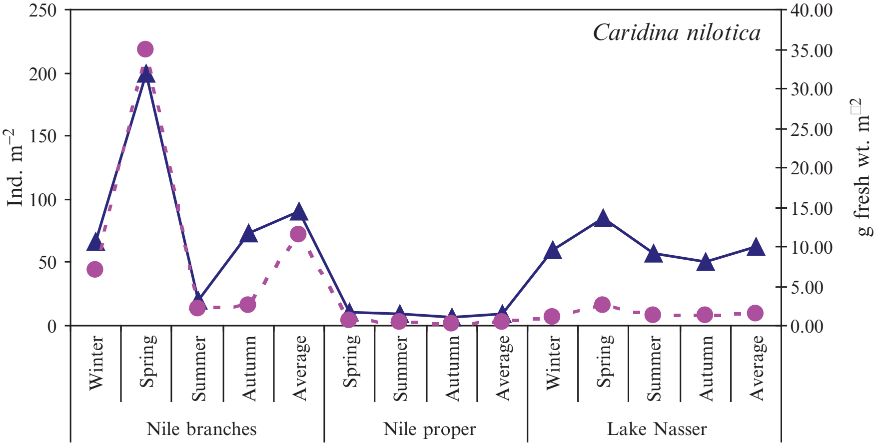


Fig. 3 The African shrimp *Caridina nilotica* is widespread across the Nile basin, and occurs in the lower part of the valley, in Egypt, as far as the river delta. The figure illustrates that the species is most common in stagnant water, but certainly is not absent from the river itself; in Lake Nasser, its abundance is more or less stable across the year, while in the delta, seasonal effects are strong (after original data by G. El-Shabrawy, Cairo)

case in *Daphnia lumholtzi* in Lake Albert, where populations under heavy predation stress developed such ornamentations, while populations without such stress had rounded heads (form *monacha*) (Fig. 3). Form *monacha* was later found in temporary waters near Khartoum by Dumont (1986).

In all, about ten species of *Daphnia*, three *Ceriodaphnia*, and three *Moina* have been found in the Nile basin. *Moina salina* (cited under the name *M. mongolica*), a brackish-water species, used to be common in Birket Qarun, but now no longer exists there. The genus *Simocephalus* is composed of predominantly littoral animals. Four widely distributed species occur in the Nile basin. The largest *Daphnia* of all, *Daphnia magna*, used to be known from the lower Nile in Egypt, where it occurred in temporary waters, often together with *Daphnia similis*. Currently, both have become rare or have disappeared. Surprisingly, in the early 1990s, *Daphnia magna* invaded Lake Victoria. Its appearance was linked to a profound alteration of the food web of the lake. According to Jonna & Lehman (2002), a temporarily relaxed planktivory occurred which permitted this large-sized zooplankter to (temporarily?) establish itself in this eutrophic, nutrient-rich environment.

D. barbata, is an endemic of tropical Africa. *D. lumholtzi* extends widely in Asia and even reaches Australia. *D. longispina,* finally, may in reality be a mix of species that may turn out to be biogeographically the most interesting of all.

Of the small-sized Bosminidae, *Bosmina longirostris* has been found basin-wide, while *Bosminopsis deitersi* occurs in the source lakes and down to the Sudd swamps.

Of the littoral Cladocera (not listed here), most species richness is to be found in the various lakes, ponds and swamps of the basin. The largest number of species is in the family Chydoridae, followed by the Macrothrichidae, and few (poorly studied) Ilyocryptidae. A couple of ctenopods (Sididae) also occur. Quite a few entries to this list are all but definitive, and the nomenclature of several genera and species may change in the future. For example, the "cosmopolitan" *Alona rectangula* has recently been re-assigned to the genus *Coronatella* (Van Damme & Dumont, 2008) and split into several species. "*Alona bukobensis"* from Lake Victoria belongs to this genus, but at least two more species are currently known from the lower Nile valley: *Coronatella rectangula* from the delta lakes, and *Coronatella anema* from temporary waters across the basin.

In all, there is a strong preponderance of tropicopolitan species, but many have not been found North of the Sudd swamps. Two *Chydorus* species (*C. tilhoi and C. kallipygos*) parallel *Thermodiaptomus galebi* in that they occur in the Nile basin plus Lake Chad. Whether any species are restricted to the great lakes of the East African plateau is, at this point in time, impossible to decide but appears improbable, in view of the ease of passive dispersal that is so typical of anomopods. The total number of Cladocera in the Nile basin currently stands at approximately 75 species. Exact numbers cannot be given, and more species surely exist. Any sizeable lake with a good choice of sub-environments should have about 50–55 cladoceran species (Dumont & Segers, 1996). The equatorial source lakes show a sizeable degree of species complementarity with the delta lakes, the latter being inhabited by a mix of African and Palaearctic species.

5 Anostraca (Fairy Shrimp)

Although large calanoids and *Daphnia* abound in ephemeral waters, the most archetypical crustaceans living in such environments are the fairy shrimp (Anostraca). By their large size (often in the range of several centimeters) and slow upside-down swimming, they are easy prey for fish and, to a lesser extent, for waterbirds. Consequently, they only occur in rainpools, or salt lakes, or high mountain lakes. A prominent family in Africa is the Streptocephalidae, of which most species show restricted ranges. In the Nile basin, especially the lower valley, their habitat has been severely affected by millennia of human interference, especially irrigation. The species *Streptocephalus torvicornis* is widespread east and west of the Nile and thus must have crossed the Egyptian Nile valley. This curious situation is analogous to that of certain Irano-Turanian dragonfly species, that occur in the Maghreb and the Levant, but rarely if ever show up in lower Egypt (Dumont, 2009). Its current range is circum-mediterranean in a broad sense, with North Africa its probable cradle. There are two subspecies, and the "Egyptian" one is probably *S. torvicornis bucheti* (Dumont et al., 1995).

In Nubia and Sudan, *S. proboscideus* replaces *S. torvicornis*. Its range extends beyond East Africa, and reaches southern Africa. The Blue Nile and the Ethiopian plateau are, however, home to *S. rotschildi*. Three more species occur sahel-wide (i.e. from

Senegal to Sudan) but appear to be less abundant than the foregoing: *S. rubricaudatus*, *S. sudanicus* and *S. vitreus*. Some other species (*S. bouvieri, S. coomansi*, and perhaps *S. caljoni*) may be restricted to the area of the Nile source lakes, but not much information on them is available. Most of the species richness in *Steptocephalus* and other anostracan genera is found in southern Africa (Hamer et al., 1994a, b).

In brief, fairy shrimp show a picture similar to that of other crustaceans: few species restricted to particular zones of the Nile basin, and some species shared with the Sahel, others with the East African plateau.

Saline waters in the desert away from the Nile valley (e.g. Nukheila oasis) contain the brine shrimp *Artemia*. If the salinity of Birket Qarun continues to increase, it may soon be expected there as well.

6 Cyclestherida

Among the so-called "big branchiopods", *Cyclesteria hislopi* is exceptional in that it occurs in permanent waters, often together with fish, in spite of its comparatively large size and conspicuous shape and colour. It is a cyclic parthenogen in which males have rarely been recorded, and it shows a circumtropical distribution. In the Nile basin, it has been found on the East African plateau (e.g. in the Kyoga swamps: Green, 2009), and in the Sudd marshes.

7 Syncarida

Syncarida are primitive bisexual crustaceans that typically live a subterranean life in river gravels and have limited dispersal abilities. They are therefore useful in phylogeographic studies. Unfortunately, they have not been well studied, and only patchy data are available. Three species are currently known from the Nile basin: *Nilobathynella predynastica* (Dumont, 1984) from the Nile in Nubia, and *Cteniobathynella bakeri* and *Heterodontobathynella ninianae* from the shores of Lake Albert (Green, 1964, 2009; Schminke, 1973). The genera *Cteniobathynella* and *Nilobathynella* are closely related, and *Cteniobathynella*'s are typically African. No doubt, numerous species await discovery in other parts of the Nile basin.

8 Atyid Shrimp of the Genus *Caridina* (Decapoda)

The species *Caridina nilotica* is an indicator species of the Nile basin from source to delta (Richard & Clark, 2005). In the river, it is usually associated with the weedy littoral, and its densities are much lower than in lakes. Figure 3 shows abundances measured over the year in different parts of Egypt: the Nile branches, the main river, and Lake Nasser (El-Shabrawy, unpublished data). In the delta lakes, and in Birket Qarun salinity is too high for this species and *Palaemon elegans* replaces it. *Caridina nilotica* is particularly abundant in Lake Victoria, where it is split in littoral and open water (limnetic) populations. At least the latter part is only partly benthic. It does undertake extensive vertical migrations (Lehman et al., 1996) and feeds on detritus and phytoplankton (Fryer, 1960). It used to be accepted that *C. nilotica* extends south to southern Africa, but newer insights contradict that. Richard & Clark (2005) consider that in parts of the Nile basin only tediously connected to the basin, endemic species have evolved. In Lake Bunyoni in the South Ugandese volcanic uplands, for example, they have found not less than four endemic species (see also Green, 2009).

9 Pelagic Zooplankton Communities

The qualitative composition of the zooplankton communities from the source lakes to the delta shows only limited variation and is composed of 8–10 species of cladocerans and copepods. In the river current, the communities are usually diluted and, in high-energy sections like the Blue Nile gorge, they become invisible (El-Moghraby, 1972), although viable eggs are invariably carried with the flow. As soon as the current subsides, these propagules develop into new populations. Which calanoid copepod is found (with usually only one species abundant but up to three species per lake) changes according to the lake(s), and among the Cladocera, between zero and three species of *Daphnia* may co-occur, depending on season (*Daphnia*'s are mainly winter animals), fish predation levels, and degree of turbidity and trophy. The last two factors are rather strongly correlated: turbidity increases under eutrophication. In mildly eutrophic conditions, Daphnia's may at first survive better (especially *D. longispina*), but at higher turbidities they have problems dealing with the overabundance of small particles that clog their delicate filter apparatus. In the currently hypereutrophic delta lakes, for example, no *Daphnia* survive today.

Among the cyclopoids, *Thermocyclops* species are ubiquitous. Like Daphnia's, the larger and carnivorous *Mesocyclops* seem to be at a disadvantage when the state of eutrophy worsens. *Mesocyclops* is now a rarity in the delta lakes, where the dominant cyclopoid is the temperate-zone *Acanthocyclops trajani*.

The most widespread cladoceran in the basin (and probably in the world) is *Bosmina longirostris*. Unlike *Bosminopsis deitersi* and *Ceriodaphnia cornuta* that do not extend beyond the equatorial Nile, it is omnipresent. *Diaphanosoma mongolianum*, surprisingly, has been shown to extend as far south as Lake Victoria and the lakes of the Western Rift, frequently co-occurring here with *D. excisum* (Lehman et al., 1998b).

10 Zooplankton Production

The quantification of zooplankton production was one of the main targets of the International Biological Programme (IBP) of the 1960s (Morgan et al., 1980; Brylinski, 1980), with Lake George on the equator and Lake Chad in the Central

Sahel two key research sites. Estimating "secondary" production, whether on a taxon-specific or a community basis, requires the quantification of the ratio between production (P) and Biomass (B):

$$P/B = a$$

Biomass can be expressed in weight (DW = dry weight), or carbon (C), or energy (J) per unit of volume (l, m^3) or lake surface area (m^2, ha, km^2). Production is expressed in the same units, per day, month, growing season, or year. The determination of the mass of an individual zooplankter and the duration of its development stages from egg to adult is currently almost a routine measurement. The IBP allowed much information to be collected about the dependence of development times on temperature (often linear in a physiological temperature interval) as well as on the relationship between development time and body size (most larger species taking longer to develop) (Morgan et al., 1980). However, most data sets contain much noise because a measure of abundance is required as well. Zooplankton is notoriously patchy, as well in the vertical as in the horizontal plane, and consequently, abundance estimates tend to distort estimates of P/B ratios.

Most production studies consider only or mainly the crustaceans, although the rotifers may contribute significantly to total production.

In Lake George on the equator, Burgis (1971a, b, 1974) worked on *Thermocyclops crassus* (still called *T. hyalinus* at that time). Her final estimate for P was 44 mg (DW) m^{-2} d^{-1} for a standing crop of about 560 mg (DW) m^{-2}, giving a P/B = 0.08. Total zooplankton biomass was 830 mg DW m^{-2}, so the cyclopoid was clearly the dominant species of this system, in which standing crop was almost invariant over the year. Extrapolated, this leads to a production of 160 kg ha^{-1} y^{-1} or 16 t km^{-2} y^{-1}, a somewhat low value that suggests that her earlier, higher estimates of P/B were closer to the mark.

In Lake Chad where detailed production work was performed by Gras (1970) & Gras & Saint Jean (1969, 1976, 1978a, b, 1981a, b), with a synthesis by Lévêque & Saint Jean (1983), the following values were found:

- For cyclopoids (mainly *Thermocyclops crassus*, with some admixture of the larger *Mesocyclops* sp.) P/B = 0.10–0.26
- Calanoids (mainly *Tropodiatomus schubotzi*) P/B = 0.02–0.07
- *Moina micrura* (the "fastest" species of all) P/B = 0.4–0.8
- *Bosmina* and *Daphnia* P/B = 0.2–0.3

Aggregating these figures to the entire community, and extrapolating to the year, average zooplankton production in Lake Chad amounted to about 400 kg ha^{-1} y^{-1} or 40 t km^{-2} y^{-1}.

In view of the similarity between the communities of Lake Chad and the Nile basin, the productivity of the stagnant Nile waters is likely of the same order of magnitude, as well in the source lakes as in the reservoirs of the Sudan. In the lower Nile, a latitudinal factor (Brylinski, 1980) comes into play. The standing crop in Lake Nasser–Nubia varies between seasons by a factor 3 (El-Shabrawy & Dumont, 2003), and this must reflect in its production. In Birket Qarun and the delta lakes, this discrepancy in seasonal abundance widens to a factor 10. A recent complicating factor is eutrophication, which has hit Lake Victoria (Lehman, 2009) and the delta lakes as well. In the latter, surveys in 2001–2005 and the 1970s have revealed an increase in standing crop by one order of magnitude (Dumont & El-Shabrawy, 2008). Production no doubt increased in parallel.

In Lake Victoria, *Caridina nilotica* constitutes a persistent element of the pelagic community. Whether to call it planktonic, benthic, or micro-nektonic is a matter of appreciation, but Lehman et al. (1996) and Ignatow et al. (1996) quantified its contribution to the lake's economy in the 1990s, and found that its net production amounted to 52 mg C m^{-2} d^{-1}. After conversion to dry weight (DW ~ 2C) and extrapolation, this gives about 400 kg ha^{-1} y^{-1}, a figure that rivals the community production of Lake Chad in the early 1970s and at least partly explains the success of the predatory *Lates niloticus* in the lake! John Lehman's team also estimated the production of the lake fly *Chaoborus* (Lehman et al., 1998a, b) and, extrapolated, found an average production of c. 47 kg DW ha^{-1} y^{-1}, making it the single most important "zooplankter" and invertebrate predator of the lake. They found that, on average, *Chaoborus* removed 10% of zooplankton production per day.

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Freshwater Crabs and Shrimps (Crustacea: Decapoda) of the Nile Basin

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Abstract Freshwater crabs are present in almost all freshwater bodies in the Nile River basin ranging from the main river to mountain streams, and from extensive wetlands to rift valley lakes, but these decapod crustaceans are absent from the more arid regions of the Sahara and East Africa. Some 14 species of freshwater crabs (Potamonautidae) and six species of shrimps (Atyidae, Palaeomonidae) are found in the eight African countries that have at least part of their territory in the Nile drainage. The most species rich country in the Nile basin is Uganda (with more than 12 species), while the vast desert countries of Sudan and Egypt are relatively species poor and have no endemic species of freshwater crabs, and Ethiopia (although not species rich) has both widespread and endemic species. There is a clear biogeographic and taxonomic divide between the freshwater crab fauna of the Nile catchment which differs significantly from the species groups found in the neighboring Congo basin (Rwanda, Burundi, and D. R. Congo).

1 Introduction

The first authors to treat the freshwater crab fauna of Africa as a whole were Rathbun (1904, 1905, 1906), Chace (1942), and Bott (1955), and these works (especially the latter) are still used by many as the standard taxonomic references for this group. Flower (1931) and Williams (1976) focused on the freshwater crab fauna of Sudan and the Nile, while Williams (1968) revised the taxonomy of the freshwater crabs of Uganda, Kenya and Tanzania. Unfortunately, all of these contributions are now out of date, and contain a number of taxonomic inconsistencies (Cumberlidge, 1999) that make them unreliable to use to assess the freshwater crab faunal composition in the Nile basin. An updated continent-wide monograph of the freshwater crabs of Africa is not available so workers in many parts of Africa must still refer to

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original type specimens to identify material and to compile distribution records, making this a daunting task for the non-specialist. Elsewhere in Africa recent taxonomic revisions are available for the freshwater crab faunas of West Africa (Cumberlidge, 1999), Tanzania (Reed & Cumberlidge, 2006), Lake Tanganyika (Cumberlidge et al., 1999; Marijnissen et al., 2004), Angola (Cumberlidge & Tavares, 2006), and southern Africa (Cumberlidge & Daniels, 2008), but large geographic areas such as Central Africa and East Africa are in need of taxonomic revision despite recent contributions (Cumberlidge & Dobson, 2008; Cumberlidge, 2009). All species identifications, synonymies, and distribution patterns used here are based on direct observation of specimens (including all relevant type material) by the author, because most of the literature on the freshwater crabs of the Nile basin is unreliable.

The first record of the existence of freshwater crabs in the Nile (and indeed anywhere in Africa) was the description of *Thelphusa berardi* Audouin, 1826 (now *Potamonautes berardi*) from Egypt, followed several years later by *Thelpheusa nilotica* H. Milne Edwards, 1837 (now *Potamonautes niloticus*) from the Nile. More than 50 years later Hilgendorf (1892) described *Telphusa emini* from northwest Tanzania near Lake Victoria, and de Man (1901) described *Potamon floweri* (now *Sudanonautes floweri*) from the Bahr el Gebel in Sudan. Nobili (1906) added a third species of *Potamonautes* from the Ruwenzoris (as *Potamon (Potamonautes) aloysii-sabaudiae*), and Rathbun (1909) described *Potamon* (*Potamonautes*) *rodolphianus* Rathbun, 1909 from northern Kenya (now *Potamonautes rodolphianus*). This was followed by the description of two species of *Potamonautes* from Ethiopia (as *Potamon* (*Geothelphusa*) *antheus* Colosi, 1920, and *Potamon* (*Geothelphusa*) *ignestii* Parisi, 1923) (now *Potamonautes ignestii* and *P. antheus*) and another species from Mount Elgon, Uganda (as *Potamon* (*Geothelphusa*) *granviki* Colosi, 1924) (now *Potamonautes loveni* (Colosi, 1924)). Subsequent contributions to the freshwater crab fauna of the Nile basin were made by Rathbun (1935) (*Potamon (Geothelphusa) amalerensis* Rathbun, 1935), Chace (1942) (*Potamon mutandensis* Chace, 1942), Bott (1955) (*Potamonautes (Gerdalopotamonautes) gerdalensis* Bott, 1955), and Corace et al. (2001) (*Potamonautes rukwanzi* Corace, Cumberlidge, & Garms, 2001) (see Table 1).

2 Overview of the Decapod Fauna of the Nile System

Freshwater crabs are an ecologically successful group of large and conspicuous decapod crustaceans occurring widely in most tropical and subtropical regions of the world. In continental Africa freshwater crabs of the family Potamonautidae Bott, 1970, are represented by 11 genera and more than 120 species (Cumberlidge, 1999; Cumberlidge et al., 2008; Yeo et al., 2008). Crabs of the genus *Potamonautes* MacLeay, 1838, are abundant in most parts of Africa, are found in almost all available freshwater bodies, and are clearly well-adapted and successful (Bott, 1955; Cumberlidge, 1999). Freshwater crabs are common throughout the Nile river basin

Table 1 Species of freshwater decapod crustaceans (Potamoidea: Potamonautidae and Caridea: Atyidae, Palaemonidae) found in the Nile River basin. Species that are endemic to the Nile catchment are shown in bold type. Introduced species are also included. Taxonomic authorities are provided in the text

Taxon	Countries of occurrence	IUCN conservation status
POTAMOIDEA, POTAMONAUTIDAE		
Potamonautes aloysiisabaudiae	Uganda, D. R. Congo	LC
Potamonautes amalerensis	Uganda	DD
Potamonautes antheus	Ethiopia	VU
Potamonautes berardi	Egypt, Sudan, Ethiopia, Uganda, Tanzania, Rwanda	LC
Potamonautes emini	Uganda, Tanzania, Burundi	LC
Potamonautes gerdalensis	Kenya, Tanzania	VU
Potamonautes ignestii	Ethiopia	VU
Potamonautes loveni	Uganda, Kenya	LC
Potamonautes mutandensis	Uganda	EN
Potamonautes niloticus	Egypt, Sudan, Ethiopia, Uganda, Kenya, Rwanda	LC
Potamonautes rodolphianus	Kenya	DD
Potamonautes rukwanzi	Uganda	EN
Sudanonautes floweri	Uganda, Sudan, Central African Republic, D. R. Congo, Congo, Gabon, Cabinda, Cameroon, Nigeria	LC
CARIDEA, ATYIDAE		
Caridina nilotica	Egypt, Sudan, Ethiopia, Uganda, Kenya, Tanzania, southern Africa	
Caridina bunyonyiensis	Uganda	
Caridina gordonae	Uganda	
Caridina pseudonilotica	Uganda	
Caridina subventralis	Uganda	
CARIDEA, PALAEMONIDAE		
Macrobrachium niloticum	Egypt, Sudan, Kenya, Cameroon, Central African Republic, D. R. Congo	
Macrobrachium rosenbergii	Introduced species in Egypt (native to Thailand)	
ASTACOIDEA, CAMBARIDAE		
Procambarus clarkii	Introduced species in Uganda and Kenya (native to the USA)	

but are absent from the more arid regions of the Sahara and the Horn of Africa. Despite the fact that freshwater crabs are among the most important invertebrates inhabiting African fresh waters, until recently they were only poorly known. This situation is now changing and there is currently an upsurge of interest in freshwater crab taxonomy, identification, phylogeny, diversity, distribution patterns, and conservation status (Cumberlidge, 1999; Daniels et al., 2006; Cumberlidge & Daniels, 2008; Cumberlidge et al., 2008; Yeo et al., 2008). As a result, our present knowledge of African freshwater crab biology in northeastern Africa has advanced greatly since the earlier contributions by Flower (1931), Chace (1942), Bott (1955), and Williams (1968, 1976, 1991). Some 13 species of freshwater crabs are found in the eight African countries that have at least part of their territory in the Nile drainage in Egypt, Sudan, Ethiopia, Uganda, Kenya, Tanzania, and Rwanda, reaching as far south as the Kagera River in Burundi. This is a relatively small number of species compared to the rest of the Afrotropical region whose fauna comprises 137 species in 20 genera and two families (Potamonautidae and Potamidae Ortmann, 1896) (Cumberlidge et al., 2008; Yeo et al., 2008). These decapods are present in all of the Nile's freshwater ecosystems, from the headwaters south of the equator north to the delta in Egypt where it flows into the Mediterranean Sea. Some species are widespread and common throughout the Nile River basin, some have more limited distributions and occur only in a particular region, while others are point endemics that are only found in a single locality.

All of the freshwater crabs in northeastern Africa belong to the exclusively Afrotropical freshwater crab family Potamonautidae. The freshwater crab fauna of the Nile basin is dominated by species of *Potamonautes* which is the largest and most cosmopolitan of the African genera, and includes more than 70 species distributed throughout sub-Saharan Africa (Cumberlidge, 1999; Cumberlidge et al., 2008; Yeo et al., 2008), with about one fifth of these species occurring in the Nile basin. Besides large rivers and small streams, freshwater crabs are also found in a number of lakes in Ethiopia, Uganda, and Kenya, not all of which are directly connected with the Nile River basin. Thirteen species of *Potamonautes* occur in the Nile River basin plus one species of *Sudanonautes* Bott, 1955, which represents the easternmost outlier of a West and Central and African genus (Cumberlidge, 1999). Shrimps of the family Atyidae are also found throughout the Nile River basin, with the commonest species (*Caridina nilotica* (P. Roux, 1833)) distributed widely in eastern and southern Africa from the Nile basin to South Africa (Monod, 1980), and there is a single record of this species occurring in Lake Upemba in the Congo basin (Roth-Woltereck, 1942). *Caridina nilotica* is part of a taxonomically unstable species complex whose distribution includes not only the entire eastern part of Africa from Egypt to South Africa, but also extends eastward to include the Indo-West Pacific region as far as southern Japan, Australia and Polynesia.

In Lake Victoria *C. nilotica* is abundant and is a major prey item of the Nile perch. In Lake Bunyonyi in Uganda *C. nilotica* is absent but there are four endemic species of *Caridina* in this isolated crater lake that is close to, but not connected to the Nile catchment (Richard & Clark, 2005). Shrimps of the genus *Macrobrachium* (Palaemonidae) such as *M. niloticum* (P. Roux, 1823) are also found in this system in the Nile in Egypt, the White Nile, and Lake Turkana, as well as in Lake Chad and the Chari and Logone Rivers in Central Africa (Monod, 1980). The Thai species *M. rosenbergii* has been introduced into Egypt for aquaculture.

3 Biology

Freshwater crabs are present in almost all freshwater bodies associated with the Nile River catchment ranging from mountain streams to large lowland rivers, and from extensive wetlands to rift valley lakes. In seasonally arid areas some species are semi-terrestrial, live in burrows, and move about on land at night. All African freshwater crabs are very similar in terms of their breeding strategy (they all have direct development from egg to hatchling crabs, and they all lack larval stages) but they differ widely in their choice of habitat within the continent's freshwater ecosystems (Cumberlidge, 1999). The complicated topography and equally diverse habitats found in the Nile River catchment is no doubt responsible for much of the diversity and endemism of the freshwater crabs. Freshwater crab populations living in crater lakes or in highland streams often become isolated due to the fragmentary nature of these habitats coupled with the limited dispersal ability of crabs associated with their low fecundity and direct development (Cumberlidge, 1999). These animals are the largest macro-invertebrates in African freshwater ecosystems and there is some evidence that they occupy key positions in aquatic food webs and that they dominate benthic invertebrate communities in terms of biomass (Hill & O'Keeffe, 1992; Somers & Nel, 1998; Dobson et al., 2002).

A large part of our present knowledge about the freshwater crabs of the Nile River basin is the result of long-term studies of onchocerciasis (river blindness) in the highland areas of East Africa (the Ethiopian highlands, the Ruwenzoris, and Mount Elgon). Those investigations were aimed at identifying associations between freshwater crabs and the aquatic larval stages of the biting blackflies of the genus *Simulium* that serve as vectors for the parasite *Onchocerca volvulus*. The immature stages of *Simulium* need to develop in fast-flowing rivers and streams, and must attach themselves either to stones or to the carapace of river-living species of freshwater crabs in order to complete their development into adult flies (McMahon, 1951; McMahon et al., 1958; Barnley & Prentice, 1958; Williams et al., 1964; Crosskey, 1990; Williams, 1991). Control measures for the spread of river blindness focus on limiting the numbers of blackflies, and one possibility for such control involves understanding the relationship between *Simulium* larvae and freshwater crabs.

4 Freshwater Crabs of the Nile System: Egypt, Sudan, and Ethiopia

4.1 Egypt

Two common and widespread species of freshwater crabs – *Potamonautes berardi* (Audouin, 1826) and *Potamonautes niloticus* (H. Milne Edwards, 1837) – are found throughout the vast expanse of the Nile River basin from the delta in Egypt to Lake

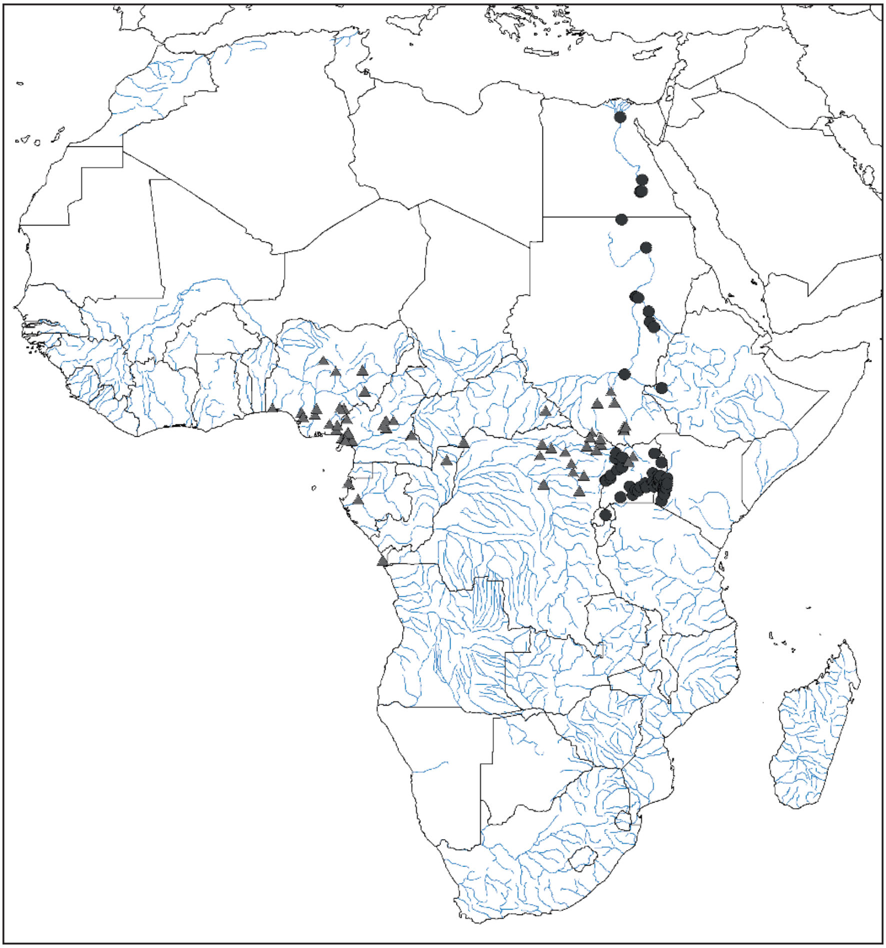

Fig. 1 Distribution of *Potamonautes niloticus* (*black circles*), a common species of freshwater crab endemic to the Nile River basin, and of *Sudanonautes floweri* (*black triangles*), a widely distributed West and Central African freshwater crab, whose range extends into the upper Nile river basin in Uganda

Victoria and its tributaries in equatorial Africa (Fig. 1). *Potamonautes berardi* is a common aquatic river crab recognized by its uniform brown colour, its small size at maturity, and by the smooth margins of its anterior carapace. *Potamonautes berardi* occurs in the major channels of the Nile and its tributaries and has a wide distribution in the Nile River basin in Egypt, Sudan, Ethiopia, Uganda, Tanzania, and Rwanda (Williams, 1976; Cumberlidge, 1997, 1998).

Potamonautes niloticus is a large and common species with a very wide distribution that is known from more than 60 localities in six countries associated with the Nile River and its tributaries in Egypt, Sudan, Ethiopia, Uganda, Kenya, and Rwanda. This species is easily recognized by the rows of distinct spines along the anterior margins of its carapace, and its populations are abundant enough in Lake Victoria to support small-scale local fisheries. *Potamonautes niloticus* occurs in a range of aquatic habitats including the major channels of the Nile itself and its lowland tributaries, in small and large lakes associated with the river basin, as well as in small clear fast-flowing mountain streams with rocky beds, and sluggish warm lowland streams with muddy bottoms (Bott, 1955; Williams, 1964; Cumberlidge, 1997, 1998). This species is completely dependent on aquatic habitats and it never leaves the water whether it is found in streams, rivers, or lakes. The Nile River delta in Egypt places two Afrotropical species (*P. berardi* and *P. niloticus*) in close proximity to the Palaearctic species *Potamon potamios* Olivier, 1804 (Potamidae), an eastern Mediterranean taxon whose range extends into the Sinai Peninsula in Egypt (Brandis et al., 2000). The freshwater crab species list for Egypt is therefore relatively impoverished and includes just three species (none of which is endemic to that country), but these belong to two genera and two families.

4.2 Sudan

Despite being Africa's largest country, Sudan has only three species of freshwater crabs: *P. berardi* and *P. niloticus* which occur along the entire course of the river including Sudan, and *Sudanonautes floweri* (de Man, 1901) which is found in the vast swamps of the Sudd in the Bahr el Gebel in southwestern Sudan, and south into the Acholi District of northwestern Uganda. *Sudanonautes floweri* is a large species easily recognised by its purplish brown body and its contrasting yellow–orange postfrontal crest and yellow orbital border (Cumberlidge, 1999). A fourth as yet undescribed species occurs in the streams draining the Imatong Mountains on the Sudan–Uganda border (Cumberlidge, in prep.). Despite its presence in the Nile basin *S. floweri* is actually a widespread West and Central African species that is on the eastern edge of its range in Sudan and Uganda. It has a wide distribution in the Niger, Chad and Congo basins (in the rivers Benue, Chari, and Congo) (Rathbun, 1921; Balss, 1936; Monod, 1980; Cumberlidge, 1995, 1999; Cumberlidge & Daniels, 2008). This species prefers the moister regions of the woodland and guinea savanna zones from central Nigeria, northern Cameroon, and the Central African Republic reaching as far eastward as southern Sudan and northeast Uganda (Cumberlidge, 1999). *Sudanonautes floweri* is also common in the humid tropical rainforest habitats in southeast Nigeria, south Cameroon, Bioko, Central African Republic, D. R. Congo, Congo, Gabon and Cabinda (Angola) (Cumberlidge, 1999; Cumberlidge & Tavares, 2006; Cumberlidge & Daniels, 2008). *Sudanonautes floweri* is an ecologically versatile species that is equally at home in both aquatic and semi-arid environments and lives in shallow streams, rivers, and ponds, as well as in burrows near streams and rivers (Rathbun, 1921; Cumberlidge, 1995, 1999). This species is also found on land either next to water or some distance away, because it is capable of breathing air, and can function well for long periods out of water. The widened and highly arched carapace, and the lack of teeth on the anterolateral margins of the carapace are features often associated with air breathing and burrow living (Cumberlidge, 1999). This body shape contrasts with the flattened, deeply grooved and spiny carapace of exclusively aquatic river living species such *P. niloticus*.

The type locality of *S. floweri* is the Bahr el Gebel in southwestern Sudan between the Albert Nile and the White Nile where the river spreads out to form the great open wetland of the Sudd, comprising standing waters and flooded land dominated by papyrus and grass swamps (Beadle, 1981). The lentic waters of this vast swamp have high rates of organic decomposition and persistently low oxygen levels, high carbon dioxide levels, and reduced light levels, but the steady current flowing northwards through the channels prevents complete stagnation. This low-oxygen environment may explain the absence of *P. niloticus* and *P. berardi* from the Sudd, but this is apparently not a problem for the air-breathing species *S. floweri*. In Nigeria and Cameroon (but not in the Nile River basin) *S. floweri* serves as an important second intermediate host to the human lung flukes *Paragonimus uterobilateralis* and *P. africanus* (Voelker & Sachs, 1977; Sachs & Cumberlidge, 1990; Cumberlidge, 1999).

4.3 Ethiopia

The lower reaches of the Blue Nile in western Ethiopia support the common Nile crab *P. niloticus*, while *P. berardi* is more widely distributed in the highland areas in Amhara, Southern, and Oromia Regions. The rivers draining the Ethiopian highlands in the Blue Nile region of western Ethiopia in the Amhara Region host two large endemic species of freshwater crabs: *P. antheus* (Colosi, 1920) and *P. ignestii* (Parisi, 1923). *Potamonautes antheus* occurs south in the Gambella, Oromia and Southern Regions, while the rivers draining the southwestern Ethiopian highlands flow south into Lake Chew Bahir in the Southern region where an undescribed species is found (Cumberlidge, in prep.). *Potamonautes ignestii* is found near Gondar in the northwestern highlands in the Lake Tana catchment area which includes the source of the Blue Nile, and this area supports a second (as yet undescribed) species of freshwater crab (Cumberlidge, in prep.). It is likely that other species will be discovered when exploration in Ethiopia improves.

4.4 Freshwater Crabs of the Upper Nile Basin: Uganda, Kenya, Tanzania, Rwanda, and Burundi

The southernmost part of the Nile catchment comprises the Lake Victoria basin and its associated lakes (Kioga, Albert, Edward, George) and their tributaries in Uganda, Kenya, Tanzania, Rwanda, and Burundi. Lake Turkana in northern Kenya is included here because this large lake was isolated from the Nile basin relatively recently.

4.4.1 Uganda

The vast majority of the freshwater ecosystems in Uganda are part of the Nile River basin. Lake Victoria is the largest of the lakes in this region, and while its northern shore is in Uganda, its northeastern shore is in Kenya, and its southern and western shores are in Tanzania. Most (but not all) of the major lakes in this part of the Nile basin have populations of freshwater crabs. For example, *P. niloticus* is found in Lake Victoria, the Victoria Nile, Lake Albert, and the Albert Nile (and probably Lake Kioga) but there are no records of any species of freshwater crab from either Lake George or Lake Edward, despite efforts to collect there. It is of interest to note that although *P. niloticus* occurs commonly in Lake Victoria in Uganda and Kenya, this species has never been recorded from the Tanzanian part of this lake. Besides lakes, *P. niloticus* is also found in the lower reaches of the rivers and fast-flowing streams draining highland areas in Uganda. The series of small isolated crater lakes in western Uganda are not strictly speaking part of the Nile drainage, and most of these do not support populations of freshwater crabs (as far as we know). Exceptions to this are Lakes Mutanda and Bunyonyi in the Kigezi District of western Uganda where *P. mutandensis* (Chace, 1942) is found (Chace, 1942), and Lake Rukwanzi, a crater lake in the Ruwenzoris, where *P. rukwanzi* Corace, Cumberlidge, and Garms, 2001, occurs (Corace et al., 2001).

The shrimp *Caridina nilotica* (Decapoda, Caridea, Atyidae) is a widely distributed species found throughout the Nile basin and elsewhere in eastern and southern Africa. Interestingly, Lake Bunyonyi in southwestern Uganda lacks *C. nilotica* but supports four endemic species of *Caridina* (*C. bunyonyiensis* Richard & Clark, 2005, *C. pseudonilotica* Richard & Clark, 2005, *C. subventralis* Richard & Clark, 2005, and *C. gordonae* Richard & Clark, 2005) (Richard & Clark, 2005). The Louisiana red claw crayfish *Procambarus clarkii* (Girard, 1852) (Astacoidea: Cambaridae) has been introduced to several parts of East Africa, including some localities in the Nile River basin. *Procambarus clarkii* is a relatively large, prolific, aggressive, burrowing crayfish that is an invasive species worldwide (Holdich, 1999; Howard & Matindi, 2003) that has been reported to have had severe ecological impacts on native populations of fish, plants, and freshwater crabs in Lake Naivasha in Kenya (Foster & Harper, 2006a,b, 2007). The introduction of *P. clarkii* in Lake Bunyonyi in Uganda is a cause for concern because it has taken over the lake and is doing so well that populations of the native freshwater crab species (*P. mutandensis*) might well be negatively impacted.

The Rwenzori (also written as Ruwenzori) Mountains in western Uganda host populations of freshwater crabs in the fast-flowing mountain streams flowing through moist tropical forest, in the lowland major rivers flowing through dry savanna, and in some of the small crater lakes associated with the western rift valley. *Potamonautes aloysiisabaudiae* Nobili, 1906, is the commonest species at higher altitudes in the upper reaches of the Kigezi and Rwenzori Rivers draining the Rwenzori Mountains. This species is also found on the D. R. Congo side of the border in rivers that are part of the Congo basin. The warmer lower reaches of these rivers are home to *P. niloticus*, but this species is not found in the cooler high altitude waters of these systems. Williams (1976) reported that *P. idjiwiensis* (previously known only from Lake Kivu) also occurs in the Rwenzoris but this record has not been confirmed here by direct reexamination of material.

The highlands east of Lake Victoria in eastern Uganda near the border with Kenya support a number of species of freshwater crabs including *P. amalerensis* Rathbun, 1935, from Mount Debasien, and *P. niloticus* and *P. loveni* (Colosi, 1924) from Mount Elgon. Freshwater crabs from the forested slopes of Mount Elgon in Uganda that were collected by T. R. Williams and his colleagues during surveys in the 1960s proved to belong to two new species of *Potamonautes* and these are currently being described (Cumberlidge & Clark, in prep.). In this part of Africa, wherever *P. niloticus* occurs in fast-flowing upland streams with turbulent water it is often associated with the blackfly *Simulium neavei* the vector of *Onchocerca volvulus* that causes onchocerciasis (river blindness) in humans (Hynes et al., 1961; Williams, 1961, 1962, 1965, 1970; Williams et al., 1961).

4.4.2 Kenya

This largely semi-arid country includes a number of rivers that are seasonal, and in many areas freshwater resources are scarce at most times of the year. The Nyanza and Western Provinces of southwestern Kenya are the only parts of this country that lie in the Nile river basin; the streams and rivers that flow south and west into the northeastern corner of Lake Victoria have healthy populations of *P. niloticus*. This species extends for considerable distances up these rivers until it reaches altitudes where the waters are too cold for its liking. A second species, *P. gerdalensis* Bott, 1955, is also found in the Nyana Province of southwestern Kenya (and across the border into the neighboring part of Tanzania) where it occurs in rivers entering Lake Victoria from the north and east (Bott, 1955; Reed & Cumberlidge, 2006). This species seems to replace *P. niloticus* in ion deficient lowland rivers (Shaw, 1959a, b; Williams, 1976). The northern parts of the Rift Valley Province and Eastern Provinces in northwestern Kenya lie in a very hot arid region with vast stretches of dry country that includes Lake Turkana that is associated with one small endemic species of freshwater crab, *P. rodolphianus* (Rathbun, 1909). Although Lake Turkana is not presently connected to the Nile River basin, it was isolated relatively recently and is currently fed by rivers flowing south from the southern Ethiopian highlands. The ancient connections of this lake with the Nile basin are indicated by the presence of two nilotic species of freshwater shrimps, *Caridina nilotica* and *Macrobrachium niloticum* in Lake Turkana.

4.4.3 Tanzania, Burundi, and Rwanda

The rivers that rise in Rwanda and Burundi and flow across northwestern Tanzania into the northwestern corner of Lake Victoria host populations of the common Nile crab, *P. niloticus*. In addition, the streams and rivers of the Bukoba region of northwestern Tanzania support populations of two other species, *P. emini* (Hilgendorf, 1892) and *P. berardi. Potamonautes emini* has also been recorded from Lake Victoria in this part of Tanzania (Williams, 1976; Reed & Cumberlidge, 2006).

5 Biogeography

The freshwater crab family Potamonautidae is found throughout the African continent and is endemic to the Afrotropical region (Cumberlidge et al., 2008; Yeo et al., 2008). The two genera of freshwater crabs found in the Nile basin (*Potamonautes* and *Sudanonautes*) are not endemic to this system but the majority of species of *Potamonautes* (8 out of 12 [66.6%]) are endemic to the river basin and its nearby lakes, with only *P. aloysiisabaudiae*, *P. berardi*, *P. emini*, and *P. loveni* also occurring outside of the river basin (as does *S. floweri*).

Figure 1 summarizes the distribution patterns of *P. niloticus,* a widespread and exclusively nilotic species, and *S. floweri* (a species with a distribution that includes the Nile, Congo, Chad and Niger River basins) based on combined distribution data from the author and from the recent literature (Cumberlidge, 1997, 1998, 1999; Reed & Cumberlidge, 2006). The vast Nile River basin has distinct nilotic species (such as *P. niloticus*) as well as a number of local or regional endemics that are all from highland regions, mostly in Ethiopia (*P. antheus* and *P. ignestii*) and Uganda (*P. aloysiisabaudiae* and *P. amalerensis*) (Table 1). The most species-rich country in the Nile basin is Uganda (with nine species). The vast desert countries of Sudan and Egypt are relatively species poor and have no endemic species of freshwater crabs, while Ethiopia (although not species rich) has both widespread and endemic species. There is a clear biogeographic and taxonomic divide between the freshwater crab fauna of the Nile catchment (Table 1) and the Congo basin (Rwanda, Burundi, and D. R. Congo), with only *P. aloysiisabaudiae* and *S. floweri* being found in both river basins. The same can be said for the parts of the neighboring countries of Tanzania and Kenya that lie outside of the Nile basin (Reed & Cumberlidge, 2006). It of interest to note that the freshwater crab faunas of Uganda, Kenya, and Tanzania are all distinct from each other, except for a few species whose distributional ranges overlap the borders between these countries (Reed & Cumberlidge, 2006).

The present assessment of freshwater crab biodiversity in the Nile (13 species in two genera, with six more species of *Potamonautes* in the process of description) is likely to be an underestimate because the absence of records for freshwater crabs in many parts of the Nile basin may be the result of uneven collecting efforts that have left large areas unsurveyed. The Nile basin is home to five taxa whose conservation status warrants their inclusion in the IUCN Red List (IUCN, 2004) as either vulnerable or endangered (Table 1). Although great advances have been made recently in our knowledge of African freshwater crabs in general, our present state of knowledge of the distribution of freshwater crabs in the Nile basin makes it difficult to draw firm conclusions about the meaning of the absence of records for the areas that have not yet been surveyed, especially the more inaccessible places that lie well away from population centers and roads.

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The Nile Benthos

Gamal M. El-Shabrawy and Mohamed R. Fishar

Abstract Benthic macro and micro-invertebrates include those biota that spend a significant portion of their life on or in the bottom. Nile benthic macroinvertebrates (molluscs, worms and crustaceans) exhibit a marked variation in composition and abundance, reflecting a range of microhabitats but a comprehensive inventory of the taxa present is still lacking. Meiobenthos (nematodes, flatworms, and microcrustaceans) has to date remained almost unstudied. Macroinvertebrate species richness in Egypt amounts to about 7–31 species at individual bank-side sites of the river and delta and the macrobenthos of the White Nile and its lakes is represented by about the same number of species. The sandy bed of the White Nile is sparsely populated, with the larvae of small Chironomidae prominent. Information about the Blue Nile is scarce, but its benthos appears to be poor, because of torrential flow and drastic changes in water level. Generally, benthic invertebrates of the Nile lakes have low diversity compared with temperate lakes. Twelve species of molluscs, 14 species of insects and three species of oligochaetes are known from Lake Victoria. The benthic community of Lake Turkana includes a sponge, a bryozoan, 8 gastropods, 3 bivalves, 17 ostracods, 23 insects and several hydracarines and annelids. *Caridina nilotica*, *Potamonautes niloticus* (Crustacea), *Limnodrilus hoffmeisteri*, *Branchiura sowerbyi* (Oligochaeta), *Corbicula fluminalis*, *Cleopatra bulimoides* and *Melanoides tuberculata* (Mollusca) occur Nile-wide.

1 Introduction

Benthic invertebrates, usually classified as macro- and meiobenthos, play an important role in the cycling of material and in energy flow. The main distinction between the two groups is size, with a zone of overlap that may cut across taxonomic borders. Large oligochaetes, for examples, are macrobenthic, while small species

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are classified as meiobenthic. Meiobenthos is mainly composed of nematodes and other small worms, and microcrustaceans such as ostracods and copepods. In many areas of the world, meiobenthos has been much less well studied than macrobenthos, and the Nile is no exception to this rule. Limited data are available mainly for some equatorial lakes.

It may be difficult to define what species are benthic, and what species are not. The shrimp *Caridina*, for example, may as well lead a benthic as a planktonic life (for lake Victoria, see Lehman, 2009). The larva of the phantom midge, *Chaoborus,* likewise spends part of its life hidden in the bottom sediment, and part swimming in the plankton (see further). Other species may not be strictly associated with bottom sediments, but live among macrophytes (see Section 4), and are periphytic, or they live on rocky substrates, such as the mussel *Etheria* and the larvae of simuliids (blackflies). Within the context of this articles, we will consider all these as “benthic”.

Benthic, especially macrobenthic, production generally exceeds that of zooplankton (Liang & Liu, 1995). It integrates change in physical, chemical and ecological characteristics of its habitat over time and space (Milbrink, 1983) and plays a key role in the accumulation and transfer of contaminants to higher trophic levels (Amyot et al., 1994). Because of this, benthic communities are useful for detecting alterations in aquatic ecosystems (Dickman et al., 1990). Macrobenthos species offer advantages to water quality surveys because (a) they inhabit all kinds of waters, (b) they are sedentary, unable to avoid environmental disturbances, (c) they have long life cycles compared to planktonic groups, (d) their responses to different environmental conditions are known, (e) they are in the middle of the aquatic food web, reflecting the productivity of trophic levels below and above.

In spite of this, ecological formation on invertebrates, large and small, in Egypt is sparse. Most studies are taxonomic (Hussein et al., 1988; Ali, 1989; El-Shimy et al., 1995; Ibrahim et al., 1999) or address small areas (Abdel Aal, 1979; El-Shimy & Obuid-Allah, 1992; Abdel Salam, 1995; Abdel Gawad, 2001; Fishar & Williams, 2006, 2008; Fishar et al., 2006).

2 Spatio-Temporal Longitudinal Variation

The macrobenthos of the Nile, mainly composed of Crustacea, Molluscs and Annelida, varies in density, biomass and diversity from the delta to Lake Nasser. Its density increased from 1,400–1,700 ind m^{-2} in the Nile branches and from Cairo to Aswan, to 2,075 ind m^{-2} at Aswan reservoir, followed by a sharp decrease to 95 ind m^{-2} in Lake Nasser (Fig. 1) (Iskaros, 1988; Fishar, 1995; El-Shabrawy, unpublished). Biomass in the Nile and its branches (649 and 142 g fresh wt m^{-2}) was also much higher than in Aswan reservoir and Lake Nasser (17 and 3.5 g fresh wt m^{-2}, Fig. 2). This mainly reflected the abundance of two large bivalves (*Mutela* and *Caelatura*). Crustacea are common at Aswan reservoir and in lake Nasser, forming 25–35% of total benthos, with *Caridina nilotica* (Decapoda) dominant. Mollusca are even more abundant in the Nile branches and the Cairo-Aswan Nile, forming 20–95% of the

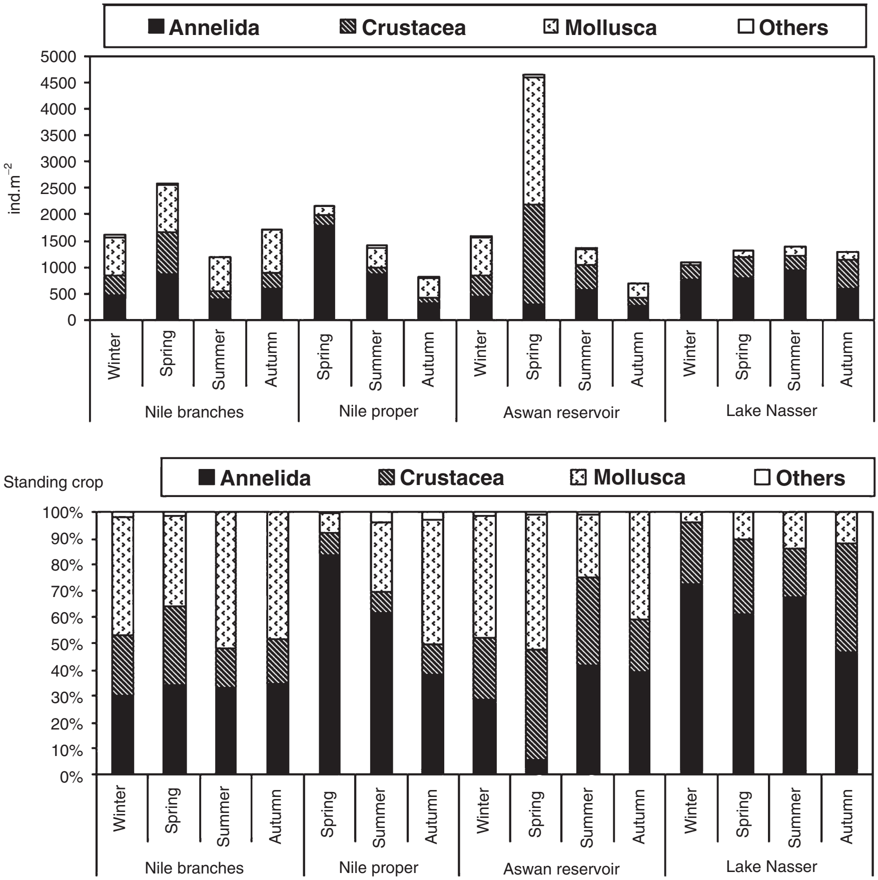

Fig. 1 Mean abundance and proportion of the three main groups of the macrobenthos by geographic sector and by season in the River Nile (original)

total in 2007 (El-Shabrawy, unpublished). Ramadan et al. (2000) mentioned that the bivalve *Corbicula consobrina* is abundant and peaks during spring and winter in the Nile (Cairo-Aswan). Type of sediment is the main factor affecting mollusc distribution. Sandy-mud bottoms are preferred over sandy or gravely sand bottoms. The widespread *Melanoides tuberculata* reaches up to 240 ind m^{-2} at Aswan reservoir in spring with highest biomass, 25.3 g fresh wt m^{-2}, in the delta branches in autumn (Fig. 3) (El-Shabrawy, op. cit.). Annelida are well represented in Lake Nasser and the Egyptian Nile, forming 62% and 68% of total density. Iskaros (1988) found that they made up 50% and 47% of total biomass at Lake Nasser and Aswan Reservoir. *Limnodrilus hoffmeisteri* reached a maximum of 1,500 ind m^{-2} between Cairo and Aswan in spring (Fig. 3). The nearly monogeneric assemblage of tubificid worms, with *L. hoffmeisteri* most abundant, indicates that the river is somewhere between gross organic pollution and simple eutrophication (Brinkhurst, 1974).

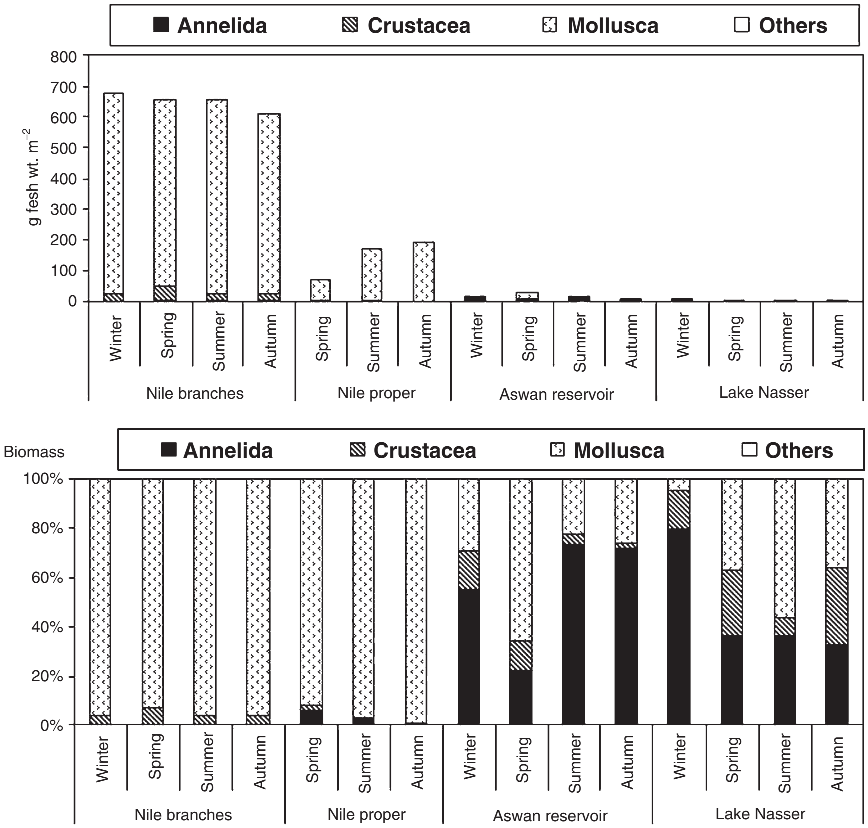

Fig. 2 Mean biomass and proportion of the three main groups of the macrobenthos by geographic sector and by season in the River Nile (original)

Many authors have noted a longitudinal zonation in rivers although it is recognised (Vannote et al., 1980) that a river is a continuum that changes gradually rather than in a stepwise manner. Illies & Botosaneanu (1963) broadly divided rivers into the eroding rhithron in the upper course, and a depositing potamon in the lowland section. Fishar & Williams (2006) showed that the Nile fauna from Aswan to Cairo can be described as a potamon. The insect fauna contains ubiquitous groups such as chironomids but is dominated by Odonata, Coleoptera and Corixids characteristic of lowland weedy reaches. Plecoptera are absent and Trichoptera limited whilst Ephemeroptera are represented only by *Baetis, Caenis* and Potamanthidae. Thus the EPT (Ephemeroptera/Plecoptera/Trichoptera) of the rhithron are poorly represented. The greatest diversity of insects occurs in macrophyte stands, little represented in the rhithron zone. The mollusc fauna is diverse throughout the river and includes gastropods and bivalves, typical of weedy and mud-depositing habitats. Only *Ferrissia* sp., a river limpet which clings onto solid surfaces, and some bivalves such as *Sphaerium* sp. and *Corbicula* sp. are found in sand. The worms and

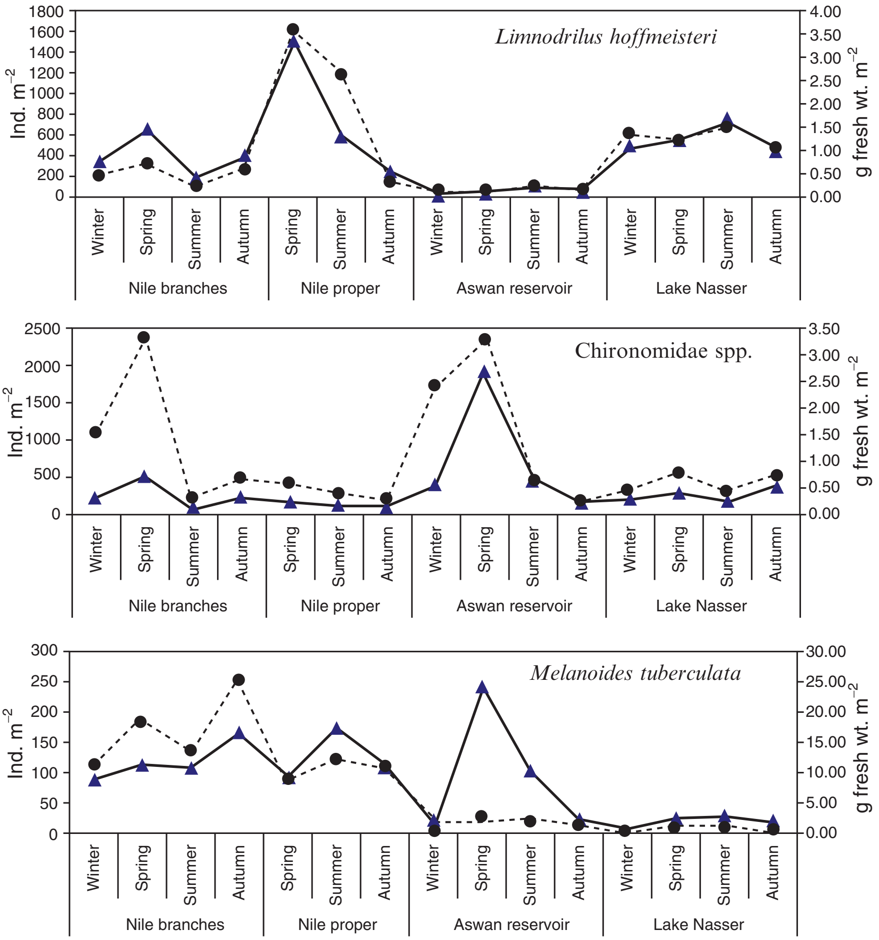

Fig. 3 Mean abundance of the dominant macrobenthic species by geographic sector and by season in River Nile (original)

leeches present are also typical of lowland reaches. *Caridina nilotica*, *Potamonautes niloticus* (Crustacea), *Limnodrilus hoffmeisteri*, *Branchiura sowerbyi* (Oligochaeta), *Corbicula fluminalis*, *Cleopatra bulimoides* and *Melanoides tuberculata* (Mollusca) are present along the whole Nile system.

3 Diversity of the Macrobenthos

Lotic ecosystems show unidirectional water movement, maintaining such processes as organic matter transport, sediment deposition and the formation of longitudinal gradients (Vannote et al., 1980). These factors directly or indirectly influence the resident biological communities (Ward, 1998). Fluvial continuity allows the colonization of river reaches downstream from upstream habitats. Abdel Gawad (2001) listed twenty eight species of annelida, mollusca and arthropoda (60%, 28% and 12% of total macrobenthos density) at Helwan region. Ramadan et al. (2000) recorded twenty species of mollusca (fourteen gastropods, six bivalves) between Esna and El-Kanater El Kharia. (El-Shabrawy, unpublished) listed 46 and 51 benthic species (of them 23 and 29 mollusca) in the Nile (Cairo-Aswan) and its branches, respectively. The documented taxon richness of macroinvertebrates in the Nile currently adds up to 51 taxa with 7–31 spp. at individual bank-side sites (but see further for evidence that this represents either a strong underestimate, or many species have gone extinct in the course of the twentieth century). Mid-stream biodiversity is lower (0–19). Lowest diversity occurs at polluted sites, highest at sites with high levels of sedimentation (Fishar & Williams, 2006). Information on macroinvertebrate diversity in large rivers from the United States and Europe can be used for comparison. Moyle (1940) collected a total of 111 taxa in a survey of the Upper Mississippi basin, whereas Elstad (1986) recorded 144 taxa in 1975 and 131 taxa in 1976–1977. Newell (1998) identified 55 taxa from the Columbia River, USA and Duane et al. (2004) recorded about 260 species in the Missouri River. In comparison, the invertebrate taxon richness of the Nile is low. A comparison between the macroinvertebrate taxon richness of the Nile and that of the Rhine over the past 80 years (CIPR, 1991) (Fig. 4) shows that macroinvertebrates in the Rhine fell from about 120 taxa in the 1920s, with strong insect representation, to about 27 taxa in the 1970s with far fewer insect species present. The current macroinvertebrate diversity

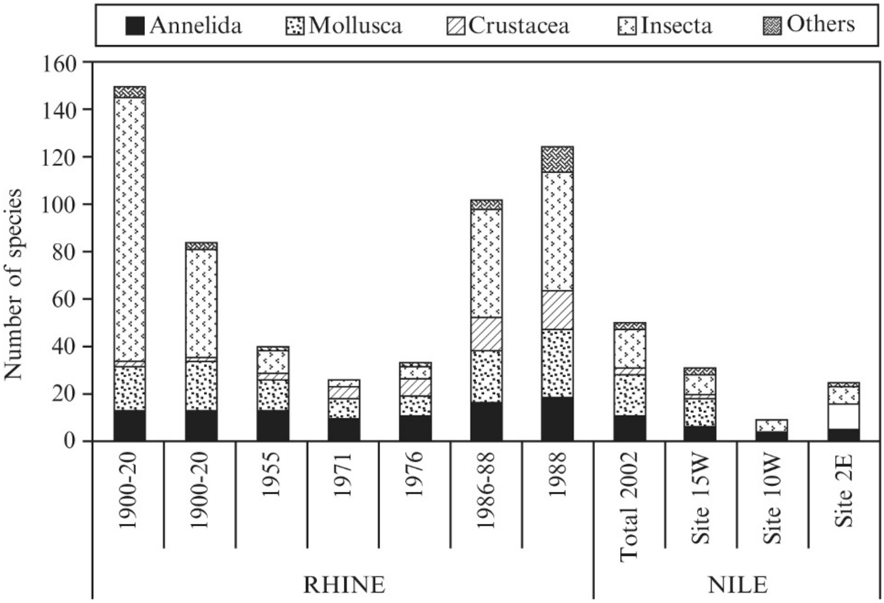

Fig. 4 Comparison of invertebrate diversity in the Nile and Rhine Rivers (after Fishar et al., 2006)

in the Nile is similar in number and composition to that of the Rhine in the 1950s. Subsequent improvements in the Rhine have been the result of two actions: pollution control and habitat restoration. The diversity of Nile macroinvertebrates is therefore probably lower than before. Flow regulation and pollution as a result of urbanisation and population growth since the nineteenth century may be the main reasons for this. However, in the case of the Nile (and many other rivers of Africa), taxonomy is lagging behind international standards and inventories – especially made in an ecological context – are far from accurate. Thus, in the case of the White Nile – the 50 + species on record are only a fraction of the 300 + that taxonomic surveys of adult Diptera alone have brought to light (see Dumont, 2009, and Green & El-Moghraby, 2009, for further details, mainly taken from the work of D. J. Lewis).

4 Macroinvertebrates as Indicators of Pollution

Biological criteria to develop a biotic pollution index can be used in conjunction with physical–chemical data. Many biotic indices are based on the pollution tolerance of macro-invertebrates. Benthic invertebrates are useful because they are long-lived, sessile, and the diversity of species may indicate water quality conditions over a period of months; chemical records are relevant only for the time of their measurement. Intermittent pollution can be easily missed by chemical sampling. Macro-invertebrates are fairly easy to identify, and do not require the skills of highly specialised taxonomists (Hellawell, 1986).

The use of biotic indices for pollution monitoring in rivers was developed in Europe and in the United States (Rosenberg & Resh, 1993). Indices have been developed using Protozoa (Jian & Yun, 2003), diatoms, macrophytes, and fish (Plafkin et al., 1989; Iliopoulou-Georgudaki et al., 2003).

One of the simplest methods using macroinvertebrates was developed in the UK. The first version (ISO-BMWP, 1979) scores each family present from 1–100 and has two scales, one for depositing and one for eroding habitats. Later, the scoring was simplified to 1–10 and the scale for depositing zones was excluded.

The simplicity and reliability of this BMWP score has made it an attractive model for adaptation to countries other than Britain, especially to countries in which taxonomy is not well developed. Fishar and Williams (2008) described a related Nile Biotic Pollution Index (NBPI) for Egypt. Seven chemical variables were used to and Biological data were collected from the same sites using Artificial Substrate Samplers (ASS). A biotic pollution index (NBPI) was based on the presence of invertebrate taxa identified to family level using the BMWP scoring system supplemented by the "Saprobien" System. The Average Score per Taxon (NBPI-APTS) was also calculated. The NBPI-ASPT performed a little better in the river as a whole as a pollution indicator than the NBPI. In clean waters, there was a wide range of NBPI scores, suggesting that the diversity of taxa also depends on other aspects of habitat quality. Conversely, in the polluted delta the scoring of individual taxa is critical, as one high scoring taxon may have a distorting effect.

This is useful information for an overall ecological assessment of the river. The relatively low taxon richness in the Nile and great variability of NBPI score at clean sites is of concern for the future management of the Nile, however.

5 Macroinvertebrates Associated with Macrophytes

Sampling large rivers such as the Nile is marred by logistic difficulties. Fishar & Williams (2006) used three sampling methods (Ekman Grab, macrophyte sweep netting and Artificial Substrate Samplers, ASS) for monitoring macroinvertebrate diversity. They found that the average number of taxa collected per sample from the banks by each method indicates that the ASS were by far most efficient with 7.2, followed by macrophytes with 3.4 and only 2.4 for the grab samples. The Nile was characterized by its large number of plant species that forms a mosaic of communities (see also Zahran, 2009). The habitats created by the combination of emergent plants and open water are prolific areas for insect development (Magee et al., 1999) since a part of providing habitat, decaying plant material supplies food for aquatic detritivores (some midges and mayflies), and creates refuges, allowing successful avoidance of predation in vegetated areas (Evans et al., 1999). Macroinvertebrate assemblages appear to be strongly influenced by vegetation (Battle et al., 2001). In Egypt, they are rich in insects such as Ephemeroptera, Odonata, Hemiptera, Coleoptera, Trichoptera, Lepidoptera and Diptera (Agami, 1989). Many ecological and taxonomical studies on Nile insects are available (Ali et al., 1993; Geene, 1994). Mohamed (2007) studied the insect community in the Nile at Cairo: 44 genera belonging to Diptera (85% of total insect density), Ephemeroptera (6%), Odonata (5%), Trichoptera (2%), Hemiptera (2%), Coleoptera (0.3%) and Lepidoptera (0.01%) were found. Diptera comprised 13 genera in 7 families. Ephemeroptera was represented by *Baetis* sp. and *Caenis* sp., and Odonata by at least *Ischnura* sp., *Trithemis* sp., *Orthetrum* sp., and *Sympetrum* sp. Trichoptera, Hemiptera, Coleoptera and Lepidoptera were represented by 3, 4, 12 and 2 genera, respectively. Dumont (1980) stated that 52 + species of Odonata occur in Egypt (and therefore, as stated earlier, the 51 species of the total benthos must be a severe underestimate, even if some species may have gone extinct by river pollution). Chironomid larvae were abundant, reaching 1920 ind m^{-2} at Aswan reservoir in spring (Fig. 3) and represented by 15 and 12 species in Lake Nasser and Aswan reservoir, respectively (Iskaros, 1988). The different macrophyte communities of Lake Nasser (dominated by *Najas* spp.) and the reservoir/river system north of Aswan High Dam (*Potamogeton crispus–Ceratophyllum demersum* association predominant) clearly reflect this (Springuel & Murphy, 1991).

6 Invasive Macrobenthic Species in Egypt

Many alien species have been introduced to the Nile in Egypt. The following are examples of Mollusca and Crustacea reported by Ibrahim and Khalil (2004) (see also Dumont, 2009; Van Damme & Van Bocxlaer, 2009). The mollusc *Helisoma* *duryi* is a North American species, first recorded in Egypt in 1980. It had been suggested as a biological control agent of *Biomphalaria* and *Bulinus*, intermediate hosts of schistosomiasis.

The red swamp crayfish, *Procambarus clarkii,* and the White River Crawfish, *Procambarus zonangulus*, indigenous to the United States and Mexico, have been introduced to Egypt in the early 1980s and now coexist in mixed populations throughout the Nile (Ibrahim et al., 1997). They are large and prolific (a female can produce over 600 young), have a burrowing life-style (causing damage to levees, barrages and irrigation systems), and are adapted to areas with seasonal fluctuations in water levels which they survive in burrows. *Procambarus clarkii* is voracious, preying on various crustaceans, molluscs and small fish, as well as on their eggs and fry. It is the most common of the two and is noted for attacking fish in trammel nets, leading to economic losses. But it also feeds on benthic snails, making itself useful as a biological schistosome control agent, and it is readily consumed by the local population. Its carapace is used as forage for cattle, and it serves as a bio-indicator of trace metals which it accumulates in its tissues.

7 The White and Blue Nile

The known macrobenthos of the White Nile system is represented by 52 species (see earlier, for a caveat on this figure). Monakov (1969) produced a seminal paper on the benthos that still forms the backbone of our knowledge. The sandy bed of the White Nile is sparsely populated by larvae of Chironomidae (*Glyptotendipes* sp., *Cryptochironomus* sp.); Oligochaeta (*Limnodrilus hoffmeisteri*) predominate on clay or sandy bottoms with small quantities of silt, near river banks or at shallow depths. Molluscs were often absent while Hirudinea, Trichoptera larvae (*Oecetis* sp., *Chematopsyche* sp.,) and larvae of Ephemeroptera were rare. The general biomass of the benthos was low in the bed of the river (0–0.2 g m^{-2}), increasing to 4.9 g m^{-2} near the banks. There was little difference in number of bottom animals between autumn and spring. The benthos of the Sobat River differed little from that of the White Nile. The clayey bottom of the bed was sparsely populated by Chironomidae (*Polypedilum* sp., *Clinotanypus* sp., *Stictochironomus* sp., *Cryptochironomus* sp.) and Trichoptera. The total biomass of the benthos in the middle of the river was about 0.2 g m^{-2}. But near the mouth of the Sobat, large zones were invaded by the big bivalve, *Etheria elliptica*. The colonies of these molluscs provided a habitat for a rich fauna of Ephemeroptera and Trichoptera. The genera *Amphipsyche*, *Cheumatopsyche*, *Aethaloptera* and *Ecnomis* predominated. In the same place *Eupera parasitica* (Mollusca) was found.

The bottom fauna of Jebel Aulia reservoir differed greatly from that of the river and flood-plain water bodies. The share of Mollusca increased (17 species recorded). *Corbicula consobrina*, *Corbicula cunningtoni*, *Sphaerium abyssinicum* and *Cleopatra bulimoides* predominated. Chironomidae were represented primarily by species of the genus *Cryptochironomus* and *Stictochironomus* but the total number of species of Chironomidae also increased. Among Oligochaeta, *Limnodrilus hoffmeisteri, L. udekemianus,* and *Stylodrilus heringianus* predominated (Monakov, op. cit.).

Information about the benthos of the Blue Nile is scarce (Vijverberg et al., 2009). The inshore benthic fauna is poor, probably because of drastic seasonal changes of water level (Rzóska, 1976). Hammerton (1976) reported the presence of large numbers of the giant mussel *Etheria elliptica* attached to rock outcrops in the river between Diem and Roseires.

8 Lakes

Lakes show considerable heterogeneity in spatio-temporal benthos distribution. Because the bottom of turbid shallow lakes is often situated in the aphotic zone, anoxic conditions tend to develop here, especially where highly organic sediments occur, and the benthos of such muddy bottoms is poor in species. Typical inhabitants of such sediments are tubificids and chironomids. The benthic fauna of tropical lakes has been largely neglected by limnologists despite its role in the transfer of matter and energy. Generally, however, benthic invertebrates of African lakes appear to have low species diversity in comparison with temperate lakes.

8.1 Lake Victoria

In the past four decades Lake Victoria has undergone ecological changes that have affected all levels of its ecosystem (Witte et al., 1992; Lehman, 2009). The result has been a dramatic reduction in species richness and extinction of indigenous fauna and flora. The phytoplankton is dominated by Cyanobacteria. The zooplankton moved from a calanoid to a cyclopoid-dominated community. Among fish, about 200 cichlid taxa have been lost (Barel et al., 1991). The native tilapia (*Oreochromis esculentus*), previously a fish of great commercial importance, has fallen to insignificant numbers (Goldsmidt & Witte, 1992). It is almost certain that many the macrobenthos components insects, crustaceans and molluscs have also been affected by this altered trophic structure. In 1984, 12 species of mollusc, 14 species of insects and three species of oligochaetes were identified in the open lake and Winam gulf (Muli & Mavuti, 2001). Nematodes and ostracods were also present but did not make up a major part of the community. The gulf had higher species richness than the main lake. The molluscs were dominated by the gastropods *Melanoides tuberculata* and *Bellamya unicolor* and by three species of Bivalvia, *Caelatura hauttecouri*, *Mutela bourguignati*, and *Corbicula fluminalis*. Oligochaeta were represented mainly by *Branchiura sowerbyii* and *Alma emini*, with *B. sowerbyii* dominant. Other abundant macroinvertebrates included the larvae of aquatic insects of the families/orders Chironomidae, Ephemeroptera, Odonata and Trichoptera (Muli & Mavuti, 2001). In 1994/1995, the benthic fauna of main lake and Winam gulf had simplified and was composed mainly of oligochaetes and molluscs. Insect nymphs and Hirudinea were also present but did no longer make up a major part of the community. Nematodes and ostracods were not encountered. Twelve species of molluscs, 19 species of insects, four species of oligochaetes and two species of Hirudinea were identified throughout the lake. The gulf still had higher species richness (31 species) than the main lake (22 species). Comparing the two sampling periods, there has been a shift in abundance, from an Oligochaeta and Insecta dominated community in 1984, to a community dominated by Mollusca and Oligochaeta. The abundance of Tubificidae and Sphaeriidae seems on the increase, while that of insects still decreases (Muli & Mavuti, op. cit.). Mbahinzireki (1994) and Ligtvoet & Witte (1991) observed a similar trend in the Uganda and Tanzania portions of Lake Victoria.

The accidental introduction of water hyacinth (*Eichhornia crassipes*) in 1988, beside a number of negative effects, gave a new boost to benthic diversity and abundance. The floating mat of *Eichhornia* provides habitats for colonization by aquatic macroinvertebrates. The outer fringes of the vegetation at the interface with the open water are well oxygenated and support abundant invertebrate communities. Deeper into the bed of vegetation, the oxygen concentration in and below the root mat declines. This is mirrored by a decline in abundance and diversity of invertebrates and an increase in low oxygen-tolerant species (Masifwa et al., 2001).

8.2 Lake Turkana

Substrate variability in the shallow waters of lake Turkana is high. Much of the lake's shoreline is sand or rock-shingle bottoms, particularly on the south and west sides. Muddy and vegetated shallows are more restricted. Deep water substrates are almost entirely fine-grained silty muds. The lake is holomictic except in a few shallow silled embayments. Dissolved oxygen is almost always plentiful (for more details, see Johnson & Malala, 2009). The known benthic community of the lake is represented by a sponge (unidentified), a bryozoan (unidentified), 8 gastropods, 3 bivalves, 17 ostracods, 23 insect species and several hydracarines and annelids. Three benthic faunal associations have been identified: (1) a littoral, soft bottom association, dominated by the ostracod *Hemicypris kliei*, naucorid water bugs, and the corixid, *Micronecta* sp. This association is found throughout the basin in water depths less than two meters. Most lakeside lagoons contain these two species exclusively. The ostracods *Ilyocypris gibba*, *Potamocypris worthingtoni*, *Cyprideis torosa*, naucorids and several species of swimming beetles are also associated with vegetated soft bottoms. (2) A littoral, rocky bottom association composed of stonefly and mayfly larvae, gastropods (*Gabbiella rosea, Ceratophallus natalensis*), a leech (*Placobdella fimbriata*) and a sponge. Ostracods are rare on both vegetated and barren littoral rocky bottoms, except where they border on mud bottoms. This association is mostly found in the southern part of the lake, where hard bottoms are common. (3) A profundal, muddy bottom association, composed of stunted gastropods

(*Melanoides tuberculata*, *Cleopatra bulimoides*, *Gabbiella roses* and *Gyraulus* sp.), chironomids and ostracods. Sandy bottoms are generally devoid of benthos at all depths (Cohen, 1986). Infaunal invertebrates, particularly bivalves, which frequent high energy sandy bottoms in other African lakes, are absent from Lake Turkana. Epifaunal ostracods are prevented from feeding on shifting sandy substrates, and macrophytes also have difficulty in colonizing them. Geographic distribution of benthic invertebrates within the lake mostly follows habitat variations with depth. With the exception of some of the rocky bottom species from the South Basin, all common taxa occur throughout the lake wherever local substrate, water chemical and feeding conditions are appropriate. Most of the invertebrate species present in the lake benthos have adaptations for long range, passive dispersal. Depth range and faunal association studies of the common invertebrate taxa show two associations related to water depth and which parallel the two soft bottom associations mentioned above. Most probably, these associations are only secondarily correlated with water depth, being principally regulated by food availability (Cohen, op. cit.).

8.3 Lake George

The benthos is dominated by dipteran larvae, viz. two species of *Chaoborus* and many unidentified chironomid larvae. Oligochaetes are the second important constituent. Mollusca are represented by *Melanoides tuberculata*, mainly at the shores, owing to the unstable soft mud of the central region. The benthos found in the top 20cm is composed of chironomids, *Chaoborus*, and ostracods. Oligochaetes even occur up to depths of 40cm. This community is depauperate in species and groups, because of the deoxygenated substrate and has a mean standing crop of 1.2g m^{-2} (dry weight). All species are detritivores, except one or two chironomids which are partly carnivorous, and *Chaoborus* which retreats into the mud during the day, but moves into the water column to feed on zooplankton at night. Only close to the shore, where sand, clay and gravel occur, a richer community, composed of molluscs, nematodes, and insects is found. Its dependence on the nature of the substratum is similar to that in Lake Chad (Dumont, 1992). Beadle (1981) considered that the low diversity of benthic fauna in Lake George may be a result of its young age (4,000 years ago), following a period of volcanism and desiccation.

8.4 Lake Tana

Relatively little is known about the benthic invertebrate of this large, relatively shallow lake at the origins of the Blue Nile (Vijverberg et al., 2009). Bacci (1951–1952) recorded 15 mollusc species, of which *Bellamyia unicolor abyssinica* is likely endemic. Recent work showed that oligochaetes, *Chaoborus* spp. and chironomids occur both inshore and offshore (Tewabe et al., 2005).

8.5 Delta Lakes

The Nile Delta supports salt marshes and brackish shallow lakes (Mariut, Edku, Borullus and Manzalah). Before the Nile damming (1902, 1970), the lakes were under strong marine influence for about two thirds of the year, to be flushed and freshened by the river flood in the remaining third. The first more or less reliable data on invertebrates appear in a paper by Steuer (1942). The invertebrates were a mix of marine and freshwater species, with plenty of biota tolerant of strong fluctuations in salinity. Thus, marine-origin cirripeds (*Balanus improvisus*) settled on the stems of Phragmites, side by side with the Caspian-origin colonial cnidarian *Cordylophora caspia*. The macrobenthos also contained two species of mysids, two polychaetes of the genus *Nereis*, the serpulid *Ficopomatus enigmatica*, and three amphipods, including the burrowing *Corophium orientale*, besides freshwater organisms like insect larvae of several midge groups (e.g. *Cricotopus*) and even damselfly larvae (Steuer, op cit.). After AHD (Aswan High Dam) construction, the benthic communities became subject to dulcification and eutrophication. The species preferring eutrophic habitats (tubificidae and gastropods) increased, true marine species disappeared, some brackish-water species survived. Progressive extension of the area of aquatic vegetation (*Potamogeton* belt) lead to a diversity and abundance of species that live on water plants, at the expense of those living on uncovered bottom. El-Shabrawy (2002) listed 33 macrobenthic species in Lake Borullus, 13 arthropods, 8 annelids and 12 molluscs. That number is three times that of 1978 (Aboul Ezz, 1984), reflecting an increasing macrophyte cover (Fig. 5), since 21species were associated with lake macrophytes (El-Shabrawy, op. cit.). In the meiobenthos, Ostracoda are normally as trustworthy indicators of salinity as zooplanktonic copepods. Ramdani et al. (2001) mentioned three extant species: *Cyprideis torosa* extends from oligohaline to mesohaline environments; *Limnocythere inopinata* and *Loxoconcha elliptica* are oligohaline species. In

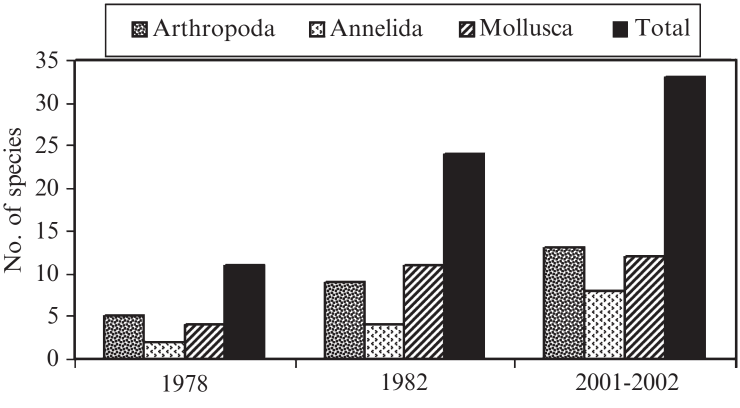

Fig. 5 Changes in the diversity within macrobenthic groups in Lake Borullus from 1978 to 2002 (original)

sediment deposits, only *Cyprideis* was found throughout a core spanning at least the twentieth century; the two freshwater species appeared before 1950, possibly shortly after 1900, suggesting a saline crisis around the beginning of the twentieth century. Abdel Mola (2003) recorded 15 macrobenthic species, belonging to 4 groups viz. 6 arthropods, 4 annelids, 4 molluscs and 1 coelenterate in Lake Manzalah. *Balanus* sp, *Gammarus locusta*, *Sphaeroma serratum, Corophium orientale*, *Chironomus* larvae, *Ficopomatus enigmaticus, Hedastia diversicolor, Polydora ciliata*, *Chaetogaster limnaei*, and *Semisalsa sp,* were abundant. The standing crop showed lowest density (ca 700 ind m^{-2}) in winter, and was highest (7,000 ind m^{-2}) in summer. In 2007, El-Shabrawy (unpublished) found that macrobenthos (representing 26 species) was high in spring and winter (970 and 720 ind m^{-2}), and at minimum in summer, 330 ind m^{-2} (Fig. 6). Chironomids, *Limnodrilus hoffmeisteri* and *Melanoides tuberculata* were abundant and widely distributed. The first survey on Lake Mariut by Samaan & Aleem (1972) revealed that a mac-

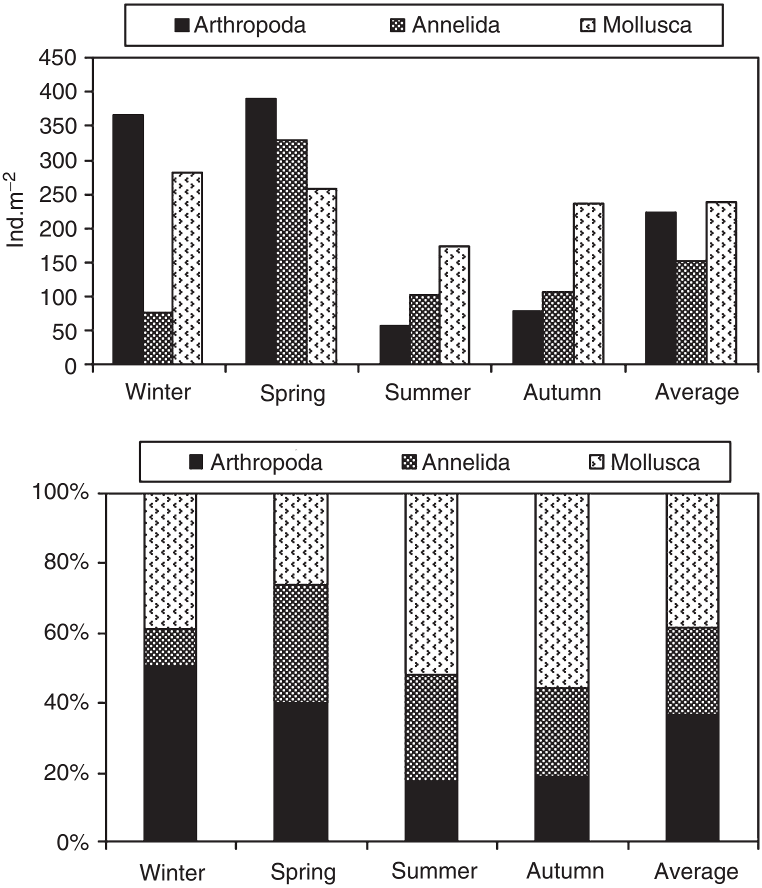

Fig. 6 Mean abundance and proportion of the three main groups of the macrobenthos by season in Lake Manzala (original)

robenthos assemblage of mainly three species, *Nereis diversicolor, Corophium volutator* and *Melanoides tuberculata*, composed 95% of total biomass. Abdel Aziz (1987) came to the same conclusion. Bernasconi & Stanley (1994) found a bottom fauna characterized by 78% of gastropods. Kossa (2000) recorded 14 benthic species, dominated again by gastropods. Aboul Ezz & Abdel Aziz (1999) listed 30 species, belonging to six groups: Oligochaeta (1 species), Polychaeta (3 species), Nematoda (1 species), Crustacea (8 species), insect larvae (3 species), Gastropoda (12 species), and Bivalva (2 species). *Hydrobia stagnorum*, *Paludestrina minuta*, and *Pomatiopsis* sp. were dominant. Insecta were represented by chironomids and Odonata (Fig. 7).

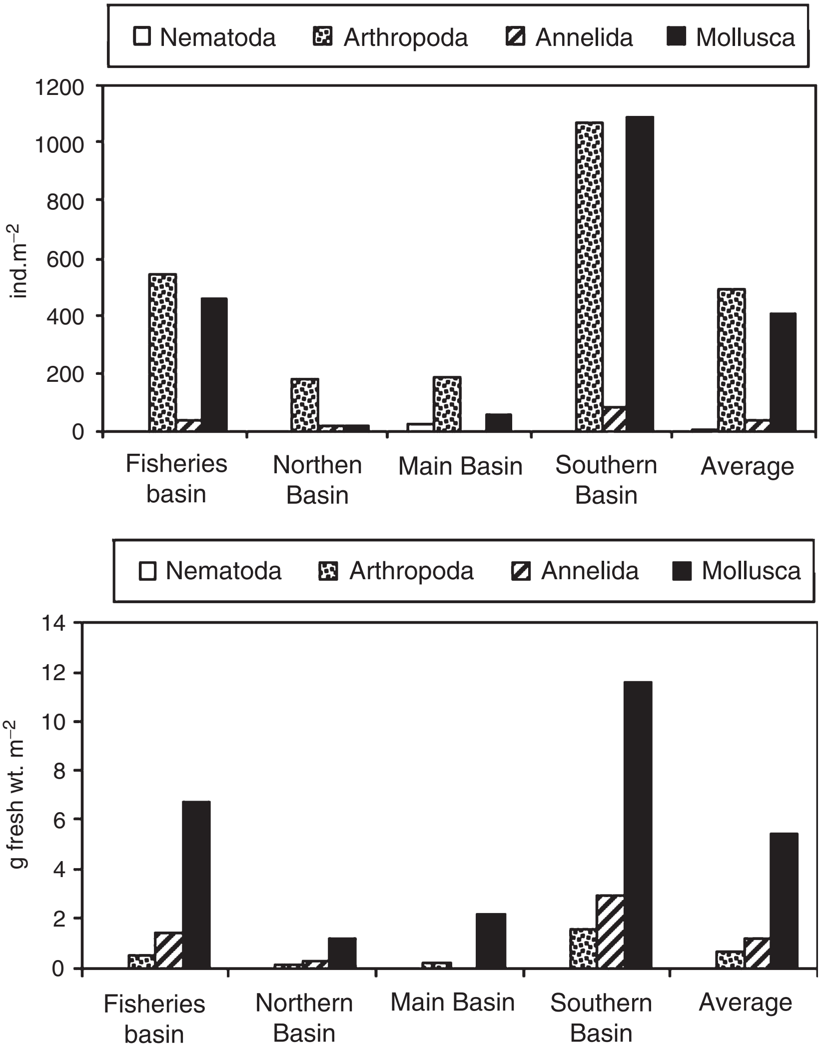

Fig. 7 Mean abundance and biomass of the three main groups of the macrobenthos by geographic sector in Lake Mariut (original)

9 Determinants of Diversity and Density of Benthos

The Nile benthos, in spite of gaps outlined earlier, exhibits a marked variation in taxonomic structure and abundance. Substratum type, water depth, sediment chemical properties, salinity (in the delta, Toshka and Fayum lakes), predation, and food come forward as the determining factors (Sibley et al., 1998). Soil texture plays a major role too: grain size should neither be too coarse nor too fine, but such effects vary with taxonomic groups. Winnel & Jude (1984) stated that bottom-dwelling invertebrates avoid coarse sediment, which could damage their soft integument by abrasion. Wiley (1981) mentioned that chironomids are burrowers, that actively seek out soft sediment. McLachlan & McLachlan (1971) found an adverse effect of coarse sand on Chironomidae. In Lake Nasser, El-Shabrawy & Abd El-Regal (1999), found a negative correlation between coarse sand and benthos, while *Limnodrilus* and *Chironomus* larvae were abundant on clay and loam. Benthos abounds in the Ethiopian rift lakes on medium and fine grained sand, while a reduced number of species occurs on silty and organic bottoms as well as on coarse sands (Tudorancea et al., 1989). In Lake Chad, molluscs and tubificids were associated with clay, while most insects are associated with sand (Dejoux et al., 1971). In Lake Kariba, Zimbabwe, coarse sand had an adverse effect on chironomids in the littoral, while a positive relation was found between organic carbon and chironomid biomass in profundal mud in winter (McLachlan & McLachlan, 1971). Particle size may favour some organisms but cannot be entirely responsible for their distribution. Other factors associated with the substrate are sediment consistency and chemistry. In lake Awasa, where the mid-lake sediment is semi-liquid and flocculent, no benthic fauna exists beyond 8–10 m depth (Tudorancea et al., op. cit.).

Abdel Gawad (2001) & Fishar (1995) claimed that in the Nile and Lake Nasser shallow water is beneficial to benthos. Average biomass in the littoral (7.21 g) is higher than in the main channel (3.45 g) (El-Shabrawy & Abd El-Regal, 1999). Benthic depth distribution in most Ethiopian Rift valley lakes is also characterized by peaks in shallow zones (Tudorancea et al., 1989). Finally, higher abundance of benthic organisms in the shallows were observed in African lakes such as Chilwa (McLachlan, 1979), Nakuru & Turkana (Cohen, 1986).

Dissolved oxygen in water and sediment may be a significant limiting factor in tropical lakes with marked thermoclines and oxylines (Beadle, 1981). Thus, during summer and autumn chironomids in the main channel of Lake Nasser respond to anoxy of the sediment by and migrating to shallower places with a better oxygen content.

Chemical properties of sediment affect benthos distribution. Mercedes (1987) found a correlation between *Limnodrilus hoffmeisteri* and conductivity in the Parana River, Argentina. Verdonschot (1987) recorded a positive relation between *L. hoffmeisteri* and pH, bicarbonate, calcium and nitrate. McLachlan & McLachlan (1971) observed a correlation between organic enrichment and Chironomid larvae and Oligochaeta. In Lake Nasser, *Limnodrilus hoffmeisteri* positively related with EC ($r = 0.66$) and organic mater ($r = 0.57$) (El-Shabrawy & Abd El-Regal, 1999).

Environmental effects on particular organisms indirectly affect other organisms which interact with them as prey, predators, competitors or symbionts. Competition and predation between benthic species has, however, been little studied in a Nilotic context. Only circumstantial evidence is available. Thus, Roback (1980) claimed that *Chironomus* larvae inhabit the littoral of lakes characterized by abundant macrophytes for protection. The abundance of benthos in the littoral of Lake Nasser may be due to the abundance of such "shielding" macrophytes (see Zahran, 2009).

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Freshwater Molluscs of the Nile Basin, Past and Present

Dirk Van Damme and Bert Van Bocxlaer

Abstract The malacofauna of the Nile is poor compared to that of the Congo and its degree of endemicity is lower. While the highest species richness of the Congo Basin is in stenotopic taxa that live in the rivers and lakes, the highest diversity in the Nile Basin occurs in eurytopic taxa living in fringe habitats such as temporary pools. The paucity of endemics that need perennial waters as well in the Lower Nile as in the White Nile confirms the geological evidence indicating instability and discontinuity in water supply during Plio-Pleistocene times.

The fauna of the Nile is predominantly Afrotropical in the Lower Nile and exclusively Afrotropical south of the junction of the White Nile and Blue Nile. Of all sub-basins, the degree of endemicity (either zero or two species) is lowest in the Equatorial Nile, indicating that the perennial aquatic environment in this sub-basin is young (probably Holocene) and lending support to the idea that the Bahr el Arab and White Nile Transcontinental Rift System were hydrologically unstable, with endorheic, alkaline lakes during most of the Plio-Pleistocene (Salama, 1997).

In the Lower (Egyptian) Nile and in the Ethiopian Highlands palaearctic faunal components occur, consisting of widespread species and of a limited number of endemics of palaearctic origin, related to Levantine species. Most of these taxa first appear in the fossil record around 2.5 Ma. There is no evidence that the Nile functioned as an invasion route for Eurasiatic species prior to that time. Only *Theodoxus niloticus* is possibly of Paratethyan origin and may have invaded in the Late Miocene. The main invasion of freshwater molluscs into Africa appears to have occurred via the Horn of Africa in Middle and Late Miocene times.

In the East African Rift, a diversified fauna occurs that only shares a fraction of species with the Nile Basin north of the Albert Nile (> ~5° N). In the equatorial headwaters, some species from southern Africa reach their northern limit, but the main community consists of species that are either endemic to one of the rift lakes or endemic to the region stretching from Turkana to the Kivu Basins. There hence exists a distinct East African bio-province, that was already recognisable in

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Pliocene assemblages and that had developed before the present lakes formed in the Late Pleistocene. Concerning the young age of Lake Victoria and the occurrence of an endemic cichlid superflock in the lake, the fossil molluscan record points to a persistence in the East African Rift of freshwater bodies sufficiently extensive to harbour a molluscan community – and *ipso facto* also fish – during periods of aridity/hyperaridity. The hypothesis of Verheyen et al. (2003, 2004), that the stem lineages of the East African haplochromines, presently inhabiting Lakes Victoria, Kyoga, Rukwa, Albert, George, Edward and surrounding waters, already existed during the Late Pliocene is consistent with the fossil evidence. The location of the area(s) of refuge (around Mount Elgon?) remains hypothetic, however.

The fossil records of the Turkana Basin, Tugen Hills and Albertine Basin show that around the Miocene/Pliocene boundary, two distinctive tropical molluscan palaeo-bioprovinces existed in equatorial Africa: an East African and a Congolian province. Regular incursions in both provinces during the Pliocene by elements of a third group, the so-called ‘Nilotic’ community, indicate the presence of a third distinctive Afrotropical palaeo-bioprovince situated more to the north. The molluscan community of the Chad Basin contains the same ‘Nilotic’ species (or closely related forms) as found in the Egyptian and Sudanese Nile but is more diverse, particularly in unionoids. Considering the climatic instability in the region of the different Nile Basins north of ~5° NL, the Neogene Chad-Eosahabi/Palaeosahabi system *sensu* Griffin (2006) is considered the most likely region of origin of the ‘Nilotic’ malacofauna, while the southern part of the Chad Basin (Chari-Logone system) may have acted as a refuge of this ‘Nilotic’ fauna during arid phases.

During Late Pliocene and Pleistocene wet phases the White Nile may have contained a perennial hydrological system, creating opportunities of exchange of aquatic faunas with Chad and the East African Rift System.

1 Introduction

The taxonomy and ecology of the Modern freshwater gastropod fauna of the Nile basin is well known. Research on freshwater molluscs of the Lower Nile started 200 years ago by French explorers such as Guillaume-Antoine Olivier (1801–1807), Jules-Cesar Savigny, who made the figures for the natural history volume of the ‘Description de l’Egypte’ (see Audouin, 1826), and Fréderic Cailliaud (1826). The first large collections from the Great Rift lakes were made some 30 years later, in 1859 by John Hanning Speke (molluscs reported by Dohrn, 1864). But some parts of the Nile Basin, in particular the Sudd area in Southern Sudan and the Blue Nile-Awash watershed in the Ethiopian Highlands, only were explored as late as the second half of the twentieth century (Brown, 1965; Brown et al., 1984; Brown, 1994).

The fact that African freshwater snails were so intensely studied in these early days is not primarily related to the nineteenth century’s fascination with the search for the Sources of the Nile but with the discovery, in the early twentieth century, that the freshwater snail genera *Bulinus* and *Biomphalara* are the intermediate hosts of trematodes causing human schistosomiasis (bilharziasis), a disease afflicting tens of millions of people in the tropics. This induced the World Health Organisation to allocate funds for studying African freshwater molluscs. From 1950 onward, two research centres were established, the Experimental Taxonomy Division of the Natural History Museum, London and the Mandahl-Barth Research Centre for Biodiversity and Health (formerly the Danish Bilharziasis Laboratory), Copenhagen.

The results of the malacological investigations on gastropods were compiled by David Brown (NHM) in his monograph 'Freshwater snails of Africa and their medical importance' (Brown, 1980, 1994). In the last two decades funding for gastropod research has been divided among several parties, and the focus of the research shifted. Modern research on African gastropods is mainly directed at endemic species flocks inhabiting (putative) long-lived lake systems, such as L. Tanganyika, L. Malawi and L. Victoria, and their evolutionary importance (e.g., West et al., 2003; Wilson et al., 2004; Genner et al., 2007; Glaubrecht & Strong, 2007; Sengupta et al., 2007). This research follows in the wake of molecular investigations on lacustrine cichlid species flocks and the claim that these lakes are 'living laboratories of evolution' (Martens, 1997; Rossiter & Kawanabe, 2000). Overview articles treating the African representatives of a particular family (e.g., Jorgensen et al., 2008) unfortunately remain rare, making it difficult to establish relationships between species of different hydrological basins and between lacustrine and fluvial ones.

African freshwater bivalves, being virtually of no economic or medical importance, have, in comparison to gastropods, been far less investigated. The major taxonomic reference works are 'Studies on African freshwater bivalves' by Georg Mandahl-Barth (Mandahl-Barth, 1988) and a synoptic inventory by Daget (1998). Mandahl-Barth's study exemplifies the taxonomic concepts prevailing in western malacology during the second half of the twentieth century, viz. that most species described by earlier workers are ecophenotypic variations or geographic races of a limited number of polymorphic, widespread biospecies. As a result, the Afrotropical unionoids (59 species), as treated by Mandahl-Barth (1988), was the least diverse of all tropical naiad faunas. Although Mandahl-Barth's work remains important, his taxonomic views are no longer followed (Daget, 1998; Graf & Cummings, 2007a, b; Van Bocxlaer & Van Damme, in press; Van Damme pers. data). Reversal of the lumping trend is related to the sudden dramatic world-wide interest in freshwater bivalves, presently considered a central item in biodiversity research and conservation biology. There exist now a general consensus that the large unionoid bivalves are the group of freshwater organisms most vulnerable to environmental stress (Ricciardi & Rasmussen, 1999; Lydeard et al., 2004). The observation that they are decimating world wide at an alarming rate (70% of the 300 species in North America are extinct or red-listed) (Bogan, 1993, 1996) emphasises this clearly. The result is that African freshwater bivalve research at present mainly focuses on mapping biodiversity and classifying taxa. Whereas current freshwater gastropod research is mainly financed from an evolutionary perspective, the main funding for freshwater bivalve research is provided by wildlife conservation instances. In 2002, a Mussel Project (Musselp; Dr Daniel L. Graf and Dr Kevin S. Cummings) was set up, aimed at providing a global classification of unionoid diversity. This project unites the main unionoid collections of the world and is hosted by the USA

Academy of Natural Sciences (http://www.mussel-project.net/). With respect to the Nile, a team, in collaboration with the University of Cairo, is working on a research project named Mashrua Al Mahar, which studies the biodiversity of the unionoid fauna of the Egyptian Nile.

The IUCN is currently making threat assessments of the freshwater molluscs of the Nile Basin as part of the Pan Africa Biodiversity Project (2005–2009). A regional approach is being used; the malacofauna of the Great Lakes region is treated as part of the Eastern Africa Freshwater Biodiversity Assessment (Darwall et al., 2005), that of the Egyptian Nile will be treated in the assessment of Northern African, to be published in 2010 (Cuttelod et al., 2007), and that of the Mountain Nile, White Nile and Blue Nile in the Northeastern assessment (to be published in 2010).

Truly unique is the completeness of the African fossil record of Late Tertiary freshwater molluscs and the length and intensity of palaeontological investigations on the subject. Research was initiated in Egypt in the nineteenth century as part of the efforts to reconstruct the evolution of human civilisation along the Nile (von Martens, 1886; Germain, 1909). In the region of the Great Lakes, the earliest palaeontological investigations such as the Wayland Expedition and the Cambridge Expedition started in the Albertine Basin around 1920 but the interest in these rich fossil malacofaunas was minimal (Cox, 1926; Fuchs, 1934, 1936). In the 1970s, the African Rift Valley, in particular the Turkana Basin, produced impressive hominid finds and was acclaimed the cradle of mankind. A steep increase of research on other fossil groups followed (e.g., Harris et al., 1988; Leakey & Harris, 2003). The study of the fossil molluscs proved important not only for palaeoenvironmental reconstruction and biostratigraphy but it also yielded interesting insights in evolutionary processes (Williamson, 1981a, 1981b, 1990; Van Damme, 1984; Van Damme & Pickford, 1994, 1995, 1999, 2003; Van Bocxlaer & Van Damme, in press).

2 Composition of the Modern Nile Fauna in a Continental Perspective

About 58 genera of freshwater gastropods and 17 genera of freshwater bivalves occur in Africa, not taking into account the malacofauna of the Maghreb with its many endemic creno- and stygobiont hydrobiids (~15 genera) (Ghamizi, 1998), the endemic thalassoid paludomids (formerly thiarids) of Lake Tanganyika (~18 genera) (West et al., 2003) and those restricted to brackish waters (~20 genera) (Brown, 1994; Daget, 1998).

The Nile harbours about 25 gastropod genera (Table 1) and 11 bivalve genera (Table 2), which represent 43% and 65% of all African genera, as mentioned above (Brown, 1994; Daget, 1998; Graf & Cummings, 2007b). These are low percentages considering the geographical extent of the Nile Basin and the climatic zones it covers. Moreover, the basin includes a vast range of aquatic habitats and ecosystems,

Table 1 Freshwater Gastropods of the Nile, Chad and Turkana Basins

		Nile Basin					
Species		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region	Chad Basin	Turkana Basin/ Omo Delta
PROSOBRANCHIA							
Neritidae							
Theodoxus niloticus	E/P	X	?				
Viviparidae							
Bellamya unicolor		X	X	X	X	X	
Bellamya phthinotropis	E				Vi		
Bellamya costulata	E				Vi		
Bellamya jucunda	E				Vi		
Bellamya constricta	E				Vi		
Bellamya trochlearis	E				Vi		
Bellamya rubicunda	E				Al		
Ampullariidae							
Pila ovata		X			X	X	
Pila wernei				X		X	Om
Lanistes carinatus		X		X	X		
Lanistes ovum				X		X	
Valvatidae							
Valvata nilotica	E/P	X	X				
Hydrobiidae							
Hydrobia ventrosa	P	X					
Hydrobia musaensis	E/P	X					

(continued)

Table 1 (continued)

		Nile Basin					
Species		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region	Chad Basin	Turkana Basin/ Omo Delta
Pomatiopsidae							
Tomichia sp. n.	E						Tu
Bithyniidae							
Gabbiella humerosa complex					X		
Gabbiella senaariensis		X		X		X	
Gabbiella kichiwambae	E				X		
Gabbiella parva	E				X		
Gabbiella schweinfurthi	?E			X			
Gabbiella barthi	E				X		
Gabbiella candida	E				Al		
Gabbiella walleri	E				Al		
Gabbiella neothaumiformis	E					X	
Gabbiella tchadiensis	E					X	
Gabbiella rosea	E						Tu
Thiaridae							
Melanoides tuberculata		X	X	X	X	X	Om, Tu
Pleuroceridae							
Cleopatra bulimoides		X	X	X	X	X	Om
Cleopatra sp. indet	?E						Tu
Cleopatra guillemei					X		
Cleopatra cridlandi	E				Vi		
Cleopatra hemmingi							X
Potamididae							
Pirenella conica		X					
PULMONATA							

Lymnaeidae							
Lymnaea natalensis		X	X	X	X	X	
Lymnaea columella	Int	X					
Lymnaea truncatula	P	X					
Lymnaea stagnalis	P	X					
Ancylidae							
Ancylus fuviatilis	P/Mnt		X				
Ancylus regularis	E/P/Mnt		X				
Burnupia edwardiana	E				Ed		
Burnupia stuhlmanni	E				Vi		
Ferrissia isseli		X	X	?			
Ferrissia clessiniana	?E	X					
Ferrissia l'hotelleriei	?E	X					
Ferrissia pallaryi	?E	X					
Ferrissia kavirondica	E				Vi		
Ferrissia eburnensis						X	
Planorbidae							
Planorbis planorbis	P	X					
Afrogyrus coretus		X	X	X	X	X	
Armiger crista	P/Mnt		X				
Ceratophallus natalensis			X	?	X	X	
Ceratophallus kigeziensis					X		Tu
Ceratophallus kisumiensis	E				Vi		
Ceratophallus bicarinatus			X		Al	X	
Ceratophallus subtilis	E				Vi		
Ceratophallus concavus	E				Vi		

(continued)

Table 1 (continued)

		Nile Basin					
Species		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region	Chad Basin	Turkana Basin/ Omo Delta
Ceratophallus crassus	E				Vi		
?Ceratophallus apertus	E				Ed		
?Ceratophallus faini	E				Al		
Gyraulus costulatus		X	X	X	X	X	
?Gyraulus sp. indet.							Tu
Lentorbis junodi				X	X	X	
Segmentorbis angustus		X	X	X	X	X	Tu
Segmentorbis eussoensis				X	?		
Segmentorbis kanisaensis				X		X	
Biomphalaria pfeifferi			X	X		X	
Biomphalaria choanomphala	E				Vi, Al, Ky		
Biomphalaria elegans	E				Al		
Biomphalaria smithi	E				Ed		
Biomphalaria stanleyi					Al	X	
Biomphalaria alexandrina	E	X		X			
Biomphalaria sudanica				X	X	X	
Biomphalaria tchadiensis	E					X	
Helisoma duryi	Int	X					
Bulinus africanus			X		X		
Bulinus nasutus					X		
Bulinus jousseaumei						X	
Bulinus ugandae			X		X		

Bulinus umbilicatus				X		X	
Bulinus obtusus						X	
Bulinus hexaploidus	Mnt		X				
Bulinus octoploidus	Mnt		X				
Bulinus transversalis	E				Vi		
Bulinus trigonus	E				Vi, Ed		
Bulinus natalensis/tropicus com			X				
Bulinus truncatus		X	X	X	X	X	
Bulinus permembranaceus	Mnt				X		
Bulinus forskalii		X	X	X	X	X	X
Bulinus scalaris			X				
Bulinus reticulatus			X		X		
Physidae							
Physa acuta	Int	X	X				
Total n species	92	29	25 (26)	21 (23)	50 (51)	27	11
Total Palaearctic species	11	8	4 (5)	0	0	0	0
Total montane species	6	0	5	0	1	0	0
Total endemic species	37 (42)	5 (8)	2 (3)	1?	27	3	2 (4)
Total introduced species	3	3	1	0	0	0	0

Abbreviations: E: endemic; P: Palaearctic; Int: introduced; Mnt: montane; Al: L. Albert & Albert Nile; Ed: Lake Edward; Ky: Lake Kyoga; Om: Omo Delta; Tu: Lake Turkana; Vi: Lake Victoria.

Table 2 Freshwater Bivalves of the Nile, Chad and Turkana Basins

		Nile Basin					
Species		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region	Chad Basin	Turkana Basin/ Omo Delta
UNIONOIDA							
Unionidae							
Unio abyssinicus	E/P/Mnt		X				
Unio dembeae	P		X				
Coelatura aegyptiaca		X		X	X	X	Om
Coelatura gabonensis						X	
Coelatura bangoranensis	E					X	
Coelatura bakeri	E				Al, Ed		
Coelatura stuhlmanni	E				Al, Ed		
Coelatura hauttecoeuri complex	E				Vi, Ky		
Coelatura alluaudi	E				Vi		
Coelatura cridlandi	E				Vi		
Nitia teretiuscula	E	X		X		X	
Nitia monceti	E				Vi		
Nitia acuminata	E			?	Al		
Nitia chefneuxi (extinct?)	E						?Om
Nitia mutelaeformis	E					X	
Iridinidae (=Mutelidae auct.)							
Aspatharia chaiziana				X		X	
Aspatharia pfeifferiana						X	
Aspatharia marnoi	E			X			
Aspatharia divaricata	E				Vi		
Chambardia rubens		X		X		X	

Chambardia wismanni						X	
Chambardia wahlbergi		X		X	X	X	Om
Chambardia tabula						X	
Chambardia letourneuxi	E	X					
Chambardia trapezia	E				Vi, Al, Ed		
Chambardia bourguignati	E				Vi		
Mutela dubia		X		X	Al, Ed	X	Om
Mutela joubini						X	
Mutela rostrata		X		X	Al, Ed	X	Om
Mutela bourguignati	E				Vi		
Mutela alluaudi	E				Al, Ed		
Etheriidae							
Etheria elliptica			X	X	X	X	Om
VENEROIDA							
Corbiculidae							
Corbicula fluminalis		X	X	X	X	X	Om,?Tu
Pisidiidae (=Sphaeriidae auct.)							
Sphaerium hartmanni complex		X	X	X	X	X	
Sphaerium victoriae complex					Vi, Al, Ed		
Sphaerium stuhlmanni	E				Vi		
Sphaerium regulare	E				Vi		
Sphaerium nyanzae	E				Vi		
Pisidium pirothi		X	X	X	X	X	
Pisidium fistulosum	E				Vi		
Pisidium amnicum	Int	X					
Pisidium kenianum			X				
Pisidium armillatum	Mnt				X		
Pisidium invenustum	Mnt				X		

(continued)

Table 2 (continued)

Species		Nile Basin				Chad Basin	Turkana Basin/ Omo Delta
		Lower Nile	Blue Nile/ Ethiopian Highlands	Upper Nile/ White Nile	Great Lakes region		
Pisidium montigenum	Mnt				X		
Pisidium ethiopicum	E/Mnt		X				
Pisidium casertanum	P		X		X		
Pisidium subtruncatum	P						
Eupera ferruginea		X	X	X	X	X	
Eupera crassa	E				Vi		
Total n species:	51	12	11	13 (14)	32	18	6 (7)
Total Palaearctic species	4	4	3	0	1	0	0
Total montane species	5	1	2	0	3	0	0
Total endemic species	25	3	2	2 (3)	16	2	1?
Total introduced species	1	1	0	0	0	0	0

Abbreviations: E: endemic; P: Palaearctic; Int: introduced; Mnt: montane; Al: L. Albert & Albert Nile; Ed: Lake Edward; Ky: Lake Kyoga; Om: Omo Delta; Tu: Lake Turkana; Vi: Lake Victoria.

encompassing a large river delta that connects to the Mediterranean palaearctic zone, a lower Nile surrounded by desert, several extensive artificial lakes, e.g., Lake Nasser, a drowned upper Nile with extensive swamps and floodplains in tropical lowland (the Sudd) and montane bogs and the extensive lake Tana in the Ethiopian Highlands, large equatorial rift lakes such as Lake Albert, Lake Edward and Lake Victoria and glacier lakes on the Rwenzoris (Thieme et al., 2005).

When a comparison of the mollusc fauna of the two largest African freshwater systems, the Nile and the Congo, is made at species level, the low diversity of the Nile becomes even more obvious. The Nile is the second largest drainage system of Africa, only surpassed by the Congo (Goudie, 2005). Compared to the Nile, the habitats in the Congo Basin are less diversified, consisting mainly of rainforest rivers and large rift lakes (Thieme et al., 2005). Brown (1994), comparing the species richness of the fluvial snail faunas of the Nile and Congo Basins with exclusion of the large lakes, pointed out that the number of gastropods known from the Nile Basin is about half that of the Congo, namely 51 to 96 species (taking *Ferrissia* and *Burnupia* into account as genera only) and the proportion of endemics is much lower, namely 10 out of 51 species. In bivalves, biodiversity is equally lower in the Nile Basin, with a total of 28 species versus 38 in the Congo drainage. The degree of bivalve endemism is dramatically lower in the Nile Basin with only 5 endemic species compared to 18 in the Congo Basin (Daget, 1998; Graf & Cummings, 2007a, b).

Moreover, the molluscan faunas of both basins have a significantly different community composition (Fig. 1), reflecting important ecological differences. In the Congo Basin prosobranch snails and unionoid bivalves are overwhelmingly dominant, while in the Nile Basin pulmonate snails and pea and basket mussels (Sphaeriidae and Corbiculidae) are more abundant. Concerning gastropods, the ratio prosobranchs to pulmonates is 74/22, thus >3/1, in the Congo Basin, while in the Nile Basin this ratio is reversed, namely 15/36 or <1/2. For bivalves, the ratio unionoids to veneroids in the Congo Basin is 25/10 while in the Nile Basin it again is reversed, namely 13/18.

A contrast in species richness between the Nile and Congo Basins can also be observed in the brackish water faunas; the relative poverty of the Nile fauna is apparent. In the oligohaline to mesohaline waters of the Congo estuary six gastropod genera (*Neritina, Hydrobia*,?*Potamopyrgus* (probably a distinct genus), *Tympanotonus*, *Pachymelania* and the pulmonate *Melampus*) and two bivalve genera (*Egeria* and *Iphigenia*) occur, one *Egeria* species being endemic (Pilsbry & Bequaert, 1927; Brown, 1994; Daget, 1998). In the oligo- to mesohaline part of the Nile estuary two gastropod genera (*Hydrobia, Pirenella*) and two bivalves (*Cerastoderma* and *Scrobicularia*) occur. None are endemic (Van Damme, 1984).

The two African basins are hence inhabited by what is essentially a different molluscan community. The explanation for this phenomenon becomes clear when the reproduction, the dispersal strategies and the habitat preferences of the diverse groups (Fig. 1) are taken into consideration.

African freshwater prosobranchs have separate sexes and reproduce via cross-fertilisation, except for parthenogenetic *Melanoides* and hermaphroditic *Valvata* (Brown, 1994). Prosobranchs are viviparous, ovoviviparous or oviparous (Brown,

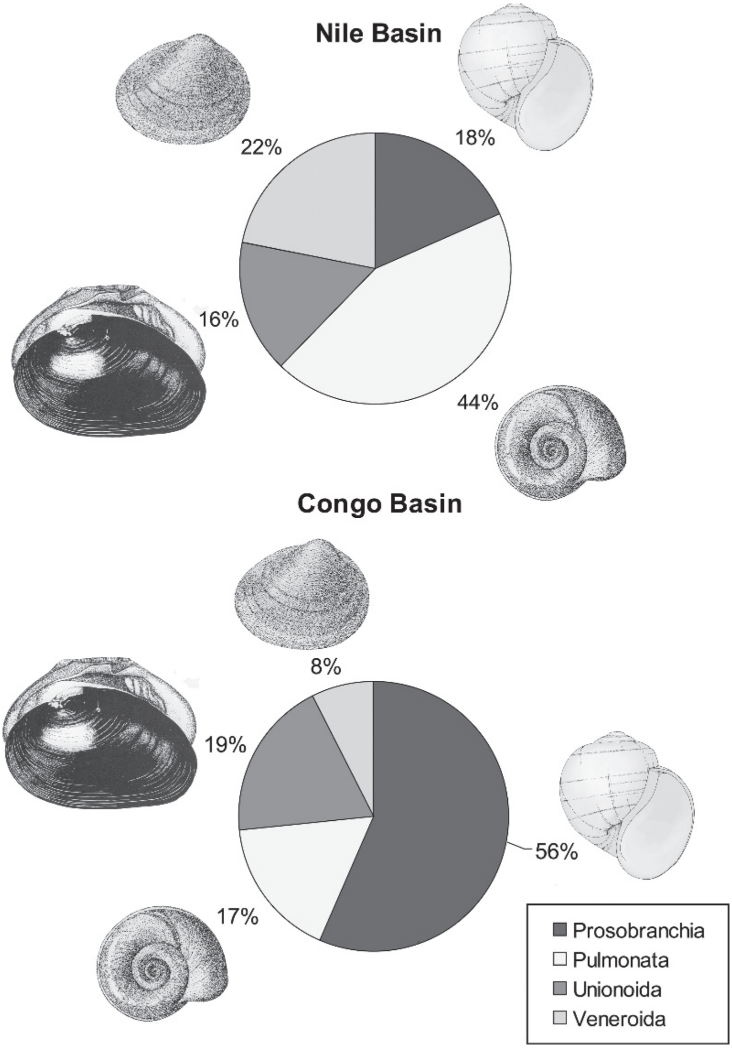

Fig. 1 Taxonomic differences at a high hierarchical level in the composition of the malacofauna of the Nile and Congo Basins.

1994) and the number of young produced is usually limited. The young have generally a cryptic lifestyle, hiding in the sediment or between vegetation. Prosobranch species are gill-breathers. Most have a relatively thick shell and operculum, protections against predators. They are benthic or endobenthic organisms that favour well oxygenated habitats and colonise open substrates in rivers and lakes along a vertical gradient from the littoral to sizeable depths (over −50 m). Dispersal capacities of most prosobranchs are low, except for the parthenogenetic and hermaphroditic taxa, due to their mode of reproduction and life style (Van Damme, 1984; Brown, 1994).

African unionoids (Unionidae, Iridinidae, Etheriidae) also reproduce sexually, breath through gills and live in the sediment (endobenthic) except for the river oyster *Etheria elliptica*, which lives cemented to hard substrates. They have adapted their reproductive strategies to life in freshwater streams and rivers by two important aspects, viz. parental care and parasitism. Both counteract the unidirectional drag to the ocean by river currents that planktonic larvae would experience (Graf & Cummings, 2006). Since active dispersal capacities are limited in unionoid bivalves, their dispersal capacity is mainly determined by the dispersal capacities of their fish host. Many unionoids are highly selective as to the type of sediment they settle in. They also tend to aggregate as a result of their mode of reproduction and limited active dispersal capacities, so that populations can be strongly localised (Van Damme, 1984).

African pulmonates are hermaphroditic and oviparous (Van Damme, 1984). They have no operculum, a fragile shell and a mantle cavity that serves as an air-breading organ (lung), lacking true gills (Brown, 1994). They hence stay close to the water surface, avoiding turbulent waters and have difficulties in colonising depths. Pulmonates favour shallow waters with aquatic vegetation, on which they depend not only for protection but also for food (they are microfeeders scraping off Aufwuchs) and for reproduction, i.e., the deposition of their egg clusters (Brown, 1994). In general, pulmonates inhabit more marginal, less stable (both in terms of longevity and water conditions) water bodies than prosobranchs. Due to their reproductive strategy and the fact that their eggs (1 to 100 per cluster) are encapsulated in a drought resistant, gelatinous substance, they easily disperse via zoochory.

Corbiculid mussels are known for their great invasive potential, partly induced by their wide spectrum of reproductive strategies (Glaubrecht et al., 2006). Sphaeriid mussels are self-fertilising hermaphrodites that developed parental care via brooding, producing viviparous, crawl-away juveniles (Park & Ó Foighil, 2000; Korniushin & Glaubrecht, 2006). Juvenile pea clams (Sphaeriidae) do not only live on the bottom but crawl on plants using their sticky foot. They also are easily dispersed by water birds and water insects, clutching at their legs and feathers (for an overview on zoochorous dispersal see Van Damme, 1984 and Wesselingh et al., 1999).

The Congo Basin is hence inhabited by a molluscan fauna with high species richness in benthic or endobenthic K-strategists, while in the Nile system the number of K-strategists is limited and that of r-strategists is markedly higher. The most speciose group in the Nile is the family Planorbidae, particularly well-represented by the genus *Bulinus*. This taxon can be used as an example of diversification and speciation in the Nile basin, because it has been intensely studied (see Brown, 1994). *Bulinus* is highly eurytopic, excelling in exploiting all kinds of stagnant waters such as small seasonal water bodies, pools in floodplains, artificial ponds, dams, etc. and is not well presented in flowing waters and lakes. Moreover, *Bulinus* is able to survive droughts. Reproduction occurs by both cross-fertilisation (outcrossing) and self-fertilisation (selfing). While outcrossing, maintaining heterogeneity in a population, seems to be preferred; virgin individuals introduced zoochorously in newly formed pools will successfully self-fertilise (Brown, 1994). Brown (1994) suggested that the ability of self fertilisation, resulting in numerous ‘biotypes’ with different fixed heterozygous loci, probably gave rise to polyploidy. *Bulinus* species originally are diploid, but the extremely successful and eurytopic *B. truncatus*, is tetraploid. *Bulinus truncatu*s has a considerable aestivation capacity and is a successful colonist of all kinds of artificial biotopes such as irrigation systems and man-made lakes as far north as Portugal, Sardinia and Corsica and as far south as the DRC and Congo. Other polyploids, namely the tetraploid *B. membranaceus*, the hexaploid *B. hexaploidus* and the octoploid *B. octoploidus* are adapted to high altitudes (Kenyan mountains, Ethiopian highlands). From this evidence Brown (1994) postulated that polyploidy enabled *Bulinus* to extend successfully to extremely altered/stressed habitats as well as to colder regions, i.e. Mediterranean Europe and the Afrotropical montane region.

Most of the malacofauna of the Nile Basin – except for that of the large lakes – did not originate by diversification and speciation within the river and its tributaries *sensu stricto*, but via founder effect divergence in temporary waters after faunal exchange (via hydrological contacts) with the main hydrographic system. In contrast, the malacofauna of the Congo Basin diversified *in situ* in streams. The fundamental difference in natural history, diversity and evolution of the malacofaunas of the two largest African Basins reflects a difference in environmental stability. The Congo fauna is the product of selection and speciation in a stable environment since Miocene times (Goudie, 2005), favouring diversification in K-selective stenotopic taxa with a low to modest dispersal capacity. Speciation, according to the distribution patterns observed, occurred within fluvial habitats, e.g., either in tributaries that temporally became geographically or ecologically isolated from the rest of the hydrographic network or in surface waters of smaller basins that became subsequently connected. The Nile Basin on the other hand represents a much less stable hydrological system, that suffered major changes during its Cenozoic history, with the birth of the modern Nile happening only ~25 ka ago (Issawi & McCauley, 1992; Goudie, 2005). The Nile fauna, as such, is the product of selection and speciation in a highly instable and stressed environment, which favoured diversification in r-selective eurytopic taxa with high dispersal capacities.

3 Cenozoic History of the Nile Basin and Its Molluscan Fauna

3.1 Oligocene Times

During Oligocene times, part of the area occupied at present by the Nile Basin may have been occupied by the Qena river system, flowing initially west and subsequently southwest (Goudie, 2005). Though numerous Oligocene molluscan sites are known from northern Africa (Mauritania to Egypt and Sudan), no fossils indicative for the presence of a large river have been recovered. The malacofauna is extremely poor, consisting – with exception for one planorbid snail (gen. sp.

indet.) – exclusively of ampullariids (*Lanistes, Pila, Pseudoceratodes*) (Van Damme, 1984). This monotonous fauna of air-breathing snails indicates that the dominant palaeo-environment during that period was tropical stagnant swamp with conditions similar to the present Sudd. During the Oligocene, the Arabian Peninsula was breaking away from Africa (Schattner et al., 2006). In the region of Thaytiniti (Oman) a molluscan fauna of Oligocene age (corresponding to the Fayum L 41 level, Martin Pickford, pers. comm.) has also been discovered but unfortunately only perfunctorily sampled. On the Arabian Peninsula, ampullariids indicative for the same paludinal palaeo-environment as in the Qena Basin, are equally dominant, but the marked compositional differences on genus and on species level do indicate a geographic separation between the faunas of eastern Arabia and northern Africa and little exchange between both regions in the Oligocene (Van Damme, pers. data).

3.2 Miocene Times

Fossil exchange during the early Miocene is poorly documented. Some freshwater gastropods may have invaded from tropical Asia, such as e.g. *Melanoides*. Fossil assemblages in the northern part of the East African Rift indicate that most molluscan genera recently occurring in the Afrotropics were already present in the Middle Miocene, some possibly having arrived from Eurasia in earlier times. The Late Cenozoic (Early Miocene to present) history of the Afrotropical malacofauna is best recorded in deposits of the East African Rift System, namely in the Albertine Basin (Uganda-Congo) (Adam, 1957, 1959; Williamson, 1990; Morris, 1995; Van Damme & Pickford, 1994, 1995, 1999, 2003), the Turkana Basin (Kenya-Ethiopia) (Williamson, 1981a, 1981b; Van Damme, 1984; Williamson, 1985; Van Bocxlaer et al., 2008; Van Bocxlaer & Van Damme, in press), the Tugen Hills (Central Kenya) and Rushinga Island (L. Victoria, Kenya) (Van Damme, 1984; Pickford, 1986; De Groeve, 2005). All these regions are, or were once part of the Nile Basin.

During the Late Miocene, between ~8.0 and 5.4 Ma (Late Tortonian and Messinian stages) northern Africa and Arabia experienced a humid phase (the Zeit Wet Phase) due to the initiation of the Asian/African monsoon ~8.0 Ma (Griffin, 1999, 2002; Böhme, 2004). At the onset of that wet phase the Eonile (Said, 1981, 1993) arose. Originally, this was a modest river not reaching far beyond the Egyptian-Sudanese border. But during the Messinian salinity crisis ~5.96–5.33 Ma, the Mediterranean dried out and brackish lakes formed on the bottom (Krijgsman et al., 1999). The Eonile eroded an impressive canyon from Aswan till the Mediterranean floor with a width varying between 10 and 20 km and a depth of 170 m at Aswan and 2,500 m north of Cairo (Said, 1993; Butzer, 1999; Griffin, 1999). At the end of the Messinian stage the Eonile ended in the oligohaline Palaeolake Cyrenaica, at the bottom of the eastern Mediterranean (Issawi & McCauley, 1992; Griffin, 1999, 2002; Goudie, 2005; Griffin, 2006). The last stage of this palaeolake is better known as Lago Mare (~5.5 Ma), since most deposits are located in Italy.

A major part of Modern African fish families were first recorded in the Late Miocene, namely the Osteoglossidae, Mormyridae, Gymnarchidae, the barbid genus *Barbus*, Distichodontidae, Characidae, most Bagridae, Tetraodontidae and Schilbeidae (Stewart, 2001). Channidae were considered to have crossed from Eurasia during this period (Böhme, 2004) but a recent discovery of Oligocene remains in Egypt (Murray, 2006) contradicts this, suggesting that the observed pattern could be due to preservational bias.

It has been suggested that the major Late Miocene invasion route between Eurasia and Africa for freshwater organisms was via the above-mentioned Mediterranean palaeolake southwards into Africa via the Eonile (e.g., Stewart, 2001, based on fish distribution). The molluscan record does not confirm this (see Heller, 2007 for an in depth discussion). During the Late Messinian, the Eonile had formed a deep canyon. Similar modern canyon rivers confined within vertical walls, with denuded rocky bottoms, and additionally with seasonal water fluctuations are poor migration routes for benthic prosobranchs and endobenthic unionoids. This is exemplified by their absence from the Grand Canyon of the Colorado river (USA) (Spamer & Bogan, 1993), from the gorge of the Blue Nile (Brown, 1994), and from the rapids of the Matadi-Boma Channel (Lower Congo), where only rheophilous gastropods adapted to adhere to rocks and the cementing river oyster *Etheria elliptica* occur (Brown, 1994; Graf, pers. comm., 2007). A second argument is the absence of Paratethyian molluscs in north-eastern Africa. This conspicuous absence remains a major zoogeographic riddle (Heller, 2007). Palaeolake Cyrenaica/Lago Mare was fed by water from the more eastward located brackish/freshwater Euxinian and Pannonian palaeolakes (Dacic Basin) (Magyar & Sztanó, 2007) and was inhabited by a highly typical Pannonian euryhaline community consisting of Neritidae, Thiaridae, Melanopsidae, Hydrobiidae, Cardiidae (of the endemic subfamily Limnocardiinae) and Dreissenidae (Esu, 2006). Remnants of this Paratethyian fauna, in particular species of the genus *Melanopsis*, different hydrobiid genera, and *Psilunio* presently occur all around the Mediterranean Basin. The main exception is the Mediterranean rivers in a region from Libya east to Sinai (Heller, 2007). The presence of the abovementioned genera in the rivers around the western Mediterranean proves that these Pannonian molluscs succeeded in moving from Palaeolake Cyrenaica stream upwards, reaching the parts of river basins that presently lie above sea level. The absence of Pannonian relicts in Quaternary deposits of the Nile system suggests that in contrast to the rest of the Mediterranean basins, either the Eonile was not colonised by a Pannonian malacofauna, or that all traces of this fauna were subsequently wiped out (though the Pannonian molluscs were/are highly eurytopic). No Afrotropical fossils have yet been found in the rich Lago Mare deposits nor inversely have any Paratethyian fossils been recorded from north-eastern African deposits. This suggests that, in contrast to the basins in the Maghreb, the Iberian Peninsula, Italy and the Levant, there was limited interchange of malacofaunas between the palaeo-lake Cyrenaica/Lago Mare and the river systems of north-eastern Africa (Eonile and Palaeosahabi). A possible exception may be the snail *Theodoxus niloticus* (Neritidae), endemic to the lower Nile (and Blue Nile?). This species is euryhaline and rheophilous, and may have been able to invade the canyon of the Eonile via Palaeolake Cyrenaica. Brown (1994) states that *T. niloticus* appears closely related to *T. jordanicus* from the Levant. This is correct, but does not automatically imply a recent arrival in Africa, certainly since representatives of the Neritidae are morphologically conservative and possess a limited number of diagnostic features. A last argument against the Palaeolake Cyrenaica-Eonile as an invasion route is the discrepancy in time. The palaeotropical freshwater molluscs that invaded Africa during the Late Miocene appear around 7–6 Ma in the fossil record, i.e. before the Messinian Salinity Crisis took place. The appearance of the Asiotropic unionids in Africa hence occurred at a time when the Mediterranean was still a sea, and hence a barrier.

Reconstructions of the palaeo-environment and tectonic events in the Ethiopian Rift during the Late Miocene–Early Pliocene (Redfield et al., 2003) show the existence of a broad connection (the Danakil Isthmus) between Yemen and Ethiopia in Miocene times. South of that land bridge, a string of lakes and rivers stretched out along the axis of the Danakil-Awash valley towards Kenya (Redfield et al., 2003). Environmental conditions in the region of the Horn of Africa during the Late Miocene were hence suitable for molluscan invaders (e.g. the unionid genus *Pseudobovaria*; Van Damme pers. data) while conditions in the Mediterranean-Eonile region were not, and those in the Sinai-Gulf of Suez region were suboptimal, with playa-like brackish waters/badland conditions (Griffin, 1999).

3.3 Pliocene Times

In the early Pliocene, water levels in the Mediterranean rose, and the canyon of the Eonile became a marine gulf extending as far south as Aswan. This marine gulf phase separates the earlier Eonile stage and the subsequent Palaeonile stage *sensu* Said (1981). The latter can be defined as the period during which a freshwater river again extended north to the region of Cairo. The Palaeonile was a regional river that did not extend beyond Egypt and supposedly was active from ~4.0 till 1.8 Ma, i.e., almost during the whole Pliocene epoch (Said, 1981; Butzer, 1999). A long and continuous active phase appears however unlikely in the light of our present knowledge of the climatological dynamics and the occurrence of marked dry/wet phases in Pliocene eastern Africa (Trauth et al., 2005).

The Pliocene-Early Pleistocene palaeo-hydrography of the Nile Basin in regions south of Egypt remains poorly documented and the reconstruction summarised below remains conjectural. It is assumed by Salama (1987, 1997, 2005) that a series of endorheic basins had formed along the axis of an ancient rift in the region at present occupied by the White Nile. These basins are suggested to have contained episodic shallow and alkaline palaeolakes extending from the Sudd till southern Kordofan. Salama (2005) recognises from south to north eight of such closed lake basins: (1) Palaeolake Sudd, fed by the Bahr el Arab, the White Nile and the Sobat River, (2) Palaeolake Adar with the Adar river, (3) Palaeolake Nuba, fed by the khor Abu Habil, (4) Palaeolake Gezira in which some rivers from the Ethiopian

Highlands ended (including the Blue Nile?), (5) Palaeolake Atbara with the Atbara River, (6) Palaeolake Gash with the Gash River, (7) Palaeolake Bayuda, fed by the Wadi El Melik and the Wadi El Mogaden and (8) Palaeolake El Qaab in which the Wadi Howar discharged. At what periods these lakes existed and whether they existed simultaneously is unknown. According to Salama (2005) is it possible that these shallow alkaline lakes, situated in the 'Intercontinental Rift', became interlinked (and fresh) during wet phases. According to this scenario a Pliocene White Nile may have formed intermittently during the Late Pliocene-Early Pleistocene, establishing an aquatic migration route not only in north-south direction but equally in a west–east sense, i.e. between the Chad Basin and the Turkana Basin (see further). As to the existence of a Pliocene Blue Nile, if such a river existed, it probably did not run north-westwards to the Nile Basin but eastwards to the Red Sea (Goudie, 2005).

Still more to the south, the area of the Great Lakes drained west into the Palaeo-Congo, the continental divide being situated along the western shoulder of the Gregory rift (Van Damme & Pickford, 2003; Goudie, 2005). The main drainage east of this rift shoulder was in a north-south direction. It consisted of the Palaeo-Omo river, originating on the Ethiopian Plateau, the Turkwell-Kerio system and the Palaeo-Turkana river *sensu* Feibel (1999), a vast system that reached the Indian Ocean at the equator (see Fig. 2).

No fossil assemblages of Pliocene age are known from the Nile Basin in Egypt and Sudan. However, 'Nilotic' faunas, i.e. faunas that consist for an important part of species presently occurring in the White Nile and the Nile, appear in the Turkana Basin and Albert Basin at several stages during the Pliocene. These provide evidence of the molluscan fauna that existed north of these basins. The appearance of these Nilotic invaders, e.g., *Valvata* sp., and *Coelatura aegyptica* (Van Bocxlaer et al., 2008), in the Turkana Basin coincides with a wet phase ~2.0–1.8 Ma that was not confined to the basin only (Brown & Feibel, 1991) but was widespread over East Africa (Trauth et al., 2005). In the Albertine Basin similar invasions occurred around that time (Van Damme & Pickford, 1994, 1999). These data hence seem to corroborate Salama's hypothesis.

The 'Nilotic' invaders of tropical origin (not the palaeartic ones such as *Valvata*) may have originated in the region of the Chad Basin, actually using the Sudanese Nile as intermittent stepping stone during wet phases (see further). The appearance during Pliocene times (from ~3 Ma onward) of Palaeartic taxa closely related or identical to species occurring in the Levant (e.g., *Unio dembeae, Corbicula fluminalis*) indicates that a new hydrographic connection had been established with Eurasia. Since the Street of Bab el Mandeb, connecting the Red Sea with the Indian Ocean has been open from around 4.5 Ma till the present (Redfield et al., 2003), the only possible invasion route was via the Sinai. These invaders, being cold water taxa, must have followed the Levant-Sinai-Nile route during wet but relatively cold phases. During the Late Pliocene, species belonging to the tropical snail genera *Bellamya* and *Melanoides* are also found in Levantine deposits (Sivan et al., 2006; Heller, 2007). These species may hence have followed the same Sinai-corridor out of Africa during wet but relatively warm phases. However, since the genera *Bellamya*

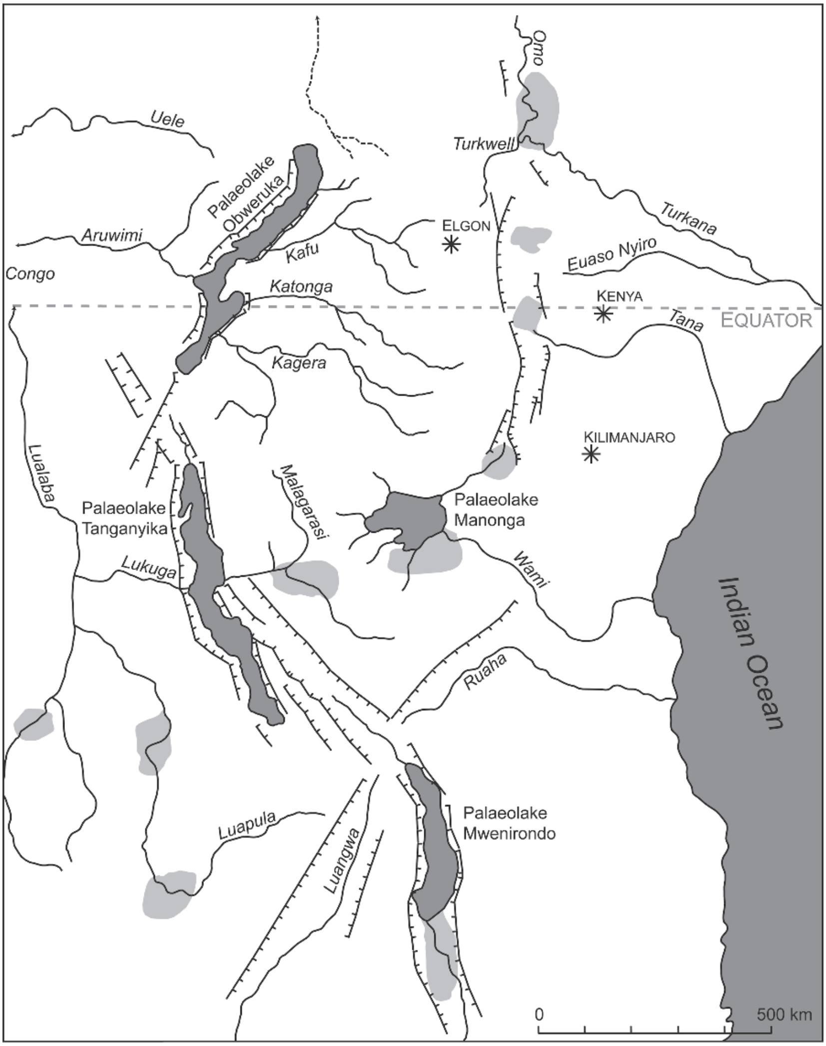

Fig. 2 Hydrographical configuration in the Great African Rift region in the Early Pliocene (ca 4 Ma). A large and deep rift lake in the Albertine Basin, Palaeolake Obweruka, started to divide into a southern and a northern basin by the rising Rwenzori Horst. Palaeolake Tanganyika may either have already reached its present configuration (as is figured) or may still have been confined to the Southern Basin of the Tanganyika Trough. Both lakes at that time drained westwards to the Congo. Early Pliocene Palaeolake Mwenirondo was probably confined to the northern Livingstone Basin, possibly extending in the Ushishya Basin of the Malawi Trough (as is figured). The region of present Lake Victoria was drained by rivers flowing westward to Palaeolake Obweruka. South of this drainage the shallow Palaeolake Manonga filled the Wembere-Manonga Basin (max. depth: ~20–30 m) (Tanzania), draining eastwards towards the Indian Ocean. In the Turkana region, the Palaeo-Omo meandered through a shallow basin (intermittently filled with short-lived lakes) southwards to the Indian Ocean via the now defunct 'Turkana River'. The coastal outline of East Africa represented in the figure does not take into account marine transgressions during that period (after Van Damme & Pickford, 2003). Light grey zones indicate swamps and temporal lakes.

and *Melanoides* are actually better represented in tropical Asia than in Africa, they may have invaded the Levant from the Iranian region (Heller, 2007). There is no indisputable evidence that the Nile or the Sinai land bridge ever was used by fresh water molluscs for dispersal northwards, in contrast to a considerable number of (non-primary) freshwater fish (Goren & Ortal, 1999).

3.4 Pleistocene – Modern Times

During an early Pleistocene dry phase, from ~1.7 Ma, the Palaeonile in Egypt became a seasonal river (wadi) (Goudie, 2005), and finally ceased flowing. After this dry phase, around 1.5 Ma, the Protonile *sensu* Said (1981) was formed but, as its predecessors, it remained largely confined to Egypt. It is only in the mid-Pleistocene, around 700 ka that the first extensive Nile system, the Prenile *sensu* Said (1981), came into existence. It was fed by water from southern Sudan and from the Ethiopian Highland as, due to a tilting of the Ethiopian plateau, the Atbara and Blue Nile started flowing north and westwards rather than to the Red Sea (Goudie, 2005). The Prenile pushed into Egypt across the Nubian Swell by a series of cataracts. This vast river existed until ~200 ka, when hyperarid conditions set in and perennial flow ceased. About 120 ka ago, the Neonile *sensu* Said (1981), significantly less vigorous than the Prenile, originated (Goudie, 2005). Due to tectonic changes, the region of the Great Lakes tilted northward around 30,000–25,000 BP (Pickford et al., 1993) and became part of the Nile catchment.

With the help of modern dating techniques, in particular thermoluminescence, the complex palaeohydrography/limnology of the Nile basin during these Middle and Late Pleistocene times has been largely elucidated. During wet phases, respectively around 400, 320–250, 240–190, 155–120, 90–65 and 10–5 ka, corresponding with Marine Isotope Stage (MIS) 11, 9, 7, 6/5e, 5a or 5c and the Holocene wet phase, the Protonile and the Late Pleistocene-Holocene Neonile were (re)activated and extensive endorheic lakes as well as lakes connected with the Nile (Fayum lakes) formed in Egypt (Szabo et al., 1995; Churcher et al., 1999; Smith et al., 2004, 2007). Further southwards along the axis of the basin of the White Nile a palaeolake with a length of >500 km formed around 400 ka and there is evidence for several very high White Nile stands between 250 and 15 ka (Williams et al., 2001, 2003; Salama, 2005). During intermittent arid phases, the Nile became wadi-like, in particular during the Glacial Maximum around 16,000 BP, as mentioned above. The present hydrographic system came into existence around 12,000 BP when Lake Tana, Lake Victoria and Lake Albert, after having dried out during the last hyperarid phase, spilled over into the Blue, the Victorian and the White Nile (Goudie, 2005).

The fossil record from the Fayum depression, Kom Ombo, Bir Tarfawi, Bir Sahara, Kurkur Oasis, Kharga, Nubia and Kordofan, shows that during Middle to Late Pleistocene times the molluscan fauna was essentially the same as the present one (see Van Damme, 1984 for a detailed overview). The only difference is the ratio Palaearctic/Afrotropical species, which fluctuates with temperature. It should be pointed out that, with one exception in Lower Egypt, no fossil assemblages have been found that consist exclusively of palaearctic or afrotropical species (Van Damme, 1984). It would hence appear that temperatures, at least during the periods from which molluscan assemblages are known, did not descend below those occurring presently on the Ethiopian plateau, nor did they become too high to sustain palaearctic species.

The Late-Pleistocene or Holocene Nile deposits do not show evidence that the equatorial malacofauna from the Great Lakes region dispersed north into the White Nile after a hydrographic connection was established. On the contrary, during the Holocene some 'Nilotic' species, such as *Coelatura aegyptiaca* and *Mutela dubia,* did penetrate as far south as Lake Albert (Graf & Cummings, 2007b) and as far east as the Omo River delta, although not into Lake Turkana itself (Van Bocxlaer & Van Damme, in press).

3.5 Where Did the Nilotic Malacofauna Originate and Where Did It Survive During Hyperarid Phases?

The Late Cenozoic evolution of the palaeohydrography and palaeohydrology of the Nile Basin, sketched above, shows that the aquatic ecosystems in the Nile basin were highly unstable partly due to tectonic changes and mainly due to climatologic shifts. The absence of endemic Afrotropical molluscs in the Nile Basin north of the Great Lake region, except for two or one species of *Chambardia* that are able to aestivate during dry periods (see further), confirms the lack of persistence of perennial waters trough time.

In northeastern Africa, north of ~5° N, conditions were unsuitable for the evolution and persistence of groups such as unionoids and prosobranchs that presently populate the Nile (see discussion Congo/Nile fauna). Yet the fossil record indicates that a typical 'Nilotic' malacofauna existed and persisted from the Early Pliocene onward. These two statements appear to be contradictory, but it should be noted that the term 'Nilotic' is biogeographically misleading since this concept indicates similarities between faunas occurring in the Nile, the Chad, the Niger and the Senegal Basins, in contrast to e.g. faunas with Congolian affinities. Since the Nile is the largest African river it was implicitly assumed by former researchers (e.g., Huckriede & Venzlaff, 1962) that during the former African 'Pluvial Stages', the 'Nilotic' fauna had invaded these other basins from the Nile. The African Pluvial/Interpluvial chronological concept used by these authors, analogous to the Glacial/Interglacial stages, has been completely abandoned.

The presently available geological data make the hypothesis of a Plio-Pleistocene Nile as a centre of faunal diversity highly questionable. But if not from the Nile Basin, where did the 'Nilotic' fauna come from? Of all the basins mentioned above, the Niger Basin has the lowest percentage of 'Nilotic' species; less than one third of its modern gastropod fauna is shared with the Nile

Basin (Brown, 1994). The Ethiopian Highland and the Blue Nile are improbable candidates as region of origin and refuge, due to their climatologic instability and because a connection between the Ethiopian Highland and the Nile was established only during the Middle Pleistocene (Goudie, 2005). The Senegal Basin equally is situated in a highly unstable climatologic, semi-arid zone. Therefore, the Chad Basin, in which a molluscan fauna highly similar to the one of the Nile Basin but richer occurs, seems the most probable candidate as region of origin and as refuge. Griffin (1999, 2002, 2006) reported that during the Late Miocene a hydrographical system composed of the Palaeo-Chari/Logone + Neogene Lake Chad + the Eosahabi/Palaeosahabi rivers formed the longest (>3,000 km) and most important north-south directed river system in Africa for more than 2 million years (from 7.0 to ~4.5 Ma). During the early Messinian the Palaeosahabi exited Neogene L. Chad in the northeast to join the Eonile via the Mourdi Depression. Later, during the drawdown phase, the Eosahabi eroded a channel in which the present Ounianga lakes are located, winding northwest towards the Gulf of Sirt (Libya) where it cut a canyon of 396 m (Griffin, 2002, 2006). Though the size of Neogene Lake Chad (maximal extension = 700,000 km^2) and hence the amount of water flowing north into the Sahabi system appears to have been dependent of the precessional Milankovitch cycle (Krijgsman et al., 1999), the Chadian hydrographic system was during the Late Miocene and Early Pliocene the only long-lived system where the distinctive ‘Nilotic’ fauna could have developed. This suggestion is in agreement with the (disputed) hypothesis of Lihoreau et al. (2006) concerning the existence of a separate Chado-Libyan aquatic palaeobioprovince in the late Miocene. According to Lihoreau et al. (2006), the amphibian mammal fauna (anthracotherids, hippotamids) discovered in the late Miocene deposits of Toros-Menella (Northern Chad) is clearly distinctive from the East African one (e.g., from the Turkana Basin), evidencing hydrographical discontinuity between these regions at that time (see also Griffin, 2006).

During the remainder of the Pliocene and during the Pleistocene, with increasing aridity, the Sahabi system degraded, while more to the east, the Palaeonile and subsequently the Protonile evolved (see above). Although the Chadian Basin was likely too shallow to harbour a lake during hyperarid periods, the headwaters of some of its tributaries, such as the Chari and Logone, are situated so far south in the tropical rainforest belt that the Chadian molluscan community must have persisted there during arid times. During wet periods this fauna may not only have extended northwards again into the Chad Basin but may also have invaded the Nile Basin via the shallow watershed divide between the Chari and the Bahr el Arab south of Jebel Marra (from where the White Nile-Sudd Basin could be re-colonised) or via the divide of the Bahr el Gazal with the Wadi Howar northeast to the Nile in Egypt. Another possibility would be via the so-called Radar Rivers *sensu* McCauley et al. (1982) (see also Issawi & McCauley, 1992). These rivers channels, revealed under the Great Selima Sand Sheet by radar shuttle, were initially considered to run in a south-westward direction, forming a Nile-Chad connection during the Late Cenozoic. However, the direction of this drainage system has been disputed and in addition there is no way to date this system(s) (Goudie, 2005).

In conclusion it can be stated that the 'Nilotic' malacofauna probably did originate around the onset of the Pliocene in what Lihoreau et al. (2006) call the Chado-Libyan palaeobioprovince and that the area of refuge during hyperarid phases were the southern headwaters of the Chad Basin.

3.6 The Vanished Long-Lived Lakes in the Nile Basin, Their Thalassoid Malacofauna and Their Contribution to the Equatorial Malacofauna

According to the geological and biological evidence the lakes in the Albertine Basin, i.e., L. Albert and L. Edward, are young, namely about 25,000 years and their ecosystems may well be much younger (Pickford et al., 1993). The degree of endemism in their molluscan faunas is low as are the morphological differences with the malacofauna of the Albert and White Nile, into which these lakes drain. These inconspicuous differences are quite recent. From about 7.5 till 2.5 Ma a giant rift lake, Palaeolake Obweruka (surface: 27,000 km^2), persisted in the Albertine Basin that during most of its existence paralleled present Lake Tanganyika (present surface area: 32,900 km^2, present maximum depth: 1470 m) in size, depth and general configuration (see Fig. 2). Both lakes originated during the same geological time, the Late Miocene, were about 300 km apart and were part of the palaeo-Congo drainage. Of prime interest for malacology is that both stand faunistically completely apart from all other recent and all known former African lakes because of the presence of a thalassoid malacofauna.

As in Lake Tanganyika, the molluscs of Palaeolake Obweruka have a peculiar marine-like appearance. The strange marine-like (= thalassoid) gastropods of Lake Tanganyika have fascinated geographers and biologists since John Hanning Speke presented them to the Royal Geographic Society in 1859. They were promptly used as prime evidence by the proponents of the theory that Lake Tanganyika was a part of the Tethys Sea that had become landlocked during the Jurassic (Moore, 1903). Since, these notions have been proven erroneous. Lake Tanganyika has an estimated age of about 7 Ma, and the marine-like morphology of its molluscan inhabitants evolved via convergence. The studies on neogene African lakes indicate that Palaeolake Obweruka is the only African lacustrine system known with an age equal to that of Lake Tanganyika and in which a thalassoid malacofauna developed. Lakes such as present Lake Victoria, Albert and Edward whose ecosystems have an age in the range of 10,000 to 20,000 years, or modern L. Malawi, whose physical-chemical conditions have only become suitable for freshwater molluscs since 95 to 130 ka ago (Cohen et al., 2007), are exclusively inhabited by malacofaunas that show modest degrees of divergence from their ancestral fluvial morphotypes.

In the decades following the marine origin debate, different proposals about the causality of the exorbitant shell ornamentation of the Tanganyikan shells were advanced. The predator-prey arms race hypothesis is the latest one (West et al., 1991;

West & Cohen, 1994). The ongoing controversy presently centres about the question if the thalassoid lineages evolved in the lake from a single non-thalassoid ancestor (monophyletism or at best paraphyletism) (West & Michel, 2000) or if the different thalassoid lineages originated well before the formation of Lake Tanganyika (polyphyletism) in the Palaeo-Congo system and subsequently invaded the nascent Lake Tanganyika (Wilson et al., 2004). The two hypotheses are of equal value since, by lack of a fossil Tanganyikan record, neither can be substantiated.

In the light of this controversy and its consequences for the evolution of freshwater biota, a brief summary of the fossil record of Palaeolake Obweruka is here represented, constituting direct evidence of tempo and mode in an extremely long-lived African lake.

3.6.1 Palaeolake Obweruka I (7.5 to 4.5 My)

Geological and fossil evidence indicates that extensive lakes existed in the Albertine Basin from the onset of the rifting (around 15 Ma), but evidence for a deep and permanently stratified rift lake (anoxic deep water clays) only emerges around 8–7.5 Ma (Pickford et al., 1993).

The molluscan and fish fauna found in the earlier deposits of Palaeolake Obweruka clearly are derived from those that existed in the precursor lakes. From the onset, the evolutionary patterns in these two biota are markedly different. In the fish fauna a major evolutionary event occurred during the earliest stage. It resulted in the appearance of several endemic, molluscivorous genera, namely *Bunocharax* (Characidae), with huge molariform crushing teeth and *Nkondobagrus*, a bagrid catfish with a strongly elongated and heavily ossified snout (Fig. 3) (Van Neer, 1994; Van Damme & Pickford, 2004). Equally abundant are representatives of the bagrid genus *Chrysichthys*, molluscivores that apparently swallow rather than crush molluscs (Van Damme, pers. obs., 2008, based on stomach contents of *Chrysichthy*s from the Sanaga R. in Cameroon).

Despite the evidence for the presence of abundant molluscivorous fish, the dominant gastropod lineages, belonging to the Viviparidae and Paludomidae, which represent ~95% of the community, do show only a modest degree of morphological changes, similar to the type found in most modern African lakes. The development of extremely ornamented morphologies was restricted to some relatively rare species, e.g., the unique, spinose *Lanistes senuti* (Ampullaridae). Even within the Ampullaridae these armoured species – hence putatively better adapted to predation – appear to have only represented a minor fraction of the biomass, i.e. <5%. The low response to predation in the abundant molluscan species and the dramatic response in a few rare species in the presence of a strongly diversified molluscivore community appears to challenge the conventional concepts of arms-race theory (Vermeij, 1987).

Between 4.5 and 4.0 Ma, a marked disconformity in the stratigraphic sequence, indicating a lake level drop, was reported (Pickford et al., 1993). In the deposits postdating this disconformity a dramatic change in the composition of the molluscan

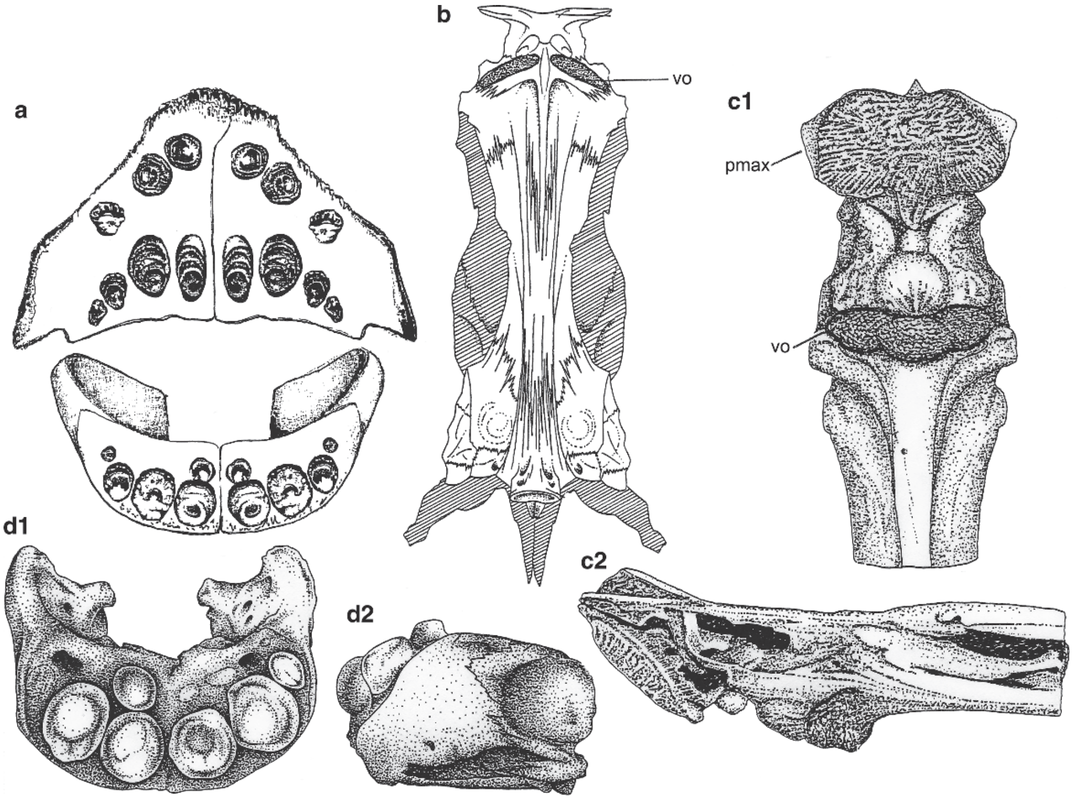

Fig. 3 Some fossil molluscivorous fish genera from the Albertine and Turkana Basins: (**a**) *Sindacharax* (Characidae), total length: 20–220 cm; widespread, common in all palaeolakes of the Turkana Basin and in Palaeolake Lusso (Albertine Basin); extinct. (**b**) *Chrysichthys* (Bagridae). Total length: 30–150 cm. widespread, extant. (**c**) *Nkondobagrus* (Bagridae), total length ≥50 cm, catfish with strongly ossified shovel-like snout, endemic to Palaeolake Obweruka, extinct. (**d**) *Bunocharax* (Characidae), total length >70 cm, endemic to Palaeolake Obweruka, Kaiso and Lusso, extinct (after Van Damme & Pickford, 2003).

assemblages was observed (Van Damme & Pickford, 1995, 1999, 2003). A severe extinction event, mainly in benthic organisms (such as molluscs and crabs) is evidenced by the fact that only a few surviving endemics (2 gastropods and 1 bivalve) are recovered, and all early thalassoids are absent. Co-occuring with the scant survivors, representatives of new invasive taxa (e.g. the Pachychilid *Potadoma*) appear in the strata of Palaeolake Obweruka II, that reached the size of Palaeolake Obweruka I (Van Damme & Pickford, 1995, 1999, 2003).

3.6.2 Palaeolake Obweruka II (4.0 to 2.5 Ma)

Shortly after the flooding of Palaeolake Obweruka II, a marked and rapid radiation did occur in each and every gastropod taxon, survivors as well as invaders, resulting in a highly diverse malacofauna composed exclusively of thalassoids. Some surviving genera (e.g. *Neothauma*), unornamented during Palaeolake Obweruka I produced the highest variability in ornamentation ever observed in a molluscan species flock (ribs, carinae and spines; Van Damme & Pickford, 1999). The stunning ornamentation, produced simultaneously in several genera can only be explained as an intensive reaction to predation (Vermeij, 1987; West & Cohen, 1994). It remains unexplained why all gastropods developed highly armoured shells, while the dominant molluscivourous fish taxa are the same as those inhabiting Palaeolake Obweruka I. The surviving lineages apparently possess the genetic possibility to produce ornamented shells, but why did this not occur before in Palaeolake Obweruka I? From the ensuing two million years an apparently unilateral arms-race with gastropods becoming increasingly more armoured is documented (Van Damme & Pickford, 1999, 2003) (Fig. 4).

3.6.3 Palaeolake Kaiso and Palaeolake Lusso (2.5 to 2.0 Ma)

The final chapter of this fascinating evolutionary story initiates around 2.5 Ma, when the rise of the Ruwenzori Horst broke up Palaeolake Obweruka. The two remnant lakes, Palaeolake Kaiso and Palaeolake Lusso, occupied the basins in which respectively Lake Albert and Lake Edward are situated at present. The palaeolakes were somewhat larger then their modern counterparts, and both were still part of the Congo catchment.

After a last phase of intense morphological changes, mainly restricted to the pachychilid genus *Potadoma*, the ecosystems of Palaeolakes Kaiso and Lusso were drastically altered. Between 2.3 and 2.0 Ma the remaining endemic lineages of molluscs and fish were replaced by a widespread malacofauna, erroneously termed ‘Nilotic’ by former authors (Adam, 1957, 1959; Gautier, 1970).

Comparing the fossil evidence of Palaeolake Obweruka to the hypotheses on the origin of the Tanganyikan thalassoids, we can conclude that several (at least 4) paludomid and pachychilid lineages invaded the lake independently.

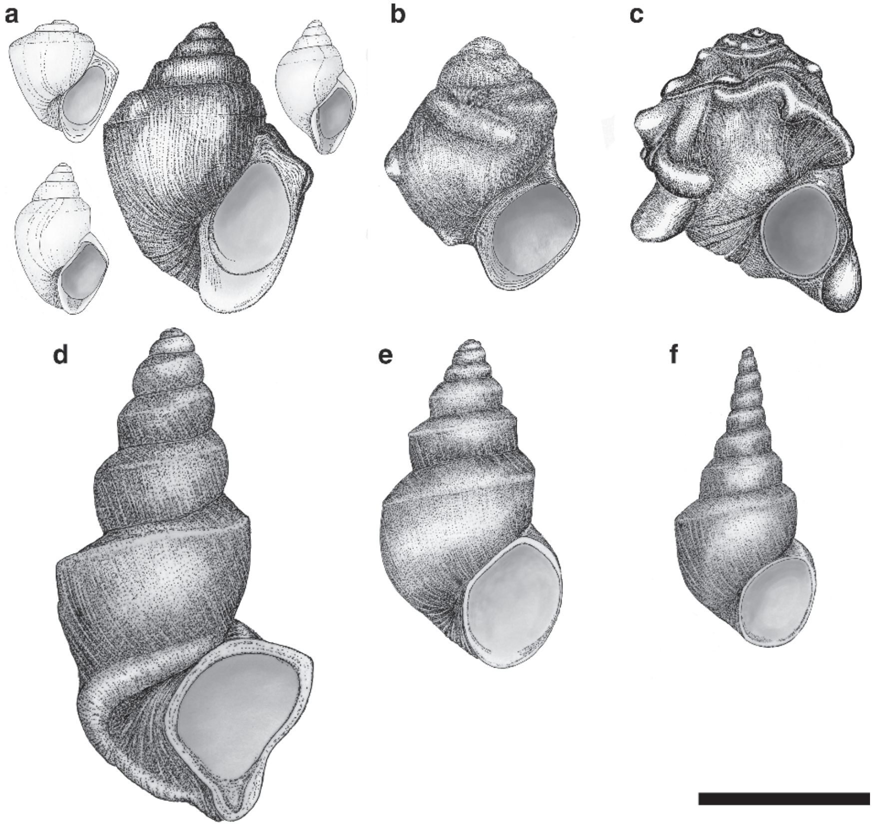

Fig. 4 The genus *Potadoma* (Pachychilidae): modes of conchyological evolution in African lakes. (**a**–**c**) Example of thalassoid evolution: an unornamented and thin shelled *Potadoma* species (*P. sebugoroensis*) gives rise to the extremely ornamented and thick *P. brevissima*. This evolution took place in long-lived Palaeolake Obweruka (Albertine Basin) over a period of ~2 million years (from 4.5 till 2.5 Ma). Such intense changes are only observed in the extremely long-lived lakes Obweruka and Tanganyika. (**d–f**) Example of non-thalassoid evolution: the fluvial *P. lomekwiensis*, with slowly but continuously enlarging whorls, evolves to *Potadoma* sp. nov., with a shell that grows first in length and subsequently rapidly enlarges in whorl size. This evolutionary development took place in the relatively short-lived Palaeolake Lokeridede (~50 ka) that existed in the Turkana Basin around 2.5 Ma. Such modest shell alterations, e.g. a shorter or smaller spire and/or weak ornamentation, are observed in all other present and former lakes, regardless of predation pressure. Included in this second group is Palaeolake Lorenyang (Turkana Basin) with an estimated age of 300 ka and hence 'long-lived' according to the prevailing definition of >100 ka (Rossiter & Kawanabe, 2000). Scale bar is 10 mm.

The thalassoid cerithioids in Palaeolake Obweruka were thus, corroborating the claim of Wilson et al., 2004 for Lake Tanganyika, likely not monophyletic. However, in Palaeolake Obweruka, the fossil evidence leaves no doubt that the invading lineages became thalassoid after having invaded the lake, as was equally proposed for the Tanganyikan fauna by West and Michel (2000). Although the most likely explanation is indeed that thalassoidism is a response to predation, the fossil record of Palaeolake Obweruka also indicates that the massive presence of specialised molluscivorous predators does not *in se* trigger a significant response, and other important factors must come into play as well.

Another interesting question is whether molluscs, originating in long-lived lakes, may subsequently spread in the hydrographical system, hence is intralacustrine evolution a main agent for maintaining diversity on the scale of a hydrographic basin or a region? In the case of Palaeolake Obweruka, the answer appears to be negative; none of the many endemics did spread outside the lake. Apparently, intralacustrine evolution in a 'long-lived' system may lead to a dead end. The most interesting conclusion that can be drawn from the Obwerukan fossil record is that in a large long-lived lake such as Palaeolake Obweruka (and by extension Lake Tanganyika) ecological insulation from the surrounding water bodies (incoming rivers, swamps, . . .) is established rapidly after the formation of the lake. Except for the invasion following the extinction event that terminated Palaeolake Obweruka I, the degree of eco-insularity appears to have been absolute (Van Damme & Pickford, 2003). A similar neat separation between lake ecosystem *sensu stricto* and fringe habitats has been noted for Lake Tanganyika. Parthenogenetic and extremely eurytopic and opportunistic species, e.g., the Asiatic species *Corbicula fluminalis*, which spread over Africa about 2.8 Ma ago (Van Bocxlaer et al., 2008), are still absent from Lake Tanganyika (Leloup, 1950).

4 Modern Biogeographic Regions of the Nile Basin

Within the Nile Basin four regions can be discerned on differences in the molluscan communities as on hydrogeological characteristics, namely:

- the Lower Nile in Egypt and North Sudan
- the Blue Nile – Lake Tana – Ethiopian Highland
- the Mountain Nile – Sudd – White Nile
- the Great Lakes

4.1 The Lower Nile in Egypt and North Sudan

This region is the part of the river extending northwards from the junction of the White Nile with the Blue Nile to the Nile Delta (Fig. 5). The most recent inventory of the malacofauna of the Egyptian part of this region is by Ibrahim et al. (1999). This study is valuable because it is the first time that the Nile has been sampled so intensively, but the taxonomy of the bivalves unfortunately is based on nineteenth century authors of the Ecole Nouvelle. The malacofauna of the Lower Nile can be discerned from that of the other regions by the presence of Palaearctic taxa. Some of these, e.g., *Lymnaea stagnalis*, *L. auricularia*, *Planorbis planorbis*, are widespread in the Palaearctic region. During the Early Holocene they occurred further south but presently they are restricted to the freshwater part of the Nile Delta (Van Damme, 1984), from which they are rapidly disappearing due to climate change (Van Damme pers. data). Five Palaearctic species are endemic, either to the Lower Nile or to the Ethiopian Highland (Tables 1 and 2). According to Brown (1994) the endemic Palaearctic snails *Theodoxus niloticus*, *Valvata nilotica* and *Gyraulus ehrenbergi* are closely related to and perhaps co-specific with Levantine species. The southern range extension of these palaearctics did fluctuate considerably during the Late Pleistocene – Holocene. During colder wet phases all these species extended as far south as northern Sudan and *Valvata nilotica* fossils are even found in the Chad Basin and the Turkana Basin, in the latter appearing for the first time around 200–150 ka (Bume Formation) (Van Damme, 1984). Two palaearctic unionids, *Unio abyssinicus* and *U. dembeae*, have presently disappeared from the Lower Nile but were abundant during the Late Pleistocene-Early Holocene cold phases. These species still occur in the Blue Nile – Lake Tana – Ethiopian Highland region and in part render the faunal community of this region distinctive (see below). Though *U. dembeae* was considered to belong to the circum-Mediterranean *Unio elongatulus* (presently *U. mancus*) complex (*U. elongatulus dembeae*) (Daget, 1998), it is probably better to consider it distinct till further research on this complex provides more information.

The number of Afrotropical endemics in the Lower Nile is extremely low (Table 1 and 2). There is only one putative speciose group, the *Ferrissia iselli* complex, with five species endemic to the Nile basin, of which three are endemic to the Lower Nile. The diversification within these small pulmonates may represent another example of rapid speciation through founder-effect, as in *Bulinus*, but it is more likely that molecular analysis will show that the genetic distinction is low or non-existing. We share the opinion of Brown (1994) who considers the number of African *Ferrissia* species to be '*highly uncertain; many are founded on shell differences but probably few are really distinct, for shell shape seems to be related to current speed and type of substratum*'. A low degree of genetic diversification has also been demonstrated for the African *Biomphalaria* representatives. All African species of this pulmonate genus cluster closely together with one South American species, *B. glabrata* (Campbell et al., 2000; Morgan et al., 2002). The taxonomic distinctiveness of *Biomphalaria alexandrina*, a species 'endemic' to the Upper and White Nile is hence rather spurious. The only solid endemic Afrotropical species of the Lower Nile appears to be the naiad *Chambardia letourneuxi* (Iridinidae), confined to the delta and probably extinct (Graf & Cummings, 2007b). It should be pointed out that many representatives of the genus *Chambardia* can aestivate and that the presence of this endemic is therefore not necessarily indicative for perennial waters.

Concerning the malacofauna of the brackish part of the Nile Delta and the saline coastal lakes we refer to the study of Barash and Danin (1992) on the coastal molluscs of Israel and Sinai, since the community composition is identical. Only a few brackish water species are found deeper inland, e.g. in the saline lake Birket Qarun, namely *Hydrobia musaensis, Pirenella conica, Cerastoderma glaucum* and *Scrobicularia cottardi*. *Hydrobia musaensis* also occurs in freshwaters (Van Damme, 1984).

4.2 The Blue Nile – Lake Tana – Ethiopian Highland

This region, that includes the watershed between the Nile and Awash systems has a malacofauna that stands apart from the rest of the Nile Basin by the occurrence of palaearctic relicts such as *Unio abyssinicus*. This species occurred throughout the Lower Nile during the Holocene but is now confined to Lake Tana (Van Damme, 1984), which is geologically young (Lamb et al., 2007) and harbours no lacustrine endemics. The main distinctive feature of the whole region is the occurrence of a limited number of endemics, namely *Bulinus hexaploidus, B. octoploidus* and *Pisidium ethiopicum*, adapted to montane conditions of small mountain streams and pools above the tree limit. A third important characteristic is the absence of all Afrotropical iridinid bivalves and all Afrotropical prosobranch taxa, except for *Bellamya unicolor* and *Melanoides tuberculata*. This region has hence the lowest species richness within the whole Nile Basin (Tables 1 and 2).

4.3 The Mountain Nile – Sudd – White Nile

The malacofauna of this vast region is appallingly poor, although extensive surface waters, namely the swamps of the Sudd and those north of the Pibor/Sobat Rivers (Machar Marshes) in southern Sudan, are included. Of the 13 gastropod species (Table 1) only one, the bithyniid *Gabbiella schweinfurthi*, may be endemic (Brown et al., 1984; Brown, 1994) and among the 11 bivalve species (Table 2) only the iridinid *Chambardia marnoi* is likely distinctive and confined to this part of the Nile, although further research may prove it to belong to the widespread *C. pfeifferiana* complex (Graf & Cummings, 2007b). The malacofauna of this region is exclusively Afrotropical. It is an impoverished version of the fauna of Lake Chad and shows only a modest relationship to the fauna of the Great Lakes.

4.4 The Great Lakes

The number of species in this region is about twice that of all other parts of the Nile Basin (Tables 1 and 2), due to the high number of endemic species in Lake Albert, Lake Edward and in particular Lake Victoria. However, it remains a pertinent question whether all these putative endemics are specifically distinct. The morphological differences between the lake-adapted endemics and the fluvio-paludal non-endemics is modest and so is the degree of intralacustrine radiation within each taxon. There actually exists only a single modestly speciose endemic clade among the gastropods of these lakes, namely that of *Bellamya* (Viviparidae) in Lake Victoria, represented by five species. An ongoing molecular investigation (Sengupta et al., 2007) indicates that this supposed 'clade' is not monophyletic, and furthermore that the COI diversity of *Bellamya* within Lake Victoria/L. Albert/L. Kyoga is low (0 to 2.2%), suggesting that either differentiation in *Bellamya* is not accompanied by strong sequence divergences or that the number of *Bellamya* species has been overestimated. Among the bivalves, the only (modestly) speciose clade is that of *Coelatura* in the lakes Victoria, Kyoga, Albert and Edward with four or five species (Graf & Cummings, 2007b) (Fig. 5). Again, it is highly unlikely that this group is monophyletic (Mandahl-Barth, 1988).

The limited diversification in the molluscs of the lakes Albert, Edward, Kyoga and Victoria is in accordance with the geological young age of the lakes (Talbot et al., 2000; Beuning et al., 2002; Goudie, 2005). However, there appears to be an important degree of persistence of this fauna during the Plio-Pleistocene, which contradicts the view that the malacofauna of the Great Lakes mainly consists of lacustrine adapted 'Nilotic' taxa (Mandahl-Barth, 1954, 1988; Scholz & Glaubrecht, 2004). The community in the East African Rift region is partly composed of species, which became taxonomically distinct during the Pliocene. For instance, the unionid species *Coelatura hauttecoeuri* and *Aspatharia divaricata,* presently endemic to Lake Victoria, appear to be no intralacustrine (= that evolved in a lake) endemics, but belong to the Early Pliocene fluvio-paludal fauna of the East African equatorial region. Fossils of these species have been recovered respectively from the Terminal Miocene of the Tugen Hills (De Groeve, 2005) and from Pliocene deposits in the Turkana Basin (Van Bocxlaer pers. data).

Van Damme and Pickford (2003), echoed by Wilson et al. (2004), reached the conclusion that even the spectacular malacofauna of Lake Tanganyika is only in part the result of intralacustrine evolution and that the lake is not primarily a '*living laboratory of evolution*', but rather a refugium for Miocene riverine taxa. Based on the fossil evidence from the Turkana Basin, the same seems to apply to the malacofauna of Lake Victoria, with the important difference that this ~12,000 years old lake may presently act as refugium for taxa of Early Pliocene age instead of Miocene ones (Van Damme pers. data).

The montane fauna of the East African Rift system is extremely poor. Only a single endemic snail has been recorded, the tetraploid *Bulinus membranaceus* in the Aberdare Range and Mau escarpment (Kenya), at altitudes between ~2,000 and 2,800 m (Brown, 1994). In waters on higher altitudes e.g. on Mount Elgon and the Rwenzoris only four pea mussels (*Pisidium casertanum*, *P. armillatum*, *P. invenustum* and *P. montigenum*) occur. *Pisidium invenustum* and *P. montigenum* hardly differ from *P. ovampicum* and may not be distinctive (Mandahl-Barth, 1988). Apparently no palaearctic species, except *P. casertanum*, which is actually a cosmopolitan cold-water species, extend this far south in East Africa.

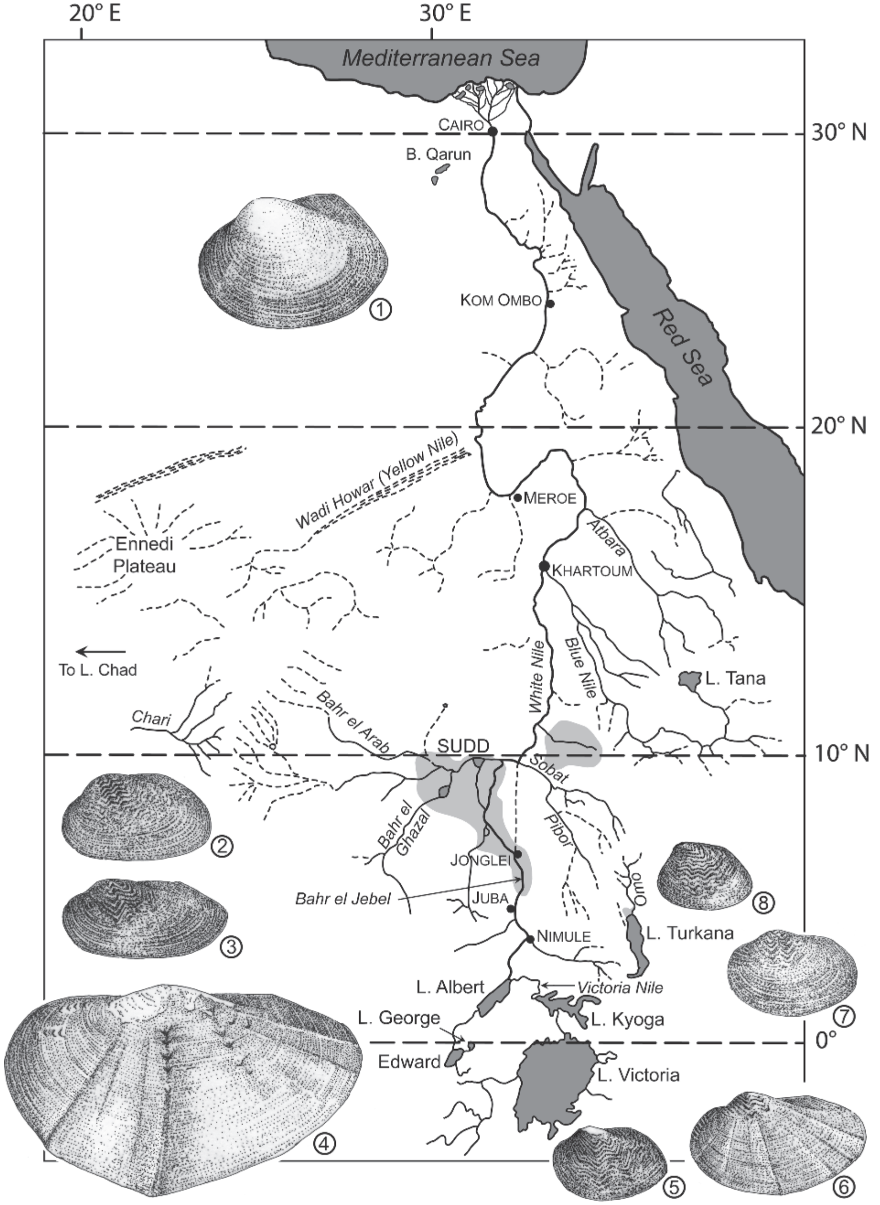

Fig. 5 The Modern Nile Basin and the distribution of representatives of the genus *Coelatura* Conrad, 1853 exemplifying the separation between the malacofaunas of the Nile north of 5° latitude and the Great Lakes region. (1) *C. aegyptiaca* (Nile, Lake Albert, Omo delta and also in the Chad Basin, Upper Niger and Senegal); (2) *C. bakeri* (Lake Albert); (3) *C. stuhlmanni* (Lake Edward); (4) *C. cridlandi* (Lake Victoria); (5) *C. hauttecoeuri hauttecoeuri* (Lake Victoria); (6) *C. alluaudi* (Lake Victoria); (7) *C. hauttecoeuri kyogae* (Lake Kyoga and the Victoria Nile); (8) *C. rothschildi* (Holocene Lake Turkana, extinct). Molluscs depicted to scale, dashed lines indicate seasonal rivers (wadis), light grey zones indicate swamps

5 Endorheic Basins Formerly Connected to the Nile

Two presently endorheic basin were previously connected with the Nile, namely the Turkana and the Chad Basins. Both connections were temporary and may have occurred repeatedly.

5.1 The Turkana Basin

The claim that a long-lived lake persisted for about 4 million years in the Turkana Basin (Cerling et al., 1979; Williamson, 1981a) has been abandoned, based on stratigraphic, geographic and palaeontological evidence (Brown & Feibel, 1988, 1991; Feibel, 1997, 1999; Van Bocxlaer et al., 2008). During its history the Turkana Basin was predominantly (~85% of the time represented by deposits) occupied by a fluvial Palaeo-Omo system that meandered through the basin and drained in the southeast towards the Indian Ocean (Brown & Feibel, 1991). Between fluvial phases, relatively short lacustrine phases, corresponding to the East African wet phases reported by Trauth et al. (2005), occurred (Brown & Feibel, 1991). Feibel (1997, 1999) recognises the following palaeolakes during Pliocene-Early Pleistocene times: (1) Palaeolake Lonyumun, existing for maximally 100 ka between 4.2 and 4.0 Ma, (2) Palaeolake Lokochot constrained between 3.5 and 3.4 Ma, (3) Palaeolake Lokeridede, existing for ~50 ka around 2.5 Ma, (4) Palaeolake Lorenyang, with a duration of up to 300 ka around 2.0 Ma, (5) Palaeolake Silbo, short-lived and possibly not a single lake but a series of several lakes around 0.9–0.7 Ma. After a long period with structural reorganisation, another palaeolake, here named Palaeolake Bume, formed in Late Pleistocene times, likely during the wet phase of 240–190 ka (MIS 7) or the one at 155–120 ka (MIS 6/5e). The name is derived from the Bume Formation (Lower Omo Basin), where its sediments were recorded (Brown & de Heinzelin, 1983). At present the Turkana Basin is occupied by the endorheic, alkaline Lake Turkana that is the remnant of a larger freshwater lake (~3 times the size of the present Turkana) in terminal Pleistocene-early Holocene times.

Ongoing research shows that the composition of the malacofauna of the Turkana Basin underwent drastic shifts since the Early Pliocene, caused by changes in hydrogeographic connections (Van Bocxlaer et al., 2008; Van Bocxlaer & Van Damme, in press). The sudden morphological shifts observed in the fossil record have originally been presented as *prima facie* fossil evidence for the punctuated equilibrium hypothesis (Williamson, 1981a, 1981b), but the advances in stratigraphy, palaeontology and taxonomy cited above have demonstrated that these pulses reflect invasions rather than bursts of intralacustrine evolution (Van Bocxlaer et al., 2008). This does not imply that no faunal evolution whatsoever was observed in the basin. Some invading fluvial lineages show marked alterations but in comparison with those that yielded the Obwerukan or Tanganyikan thalassoids, these changes remain modest (see Fig. 4). At several stages representatives of the ‘Nilotic’ community appear in the basin.

There exists no geological evidence for a Plio-Pleistocene connection between the Turkana Basin and the hydrographic basins situated to the north (Nile) and west (Chad), which contained a 'Nilotic' malacofauna (Van Bocxlaer & Van Damme, in press). The intermittent invasion of 'Nilotic' elements in the Turkana Basin suggests that such a link occasionally was established but possibly insufficiently long to leave geomorphological traces (such as the palaeo-Sahabi did).

The dominant Late Pleistocene – Early Holocene molluscan elements in the Turkana Basin are taxonomically related to those presently occurring in Lake Victoria (Cohen, 1981, 1986; Van Bocxlaer & Van Damme, in press). During the hyperarid phase of the terminal Pleistocene, surface water in the Turkana Basin must have been alkaline (Butzer et al., 1969) and in the Lake Victoria Basin only some alkaline pools may have remained (Stager & Day, 2004). Phases when the Turkana Basin held no water have also been recorded during Plio-Pleistocene periods (Brown & Feibel, 1988; 1991; Feibel, 1997, 1999). The geological data and the fossil bearing deposits in the Turkana Basin suggest that freshwater environments of a size suitable to maintain a diverse molluscan community were not or only episodically present. This raises the question where a diversified fauna may have persisted. The best candidate is the area at the base of Mount Elgon, where standing waters persisted during the aridity of the Glacial Maximum (Pickford, pers. comm., 2007).

During the early Holocene a hydrological link was established between Lake Turkana and the Nile, when Lake Turkana spilled into the Lotigipi Plain and the Pibor-Sobat system along its northwestern margin (Butzer et al., 1969; Butzer, 1971; Cohen, 1981). Since the Modern malacofauna of the Sobat-Sudd region differs markedly from the early Holocene Turkana one, there is no evidence that taxa from Turkana migrated northwards via this connection. Alternatively some 'Nilotic' species (e.g. *Coelatura aegyptiaca, Mutela rostrata, M. dubia*) did reach the basin but remained restricted to the fresh waters of Sanderson's Gulf and the Lower Omo (Van Bocxlaer & Van Damme, in press). The lacustrine fauna of Lake Turkana has been severely decimated since the early Holocene, and is at present almost extinct due to the high alkalinity. Based on data from Cohen (1986) and material collected by Frank Brown in 2007, nine species live in the lake proper. Only *Melanoides tuberculata, Gabbiella rosea* and *Ceratophallus kigeziensis* (erroneously identified formerly as *C. natalensis*, see Brown, 1994) are still abundant. Bivalves are absent from the lake, possibly except for a few small populations of *Corbicula fluminalis*. In the fresh water of the Omo delta, a richer fauna, dominated by *Pila wernei* and *Chambardia wahlbergi,* occurs (Tables 1 and 2) (Van Damme, 1976; Van Bocxlaer & Van Damme, in press). Sampling in the Lower Omo remained restricted to occasional surface collecting of larger shells and better sampling will likely yield more species. Additional species, mainly small pulmonates, occur in smaller freshwater ponds around the main lake, e.g., in atapars (springs artificially expanded into cuvettes for watering cattle). In such a standing water we collected *Cleopatra hemmingi* in 2007 and Brown (1994) mentions *Bulinus truncatus and Biomphalaria* sp. from within or near the lake (probably the latter).

5.2 The Chad Basin

The Chad Basin forms a vast expanse in which extensive lakes were formed intermittently at least since the Late Miocene (Goudie, 2005; Griffin, 1999, 2002, 2006). The largest of these was Lake Megachad (Drake & Bristow, 2006). Its existence has been questioned during the 1980s, but SRMT-30 data and Landsat TM imagery have since provided conclusive evidence for a lake around 7,000 BP that was over 173 m deep, with an area of at least 400,000 km^2 (the largest lake may have been ca 837,000 km^2). The overflow of this early Holocene lake was not in the east towards the Nile but in the southwest, towards the Mayo Kébi River and thence westwards to the Atlantic Ocean via the Benué River (Drake & Bristow, 2006).

The fossil malacofauna of the Chad Basin has been poorly studied and the ages of most assemblages are only assumed to be Holocene. However, the arid northern part of the Chad Basin, the Bodélé Depression, undergoes strong wind erosion and it can not be excluded that some assemblages exposed by wind erosion date from the beginning of the Quaternary or earlier. Since the area is now the largest source of atmospheric dust on Earth because of deflation by a powerful north-eastern low-level jet (Washington & Todd, 2005; Koren et al., 2006), the 'Holocene' surface finds may actually consist of fossils and stone artefacts from different time periods concentrated by erosional subsidence as is the case in the Mauritanian desert (Van Damme, 1984). In the few instances where molluscan assemblages are preserved in a stratigraphic context, e.g., at the Falaise d'Angamma (N. Chad), no significant compositional differences can be observed between the Modern community and the Middle Pleistocene one. The oldest Angamma assemblages originally were estimated on the basis of mammalian fauna inference to be of Early to Middle Pleistocene age (Coppens, 1965). This date has since been revised to ~250 ka (Howell, 1978). The Angamma malacofauna is the same as the one in present Lake Chad, indicating that the modern lake fauna did persist during the terminal Pleistocene, even when Lake Chad was dry (Van Damme, 1984).

To date, radar shuttle imagery has not revealed conclusive geophysical evidence indicative for a Chad-Nile connection during Plio-Pleistocene times, although the Holocene Lake Megachad has been suggested to have spilled over towards the east (Beadle, 1981; Leblanc et al., 2006). Since there is no trace of down-cutting at the eastern edge of this vast lake, in contrast with the erosion channel in the southwest (Drake & Bristow, 2006), this Nile-Chad connection apparently was short-lived.

As already stated, the Chad malacofauna is more diversified and archaic than the one of the Nile (see Tables 1 and 2). Endemism in Modern Lake Chad is low and many so-called endemics may not be distinctive (Brown, 1994).

6 Conservation

It is difficult to assess the importance of threats in such an extensive hydrographic system as the Nile Basin. According to recent studies on the Egyptian Nile (Ibrahim et al., 1999; Van Damme pers. data) two main trends can be observed:

(1) the construction of the Aswan Dam and the ensuing reduction of the flow regime of the Egyptian Nile has resulted in a southwards extension to Lake Nasser of species that had formerly been restricted to the Nile Delta.

(2) Palaearctic, boreal species that have been in retreat since the middle Holocene and that were holding out in the Nile Delta have been rapidly disappearing during the last three decades. *Chambardia letourneuxi*, the only endemic bivalve recorded from the Egyptian Nile, has not been collected since the beginning of the twentieth century and probably is extinct. *Unio abyssinicus*, a Palaearctic relict, only surviving in Lake Tana, must be considered as threatened since it is sensitive to climate change. The same may be the case for Ethiopian montane species such as *Bulinus octoploidus* and *Pisidium ethiopicum*. The malacofauna of the White Nile – Mountain Nile and of the Sudd appears not to be threatened. According to Darwall et al. (2005) 25 species of the eastern African region (as defined by IUCN, i.e., including the lakes belonging to the Nile Basin but also L. Malawi and L. Tanganyika) are globally threatened. The main threats are increased sedimentation and habitat loss due to deforestation, drainage of wetlands, and agricultural encroachment. In our opinion, the whole bivalve fauna of Lake Victoria is showing stress. In recent decades, shells of *Coelatura* and *Mutela* appear to have grown significantly larger and thinner, possibly a combined effect of nutrient and temperature increase.

The number of introduced freshwater molluscs in the Nile Basin is low (5–6 species) and none presents an ecological threat. The American ampullariid *Marisa cornuarietis* and the planorbid *Helisoma duryi* were intentionally introduced around 1970 in the Egyptian Nile and Blue Nile, as a biological control agent against *Schistosoma* (Brown, 1994). *Helisoma duryi* is presently recorded from the whole length of the Egyptian Nile (Lofty et al., 2005) but remains relatively uncommon, while *M. cornuarietis* is rare. Another American planorbid, *Biomphalaria glabrata* used in Egypt in *Schistosoma* research, was recorded from the wild in the vicinity of Cairo around 1980 (Brown, 1994). Being an intermediate host of *Schistosoma mansoni,* its escape was considered as a serious public health hazard, but during a recent molecular study of Nile populations the species could not be identified (Lofty et al., 2005). The two other invasive gastropods, the pulmonates *Lymaea columella* and *Physa acuta*, introduced around 1940–50 in the Republic of South Africa probably via the aquarium trade (Appleton, 2003), are presently found all over Africa, including the Nile Basin. However, they do not seem to form an ecological threat, thriving mainly in polluted waters were most autochtonous species have disappeared. There are no known invasive bivalves, though it is possible that some *Corbicula fluminalis* populations in the Lower Nile, being identical to the Levantine morph (Mandahl-Barth, 1988), may be recent arrivals.

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Aquatic Insects of the Nile Basin, with Emphasis on the Odonata

Henri J. Dumont

Abstract Much work has been done on the Diptera of the Nile, because many species are vectors of disease of man and cattle. Some biogeographic work has been done on the Heteroptera, but the group that is known best is that of the Odonata. With c. 250 spp. out of an estimated 900 for Africa, the Nile is not particularly rich. Unlike the Congo basin, it lacks a high degree of endemicity. Relatively most endemic species are found on the faunistically depauperate Ethiopian plateau, followed by the East African lake zone.

Quite a few wide-ranging Afrotropical species have used the Nile valley as a pathway to reach the Mediterranean shores, while in Lower Egypt some Palaearctic species of Irano-Turanian extraction occur. There has been exchange, across Sinai with the Levant, and perhaps across the Bab-el-Mandeb passage with Arabia. Some of these exchanges have been recent, others are older, and (sub) speciation has occurred since. Old endemics of Arabia and The Levant (at genus level) may not have had anything to do with the Nile. Their ancestors may have used the Red Sea valley as a pathway for dispersal before the opening of Bab-el-Mandeb. Not only the Afrotropical fauna of the Levant is a pluvial relict of Pleistocene age; also in West Sudan, relicts of an African forest fauna are found in a mountainous Sahel environment (Jebel Marra). Oriental elements in the Nile fauna are extremely rare.

1 Introduction

Rzóska's (1976) monograph of the Nile does not contain a comprehensive, basin-wide discussion of any group of insects although in some groups, like the aquatic Hemiptera, an outline of what such an analysis might have to offer had been in place since the early 1930s. Hutchinson (1933), in a pioneer study of the water-bugs of the Sahara, had been struck by the strong northern element in the desert–water fauna, especially, though not exclusively, at higher altitudes.

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The Nile valley fauna, in contrast, was found to be almost purely "African", and served as a highway for tropical species to extend north of their tropical range. Work by Linnavuori (1971), although mainly taxonomical, later reinforced this view by better documenting the fauna of the Sudan. Information is also available for the East African lakes (for Lakes Albert–Edward, see Green, 2009). However, a recent overview of global heteropteran species richness (Polhemus & Polhemus, 2008) shows that, from a biogeographic point of view, not much further refinement, such as a basin-by-basin analysis in Africa, has been attempted to date.

2 Pests

Rzóska & Lewis (1976) devoted a chapter to "insects in general and human ecology", mainly focused on the Sudan, but with notes on other Nilotic countries. There were definitely good reasons for this paper, since a multitude of aquatic or peri-aquatic insects (=living not in but near to water) that occur here have health effects on humans and their cattle, sheep, and camels. Medical entomologists thus contributed much to overcoming the blockage to river traffic and commerce by the great marshes that had previously prevented the Egyptians, Romans and Arabs from expanding into East Africa via the Nile.

Most problems arise from the Diptera, mosquitoes and flies. With a conservative estimate of about 6,000 species, these constitute almost half of all aquatic insects of Africa (Balian et al., 2008a,b). They would certainly qualify for a comparative biogeographic analysis of the Nile basin. Among the families covered by Rzóska & Lewis (1976) was the Tabanidae (Diptera). These large flies have fossorial larvae that live in damp soil where they feed on soil invertebrates. Females of many species require a blood meal for reproduction, and bite various vertebrates and mammals including man. In doing this, the genus *Chrysops* transmits *Loa loa*, a filarial nematode worm, causing loaitis in humans. Tabanids also cause anthrax in cattle and sheep. Disease and skin irritation caused by the seasonal mass occurrence of these flies, particularly in the south of Sudan and adjacent parts of Uganda and Ethiopia (Rzóska, 1974), together with the seasonal flooding of the plains, are among the main causes for the recurrent migrations of people and their cattle in these areas (Fig. 1).

A second group of interest is the Simuliidae. Of these, Lewis (1953a, b) found more than 20 species living near running waters in the Sudan. Most of these also extend into Uganda, Congo, and Ethiopia. The adults are aerial, but the larvae live in running waters, requiring rather swift currents, and they are therefore virtually absent form marshes like the Machar and Sudd. However, elsewhere along the Blue and White Nile, they may occur in massive numbers. The females feed on the blood of a variety of hosts, and the species-group of *S. damnosum* transmits the nematode *Onchocercus volvulus* to humans during their blood meal, causing river blindness (onchocerciosis). North of Khartoum, little onchocerciosis occurs, but the bites of the flies, when numerous, cause skin irritation and infections. Another mass-species is *S. griseicolle*, widely dispersed across Africa, and a nuisance if present in great numbers, although perhaps not transmitting any disease except filariasis.

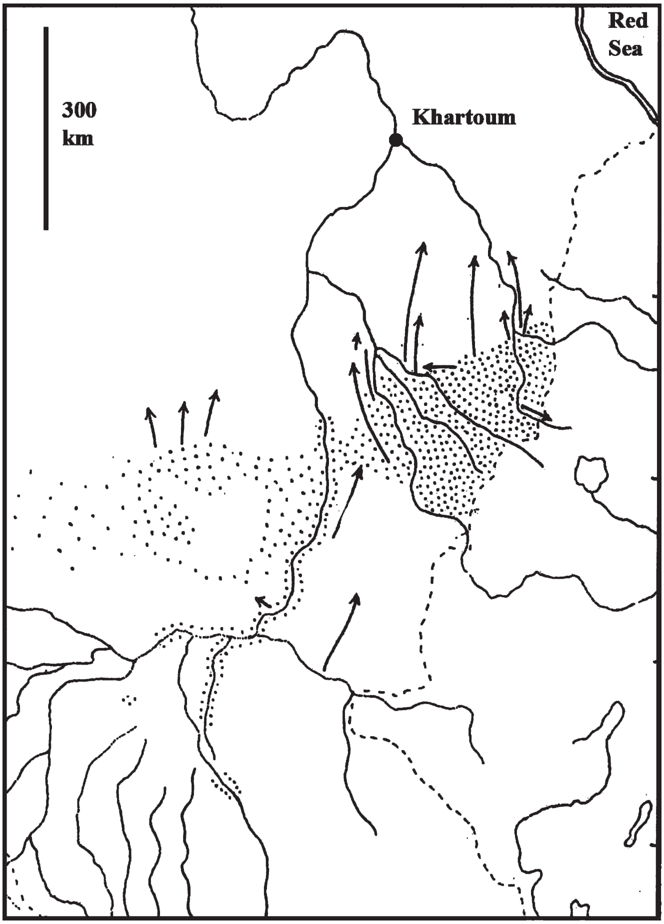

Fig. 1 Migration pathways of people and their cattle in southern Sudan and Western Ethiopia during monsoon, when massive tabanid outbreaks chase inhabitants from clayey and wet river valleys to drier sandy grounds (redrawn after Lewis, 1952; Rzóska, 1976)

Chironomidae are a complex and speciose group of mainly non-biting midges of which the larvae are aquatic. They constitute an important element of river and lake benthos. Mass emergence of imagoes is frequent, often consisting of several species emerging simultaneously. Even if not transmitting any disease, such mass emergences in the Sudan have been linked to allergies and asthma in humans exposed to the swarms (Lewis et al., 1954; Lewis, 1956a). Mass emergences worsened after the White and Blue Niles were dammed, and massive treatments with insecticides, originally including much DDT, were necessary (Rzóska & Lewis, 1976). In contrast to the chironomids, most representatives of the Ceratopogonidae feed on blood and are a nuisance to men and beast. Numerous species (30+) have been recorded from the Sudan. The partly planktonic, partly benthic. Chaoboridae too may develop in great numbers in lakes and rivers. When they emerge, alone or mixed with chironomidae, they may produce “clouds” or smoke-stacks emerging from their native lakes. Such swarms are locally harvested by the tribes along the lake shores, and may at times provide a significant contribution to their protein diet (Beadle, 1981) (Fig. 2). The production of *Chaoborus* in Lake Victoria has been determined by Lehman

Fig. 2 Massive eclosions of *Chaoborus* in the Great Lakes of Eastern Africa sometimes give an impression of smoke stacks (*top*) emerging from the lake water. When the swarms come on land to mate, they are actively chased by the local population and consumed fresh (*bottom*) (original pictures by H. J. Dumont) (*see Color Plates)*

et al. (1998). At about 40 kg ha^{-1} y^{-1}, it is comparable to that of the shrimp *Caridina nilotica*, and a sizeable contribution to the lake's secondary production.

Of true mosquitoes (Culicidae), the females of which require a blood meal before ovipositing, Lewis (1956b) recorded not less than 156 spp. in the Sudan Nile area. Their number decreases spectacularly north of Khartoum, although malaria-transmitting species of *Anopheles* can be found north as far as the Mediterranean. Other species and genera (*Aedes*, *Culex*) are vectors of viruses that cause diseases like yellow fever, dengue fever, and West Nile fever. In contrast to malaria mosquitoes, which predominantly bite at dusk or at night, they attack during daytime. They abound in the southern swamps of the Sudan, and in adjacent Ethiopia and Uganda.

Unfortunately, as with the Heteroptera, the various contributions to dipteran families in the animal diversity assessment by Balian et al. (2008) show that a biogeographic analysis of the Diptera within and between African river basins remains a task for the future.

3 Odonata

Of the aquatic insects that are numerous and prominent, completely harmless to man, and have been relatively well studied, the dragonflies are no doubt the most prominent. They have recently been called the "guardians of the watershed" (Clausnitzer & Jödicke, 2004), on account of their indicator values for ecosystem health. Some species are typical of wetlands and shallow, weedy lakes; others are restricted to running waters. Some prefer forest landscapes, other dry savanna, and a few live in (semi) deserts. Some species are typical of lowlands, others are found at (sub)alpine altitudes. Many small species (e.g. in *Chlorocypha*, of which several species are restricted to Uganda) have imagoes that are tightly linked to (running) water and endemic to a small geographic area; others (*Pantala flavescens*, *Anax ephippiger*) are migrants that may cover intercontinental distances, crossing oceans and deserts. There are two suborders: the tiny Zygoptera, and the robust Anisoptera (Fig. 3). Dragonflies are ancient insects: the ancestors of most families were in existence at the time of the breakup of Gondwanaland. On the other hand, dragonflies are sensitive to the vagaries of the climate, as well as regards temperature as humidity. Because, more than other tropical continents, Africa has suffered from recurrent droughts after the Miocene, its dragonfly fauna became sharply reduced. With slightly over 800 spp. (Dijkstra, 2007b) (but almost 900 spp. according to Kalkman et al., 2008), its species richness is just over half that of the Oriental and Neotropics.

The Nile basin is not a particularly rich area for dragonflies. Most of the continent's species richness is found in the Congo basin (including the adjacent Guinea zone to the West), where at least 40% of all African taxa occur. Many genera in both suborders are entirely or almost entirely restricted to that zone: the genus *Porpax* among Libellulidae (Dijkstra, 2006), and the genera *Umma* and *Sapho* among Zygoptera are striking examples. The mountain barrier between Nile

Fig. 3 The two suborders of dragonflies. *Pseudagrion kersteni*, a zygopteran (*above*); *Trithemis furva*, an anisopteran (*below*). Both are Afrotropical species, but relicts exist in Yemen and in Jebel Marra, Darfur, Western Sudan, where these photographs were taken in 1985 (original pictures by H. J. Dumont) (*see Color Plates)*

and Congo (Eggermont et al., 2009) thus appears to have functioned since the late Miocene. But also isolation from the East African coastal zone by the eastern rift and eastern arc mountains appears to be rather hermetic: many coastal East African taxa, including some ancient relict groups like *Coryphagrion*, do not occur in the Nile basin. On the other hand, faunal exchange along the east African highlands that stretch from Uganda to South Africa (the so-called Afromontane zone) is relatively easy. The same is more or less true for exchange across the semi-arid belt of the Sahel, west of the Upper Nile basin, although aridity limits the number of species involved.

In all, the Nile basin species count currently stands at about 250 species (Table 1). Future additions and corrections will certainly occur, and some parts of the basin (e.g. southern Sudan, where only 25 spp. are currently known from the Sudd

Table 1 List of Odonata of the Nile Basin (in bold: species with restricted ranges within the basin)

	Uganda	Sudan	Egypt	Ethiopia
Zygoptera				
Aciagrion africanum	x			
A. gracile	x			
A. hamoni	x			
A. heterosticta	x			
A. karamoja	x			
Africallagma elongatum	x	–	–	x
A. glaucum	x			
A. pseudelongatum	x			
A. subtile	x	–	–	x
A. vaginale	x			
Agriocnemis exilis	x	–	–	x
A. forcipata	?	x		
A. gratiosa	x	x		
A. inversa	x	–	–	x
A. maclachlani	x			
A. palaeforma	x			
A. sania	x	?	?	x
A. victoria	x	x		
A. zerafica	x	x		
Azuragrion nigridorsum	x	x		x
A. vansomereni	x	x		x
A. somalicum	–	–	–	x
Ceriagrion bakeri	x			
C. corallinum	x			
C. glabrum	x	x		x
C. kordofanicum	x	x		
C. suave	x	–	–	x
C. varians	x			
C. whellani	x			
Chlorocnemis nigripes	x			
C. pauli	x			
C. superba	x			
Chlorocypha cancellata	x			
C. curta	x	x		
C. jacksoni	x			
C. tenuis	x			
C. trifaria	x			
C. victoriae	x			
Elattoneura glauca	x			
E. nigra	x			
E. pasquinii	–	–	–	x
Ischnura abyssinica	–	–	–	x
I. evansi		x	x	
I. fountaineae				
I. pumilio			x	

(continued)

Table 1 (continued)

	Uganda	Sudan	Egypt	Ethiopia
Zygoptera				
I. senegalensis	x	x	x	x
Lestes dissimulans	x			
L. ictericus	x	x		
L. ochraceus	x	x		
L. pallidus	x			x
L. plagiatus	x	x		
L. uncifer	x			
L. virgatus	x			x
L. tridens	–	–	–	x
Mesocnemis singularis	x	x	–	x
M. robusta	–	x	x	
Phaon iridipennis	x	–	–	x
Platycnemis nyansana	x			
P. sikassoensis	x			
Platycypha caligata	x			x
P. lacustris	x			
Proischnura subfurcatum	x	x	–	x
Pseudagrion bicoerulans	x			
P. gamblesi	x			x
P. guichardi	–	–	–	x
P. hageni	x			x
P. kaffinum				x
P. kersteni	x	x	–	x
P. kibalense	x			
P. melanicterum	x	x		
P. rufocinctum	x			
P. salisburyense	x			
P. assegai	x			
P. glaucescens	x			
P. glaucoideum	x			
P. hamoni	x	x	x	
P. lindicum	?			
P. massaicum	x	x	–	x
P. niloticum	?	x	x	x
P. nubicum	x	x	x	x
P. sjoestedti	x	–	–	–
P. spernatum	x	–	–	x
P. sublacteum	x	x	x	x
P. sudanicum	x	x		
P. torridum	x	x	x	x
Umma sapphirina	x			
Anisoptera				
Acisoma panorpoides	x	–	–	x
A. trifidum	x			
Aeshna* cf. *yemenensis	–	–	–	x
A. ellioti	x	–	–	x

(continued)

Table 1 (continued)

	Uganda	Sudan	Egypt	Ethiopia
Anisoptera				
A. meruensis	x			
A. rileyi	x	x		
A. scotias	x			
Aethiothemis coryndoni	x			
A. solitaria	x			
Aethriamanta rezia	x			
Anasciaeschna triangulifera	x	–	–	x
Anax chloromelas	x			
A. ephippiger	x	x		x
A. imperator	x	x		x
A. parthenope		x		
A. speratus	x	x		x
A. tristis	x	x	–	–
A. aethiopica	–	–	–	x
Atoconeura eudoxa	x			
A. kenya	x	x		
A. pseudeudoxia	x			
Brachythemis lacustris	x	x	–	x
B. leucosticta	x	x	x	x
B. wilsoni	x	x		
Bradinopyga cornuta	x			
B. strachani	x	x		
Chalcostephia flavifrons	–	–	–	x
Crenigomphus abyssinicus				x
C. denticulatus				x
Crenigomphus hartmanni	x			
C. renei	x			
Crocothemis divisa	x	x		
C. erythraea	x	x	x	x
C. sanguinolenta	x	x	x	x
Diastatomma bicolor	x			
Diplacodes deminuta	x			
D. lefebvrii	x	x	x	x
D. luminans	x			
Eleuthemis buettikoferi	?			
Gomphidia bredoi	x			
Gynacantha africana	x			
G. bullata	x			
G. cylindrata	x			
G. manderica	x			
G. nigeriensis	x	–	–	x
G. sextans	x	–	–	x
G. vesiculata				
G. villosa	x	–	–	x
Hadrothemis camarensis	x			
H. coacta	x			

(continued)

Table 1 (continued)

	Uganda	Sudan	Egypt	Ethiopia
Anisoptera				
H. defecta	x			
H. infesta	x			
H. versuta	x			
Heliaeschna cynthiae	x			
H. fuliginosa	x			
H. trinervulata	x			
H. ugandica	x			
Hemicordulia africana	x			
Hemistigma albipunctum	x	–	–	x
Ictinogomphus ferox	x			
I. regisalberti	x			
I. jellianae	x			
Lestinogophus angustus	x			
L. pseudafricanus	x			
Lindenia tetraphylla			x	
Malgassophlebia bispina	x			
Microgomphus schoutedeni	x			
Micromacromia camerunica	x			
Neodythemis afra	x			
N. munyaga	x			
N. preussi	x			
Nesciothemis farinosa	x	x	x	x
Notiothemis jonesi	x			
N. robertsi	x			
Notogomphus cottarellii				x
Notogomphus dorsalis	x	–	–	x
N. flavifrons	x			
N. gorilla	x			
N. lecythus				x
N. leroyi	x			
N. lujai	x			
N. ruppeli				x
Olpogastra lugubris	x	x	x	–
Onychogomphus bwambae	x	–	–	–
O. lefebvrei	–	–	x	–
O. styx	x	–	–	–
Orthetrum abbotti	x	x	–	x
O. africanum	?	–	–	–
O. angustiventre	x	x	–	–
O. austeni	x	–	–	–
O. brachiale	x	x	x	x
O. brunneum	–	–	x	–
O. caffrum	x	x	–	x
O. chrysostigma	x	x	x	x
O. guineense	x	–	–	x
O. hintzi	x	–	–	x

(continued)

Table 1 (continued)

	Uganda	Sudan	Egypt	Ethiopia
Anisoptera				
O. icteromelas	x	x	–	–
O. julia	x	x	–	x
O. kollmannspergeri	–	x	x	x
O. kristenseni	–	–	–	x
O. machadoi	x	–	–	x
O. microstigma	x	x	–	–
O. monardi	x	–	–	x
O. ransonneti	–	x	x	–
O. sabina	–	x	x	–
O. saegeri	x	–	–	–
O. sagitta		x		
O. stemmale	x	x	–	x
O. trinacria	x	?	x	x
Oxythemis phoenicosceles	x	–	–	–
Palpopleura deceptor	x	x	–	x
P. jucunda	x	x	–	x
P. lucia	x	x	–	x
P. portia	x	x	–	x
Pantala flavescens	x	x	x	x
Paragomphus alluaudi				x
Paragomphus bredoi	x			
P. cognatus	x			
P. crenigomphoides				x
P. genei	x	x	x	x
P. pumilio	x		x	
P. serrulatus	x			
P. sinaiticus		x	x	
P. viridior	x	x		
Parazyxomma flavicans	x			
Philonomon luminans				x
Phyllogomphus annulus	x			
P. selysi	x			
Phyllomacromia africana	x	x	x	
P. aureozona	x			
P. bispina	x			
P. contumax	x	?		
P. flavimitella	x			
P. kimminsi	x			
P. melania	x	?		
P. overlaeti	x			
P. pallidinervis				x
P. picta	x	–	–	x
P. pseudafricana	x			
P. sylvatica	x			
Rhyothemis fenestrina	x			
R. semihyalina	x	–	x	x

(continued)

Table 1 (continued)

	Uganda	Sudan	Egypt	Ethiopia
Anisoptera				
Selysiothemis nigra			x	
Sympetrum fonscolombii	x	x	x	x
S. sinaiticum	–	?	x	–
Tetrathemis camerunensis	x			
T. corduliformis	x			
T. denticauda	x			
Tetrathemis polleni	x			
T. ruwensoriensis	x			
Thermochoria equivocata	x			
Tholymis tillarga	x	x	–	x
Tramea basilaris	x	–	–	x
T. limbata	x	–	–	x
Trithemis aconita	x	–	–	x
T. annulata	x	x	x	x
T. arteriosa	x	x	x	x
T. dejouxi				x
T. dichroa	x	x		
T. donaldsoni	x			x
T. dorsalis	x			
T. ellenbecki				x
T. furva	x	x		x
T. grouti	x			
T. hecate	x			
T. imitata				x
T. integra	x			
T. kirbyi	x	x	x	x
T. monardi	x			
T. nuptialis	x			
T. pruinata	x			
T. stictica	x	x	–	x
T. werneri	x			
Tritethrum navasi	x			
Urothemis assignata	x	–	–	x
U. edwardsii	x	x	x	x
Zygonoides fraseri	x	–	–	–
Z. fuelleborni		x		
Zygonyx flavicosta	x	–	–	–
Z. natalensis	x	–	–	x
Z. regisalberti	x	–	–	–
Z. torridus	x	x	x	x
Zyxomma atlanticum	x			

swamps (Mefit-Babtie, 1983) have a particularly strong species deficit. However, the information is adequate for some generalizations. The quasi-total absence of Nile-basin endemics is striking. The only species that more or less qualify are *Paragomphus pumilio* and *Pseudagrion niloticum* (but the latter was recently found in South Yemen, W. Schneider, personal communication). A peculiar range is found in *Orthetrum kollmannspergeri*, a species only recently separated from the Oriental *O. taeniolatum* (Bucchholz, 1959; Dumont & Verschuren, 2005; Clausnitzer & Dijkstra, 2005). It extends across a "sahel" belt from Somalia and Ethiopia to Darfur and Eastern Chad. It seems to prefer desert waters, both stagnant and the outflow of springs, which are otherwise species-poor environments. Although it occurs east and west of the Nile, it had never been found in the valley itself, but this also applies to most arid-land species that occur in the lower Nile valley. It has not (yet) been found in Egypt. Oriental elements in the Nile valley are extremely rare. For a long time, it was thought that *Hemicordulia asiatica*, an Oriental species, occurred on the east African plateau, which it had reached via the Nile. Recently, Dijkstra (2007a) showed, however, that the African populations represent a different species, *H. africana*, and that this is part of a small but significant assemblage of species that made it to the East African shores from the east, blown by ocean winds. In fact, the only confirmed Oriental species found in the lower and middle Nile valley is *Orthetrum sabina* (Dumont & Verschuren, 2005).

Other sub-basins of the Nile have endemics too, but not many: none in the lower Nile, and about 3% on the east African plateau and in the western rift. The East African area is where most of the fauna (c. 230 spp.) resides (Pinhey, 1961; Clausnitzer, 2005), but many species that occur here are shared with the Afromontane zone (Dijkstra, 2007a,b). Very few extend to the Congo basin, and those that do usually occur Africa-wide, or are even shared between Africa and the Oriental (e.g. *Ischnura senegalensis*, *Trithemis kirbyi*, *Orthetrum chrysostigma*, *Tholymis tillarga*). The Ethiopian plateau, a zone that is relatively species-poor (96 spp. according to Clausnitzer & Dijkstra, 2005) has the largest share of endemics: c. 13%. This impoverishment reflects a dearth of forest species, while on the other hand, riverine species, especially of the family Gomphidae, are over-represented among the endemics. Some incipient speciation may currently be going on in the Lake Turkana basin, where a pale form of *Pseudagrion torridum* (*f. orientis*) lives (Pinhey, 1964), but a closer study of this population is needed.

In the narrow valley of the Nile itself, the number of species thins out rapidly as one moves north from the great marshes. A significant number of true "African" species has made it to the lower Nile in Egypt, however, and one among these is the large *Phyllomacromia africana*, beside several *Pseudagrion* and the tiny *Agriocnemis exilis* (Dumont, 1980). This property of the Nile, to drive an Afrotropical wedge through a vast stretch of desert as far north as the Mediterranean shores, is recurrent and noted in many contributions to this book. It applies to all biota, from microscopic to megafauna (hippopotamus and Nile crocodile occurred in the delta until the eighteenth century). In fact, it is curious that not more African species have been recorded from the delta. A few may perhaps still await discovery but, like the hippopotamus and the Nile crocodile (De Smet, 1999), human intervention rather than climate may have caused their extinction, especially but not exclusively in the last two centuries. Rzóska (1976) attempts to depict the river valley before and during man's occupation, and it emerges that in Egypt and Nubia, the first major changes occurred in early dynastic times, perhaps as far back in time as 5,000 BP. Marshes were drained, and inundation plains adapted for seasonal irrigation. Many mini-sudd swamps all along the river were thus eliminated and many aquatic insects, including dragonflies, driven to extinction. More recently, river damming, population growth and the associated eutrophication and industrial expansion (see various chapters in this book) undoubtedly took a toll and caused further faunal impoverishment.

From the lower Nile, species spilled over to the Levant, especially during humid events, and some remained established in the Jordan valley and even further north. There seem to have been several colonization events, since "older" immigrants (e.g. *Pseudagrion syriacum*) meanwhile speciated, while others (e.g. *Orthetrum abbotti*) did not speciate at all. It is probably significant that in Arabia two endemic genera of zygopterans occur, *Arabicnemis* and *Arabineura*, both probably descended from African ancestors. These are believed to be relicts of old immigrations, perhaps even of Miocene or early Pliocene age, that have left no traces in the Nile valley itself. In theory, these could have reached Arabia via the coasts of Eastern Africa and the Bab-el-Mandeb passage. However, in the Levant there also exists an endemic fish genus, *Tristramella*, which has African roots, and may have invaded the Jordan valley via the Sinai. It is questionable whether such "old" immigration waves were even connected to the Nile, since prior to the Pleistocene, the present course of the river did not exist (see Talbot & Williams, 2009), while the Red Sea was not open to the Indian Ocean, may have looked like a swampy river valley, and was the real pathway of dispersal of these old biota.

A significant component of the Nile fauna, especially in its lower reaches, consists of species that extend from the arid belt of Western Asia (so-called Irano-Turanian faunal elements) to the Central Sahara, and sometimes even to the Maghreb and the Iberian peninsula. As noted above, these are mostly absent from the Nile valley itself, but necessarily had to transit across it. Examples include *Paragomphus sinaiticus*, *Onychogomphus lefebvrei*, *Ischnura evansi* and *fountaineae*, *Orthetrum ransonneti*, *Selysiothemis nigra* and, perhaps, *Lindenia tetraphylla*. Most of these are common in Arabia.

Many of the species currently found between Central Sudan and Lower Egypt are rather sturdy animals, the larvae of which endure environmental insults such as eutrophication, fluctuations in salinity and temperature, and even drying out of their environment. They overcome such periods by a rapid larval development (*Pantala flavescens*, *Anax ephippiger*), adult estivation (*Lestes pallidus*), and egg or even larval estivation in (damp) mud (*Lestes pallidus*, *Trithemis arteriosa*, *Pantala flavescens*).

Because the Nile forms a continuum between the Equator and the Mediterranean, Afrotropical species occurring in its lower course cannot be described as relicts. True, geographically isolated relicts have, however, been found in wet mountain islands surrounded by arid land. The flanks of Jebel Marra, partly draining towards lake Chad, and partly towards the Nile, provide such an environment. The Jebel Marra vegetation and climate were studied by Wickens (1976). At higher altitudes, precipitation may reach 1,000 mm per annum, and small patches of "tropical" forest survive, as well as perennial running water. A relict fauna with a high share of "tropical" species but no endemics has been found there by Happold (1966) and Dumont (1988). It comprises such species as *Chlorocypha curta*, *Pseudagrion melanicterum* and *Anax speratus*, currently found between 500 and 1,000 km further south. A pluvial spell during the

Holocene, perhaps around 6,000–7,000 BP, the period during which the Wadi Howar was last flowing (Kuper & Kröpelin, 2006), may have sufficed to bridge todays' aridity gap and allowed these species to immigrate and to hold out to the present. However, it is also possible that these relicts are older, and the result of multiple invasions.

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Fish Fauna of the Nile

Frans Witte, Martien J. P. van Oijen, and Ferdinand A. Sibbing

Abstract The total number of fish species in the Nile drainage basin, which includes the River Nile, its affluent rivers and the connected Lakes, is currently estimated at more than 800. Of these, 128 species, belonging to 27 families, occur in the River Nile. The river comprises many different habitats (e.g. the swampy Sudd) each with a different species composition. The families Cichlidae, Cyprinidae, Mormyridae and Mochokidae comprise the majority of the fish species in the Nile drainage basin. The Mormyridae and Mochokidae have more representatives in the river than in the Lakes. The same holds for the Cyprinidae, with the exception of Lake Tana that harbours almost as many cyprinid species as the river. Cichlid species dominate the fish faunas of Lakes Edward, George, Victoria and Kyoga. Especially Lakes Victoria and Kyoga and their satellite Lakes are well known for their cichlid diversity. Prior to the human induced ecological changes, these Lakes contained about 600 haplochromine cichlid species in contrast to 46 native fish species belonging to 11 other families. The haplochromine cichlids comprise at least 15 trophic groups that are morphologically adapted to feed on specific food types. The boom of the introduced Nile perch in the 1980s as well as fishery and habitat deterioration had a strong impact on the haplochromine species and many other fish species, and about 200 endemic haplochromine species may have gone extinct. In Lake Tana, which is part of the head waters of the Blue Nile, the fish fauna is dominated by the cyprinid genera *Barbus* and *Labeobarbus*. The flock of 15 endemic *Labeobarbus* species in

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this lake shows a trophic radiation similar to that of the haplochromine cichlids of Lake Victoria. Another notable inhabitant of Lake Tana is *Nemacheilus abyssinicus*, the only known representative of the Euro-Asiatic Balitoridae.

1 Introduction

In this chapter an overview is given of the fish fauna of the River Nile and its drainage basin, which includes among others the Lakes Victoria, Kyoga, Edward, George, Albert and Tana (Fig. 1). As the total number of fish species of the Nile drainage

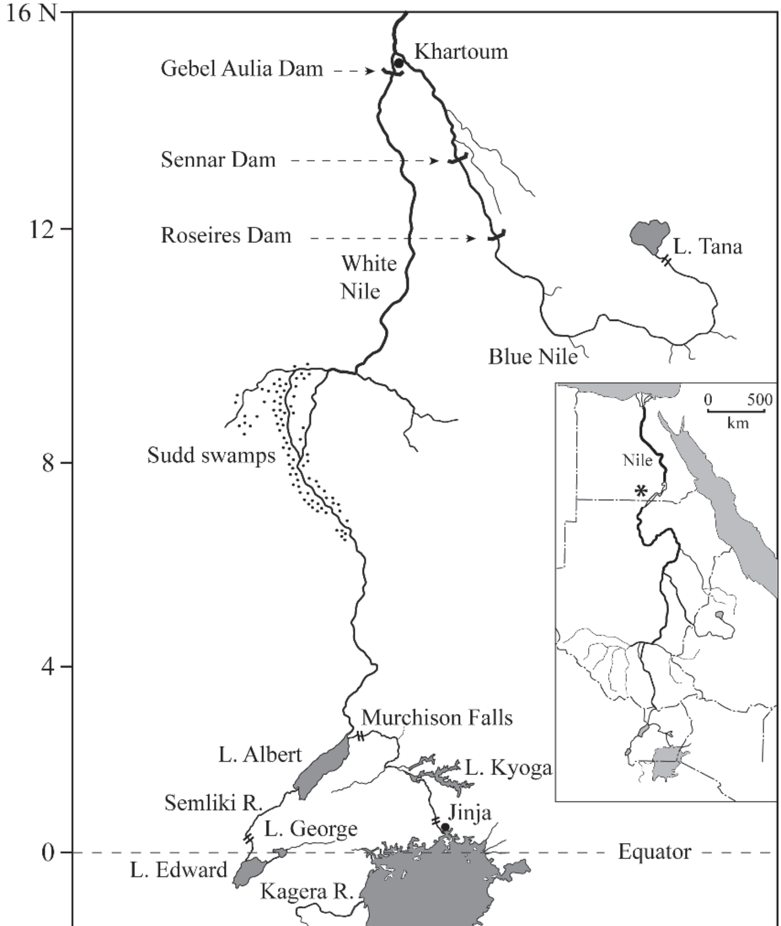

Fig. 1 Map of the River Nile and its tributaries. Asterisk in inset indicates the location of Lake Nasser/Nubia

basin amounts to over 800, it is impossible to discuss all of them. Therefore, we mainly deal with the fish families and genera that make up the Nile fauna, and give examples of representative species. A list of the fish species (+ authors) discussed in the present chapter and in the chapter Fisheries in the Nile System is given in the Appendix. Nomenclature of the higher fish taxa follows Nelson (2006). Nomenclature of the species follows the Check-List of the Freshwater Fishes of Africa (CLOFFA) parts I, II and IV (Daget et al., 1984, 1986, 1991), except for the Alestiidae (formerly African Characidae), the Schilbeidae and *Oreochromis*, for which respectively Paugy (1986), de Vos & Skelton (1990) and Trewavas (1983) are followed.

2 Ichthyofaunal Provinces

Boulenger (1907) was the first to divide Africa or the "Ethiopian region" into ichthyofaunal provinces, based on the distribution of freshwater fish. As more knowledge of the African freshwater fish became available, these provinces were modified (e.g. Poll, 1973; Roberts, 1975; Paugy et al., 1994; Hugueny & Lévêque, 1994). According to Roberts (1975), the Nile drainage basin, including the River Nile, its affluent rivers and the connected Lakes, covers several provinces. The major part of the River Nile, including Lakes Edward/George and Lake Albert (also called Lake Mobuto Sese Seko), is located in what has been defined as the Nilo-Sudan province (Fig. 2). Lake Tana and a large part of the Blue Nile have been included in the Abyssinian Highlands. The latter are considered a sub-province of the Nilo-Sudan province by Lévêque (1997). Lakes Victoria and Kyoga and the Victoria Nile were included in the East Coast province by Roberts (1975). Greenwood (1983), also included Lakes Edward and George in this province and later Snoeks et al. (1997) added Lake Kivu. However, according to Lévêque (1997) "it seems more correct to include Lake Victoria in the Nilo-Sudan province (as defined by Roberts, 1975), taking into account the affinities of the non-cichlid fauna with the Nile fauna". Recent molecular research suggests that the extensive endemic haplochromine cichlid fauna in Lakes Victoria and Kyoga also may have originated from Congolese-Nilotic ancestors rather than from East African riverine species (Seehausen et al., 2003), and that the haplochromine cichlids of Lakes Victoria, Edward, George and Albert form a monophyletic superflock (Verheyen et al., 2003). Therefore, we tentatively included the Lakes Victoria and Kyoga, and the Victoria Nile in the Nilo-Sudan province (Fig. 2). In the Nilo-Sudan province 15 endemic riverine genera (belonging to 11 families) were recognized (Table 1; Roberts, 1975). Ten of these genera occur in the Nile and its tributaries. In the Abyssinian Highlands no endemic riverine genera are present (Roberts, 1975).

An alternative map of freshwater ecoregions of the world, based on the distribution and composition of freshwater fish species, was published by Abell et al. (2008). According to this map, the Nile drainage basin covers six ecoregions: (1) the Lake Victoria basin, including Lakes Victoria, Kyoga, Edward/George and Kivu; (2) the Upper Nile, including the Semliki River and Lake Albert in the South and the Sudd in the North; (3) the Lower Nile, from Khartoum in the South to the Nile Delta and including the Blue Nile except its uppermost reaches; (4) the

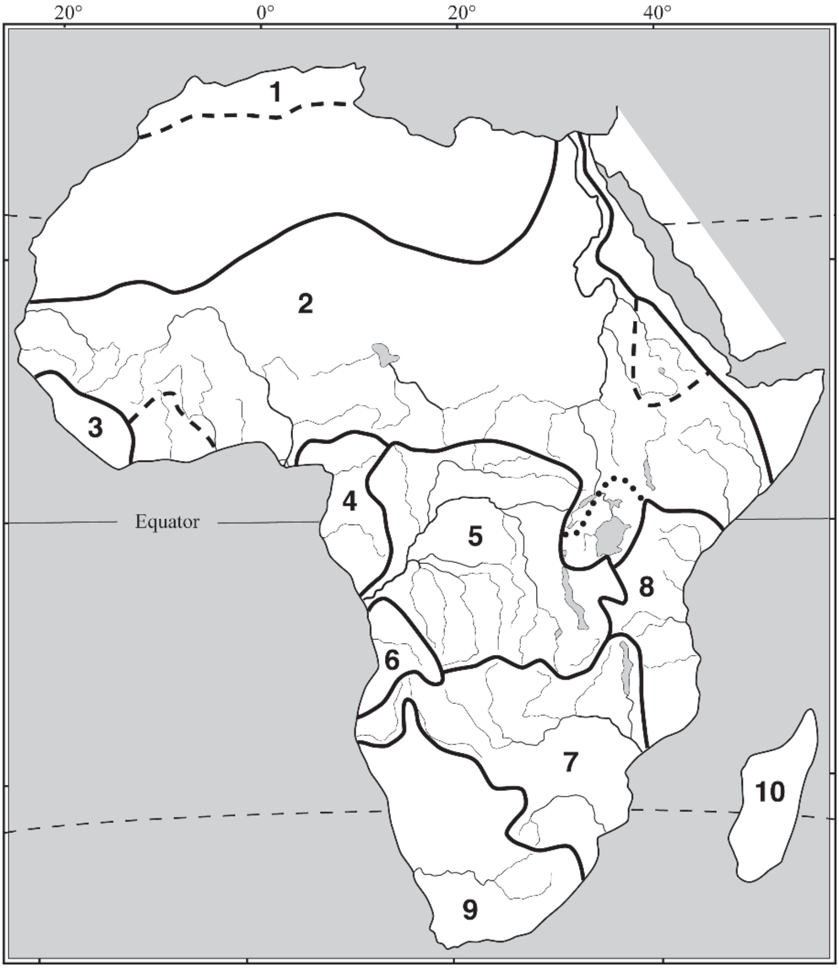

Fig. 2 Ichthyofaunal provinces in Africa, modified from Roberts (1975) and Lévêque (1997). Dashed lines indicate sub-provinces; dotted line indicates the border of the Nilo-Sudan province as suggested by Roberts (1975), which was tentatively modified based on suggestions in more recent literature (see text). 1 – Maghreb; 2 – Nilo-Sudan; 3 – Upper Guinea; 4 – Lower Guinea; 5 – Zaïre; 6 – Qaunza; 7 – Zambezi; 8 – East Coast; 9 – Southern; 10 – Malagasy province

Nile Delta; (5) the Ethiopian Highlands, defined by the two blocks of highland in Ethiopia, separated by the rift valley; and (6) Lake Tana.

3 Fish Species Composition in the Nile Drainage Basin

Greenwood (1976) referred to the fishes of the Nile drainage basin as the “extended Nile ichthyofauna” (Figs. 3 and 4). The knowledge of the fish fauna in the Nilotic Lakes is better than that in the rivers. According to Greenwood (1976), the diversity and

Table 1 Endemic riverine genera in the Nilo-Sudan province according to Roberts (1975), and their presence in the Nile drainage basin

Family	Endemic genus	Presence in Nile drainage basin
Osteoglossidae	*Heterotis*	+
Mormyridae	*Hyperopisus*	+
Gymnarchidae	*Gymnarchus*	+
Kneriidae	*Cromeria*	+
Distichodontidae	*Paradistichodus*	–
Citharinidae	*Citharidium*	–
Bagridae	*Clarotes*	+
	Pardiglanis	–
Schilbeidae	*Irvineia*	–
	Siluranodon	+
Amphiliidae	*Andersonia*	+
Mochokidae	*Brachysynodontis*	+
	Hemisynodontis	+
	Mochokus	+
Cichlidae	*Gobiocichla*	–

high level of endemicity of the fishes in some of the Lakes, the related evolutionary questions and the economic importance of many lake fishes have resulted in “rather more research being done on the fishes of the Nilotic Lakes than on the species inhabiting the Nile itself.” During the past decades this discrepancy has only increased, as research on the Lakes, in particular Victoria and Tana, has expanded enormously. In the case of Lake Victoria, research was strongly stimulated by dramatic human-induced ecological perturbations (Witte et al., 2009).

Greenwood (1976) recorded some 320 species in 60 genera in the Nile drainage basin. However, in the past decades hundreds of new cichlid species were discovered in Lake Victoria and its satellite Lakes (van Oijen et al., 1981; Witte & van Oijen, 1995; Seehausen, 1996; Kaufman et al., 1997; Witte et al., 2007a), as well as some 20 new and resurrected cyprinid species in Lake Tana (Nagelkerke & Sibbing, 1997; Nagelkerke & Sibbing 2000; de Graaf et al., 2000; Dejen et al., 2002; Stiassny & Getahun, 2007). Therefore, we currently estimate the total number of fish species in the Nile drainage basin at 800+.

4 River Nile

In the 1970s the number of fish species recorded in the River Nile was 115, of which 26 were considered endemic and 74 species were shared with the River Niger (Greenwood, 1976). The species described by Bailey (1994) in a guide to the fishes of the River Nile in the Republic of the Sudan, also numbered 115. Lévêque (1997) listed 128 fish species belonging to 27 families for the total Nile (Table 2) of which 77 are shared with the Niger (Lévêque et al., 1991). This total number is modest, compared to that of the Niger, with 243 species (36 families), and the Congo with 787 species (31 families). The difference in species numbers between these river systems is partly explained by the size of the system. The number of

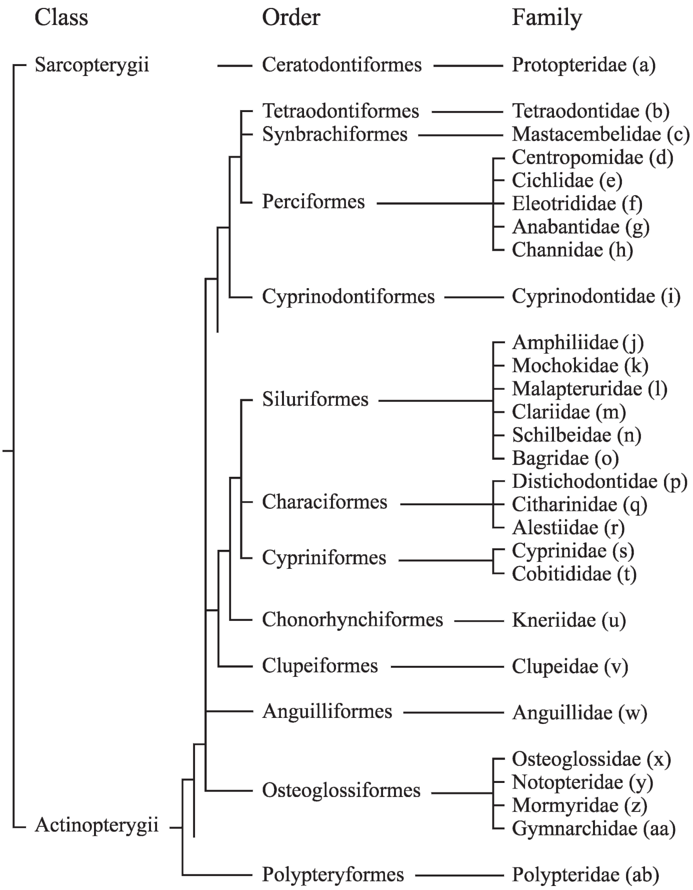

Fig. 3 Phylogenetic tree of the fish families occurring in the Nile drainage basin, based on Nelson 2006. Letters refer to representative species depicted in Fig. 4

fish species as a function of river basin area for 24 African rivers can be expressed as $Log_{10} N = 0.485 Log_{10} B - 0.571$ ($r^2 = 0.876$; N = number of species; B = basin area in km^2; Welcomme, 2003).

The Cyprinidae, Mormyridae, Mochokidae and Cichlidae together account for more than half the number of fish species in the River Nile (Table 2). The Mormyridae and Mochokidae have more representatives in the river than in the Lakes of the drainage basin (Table 3). The same holds for the Cyprinidae, with exception of Lake Tana that harbours almost as many cyprinid species as the river (Table 3). In contrast, the number of Cichlidae is considerably lower in the river than in the typical cichlid Lakes Edward, George, Victoria and Kyoga. The riverine cichlids comprise *Hemichromis fasciatus*, five haplochromine species (allocated to the genus *Thoracochromis*) and four tilapiine species, viz. *Tilapia zillii*, *Sarotherodon galilaeus, Oreochromis niloticus* and *O. aureus* (Lévêque et al., 1991).

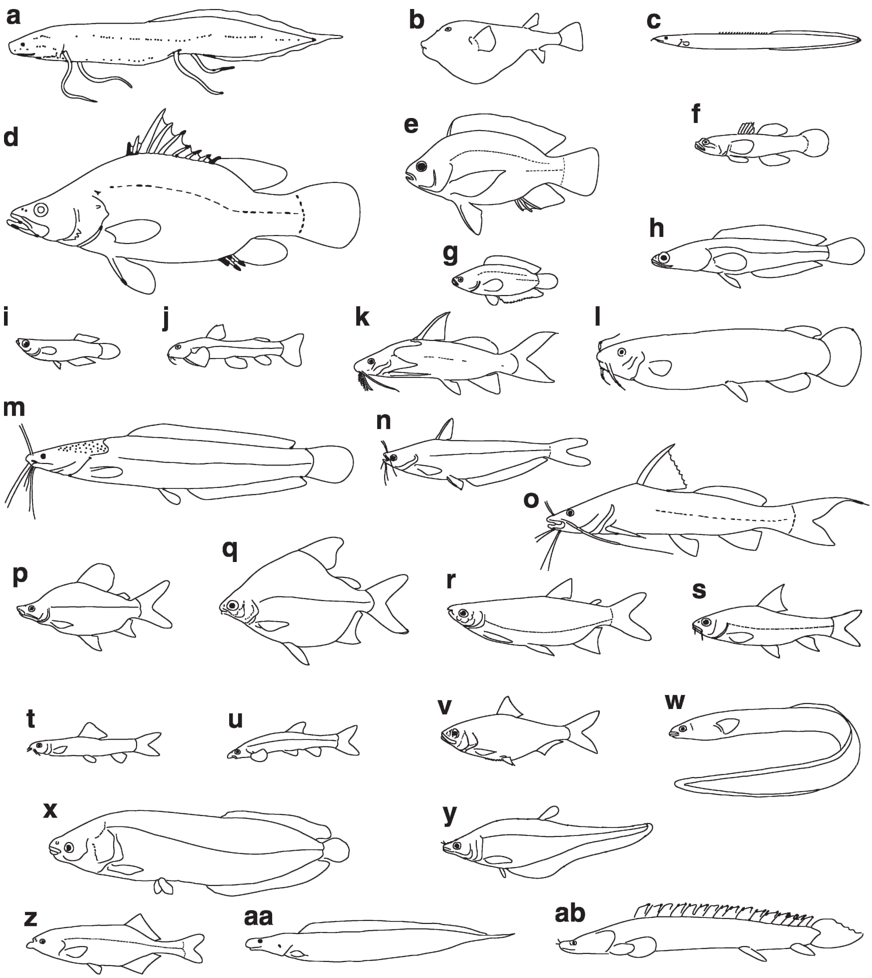

Fig. 4 Outline figures of representatives of the fish families in the Nile drainage basin. Letters refer to the families in Fig. 3. Redrawn from Nelson (1984) and van Oijen (1995)

Being the longest river in the world, the Nile comprises many different habitats, each with a different species composition. Well known is the Sudd, a swampy area of some 30,000–40,000 km^2 (Mohammed et al., 2006; Green & El-Moghraby, 2009), through which the Nile flows. Studies of the perennial wetland and the eastern seasonal-floodplain of the Sudd revealed 68 species, divided over 21 families (Table 2; Hickley & Bailey, 1986, 1987). Of these, 62 species were recorded in the permanent wetland of the Sudd (Hickley & Bailey, 1986) and only 23 species were caught in the seasonal floodplain (Hickley & Bailey, 1987). Several species from the latter habitat are known as obligatory or facultative air breathers e.g. *Protopterus aethiopicus*, *Polypterus senegalus*, *Heterotis niloticus*, *Xenomystis nigri*, *Clarias gariepinus*, *Ctenopoma muriei*, and *Parachanna obscura* (Hickley & Bailey, 1987). Concerning

Table 2 Total number of fish species in the River Nile (White and Blue) and some of its parts

Fish families	Nile	Sudd	L. Nubia
Protopteridae	2	1	–
Polypteridae	3	2	–
Anguilidae	1	–	–
Clupeidae	1	–	–
Osteoglossidae	1	1	–
Notopteridae	1	1	–
Mormyridae	15	8	4
Gymnarchidae	1	1	–
Kneriidae	1	–	–
Alestiidae	8	5	3
Distichodontidae	7	5	–
Citharinidae	2	3	2
Cyprinidae	25	9	4
Balitoridae	1	–	–
Bagridae	6	5	4
Schilbeidae	5	3	2
Amphiliidae	1	–	–
Clariidae	7	2	1
Malapteruridae	1	–	–
Mochokidae	15	5	2
Cyprinodontidae	7	4	–
Channidae	1	1	–
Centropomidae	2	1	1
Eleotridae	1	1	–
Cichlidae	10	7	2
Anabantidae	2	2	–
Mastacembelidae	–	–	–
Tetraodontidae	1	1	–
Total families	27	21	10
Total species	128	68	25

biomass, important species in Lakes and channels of the perennial wetland were the catfishes *Synodontis schall*, *S. frontosus* and *Auchenoglanis biscutatis*, the alestiid *Alestes dentex* and the osteoglossid *H. niloticus* (Hickley & Bailey, 1986). According to Hickley and Bailey (1986), "with exception of zooplanktivores all components of the trophic spectrum are well represented in lake communities" of the Sudd. In seasonal floodplains *Ctenopoma murei*, *Epiplatys spilargyreius*, *C. gariepinus*, *O. niloticus* and *P. obscura* were prominent (Hickley & Bailey, 1987).

A study of Lake Nubia (the part of man-made Lake Nasser within the Sudanese borders), using gill nets with stretched meshes ranging from 40 to 200 mm, revealed 25 fish species belonging to ten families (Table 2; Ali, 1984). Here the most important species were *Labeo niloticus*, *Lates niloticus*, *Hydrocynus forskalii* and *Alestes baremoze*.

Twelve freshwater fish species, including five cichlid species and the catfish *C. gariepinus*, are known from Lake Borullus of the Nile Delta (Dumont & El-Shabrawy, 2007).

Table 3 Number of fish species in the River Nile (White and Blue) and in lakes connected to it (Greenwood, 1966, 1974; Lévêque et al., 1991; Lévêque, 1997; Witte & van Oijen, 1995; Seehausen, 1996; Kaufman et al., 1997; Snoeks, 2000; Nagelkerke & Sibbing, 2000; de Graaf et al., 2002)

Fish families	R. Nile	L. Vict/Kyoga	L. Edw/G	L. Alb	L. Tana
Protopteridae	2	1	1	1	–
Polypteridae	3	–	–	1	–
Anguilidae	1	–	–	–	–
Clupeidae	1	–	–	–	–
Osteoglossidae	1	–	–	–	–
Notopteridae	1	–	–	–	–
Mormyridae	15	7	2	7	–
Gymnarchidae	1	–	–	–	–
Kneriidae	1	–	–	–	–
Alestiidae	8	2	–	5	–
Distichodontidae	7	–	–	–	–
Citharinidae	2	–	–	4	–
Cyprinidae	25	17	4	5	24
Balitoridae	1	–	–	–	1
Bagridae	6	1	1	3	–
Schilbeidae	5	1	–	2	–
Amphiliidae	1	–	–	–	–
Clariidae	7	6	4	2	1
Malapteruridae	1	–	–	1	–
Mochokidae	15	2	–	3	–
Cyprinodontidae	7	7	4	2	–
Channidae	1	–	–	–	–
Centropomidae	2	(1)	–	2	–
Eleotridae	1	–	–	–	–
Cichlidae	10	ca 600 (+4)	60	10	1
Anabantidae	2	1	2	–	–
Mastacembelidae	–	1	–	–	–
Tetraodontidae	1	–	–	–	–
Total families	27	12 (+1)	8	14	4
Total species	128	600–700	78	48	27

Numbers within brackets concern introduced taxa (see text).

5 Lake Albert

Lake Albert, with a surface of 6,800 km^2 and a maximum depth of 58 m, is the only major Nilotic lake that is not isolated by falls from the River Nile (Fig. 1). Consequently, many species in this lake also occur in the river. A total of 48 species belonging to 14 families has been reported for Lake Albert (Table 3; Greenwood 1966, 1974). The degree of endemism is relatively low (ca 13%); one endemic cyprinid, one centropomid and four haplochromine cichlid species (Greenwood, 1974, 1976). In contrast to the other Lakes, it shares the families Polypteridae, Citharinidae, Malapteruridae and the Centropomidae with the River

Nile (Table 3; note that the Nile perch – *Lates niloticus*, Centropomidae – was introduced into Lakes Victoria/Kyoga in the 1950s; see chapter on Fisheries in the Nile System). Further, compared to the other Lakes, Lake Albert has a relatively high number of species belonging to the families Alestiidae and Bagridae (Table 3). In contrast, the number of cichlid species is relatively low. Among the ten reported cichlid species from Lake Albert, four are tilapiines: viz. *Tilapia zillii*, *Sarotherodon galilaeus*, *Oreochromis niloticus* and *O. leucostictus* (Greenwood, 1966; Trewavas, 1983). The other six species are haplochromines (Greenwood, 1974).

Lake Turkana (formerly called Lake Rudolf), now completely isolated from the Nile (Johnson & Malala, 2009), has a fauna similar to that of Lake Albert. It includes many species that are shared by both Lakes and by the River Nile (Greenwood, 1976).

6 Lakes Edward and George

Lakes Edward and George are isolated from Lake Albert by falls in the Semliki River (Fig. 1), which are supposed to form a barrier to most fish species migrating upriver (Greenwood, 1976). The small and shallow Lake George (270 km^2, maximum depth 4 m) and the larger and deeper Lake Edward (2,325 km^2, maximum depth 117 m) are connected through the 36 km long, river-like Kazinga Channel (Green, 2009). At least 78 fish species, belonging to 8 families, are known from these Lakes (Table 3). The fish fauna is dominated by the family Cichlidae with 60+ species (Table 3; Snoeks, 2000). These include haplochromine cichlids, more than 90% of which are endemic, and two tilapiine species, *Oreochromis niloticus* and *O. leucostictus* (Greenwood, 1974; Snoeks, 2000).

7 Lakes Victoria and Kyoga before the 1980s

With a surface area of 68,800 km^2, Lake Victoria is the largest tropical lake in the world (Lehman, 2009). Compared to other large Lakes it is relatively shallow (maximum depth 70 m). On its way to Lake Albert, the water of Lake Victoria passes through Lake Kyoga (surface area 2,700 km^2, maximum depth 8 m). Lakes Victoria and Kyoga are cut off from Lake Albert and the Nile by the impassable Murchison Falls, which are some 40 m high. Further, Lake Victoria was isolated from the Victoria Nile and Lake Kyoga by the Ripon falls. Due to the Owen Falls dam, built downstream in the 1950s, the Ripon Falls were submerged (Fig. 1). However, the dam is probably an even more effective barrier than were the falls (Greenwood, 1974).

Though Greenwood (1967, 1974) found endemic haplochromine cichlids in Lake Kyoga, he suggested that the fishes of this lake are mostly conspecific with those of Lake Victoria and that it is very likely that the latter lake was the chief source of fish stocks for Lake Kyoga. Kaufman estimated the number of haplochromines endemic to Lake Kyoga at 100 species (Turner et al., 2001). Because relatively little information is available on the cichlid fauna of Lake Kyoga, we treat them together with those of Lake Victoria. When Lake Kyoga and the satellite Lakes of Victoria/Kyoga are included, the total number of haplochromine species in the area may rise to 600 or even more (Kaufman et al., 1997). This makes the fish fauna of Lakes Victoria/Kyoga extremely rich compared to that of all other parts of the Nile system (Table 3). However, Lakes Victoria/Kyoga harbour only 46 native non-cichlid species of which 16 are endemic and 10 are shared with the River Nile (Greenwood, 1974; Lévêque et al., 1991). These non-cichlid species belong to 11 families, so at the family level the diversity in Lakes Victoria/Kyoga is distinctly lower than in the River Nile (Table 3). Two indigenous tilapiines, *Oreochromis esculentus* and *O. variabilis*, are present in the Lakes, and four species (*O. niloticus*, *O. leucostictus*, *Tilapia zillii*, *T. rendalli*) were introduced in the 1950s (Welcomme, 1988). Apart from these cichlid species, the Nile perch (*Lates niloticus*), was also introduced (Welcomme, 1988; Witte et al., 2009).

More than 500 endemic haplochromine species, all female mouth brooders, are known from Lake Victoria alone (Greenwood, 1974; Kaufman & Ochumba, 1993; Witte & van Oijen, 1995; Seehausen, 1996; Witte et al., 2007a). They made up more than 80% of the demersal ichthyomass (Kudhongania & Cordone, 1974). Other prominent species in bottom trawl catches were *O. esculentus*, *Clarias gariepinus*, *Protopterus aethiopicus* and *Bagrus docmak* (Kudhongania & Cordone, 1974). Apart from these demersal fishes, the small pelagic cyprinid *Rastrineobola argentea* made an important contribution to the fish fauna in the lake (Okedi, 1974).

Several authors raised doubts about the taxonomic status of Lake Victoria haplochromines (Sage & Selander, 1975; Turner & Grosse, 1980; Crapon de Caprona & Fritzsch, 1984; Meyer, 1987). However, ecological research corroborated in many cases the biological soundness of species distinction originally based on male colouration and small morphological differences. That is, no indications of gene flow could be found between presumed species that live in sympatry (Hoogerhoud et al., 1983; Goldschmidt & Witte, 1990; Seehausen et al., 1998b).

Lake Victoria haplochromines have been classified into 15 trophic groups, each consisting of species sharing morphological characters related to the capture, uptake and processing of their dominant food source (Figs. 5 and 6; Greenwood, 1974; Witte & van Oijen, 1990, 1995). The morphological characters that were used by Greenwood (1979, 1980) for the revision of the genus *Haplochromis* and related taxa into more than 20 genera and several subgenera, show considerable overlap with those that characterize the trophic groups. During the past decades there have been extensive debates on the validity of the genera defined in this way by Greenwood (Hoogerhoud, 1984; Meyer et al., 1990; Lippitsch, 1993; Snoeks, 1994; Seehausen, 1996; van Oijen, 1996; Seehausen et al., 1998a). Because of the disagreements, and as a considerable number of the haplochromine species from Lake Victoria cannot be assigned to the “new” genera, we prefer to keep the species in the genus *Haplochromis* and add the new generic names in parenthesis, i. e. use them as subgenera.

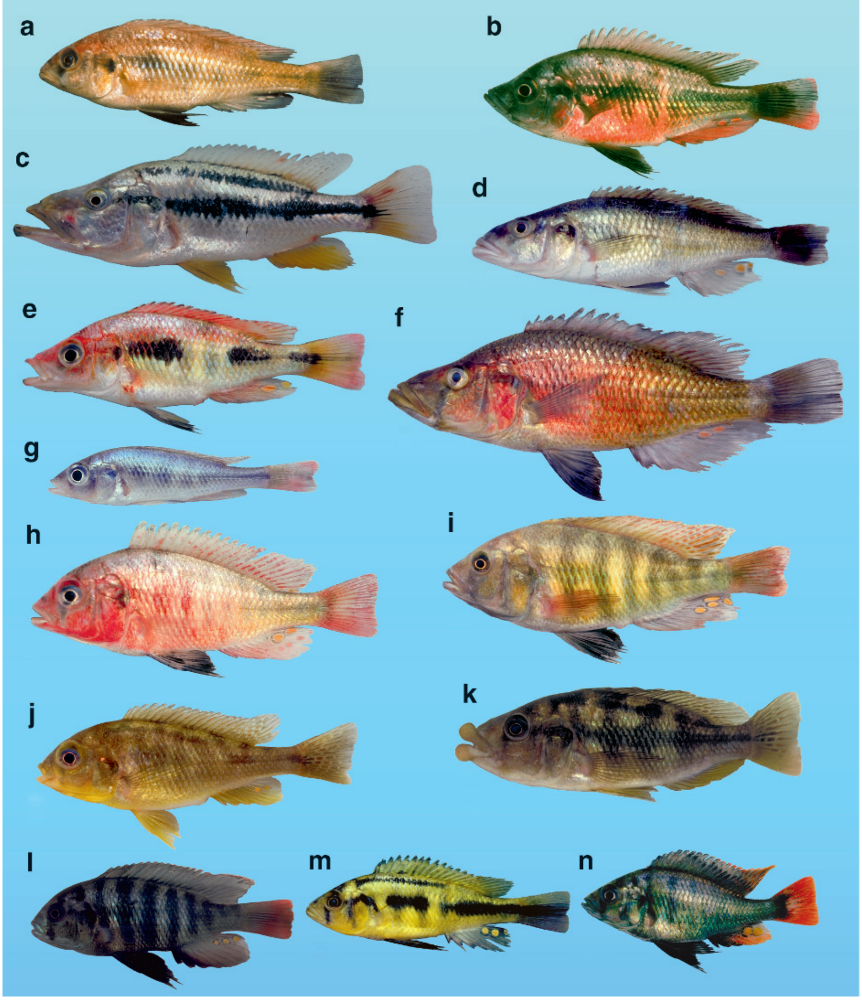

Fig. 5 Representatives of Lake Victoria haplochromine cichlids: (**a**) *H.* (*?*) *teunisrasi* (parasite eater); (**b**) *H.* (*Lipochromis*) *microdon* (paedophage); (**c**) *H.* (*Prognathochromis*) *macrognathus* (piscivore); (**d**) *H.* (*P.*) "dentex like" (piscivore); (**e**) *H.* (*P.*) "erythrocryptogramma" (prawn eater); (**f**) *H.* (*P.*) *argenteus* (piscivore); (**g**) *H.* (?) "argens" (zooplanktivore); (**h**) *H.* (*Labrochromis*) *teegelaari* (pharyngeal mollusc crusher); (**i**) *H.* (*Labrochromis*) *ishmaeli* (pharyngeal mollusc crusher); (**j**) *H.* (*Ptyochromis*) *sauvagei* (oral mollusc sheller); (**k**) *H.* (*Paralabidochromis*) *chilotes* (insectivore); (**l**) *H.* (*Neochromis*) *rufocaudalis* (algae grazer); (**m**) *H.* (*?*) "citrus" (phytoplanktivore); (**n**) *H.* (*Enterochromis*) "75" (detritivore/phytoplanktivore) (*see Color Plates)*

The trophic groups are not equally distributed over the lake. For instance, epilithic algae grazers are restricted to rocky shores and epiphytic algae grazers are mainly caught along shores with stands of rooted plants (e.g. Greenwood, 1974; Witte et al., 1992; Seehausen et al., 1997b). Insectivores and oral shelling molluscivores are mainly associated with hard substrates like sand and rocks, and

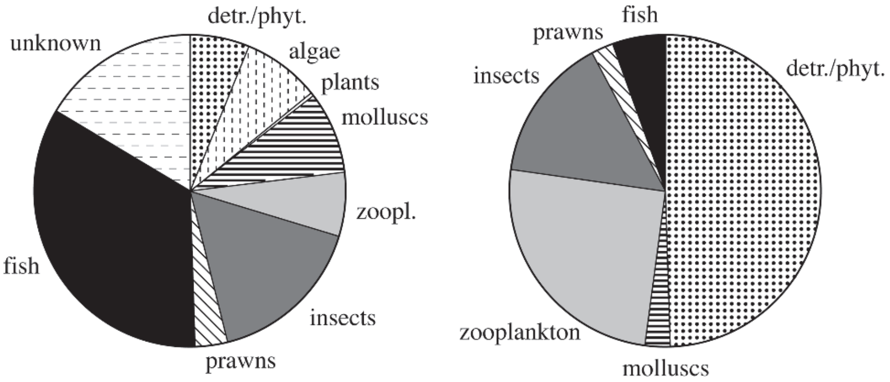

Fig. 6 Haplochromine trophic groups from Lake Victoria: (*left*) species composition in all habitats. Note that the paedophages and the scale scraper are included in the piscivores and that rare trophic types, like the parasite feeders and the crab eater, are not included; (*right*) biomass composition in sub-littoral waters (6–20 m deep)

detritivores with mud bottoms (e.g. Greenwood, 1974; Witte, 1981; Witte et al., 1992). With respect to the total number of species, the piscivores and insectivores were the most common groups (Fig. 6), however, concerning biomass the detritivores and zooplanktivores were most important, at least in the sub-littoral habitat (6–20 m deep; Fig. 6) and probably also in the open waters of the lake.

Molecular studies indicate that the 500+ haplochromine species of Lake Victoria evolved within the geologically short period of 100,000–400,000 years (Meyer et al., 1990; Nagl et al., 2000; Seehausen et al., 2003; Verheyen et al., 2003), and perhaps even in a much shorter time frame. Bottom core studies by Johnson et al. (1996) suggest that Lake Victoria fell dry completely 14,600 years ago. The reliability of the data has been questioned (Fryer, 2004), but see Stager & Johnson (2008). The origin, age and evolutionary history of the extraordinary speciose Lake Victoria haplochromines is still debated (Nagl et al., 2000; Seehausen et al., 2003; Verheyen et al., 2003; Seehausen, 2006). Nagl et al. (2000) suggested that the Lake Victoria haplochromines originated from trophic generalists, which lived in the East African river systems and in which mutations for morphological adaptations were already present as polymorphisms. Data of Seehausen et al. (2003) indicated that the Lakes Victoria/Edward flock is derived from the morphologically and ecologically diverse cichlid genus *Thoracochromis* from the Congo and Nile. Verheyen et al. (2003) explained the fast radiation of eco-morphological diversity in Lake Victoria haplochromines by their descent from the lacustrine, possibly already diversified, Lake Kivu ancestors. All four papers suggest that the Lake Victoria flock sensu stricto must be older than 14,600 years and that it is not strictly monophyletic. Rapid speciation has been suggested to be a typical feature of haplochromine cichlids (Seehausen, 2006) and is thought to be partly the result of sympatric speciation through disruptive sexual selection for conspicuous coloration (Maan et al., 2004) and strong assortative mating (Seehausen & van Alphen, 1998).

Learning in the form of sexual imprinting seems to facilitate assortative mating and reproductive isolation among closely related cichlid species (Verzijden & ten Cate, 2007).

Water clarity appears to be important for this mode of speciation and there is a significant correlation between the number of coexisting haplochromine species and transparency, among different East African Lakes and among localities within Lake Victoria (Seehausen et al., 1997a). The functional decoupling of the upper and lower pharyngeal jaws in cichlid fish may have contributed to the high degree trophic radiation of the haplochromines (Galis & Drucker, 1996).

8 Lakes Victoria and Kyoga after the 1980s

During past few decades the composition of the fish fauna in Lakes Victoria and Kyoga changed dramatically due to anthropogenic perturbations in the ecosystem. The boom of the introduced Nile perch in the 1980s as well as fishery and habitat deterioration (Witte et al., 2009) had a strong impact on the haplochromine cichlids and many other fish species (Ogutu-Ohwayo, 1990; Witte et al., 1992; Goudswaard & Witte, 1997; Goudswaard et al., 2002a,b, 2008). It was estimated that some 200 of the endemic haplochromine species may have gone extinct (Witte et al., 1992). The highly structured rocky shores and papyrus fringes, where Nile perch densities are low, were less affected by Nile perch than the sub-littoral and offshore waters (Witte et al., 1992, 2007a; Seehausen, 1996). However, the decrease in water transparency due to eutrophication may have caused hybridization among several haplochromine species, including those living along rocky shores (Seehausen et al., 1997a; Seehausen, 2006). Lake Victoria haplochromines are rather tolerant to low oxygen concentrations (Verheyen et al., 1986; Chapman et al., 1995; Rutjes et al., 2007), therefore the impact of the increased hypoxic conditions due to eutrophication (Hecky et al., 1994) may have been less severe than suggested (Witte et al., 2005).

Some satellite Lakes of Lakes Victoria and Kyoga were not invaded by Nile perch or affected by eutrophication. These Lakes, each with their own endemic haplochromines, still have a relatively pristine fish fauna, including some types of haplochromines that seem to have vanished from the main Lakes (Ogutu-Ohwayo, 1993; Mwanja et al., 2001; Aloo, 2003; Mbabazi et al., 2004).

In the course of the 1990s, after a decline in Nile perch in Lake Victoria due to intensive fishing, a slow resurgence of some haplochromine species was observed, mainly zooplanktivores and detritivores (Witte et al., 1995, 2000, 2007b; Seehausen et al., 1997b; Balirwa et al., 2003). Of each group only about 30% of the species recovered and the ratio between detritivores and zooplanktivores reversed (Witte et al., 2007a, b). Before the 1980s detritivores made up about 50% of the haplochromine biomass in the sublittoral waters and zooplanktivores about 25% (Fig. 6; Goldschmidt et al., 1993), whereas by 2001 detritivores constituted only 15% and zooplanktivores more than 80%. However, the majority of the species did not recover. Many of the highly specialized trophic types like scale eaters, parasite eaters and prawn eaters have not been caught since the 1980s, whereas piscivores and paedophages are extremely rare now, both with respect to numbers of individuals and species. Balirwa et al. (2003) suggested that conservation of biodiversity and fishery sustainability may not have to be antitheses in the management of Lake Victoria. A modelling study suggested that Nile perch prefer and grow fastest on a haplochromine prey base (Kaufman & Schwarz, 2002). If the model is realistic, it would suggest that it is worth thinking of management strategies that allow enough fishing on Nile perch to ensure an abundance of their haplochromine prey, but not so much pressure as to threaten the Nile perch stock itself (Balirwa et al., 2003). However, to allow maintenance and restoration of haplochromine diversity, the urgent measures must include serious attempts to reverse the eutrophication of Lake Victoria (Seehausen et al., 1997a; Balirwa et al., 2003; Witte et al., 2005).

Responses to the environmental changes were observed in several fish species in Lake Victoria. Reproductive strategies changed in the tilapiine cichlid *Oreochromis niloticus* (Ojuok et al., 2007) and in haplochromine cichlids and the cyprinid *Rastrineobola argentea* (Wanink & Witte 2000a; Manyala & Ojuok, 2007). Dietary shifts were observed in zooplanktivorous and detritivorous haplochromines (van Oijen &Witte, 1996; Katunzi et al., 2003; Kishe-Machumu et al., 2008), in *Rastrineobola argentea* (Wanink, 1998), in *Oreochromis niloticus* (Gophen et al., 1993; Bwanika et al., 2006; Njiru et al., 2007), in the catfishes *Bagrus docmak* and *Schilbe intermedius* (Olowo & Chapman, 1999), and the alestiid *Brycinus sadleri* (Wanink & Joordens, 2007). In all these cases the amount of macro-invertebrates in the diets increased strongly. Morphological adaptations to the increased hypoxic conditions, the decreased water transparency and the changes in diet were observed in the cyprinid *R. argentea* and in the haplochromines (Wanink & Witte, 2000b; Chapman et al., 2008; Kishe-Machama et al., 2008; Witte et al., 2008).

9 Lake Tana

Lake Tana is part of the headwaters of the Blue Nile; it has a surface area of 3,100 km^2 and a maximum depth of only 14 m (Vijverberg et al., 2009). The shallow lake is not stratified and extremely turbid; Secchi depths range from 0.3 m in the wet season to 1.8 m in some sheltered areas during the dry season (Sibbing & Nagelkerke, 2001). The ca 40 m high Blue Nile falls at Tissisat, 30 km downstream from the lake, form an effective barrier to the migration of fish from the lower Blue Nile basin into Lake Tana. Until the 1990s the fish fauna of Lake Tana had been poorly studied (Greenwood, 1976; Lévêque, 1997). Greenwood (1976) wrote that "Lake Tana, as far as can be told from its poorly studied fauna, should be considered merely as part of the Blue Nile". However, he also noted that the occurrence in Lake Tana of *Nemacheilus abyssinicus*, the only known representative in Africa of the Euro-Asiatic family Balitoridae (then placed in the family Cobitidae), "reemphasises the need for further detailed studies" on Lake Tana fishes (Greenwood, 1976). Such studies were started in the 1990s (Nagelkerke et al., 1994, 1995a, b; Sibbing et al., 1994, 1998; Dixon et al., 1996; Mina et al., 1996; Nagelkerke & Sibbing, 1996, 1997, 2000; Wudneh, 1998; Dgebuadze et al., 1999). The presence of *N. abyssinicus*, until then based on a single specimen, was confirmed in small streams close to Lake Tana and in large parts of the Ethiopian plateau (Dgebuadze et al., 1994). A single specimen was found in the deep part of the lake (Nagelkerke, 1997). The only cichlid in this highly turbid lake is the tilapiine *Oreochromis niloticus tana* and the only catfish *Clarias gariepinus*. The latter was originally described as *C. tsanensis* by Boulenger (1902) but later synonymised with *C. gariepinus* (Teugels, 1986).

In contrast to the headwater Lakes of the White Nile where haplochromine cichlids dominate, the fish fauna of Lake Tana is dominated by the cyprinid genera *Barbus* and *Labeobarbus*. Of the 93 species of freshwater fishes reported for Ethiopia (Getahun & Stiassny, 1998; Froese & Pauly, 2001; Stiassny & Getahun, 2007), 44 species are cyprinids, and in Lake Tana alone 24 cyprinid species are found (Table 3), of which 18 are endemic to the lake. The large barbs of Lake Tana (up to 100 cm) were first described by Rüppell (1836) as five *Barbus* and one *Labeobarbus* species. Later, Bini (1940) identified 10 species, including 23 subspecies, and considered them as a separate subgenus *Labeobarbus*. Inadequate descriptions and keys forced Banister (1973) to a revision of the large barbs of East-Africa. He lumped all 50 nominal species and subspecies into a single highly variable species *Barbus intermedius*, composed of two subspecies: *Barbus intermedius intermedius*, including all Lake Tana barbs, and *Barbus intermedius australis*. Following detailed morphological and ecological characters (Nagelkerke et al., 1994; Nagelkerke & Sibbing, 1997), immuno-genetics (Dixon et al., 1996), reproductive segregation (Nagelkerke & Sibbing, 1996) and ontogenetic development (Nagelkerke et al., 1995b) the large barbs of Lake Tana were upgraded from distinct morphotypes (Nagelkerke et al., 1994) into 15 endemic species in addition to the non-endemic *B. intermedius* (Nagelkerke & Sibbing, 1997, 2000). Although Mina et al. (1996) and Dgebuadze et al. (1999) only partly agreed on the specific status of the large barbs and favoured the description of the barb diversity by plastic phenotypes of *Barbus intermedius*, several follow-up studies confirmed morphological, ecological, reproductive and genetic segregation (Kruiswijk et al., 2005; de Graaf et al., 2003a,b; Palstra et al., 2004; de Graaf et al., 2005, 2008). Palstra et al. (2004) assigned all large hexaploid barbs of Lake Tana to the genus *Labeobarbus* following suggestions by Bini (1940), Berrebi (1995), Skelton (2002) and Berrebi & Tsigenopoulos (2003). This better reflects the phylogenetic distance between the hexaploid large barbs (Golubtsov & Krysanov, 1993) and the small diploid barbs of Lake Tana, also supported by molecular data (de Graaf et al., 2003b; de Graaf et al., 2007).

The last desiccation of Lake Tana was estimated in the same period (between 18,700 and 16,700 BP; Lamb et al. 2007) as that in Lake Victoria (Johnson et al., 1996; Stager & Johnson, 2008). The *Labeobarbus* species flock probably evolved from a highly polymorph *Labeobarbus intermedius* complex, still present along the shore of Lake Tana (Nagelkerke & Sibbing, 2000), by sympatric speciation following disruptive selection on trophic structures (Sibbing et al., 1998).

Varicorhinus beso is another large (up to 40 cm) cyprinid in Lake Tana. It is closely related to *Labeobarbus*, which is also apparent from some hybrids found (Nagelkerke & Sibbing, 2000). The small barb species are considered to belong to '*Barbus* sensu lato' by Howes (1987); they are diploid, have diverging instead of parallel striae on the exposed part of their scales, and smaller dorsal spines than *Labeobarbus*. Three species of small (<10 cm) barbs (*Barbus*, subgenus *Enteromius*) are known from Lake Tana: *Barbus humilis*, *Barbus pleurogramma* and the recently described pelagic *Barbus tanapelagius*. The species *Barbus trispilopleura* that was also reported from the lake (Boulenger, 1902) formed a continuous range in appearance with *Barbus humilis* and has been synonymized as a shallow water ecotype of *Barbus humilis* (Dejen et al., 2002). Molecular analyses show the genetic similarity between the benthivorous *Barbus humilis* and the zooplanktivorous *Barbus tanapelagius*, which probably evolved from the first mentioned species after production of zooplankton increased in the incipient Lake Tana (de Graaf et al., 2007).

According to Boulenger (1911), the genus *Garra* has two species in Lake Tana, *G. dembeensis* and *G. quadrimaculatus*. In a recent revision by Stiassny & Getahun (2007) the latter species was re-identified and described as *G. dembecha*, a new species that also occurs outside the lake in Eritrea, Kenya and Tanzania. Stiassny & Getahun (2007) also described two new endemic species for Lake Tana, viz. *G. regressus* (formerly *G. microstoma*, Getahun 2000) and *G. tana*.

All Lake Tana barbs and labeobarbs evolved from benthic riverine species; many adapted to new spatial and trophic niches after the origin of Lake Tana (Fig. 7 and 8; Nagelkerke & Sibbing, 1996; Sibbing et al., 1998; Sibbing & Nagelkerke, 2001; Palstra et al., 2004, de Graaf et al., 2008). The most conspicuous group, and the most deviating from the ancestral benthivore design, are the piscivores with four obligatory (prey > 80% fish) and four predominantly (prey > 60% fish) piscivorous species (Sibbing et al., 1998; Sibbing & Nagelkerke, 2001). Although limited in prey size (to ca 15% of their fork length, de Graaf et al., 2003c) labeobarbs are successful piscivores in Lake Tana, probably due to the absence of specialized and competing piscivores belonging to other fish families and the abundance of small *Barbus* and *Garra* in the proper size range of their processing capacity. Much like the polymorph *Labeobarbus intermedius* shore complex of Lake Tana, other labeobarb species feed on varied benthos (mixtures of insect larvae and detritus) and are segregated by habitat (mainly littoral rocks, littoral mud, sub-littoral or offshore benthopelagic; de Graaf et al., 2008). Whereas two species additionally take molluscs, only a single labeobarb feeds substantially on macrophytes (Sibbing & Nagelkerke, 2001; Vijverberg et al., 2009, Fig. 8). Zooplankton is partitioned among all juvenile *Labeobarbus*, adults of *L. brevicephalus* and the obligatory zooplanktivorous *B. tanapelagius* (Dejen et al., 2006). Phytoplankton seems to be a vacant food niche; it is, however, exploited by the abundant littoral *Oreochromis niloticus*. The small *Garra* species utilize the benthic algae, just like *Varicorhinus beso* which may feed more on the periphyton on littoral weeds and reed beds.

In contrast to Lake Victoria, the ichthyofauna of Lake Tana lacks fishes with extreme specialisations as found in paedophages, prawn eaters, crab eaters, parasite feeders and scale eaters. The cyprinid design, lacking oral jaw teeth, a stomach and

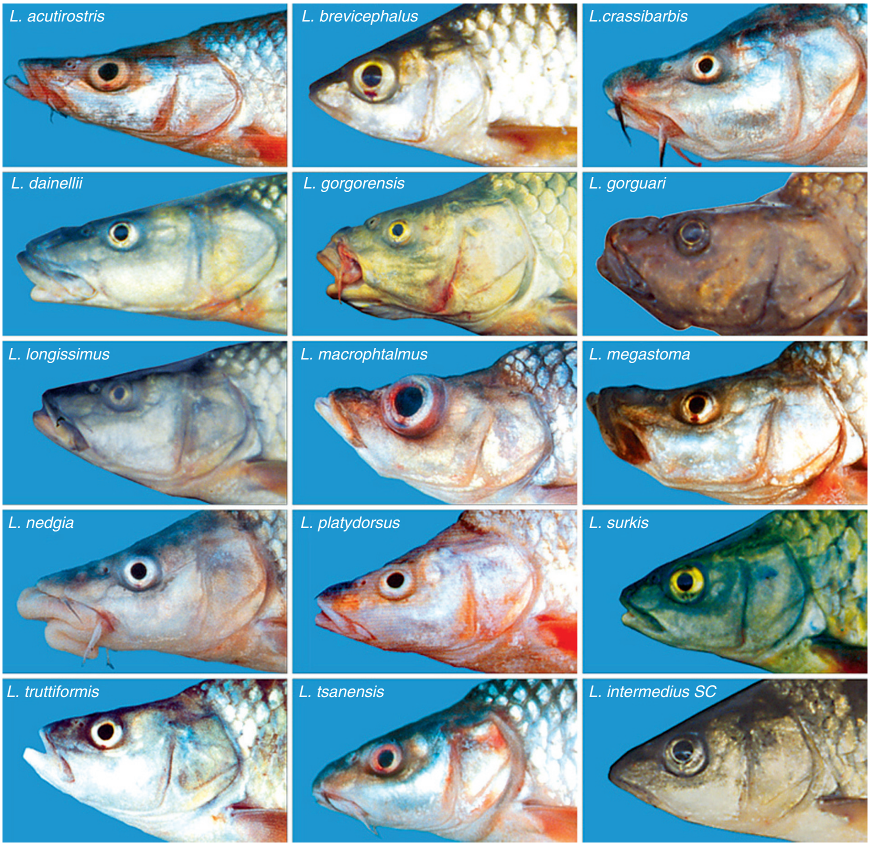

Fig. 7 Representatives of *Labeobarbus* species from Lake Tana. Obligatory piscivores (>80% fish): *L. acutirostris*, *L. truttiformis*, *L. longissimus*, *L. dainellii*, *L. megastoma*; facultative piscivores (>60% fish): *L. gorguari*, *L. platydorsus*; herbivores/molluscivores/detritivores: *L. surkis*, *L. gorgorensis*; polyphagous barbs: *L. brevicephalus*, *L. macrophthalmus*; benthivores: *L. nedgia*, *L. tsanensis*, *L. crassibarbis*, *L. intermedius* shore complex (*see Color Plates*)

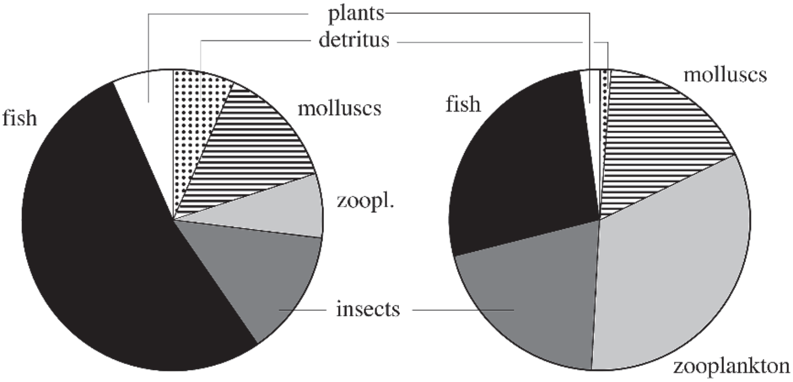

Fig. 8 Labeobarb trophic groups from Lake Tana: (*left*) species composition; (*right*) biomass composition

cellulases, may impose serious phylogenetic constraints on some trophic specializations. However, cyprinids possess highly developed and diversified pharyngeal jaws. This pharyngeal jaw system enables cyprinid fish to break down otherwise inaccessible tough and strong food types (Sibbing & Nagelkerke, 2001). Another speciality of the cyprinids is the sensory and highly muscular palatal organ required for sorting food from the non-food benthos (Sibbing et al., 1986). Equipped with these features the cyprinids found their niches mainly in the benthic zone. Their flexibility and opportunistic strength is demonstrated by the natural evolutionary experiment in Lake Tana, where they even expand into the piscivorous level due to the lack of competitors.

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Appendix

Species mentioned in the text of the chapters *Fish fauna of the Nile* and *Fisheries in the Nile system*, with authors and families to which the species belong

Species	Author	Family	Notes
Alestes baremoze	(De Joannis, 1835)	Alestiidae	Formerly *baremose*, Characidae
A. dentex	(Linnaeus, 1758)	Alestiidae	Formerly Characidae
Auchenoglanis biscutatis	(Geoffroy Saint-Hilaire, 1809)	Bagridae	
Bagrus bajad	Forsskål, 1775	Bagridae	Formerly *bayad*
B. docmak	Forsskål, 1775	Bagridae	
Barbus altianalis	Boulenger, 1903	Cyprinidae	
B. bynni	Forsskål, 1775	Cyprinidae	
B. humilis	Boulenger, 1902	Cyprinidae	
B. intermedius australis	Banister, 1973	Cyprinidae	Now *Labeobarbus*
B. intermedius intermedius	Rüppell, 1836	Cyprinidae	Now *Labeobarbus*
B. pleurogramma	Boulenger, 1902	Cyprinidae	
B. tanapelagius	de Graaf et al., 2000	Cyprinidae	
B. trispilopleura	Boulenger, 1902	Cyprinidae	In L. Tana synonym with *humilis*
Brycinus jacksonii	(Boulenger, 1912)	Alestiidae	Formerly Characidae
B. nurse	(Myers, 1929)	Alestiidae	Formerly Characidae
Clarias gariepinus	(Burchell, 1822)	Clariidae	Formerly *lazera*;
Ctenopoma murei	(Boulenger, 1906)	Anabantidae	
Epiplatys spilargyreius	(Duméril, 1861)	Cyprinodontidae	Formerly *E. marnoi*
Garra dembeensis	(Rüppell, 1836)	Cyprinidae	
G. dembecha	Stiassny & Getahun, 2007	Cyprinidae	Formerly *quadrimaculatus* (non-Rüppell)
G. regressus	Stiassny & Getahun, 2007	Cyprinidae	Formerly *microstoma*
G. tana	Stiassny & Getahun, 2007	Cyprinidae	
Haplochromis (*?*) "argens"	Cheironym	Cichlidae	
H. (*Prognathochromis*) *argenteus*	Regan, 1922	Cichlidae	
H. (*Paralabidochromis*) *chilotes*	(Boulenger, 1911)	Cichlidae	
H. (*?*) "citrus"	Cheironym	Cichlidae	
H. (*Prognathochromis*) *dentex*	Regan, 1922	Cichlidae	
H. (*Prognathochromis*) "erythrocryptogramma"	Cheironym	Cichlidae	
H. (*Labrochromis*) *ishmaeli*	Boulenger, 1906	Cichlidae	

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Species	Author	Family	Notes
H. (*Lipochromis*) *microdon*	(Boulenger, 1906)	Cichlidae	
H. (*Neochromis*) *rufocaudalis*	Seehausen & Bouton, 1998	Cichlidae	
H. (*Ptyochromis*) *sauvagei*	Pfeffer, 1896	Cichlidae	
H. (*Labrochromis*) *teegelaari*	Greenwood & Barel, 1978	Cichlidae	
H. (*?*) *teunisrasi*	Witte & Witte-Maas, 1981	Cichlidae	
H. (*Enterochromis*) "75"	Cheironym	Cichlidae	
Hemichromis fasciatus	Peters, 1858	Cichlidae	
Heterotis niloticus	Rüppell, 1829	Osteoglossidae	
Hydrocynus forskalii	(Cuvier, 1819)	Alestiidae	Formerly *forskahlii*, Characidae
Labeo altivelis	Peters, 1852	Cyprinidae	
L. niloticus	(Forsskål, 1775)	Cyprinidae	
L. mesops	Günther, 1868	Cyprinidae	
L. victorianus	Boulenger, 1901	Cyprinidae	
Labeobarbus acutirostris	(Bini, 1940)	Cyprinidae	
L. brevicephalus	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. crassibarbis	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. dainellii	(Bini, 1940)	Cyprinidae	
L. gorgorensis	(Bini, 1940)	Cyprinidae	
L. gorguari	(Rüppel, 1836)	Cyprinidae	
L. intermedius	(Rüppell, 1836)	Cyprinidae	
L. longissimus	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. macrophtalmus	(Bini, 1940)	Cyprinidae	
L. megastoma	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. nedgia	Rüppel, 1836	Cyprinidae	
L. platydorsus	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. surkis	(Rüppel, 1836)	Cyprinidae	
L. truttiformis	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. tsanensis	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
Lates niloticus	(Linnaeus, 1758)	Centropomidae	
Nemacheilus abyssinicus	Boulenger, 1902	Balitoridae	Formerly Cobitidae
Neobola bredoi	(Poll, 1945)	Cyprinidae	

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Species	Author	Family	Notes
Oreochromis aureus	(Steindachner, 1864)	Cichlidae	
O. esculentus	(Graham, 1929)	Cichlidae	
O. leucostictus	(Trewavas, 1933)	Cichlidae	
O. niloticus	(Linnaeus, 1758)	Cichlidae	
O. niloticus tana	Seyoum and Kornfield, 1992	Cichlidae	
O. variabilis,	(Boulenger, 1906)	Cichlidae	
Parachanna obscura	(Günther, 1861)	Channidae	Formerly *Channa*, Ophicephalidae
Polypterus senegalus	Cuvier, 1829	Polypteridae	
Protopterus aethiopicus	Heckel, 1851	Protopteridae	
Rastrineobola argentea	(Pellegrin, 1904)	Cyprinidae	
Sarotherodon galilaeus	(Linnaeus, 1758)	Cichlidae	
Synodontis frontosus	Vaillant, 1895	Mochokidae	
S. schall	(Bloch & Schneider, 1801)	Mochokidae	
Synodontis victoria	Boulenger, 1906	Mochokidae	
Tilapia rendalli	Boulenger, 1896	Cichlidae	
T. zillii	(Gervais, 1848)	Cichlidae	
Varicorhinus beso	Rüppell, 1836	Cyprinidae	
Xenoclarias eupogon	(Norman, 1928)	Clariidae	
Xenomystis nigri	(Günther, 1868)	Notopteridae	

Fossil Fish from the Nile River and Its Southern Basins

Kathlyn M. Stewart

Abstract The differing composition of the modern Nile River system fish faunas reflects the tectonic and climatic changes which occurred throughout the Cenozoic, particularly the late Cenozoic. The pre-Pliocene fish taxa were widespread ('nilotic') and fairly uniform in composition, with some of the earliest records of several families recorded in the Nile Valley. However geomorphological and climatic changes in much of Plio-Pleistocene northern and eastern Africa severely changed the hydrology of these areas, and the fish faunas of the Nile's southern basins experienced considerable immigration and disappearances. Exchange of fish between basins apparently occurred, particularly between the Nile and Lakes Albert and Turkana. The high humidity of the early Holocene resulted in expanded lakes and rivers, leading to exchanges between the Nile and the saharan and sahelian zones. The Nile and two of its large basins now have a fish fauna with a primarily 'nilotic' distribution, while three other basins whose faunas were isolated in the Holocene have largely endemic faunas.

1 Background

Examination of the present day fish faunas of the Nile River and its drainage system demonstrates several anomalies, among them: the modern fish fauna of the main Nile River has a significantly different composition from those of Lakes Edward and Lake Victoria, although both lakes are connected to the Nile; Lake Turkana's modern fauna is very similar to that of the Nile River although it has not been connected to the Nile for thousands of years; Lake Tana is the source for the Blue Nile, but has a fauna very different from the Blue Nile (Daget et al., 1984, 1986, 1991). These anomalies, however, are not seen in the Miocene-aged faunas from the Nile and its basins; the faunas are extremely similar (at a generic level) (Arambourg & Magnier, 1961; Gaudant, 1987; Greenwood, 1951, 1973, 1974; Greenwood & Howes, 1975; Murray, 2004; Murray & Attia, 2004; Priem, 1914, 1920; Roberts,

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1975; Robinson & Black, 1974; Stewart, 1990, 2003a; Van Couvering, 1977, 1982; Van Neer, 1992, 1994; Vignaud et al., 2002).

The differing composition of the Nile system fish faunas is very much tied to geomorphological changes which occurred throughout the Cenozoic, particularly in the late Cenozoic. Prior to the late Miocene, much of the African continent was a plateau, with few topographical barriers, and a network of rivers and basins which probably allowed movement of a relatively uniform and widespread fish fauna (Beadle, 1981; McCauley et al., 1982, 1998). During the latest Miocene, however, the lowering of the Mediterranean Sea led to the strengthening of the Nile River, while in Pliocene and Pleistocene central and eastern Africa, large-scale earth movements and volcanism occurred in association with the formation of the African Rift System (Adamson & Williams, 1980; Bishop, 1967; Hsü et al., 1977; Said, 1981, 1993). These forces created new barriers and basins, dramatically changing the hydrology of northern, central and eastern Africa.

This paper reviews the origins and distribution of the fossil fish in the Nile River and its four large southern lakes – Albert, Edward, Victoria, Tana – plus Lake Turkana to which it was recently connected**.** The data indicates that the Nile River taxa remained fairly uniform throughout the later Cenozoic, but in the southern basins the fish faunas underwent major changes in association with the dramatic geomorphological changes.

As Greenwood (1976a) stated over 30 years ago, the main problem in describing the evolutionary and biogeographic relationships of African fossil fish is that ‘few fossil remains are identified to the species level.’ The fossil record now is certainly richer than when Greenwood wrote, however most identifications are still at the level of genus, leaving the evolutionary story incomplete until more intact fossils are recovered. Further, the fossil fish record is very much biased by differential preservation and recovery of taxa. Those taxa with large, robust elements, e.g., *Lates*, are much better represented as fossils than fish such as *Citharinus*, which has elements and teeth with poor preservation potential. The more recent use of sieves during fossil recovery has resulted in a more diverse taxa, particularly of smaller and less robust fish, however most small-sized fish or those with less robust elements are virtually invisible in the fossil record.

2 The Nile River

Varying numbers exist for the number of fish taxa in the present-day Nile River *sensu latu* (including the main Nile, Victoria, Albert, White and Blue Nile), but based on Lévêque (1997) there are 127 species and 27 families; including the Claroteidae makes 28 families (Mo, 1991). Twenty of these families have a fossil record in the main Nile River valley, while the White, Victoria and Albert Nile have poor fossil records and knowledge of their modern faunas is also sparse.

According to Lévêque (1997), 27 fish species are endemic to the Nile River, while ten others are restricted to the Nile River and the rivers of eastern Africa. A full 87 species (70%) have a “nilotic” distribution, defined here as dispersion across the present saharan and sahelian zones, and including the Nile River system, the Niger River system, the Senegal River system and the Lake Chad basin. These waterways are at present separated by vast areas of desert and some highlands. The discontinuous dispersal of these faunas suggests common waterways in the past which connected these basins.

One period of faunal dispersion was during the Holocene, a time of high humidity and productive waterways across the saharan and sahelian zones of Africa. There is considerable fossil evidence that a mature, relatively uniform nilotic fauna existed at this time along the Nile River valley and across northern Africa, with sites ranging from the Nile valley westwards to Arouane, in northern Mali. These sites contained a diversity of fish taxa, including large Nile perch and catfish, and other aquatic fauna such as hippopotami and crocodiles, indicating large, permanent waterways (Daget, 1959, 1961; Petit-Maire et al., 1983; Van Neer, 1989).

However, there must also have been *previous* dispersions of a uniform fish fauna, because many of the same taxa are found in pre-Holocene fossil sites across northern, eastern and central Africa (few fossil sites exist in western Africa, and southern African fish have a different history). Many of the earliest or near-earliest records for this fauna are found in fossil sites along the present Nile River valley.

The fossil record for this fauna essentially begins with the recovery of eight families from the highly fossiliferous Eocene and Oligocene deposits in the Fayum Depression, about 100 km southwest of modern Cairo (Fig. 1). Previously in the Cenozoic the Tethys Sea had intermittently covered northern Egypt and most fish faunas were marine. Four endemic freshwater families (Protopteridae, Polypteridae, Gymnarchidae and Alestidae), and four other families (Clupeidae, Cichlidae and Latidae) are reported from the Fayum (Table 1). All are present in the modern Nile.

Two archaic genera – the protopterid *Protopterus* (lungfish), belonging to a group dating back to the Devonian, and polypterid *Polypterus*, a primitive, fleshy finned fish showing some similarities to ancient palaeonisciforms (Carroll, 1988) – have fossil records from the Cretaceous to the Oligocene. The two modern lungfish species now in the Nile River – *Protopterus aethiopicus* and *P. annectens* – were first identified in Oligocene deposits north of Fayum in what is now the western Nile valley (Greenwood, 1974; species identification is “cf”). Such species longevity indicates considerable conservatism of these taxa.

The earliest known gymnarchid teeth have been recovered from the Birket Qarun Formation (late Eocene) at Fayum (A. Murray, personal communication; personal observation), and are identical to those of modern *Gymnarchus niloticus*, an eel-like mormyroid which uses an electrical field to sense its environment. Surprisingly, while *Gymnarchus* is present in the Nile and has a modern nilotic distribution, it has no fossil record in the Nile River between the Oligocene and the Holocene. This lack may be due to sampling or preservational bias, but gymnarchid teeth are robust and distinctive, so its absence may be real.

Multi-cusped alestid teeth are reported from the Jebel Qatrani Formation (late Eocene and Oligocene) at Fayum, which are similar to teeth of modern *Alestes* and *Brycinus* species present in the Nile River (Murray, 2004; Roberts, 1975; Van Couvering, 1977). Earlier alestid teeth have been reported from other

Fig. 1 Map of Eocene/Oligocene, early and late Miocene sites mentioned in text and/or tables

northern African sites, including in Morocco, and dating from the Cretaceous to the Oligocene. These reports indicate the widespread dispersion of this endemic family already in the early Cenozoic. While Alestidae are present in the modern Nile, similar to *Gymnarchus*, this family has no fossil record in the Nile River valley between the Oligocene and the Pleistocene.

The oldest African records of the large perch *Lates* (*L. qatraniensis*), of the family Cichlidae (cf *Tylochromis*), and of the Oligocene freshwater clupeomorph *Chasmoclupea aegyptica* were also reported from the Fayum's early Oligocene Jebel Qatrani Formation (Murray, 2004; Murray & Attia, 2004; Murray et al., 2005). *Lates* has a widespread fossil record in all but southern Africa throughout the Neogene. The modern cichlid *Tylochromis* is present in West Africa and the Congo basin, but not in eastern or northern Africa. Its Oligocene presence in northern Africa (Fayum) suggests that it had a more widespread presence at that time. *Chasmoclupea* was preserved in fluviatile deposits, although clupeomorphs are usually found in marine sediments. *Chasmoclupea* is extinct; only one clupeid (*Alosa fallax*) is now present in the Nile River estuaries.

Table 1 African freshwater fish from the Eocene, Oligocene, early and late Miocene, listed by age and site. Data from Arambourg and Magnier, 1961; Gaudant, 1987; Greenwood, 1951, 1973, 1974; Greenwood and Howes, 1975; Murray, 2004; Murray and Attia, 2004; Murray et al., 2005; Priem, 1914, 1920; Roberts, 1975; Robinson and Black, 1974; Stewart, 2003a; Van Couvering, 1977, 1982; Van Neer, 1994; Vignaud et al., 2002

	Eocene/ Oligocene	Early Miocene→		Late Miocene→						
Sites → Taxa ↓	Fayum	Moghara	Chalouf	Gl. Zelten, Sahabi	Bled ed Douarah	Toros Menalla	Southern L. Albert[a]	Victoria Basin[b]	Loperot	Lothagam
Protopterus cf *annectens*	X									
Protopterus cf *aethiopicus*	X									
Protopterus sp.							X	X	X	X
Polypterus sp.				X	X	X		X	X	X
Chasmoclupea sp.	X									
Heterotis sp.										X
Gymnarchus cf *niloticus*							X			
Gymnarchus sp.						X				X
Gymnarchidae	X									
Hydrocynus sp.						X	X			X
Sindacharax lepersonnei							X			
S. lothagamensis										X
Sindacharax sp.						X				X
Alestes/Brycinus							X			X
Alestidae	X									
Distichodus sp.							X			X
Characiformes									X	
Labeo sp.							X			
Barbus sp.			X							
Cyprinidae									X	

(continued)

Table 1 (continued)

	Eocene/ Oligocene	Early Miocene→		Late Miocene→						
Sites → Taxa ↓	Fayum	Moghara	Chalouf	Gl. Zelten, Sahabi	Bled ed Douarah	Toros Menalla	Southern L. Albert[a]	Victoria Basin[b]	Loperot	Lothagam
Aff. *Bagrus*										X
Bagrus sp.			X							
Clarotes sp.				X			X			X
Auchenoglanis sp.							X			
Clarias sp.			X	X	X					X
Clariidae							X			
Synodontis sp.		X	X	X			X	X		X
Mochokidae							X			
Siluroidea/Siluriformes				X	X		X	X	X	
Semlikiichthys							X			
cf *Semlikiichthys*		X								X
Lates niloticus										X
Lates cf *niloticus*					X					
L. qatraniensis	X									
Lates sp.		X	X	X	X		X	X		X
Latidae									X	
cf. *Tylochromis*	X									
Cichlidae							X	X	X	
Percoidea				X						

[a] Includes Sinda Mohari.

[b] Includes Rusinga Island, Kavirondo.

The early and late Miocene sites of Moghara (Priem, 1920) and Chalouf (Priem, 1914) respectively, are located near the present-day Nile delta (Fig. 1). Their faunas are small, but contain the earliest African remains of the endemic catfish *Synodontis* and *Bagrus,* the cyprinid *Barbus* and an early record for the clariid *Clarias* (Table 1). All are reported from other Miocene sites in northern and eastern Africa, and all are present in the modern Nile. *Synodontis* is a small mochokid catfish which is speciose in the modern Nile. *Barbus* is suggested to have entered Africa from Saudi Arabia in the early Miocene (Otero, 2001). Modern *Clarias* is an airbreather which can live up to 18 hours out of water, can use its pectoral fins to "walk" between waterways, and is tolerant of deoxygenated waters; this may explain its ubiquity in African fossil sites.

A recent look at the *Lates* specimens from Moghara indicates that some elements almost certainly belong to *Semlikiichthys* (pers. obs; A. Murray pers. comm.), a large extinct percoid related to *Lates* (Otero & Gayet, 1999), while other elements are probably *Lates. Semlikiichthys* is also identified or tentatively identified at other Miocene sites (Stewart, 2003a) and several Pliocene sites (discussion below) (Tables 1 and 2). Many of the genera/families just described are also known from other northern African Miocene-aged sites, including Bled ed Douarah, Tunisia (Greenwood, 1973), Gebel Zelten, Libya (Arambourg & Magnier, 1961), Sahabi (Gaudant, 1987) and Toros-Menalla, Chad (Vignaud et al., 2002) (Fig. 1; Table 1), as well as in several sites in central and eastern Africa (discussed below). The widespread distribution of these genera and/or families at that time suggests a common waterway across northern Africa. Possible evidence for this waterway comes from radar imaging data and field studies in the eastern Sahara (Issawi & McCauley, 1992; McCauley et al., 1982; McCauley et al., 1998). These suggest that intermittently from the Oligocene until the Middle Miocene (ca 40 to 15 mya), streams flowed south and west from the Red Sea Mountains through what is now Egypt into the Sudan and Libya**.** About 25 mya, increased uplift of the Red Sea mountains resulted in the strengthening of several of these rivers, and there is evidence that one or more major river systems were flowing as far west as the Chad Basin, and into the Niger Basin. These rivers would have acted as conduits for the Miocene (and possibly Oligocene) fish fauna, from the Red Sea Mountains across northern Africa, resulting in widespread distribution of many of the same genera and species.

In the latest Miocene (ca 6–5 my), drying of the Mediterranean Sea basin and its rapidly lowering level altered the course of the "Nile", then a stream flowing in the vicinity of its present valley (Butzer, 1980). As the sea level fell (the Messinian Salinity Crisis) (Hsü et al., 1977), the "Nile" presumably strengthened, partly through stream capture, and became a larger more powerful drainage. This powerful river must have allowed the movement of fish in a north/south direction, which eventually opened up faunal exchange between the Nile and the southern/eastern basins.

The earliest large and diverse freshwater fish fauna which can be attributed to the "new" main Nile is from Wadi Natrun, an important late Pliocene site located on the western edge of the modern Nile delta (Fig. 2). The fish have been studied by a variety of scientists throughout the twentieth century (Greenwood, 1972; Stromer,

Table 2 African freshwater fish from the early and late Pliocene, listed by age and site. Data from Feibel, 1988, 1994; Greenwood, 1972; Greenwood and Howes, 1975; Schwartz, 1983; Stewart, 1990, 2003a, b; Stewart and Murray, in press; Stromer, 1914; Van Neer, 1992, 1994; Weiler, 1926; White, 1926

	Early Pliocene→				Late Pliocene→					
Sites→ Taxa↓	Southern L. Albert[a]	East Turkana	Kanapoi	Lothagam	Wadi Natrun	Southern L. Albert[b]	Lusso, L. Edward	East Turkana	Lothagam	Omo River
Dasyatis africana								X		
Protopterus sp.	X			X	X			X	X	
Polypterus sp.		X	X	X	X			X	X	X
Heterotis sp.				X					X	
Hyperopisus sp.	X		X		X	X		X		
?Hyperopisus					X		X			
Gymnarchus niloticus		X						X		
Gymnarchus cf *G. niloticus*	X									
Gymnarchus sp.			X	X			X	X	X	
Bunocharax sp.	X					X	X			
Hydrocynus sp.	X	X	X	X	X	X	X	X	X	
Sindacharax mutetii			X	X					X	
S. howesi			X						X	
S. deserti				X	X	X			X	
S. greenwoodi				X					X	
S. lepersonnei	X					X				
S. lothagamensis			X	X						
S. omoensis										X
Sindacharax sp.		X	X	X			X	X	X	X
Alestes/Brycinus	X						X	X		
Brycinus macrolepidotus			X							
Distichodus sp.	X	X	X	X			X	X		
*Gen.*et sp. nov.							X			
Characiformes										X

Labeo sp.	X	X	X		X			X		
Barbus sp.	X		X	X	X			X		
Nkondobagrus longirostris	X									
Bagrus sp.	X				X	X		X		
Bagrus docmak						X				
Aff. Bagrus				X				X	X	
Clarotes laticeps						X				
Clarotes sp.	X			X	X	X	X	X	X	X
Chrysichthys macrotis	X					X				
Auchenoglanis sp.	X							X		X
Heterobranchus bidorsalis						X				
Clarias sp.					X			X		
Clariidae	X		X	X		X		X	X	
Synodontis sp.	X	X	X	X	X	X	X	X	X	X
Malapterurus sp.								X		
Siluroidea/ Siluriformes			X							
Semlikiichthys rhachirhinchus	X		X	X		X			X	
Lates arambourgi										X
L. niloticus			X	X	X	X	X		X	
Lates cf L. niloticus	X					X				
Lates sp.			X	X	X			X		
Tilapia sp.					X					
Tilapiini	X									
Cichlidae	X			X			X	X		
Parachanna sp.	X									
Tetraodon sp.	X	X		X				X	X	

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[a] Includes Sinda Mohari.

[b] Includes Sinda Mohari and Kaiso.

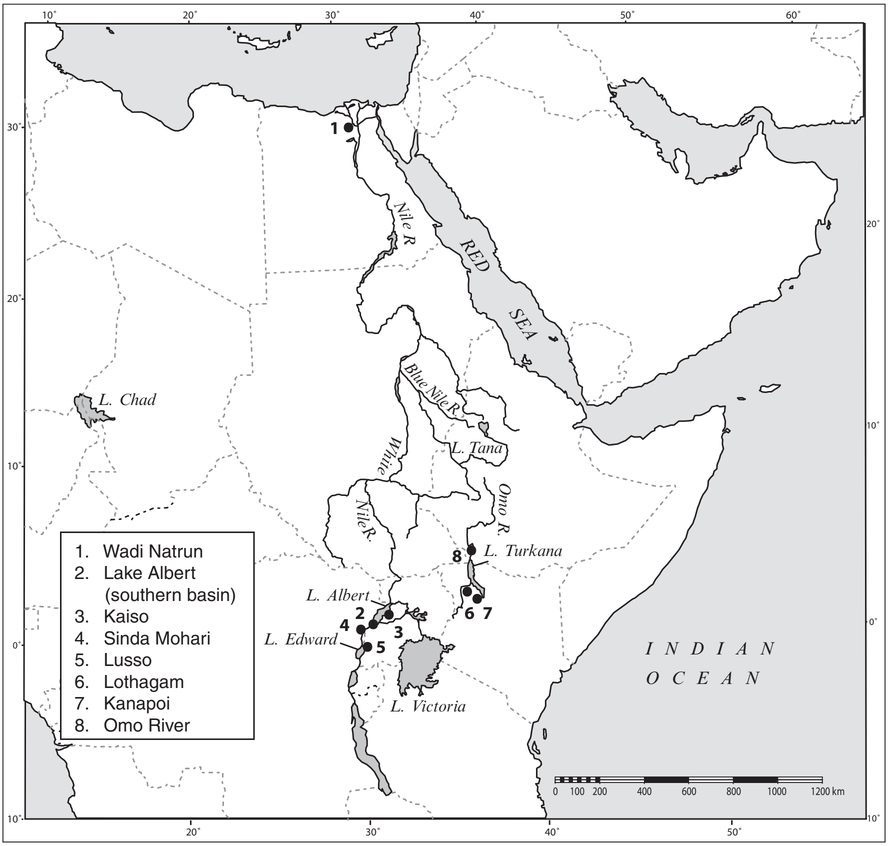

Fig. 2 Map of early and late Pliocene sites mentioned in text and/or tables

1914; Weiler, 1926) (Table 2). The site was formed during a series of marine transgressions alternating with fluvial sediments (El-Shahat et al., 1997), and while it contains some marine fish, most are freshwater. This freshwater fauna consists of several genera not recorded in previous "Nile" sites, but which are known from other Miocene northern and eastern African sites (Tables 1 and 2).

One of the more intriguing aspects of the Wadi Natrun fauna are three extinct taxa (Greenwood, 1972): the characiform *Sindacharax deserti*, a mormyrid ?*Hyperopisus* and *Semlikiichthys*, the large percoid first recorded in early Miocene Moghara. *Sindacharax* has uniquely ridged molariform teeth, which differ from *Alestes*' cusped teeth, for crushing hard objects, probably molluscs. *S. deserti* is also known from late Pliocene Lakes Albert and Turkana, indicating a connection between these basins. The last known record of *Sindacharax* is about 700,000 years ago, in the Turkana basin (Feibel, 1988). The extinct taxon ?*Hyperopisus* is also represented by very large crushing-type teeth, which show considerable similarity to the much smaller teeth of the modern mormyrid, *Hyperopisus. Semlikiichthys* seems to have disappeared at the same time as the molluscivore fish (discussion below), which may have been its chief prey.

The modern Nile fauna is dominated by the Mormyridae, Cyprinidae, Mochokidae and Cichlidae, and all are present at Wadi Natrun (Greenwood, 1972) The mormyrid *Hyperopisus* is a monotypic genus (*H. bebe*) present in the modern Nile, with a nilotic distribution. It is known from widespread early Pliocene sites in northern, central and eastern Africa. The cyprinids *Labeo* and *Barbus* have a modern African and Asian distribution; both are in the modern Nile. Both have a widespread Pliocene distribution.

No fish faunas have been reported from the main Nile Valley in the early Pleistocene, a period when the Nile may have ceased to flow until the middle Pleistocene (Said, 1981, 1993). Isolated *Lates niloticus* vertebrae were recovered in middle/late Pleistocene deposits of the White Nile near Malakal, Sudan (Fig. 3)

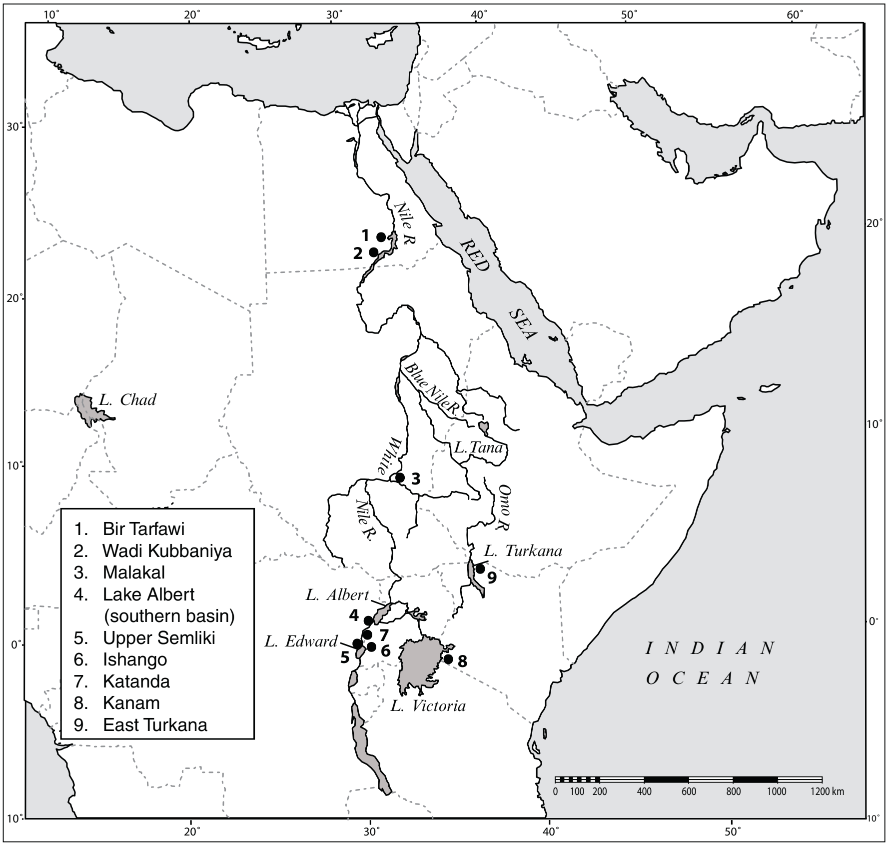

Fig. 3 Map of early, middle and late Pleistocene sites mentioned in text and/or tables

(Williams et al., 2001), indicating the presence of a reasonably large well-oxygenated body of water in this area. A much larger fauna is known from Bir Tarfawi in southern Egypt, now located in the middle of desert (Fig. 3). It dates to about 125,000 BP, and contains mormyrids, *Alestes* or *Brycinus*, *Bagrus*, *Clarias*, *Synodontis*, *Lates niloticus* and Tilapiini (Table 3) (Van Neer, 1993). All but *Alestes*/*Brycinus* are known from Wadi Natrun. Alestidae were first recorded in the Paleogene Fayum deposits, but they have no Nile River record until Bir Tarfawi, surprising, as they were widespread in pre-Miocene northern Africa; their small teeth may have precluded recovery.

The later Pleistocene was also a time of drought, seemingly through northern and eastern Africa, including the Nile. Between 40,000 and 25,000 BP, extensive evaporates along the White Nile suggest that major contributions of water from Lakes Albert and Victoria were rare or even non-existent (Adamson & Williams, 1980; Lamb et al., 2007) drastically reducing some sections of the Nile. There is also evidence from Lakes Albert and Victoria that very low lake levels prevented overflow into the White Nile prior to 11,500 years ago (Talbot et al., 2000), and similarly that low lake levels in Lake Tana prior to 15,000 years ago reduced outflow through the Blue Nile (Lamb et al., 2007), again reducing flow in the Nile (see discussion below).

Unfortunately there is little faunal evidence to determine if and which species was lost at this time. Virtually all known sites during this period are archaeological in origin, meaning taxa were biased to human selection. Accordingly, several late Pleistocene fishing sites along the Nile, with primarily *Clarias* remains, provide little insight into diversity of taxa at this time. However the late Pleistocene archaeological sites from Wadi Kubbaniya and northern (Nubian) Sudan along the main Nile (Fig. 3) contain *Bagrus*, *Synodontis*, *Tilapia* and *Lates* (Table 3), which show taxonomic continuity from the Mio-Pliocene and into the Holocene (Gautier & Van Neer, 1989). The fauna also includes the earliest records of the catadromous eel *Anguilla anguilla*, *Barbus bynni* and *Clarias* cf *gariepinus*, all of which inhabit the modern Nile. *Clarias* is tolerant of de-oxygenated waters, while *Barbus* and *Lates* are not, so presumably the Nile or its tributaries retained some areas of well-oxygenated water. Of note is the absence of *Sindacharax*, ?*Hyperopisus* and *Semlikiichthys* from the middle and late Pleistocene sites of Bir Tarfawi and the Wadi Kubbaniya sites. Their last known presence in the main Nile was in the late Pliocene at Wadi Natrun. Possibly during the extreme drought of the early Pleistocene, these taxa disappeared from the river. The specialized teeth of the former two genera may have reduced their ability to adapt to a different diet.

The Holocene onset of rains and humidity, and new inflows from the southern lakes strengthened the Nile River, and many Holocene archaeological faunas are reported from the main Nile Valley (and across the saharan and sahelian zones). The early Holocene Wadi Howar sites (Fig. 4; Table 4) (Van Neer & Uerpmann, 1989) include three taxa of fish *Heterotis niloticus*, *Barbus bynni* and *Lates niloticus*, all of which are present in the modern Nile. These sites are located on dry or seasonal wadis which could not today sustain any of these fish, all of which

Table 3 African freshwater fish from the early, middle and late Pleistocene, listed by age and site. Data from Arambourg, 1947; Brooks et al., 1995; Feibel, 1988; Greenwood, 1959, 1968, 1976b; Greenwood and Howes, 1975; Schwartz, 1983; Stewart, 1990; Trewavas, 1937; Van Neer, 1986, 1993, 1994

	Early Pleistocene→				Middle Pleistocene	Late Pleistocene→			
Sites→ Taxa↓	Southern Lake Albert	Upper Semliki River	East Turkana	Omo River	Bir Tarfawi	Wadi Kubbaniya	Nubian Sudan	Ishango	Katanda
Dasyatis africana			X						
Protopterus cf P. aethiopicus								X	X
Protopterus sp.		X	X					X	X
Polypterus bichir				X					
Polypterus sp.			X					X	
Anguilla anguilla						X			
Heterotis sp.			X						
Hyperopisus sp.	X		X						X
?Hyperopisus		X							
Mormyridae					X	X			X
Gymnarchus niloticus			X						
Gymnarchus sp.		X	X						X
Bunocharax sp.	X								
Hydrocynus sp.	X	X	X	X					
S. greenwoodi				X					
Sindacharax sp.		X	X						
Alestes/Brycinus sp.		X			X				
Distichodus sp.		X	X						
Citharinus sp.			X						
Labeo sp.		X	X						
Barbus cf altianalis								X	
B. bynni						X		X (cf)	
Barbus sp.	X	X	X				X	X	X

(continued)

Table 3 (continued)

	Early Pleistocene→				Middle Pleistocene	Late Pleistocene→			
Sites→ Taxa↓	Southern Lake Albert	Upper Semliki River	East Turkana	Omo River	Bir Tarfawi	Wadi Kubbaniya	Nubian Sudan	Ishango	Katanda
Bagrus sp.		X		X	X	X	X	X	X
Clarotes laticeps				X					
Clarotes sp.		X	X					X	
Auchenoglanis sp.		X							
Clarias gariepinis						X(cf)		X	
Clarias sp.		X	X	X	X		X	X	X
Clariidae	X								
Synodontis cf schall								X	
Synodontis cf frontosus								X	
Synodontis sp.	X	X	X	X	X	X	X		X
cf *Semlikiichthys*		X							
L. niloticus		X		X	X				
Lates cf L. niloticus	X	X						X	
Lates sp.		X	X				X	X	X
Tilapia sp.						X	X	X	
Tilapiini					X				
Cichlidae		X	X	X					X
Tetraodon sp.	X		X						

Fig. 4 Map of Holocene sites mentioned in text and/or tables

need permanent, oxygenated waters. Three extensive Holocene faunas from Abu Darbein, El Damer, and Aneibis, located along the Nile near the junction of the Nile and Atbara Rivers (Haaland & Magid, 1995; Peters, 1995), contain 21 genera with 16 named to species (Fig. 4; Table 4); all are in the modern Nile River. Continuity from the Pleistocene to the present Nile is seen with the species *Anguilla anguilla*, *Barbus bynni* and *Clarias* cf *gariepinis*, and the genera *Bagrus*, *Synodontis* and *Tilapia*. The taxa *Gymnarchus niloticus*, *Distichodus* sp. and *Tetraodon lineatus* are new appearances in the Holocene Nile, and may demonstrate emigration from other lakes or rivers. They are present in the modern Nile, but have no Nile Mio-Pleistocene fossil record, although all preserve well as fossils. A possible source of these immigrants is the Turkana basin, where they were recorded in the Pleistocene, and may have entered the Nile in the Holocene high water periods. Alternatively they could have come indirectly from the Niger or other western basins, but the Turkana route is shorter and more direct (via the Sobat and Pibor Rivers).

Table 4 African freshwater fish from the Holocene, listed by age and site. Data from Van Neer, 1988; Van Neer and Uerpmann, 1989; Marshall and Stewart, 1995; Peters, 1995; Phillipson, 1977; Robbins, 1974; Stewart, 1989

	Holocene→			
Sites→ Taxa ↓	Nile River near Atbara River	Wadi Howar sites	Gogo Falls	Turkana Basin sites
Protopterus aethiopicus	X			
Protopterus sp.				
Polypterus bichir				
Polypterus sp.	X			
Anguilla anguilla				
Heterotis niloticus	X	X		
Hyperopisus bebe	X			
Mormyrops anguilloides	X			
Mormyridae	X			X
Gymnarchus niloticus	X			
Gymnarchus sp.				
Hydrocynus sp.	X			X
Alestes/Brycinus sp.	X			X
Distichodus sp.	X			
Citharinus sp.	X			
Characiformes	X			
Labeo sp.	X			X
Barbus cf *altianalis*				
B. bynni		X		
Barbus sp.	X		X	X
Cyprinidae				
Bagrus bayad	X			X
B. docmak	X			
Bagrus sp.	X		X	X
Clarotes laticeps	X			
Clarotes sp.				
Auchenoglanis sp.	X			
Heterobranchus sp.	X			
Clarias gariepinus				
Clarias sp.	X		X	X
Clariidae	X			
Synodontis schall	X			X
S. serratus	X			
S. sorex	X			
S. batensoda	X			
S. membranaceus	X			
Synodontis sp.	X		X	X
Malapterurus electricus	X			
Lates niloticus	X	X		
Lates cf *niloticus*				
Lates sp.				X
Tilapia sp.				
Tilapiini	X			
Cichlidae			X	X
Tetraodon lineatus	X			X

3 Fish of the Nile's Southern Basins: Lakes Albert, Edward, Victoria, and Turkana

The fossil fish faunas of the southern Lakes Albert, Edward, Turkana, and to a lesser extent, Lake Victoria, are extensive compared to that of the Nile River. Detailed analysis of these faunas is ongoing and provides considerable insights both into the evolution of the African faunas, and into geomorphological changes which occurred in central and east Africa during the Plio-Pleistocene (Greenwood, 1974; Stewart, 2001). However, because the known connections of the basins with the Nile River are fairly recent, my discussions will be limited to a brief outline of their past faunas and their possible exchanges and/or influences on the Nile fauna.

3.1 Lake Albert

Modern Lake Albert is connected to the White and main Nile through the Albert Nile. Its fish fauna reflects this direct connection: all of its 14 families are present in the modern Nile. Of its 48 species (Witte, 2009), 30 are shared with the Nile (Greenwood, 1966), while 6 are endemic, and the others have a more restricted distribution**.** Twelve of Lake Albert's present-day 14 families have a fossil record. Lake Albert was initially formed as a shallow basin in the Middle/Late Miocene. At this time Africa was still a plateau, and rifting and uplift had not yet disrupted rivers which flowed westwards (the present day Kafu, Katonga and Kagera) across the Albert, Edward and Victoria basins and probably into the Congo basin (Cooke, 1958; Bishop, 1965; Bishop & Trendall, 1967). The Albert basin filled from these rivers, and provided colonizing opportunities for their fish. The Late Miocene fauna, from the southern Albert basin, including Sinda Mohari (Van Neer, 1992, 1994), overlaps completely with the Miocene northern African faunas, containing all but one of the genera/families reported (Table 1; Fig. 1), plus additional taxa. This overlap indicates that, through connecting waterways, the same northern African Miocene fauna was also distributed through central and eastern Africa (see also Lake Turkana).

Because of Lake Albert's position between the Nile and the vast fish faunas of the Congo River basin, it may have acted as a conduit for taxa between these systems.

Three taxa in the lake's Miocene deposits are not recorded in Mio-Pliocene northern Africa, including the citharinid *Distichodus*, a large characoid with bifurcate teeth, the cyprinid *Labeo*, and the catfish *Auchenoglanis. Labeo* and *Distichodus*, and to a lesser extent *Auchenoglanis*, are very speciose in the modern Congo basin, with several endemic species, and may therefore be emigrants from the Congo basin via the westward flowing rivers. The extinct, large *Sindacharax lepersonnei*, may also have derived from the Congo basin, or is endemic to Lake Albert, as it is not known elsewhere in Africa.

The appearance of 13 “new” taxa in early Pliocene southern Albert deposits (Van Neer, 1992, 1994) (Table 2; Fig. 2) suggests new inflow/outflows in the lake, possibly resulting both from large-scale tectonic movements in the Pliocene, and from a humid period where expanded lakes and rivers must have facilitated exchange of fish faunas: Lakes Turkana, Chad, and Manonga, are all reported as much expanded at this time (Feibel, 1988; Griffin, 2006; Harrison, 1997). The appearance of *Sindacharax deserti*, *Bagrus, Lates niloticus* and *Tetraodon* suggests a connection with the Turkana basin, the only other early Pliocene fauna which contains all four taxa. Depending on the location of the pre-rift watershed, western flowing rivers may have linked both basins. Alternatively, new indirect connections with the Nile may have occurred, although the Wadi Natrun fossil record does not contain all these taxa. Additionally, the appearance of *Tetraodon* and the extinct *Chrysichthys* in Pliocene Lake Albert may indicate a connection with the Congo basin, as neither taxon has a fossil record in northern Africa, and both are very speciose in the modern Congo basin; *Tetraodon* has five species, while *Chrysichthys* has 16 species (Daget et al., 1986, 1991).

The “new” extinct taxa reported from early Pliocene southern Lake Albert – *Bunocharax*, a large characoid with robust jaws and large molariform teeth, *Nkondobagrus longirostris*, a bagrid with similarities to the modern catfish *Bagrus*, and *Chrysichthys macrotis*, a bagrid catfish similar to the modern genus (Van Neer, 1994), plus *S. lepersonnei* and *Semlikiicthys* provide an intriguing look at a fauna which no longer exists, but which inhabited the Albert and Edward basins, and to a lesser extent the Turkana basin and the Nile River. The extinct taxa were large fish, growing over a half a meter. At least six taxa (including two from Lake Edward, described below) had robust, molariform teeth, with such morphology suggesting a specialized trophic niche of mollusc eating. Teeth of these taxa show considerable wear, with ridges and cusps often completely worn away, and there is considerable pitting of the occlusal surface. These characters are consistent with a diet of crushing hard objects. Several of the extant taxa also were adapted for mollusc-eating. Pliocene fossil deposits in the Albert and Edward basins contain millions of mollusc shells, providing food for the large number of molluscivores, both extinct and extant.

Fossil faunas are, unfortunately, virtually unknown from the Congo basin, which due to its proximity and connection to Albert via western rivers, may also have shared this fauna. The disappearance of huge numbers of molluscs in the Pleistocene (Van Damme & Van Docxlaer, 2009) may be linked to the disappearance of many of the molluscivore fish, which may have been too specialized to adapt to another diet. The diets of the other extinct taxa – *Semlikiichthys, Nkondobagrus* and *Chrysichthys macrotis* – are unknown, but modern *Chrysichthys auratus*, in the Nile, also preys mainly on molluscs. Relatives of the other two taxa are piscivores, and probably preyed on the large populations of molluscivore fish. By the late Pliocene in southern Albert and the Kaiso sites, all but *Bunocharax* and *Chrysichthys* have disappeared from the Albert basin.

The early Pleistocene fauna is the last large fauna known from Lake Albert (Van Neer, 1994) (Table 3; Fig. 3). It again shows several additions and disappearances compared to the Pliocene faunas, probably resulting from tectonic changes in the Western Rift. Most of the molluscivores have disappeared. When the early Pleistocene fauna is compared with the fauna of present-day Lake Albert, it appears that several genera disappear during the Pleistocene, including *Bunocharax* (extinct), *Clarotes* and *Tetraodon*. This may be due to two long periods of very low lake levels between 25,000 and 12,500 BP (Beuning et al., 1997), or between 40,000 and 25,000 BP, when extensive evaporates along the White Nile suggest that major contributions of water from Lake Albert and Victoria were rare or even non-existent (Adamson & Williams, 1980).

The similarity between the modern Nile River and Lake Albert faunas, and the lack of Albert endemics, reflects their present day connection. Without late Pleistocene fossils, it is impossible to know how many taxa in the modern lake derive from its pre-Holocene fauna, particularly after drought in the Pleistocene. Modern Albert taxa not present in the Nile but shared with Lake Victoria, like *Barbus neumayeri* (De Vos & van den Audenaerde, 1990), may reflect a late Pleistocene connection which no longer exists (Murchison Falls is a barrier to fish movement via the Victoria Nile). Fish which occur in both the Nile and Congo basins, e.g., *Xenomystus nigri* (Roberts, 1992) may have entered the Albert basin from the Congo in the Mio-Pliocene and later entered the Nile.

3.2 Lake Edward

Modern Lake Edward is connected to Lake Albert via the Semliki River, and then indirectly to the White Nile. Its fish fauna is isolated from Lake Albert and the Nile, as the Semliki River rapids are a barrier to fish. Lake Edward has only eight families of fish, which contain 81 species, of which 56 are endemic. Few species are shared with the Nile River. Of the 81 species, 74% are cichlid, and about half are endemic (Snoeks, 2000). A composition dominated by endemic cichlids has clearly neither had a recent connection with the Nile, which has only eight cichlid species, nor is it a characteristic nilotic fauna. Edward's past fauna, however, had considerable overlap with the Nile system, bearing little resemblance to its modern fauna.

None of Lake Edward's late Pliocene ten genera occur in the modern lake (Table 2; Fig. 2). The fauna, from the Lusso site, contains a mix of taxa seen in the northern African Miocene sites (*Gymnarchus, Hydrocynus, Alestes, Sindacharax, Synodontis* and *Lates niloticus*), as well as four extinct taxa. Surprisingly, the fauna differs considerably from the geographically close Lake Albert taxa, suggesting the two faunas are not connected, similar to today (Table 2). Of the four extinct taxa, one is probably shared with Lake Albert (*Bunocharax*, rare at Edward), one with the Nile (?*Hyperopisus*) and two known only in Lake Edward (*Gen et sp. nov*. and *Sindacharax* sp.). *Gen et sp.nov*. is yet another probable characid with flat crushing teeth (Stewart, 1990).

The appearance of nine "new" taxa in extensive early and late Pleistocene faunas from the Upper Semliki, Ishango and Katanda (Table 3; Fig. 3) suggest a new connection with either the Nile system or the Turkana basin. This connection may perhaps have been via Lake Albert, although the very different compositions of the Albert and Edward faunas make this unlikely. Continuing and severe tectonic movements could have created new indirect connections with the Turkana basin or the Nile, particularly as the existence of the White Nile is now documented (e.g., Williams et al., 2003).

Lake Edward is the only one of the Nile's southern lakes to have a detailed record of late Pleistocene faunal change. Very dramatic changes to the extensive Pleistocene Lake Edward fauna are recorded in the well-stratified Ishango archaeological site, where later Pleistocene levels contain large amounts of volcanic ash. These ash levels are followed by levels with drastic reductions in the fish taxa (Greenwood, 1959; Stewart, 1989). Apparently the ash, resulting from eruptions from nearby Mt Katwe, blanketed the lake and exterminated those fish most reliant on well-oxygenated waters, including *Lates niloticus*, *Barbus bynni* and *Synodontis*.

The modern Lake Edward fauna is very different from its late Pleistocene fauna, its immediate post-Katwe ash fauna, and the modern Nile and Lake Albert faunas. It does however resemble the modern fauna of Lake Victoria, in that both are heavily dominated by cichlids, with cyprinids, catfish and mormyrids (Victoria) next most common (Greenwood, 1966). Clearly Lake Edward's fauna has not been connected with the Nile since the Katwe eruption. There is some evidence that Lake Edward was connected with Lake Victoria in the latest Pleistocene (Bishop & Trendall, 1967), and this is the main source of its modern fauna.

3.3 Lake Victoria

Most geological data indicate that the present-day Lake Victoria basin was formed only in the late Pleistocene, after a period of desiccation (Beadle, 1981), although recent molecular data from modern cichlid flocks suggest that at least part of the basin has sustained enough water to support cichlids since much earlier (Verheyen et al., 2003; see also Lehman, 2009). The modern lake is indirectly connected to the Albert Nile via the Victoria Nile and Lake Albert, a connection which probably opened about 11,500 years ago (Talbot et al., 2000). However Lake Victoria's fish fauna is isolated from Lake Albert due to Murchison Falls on the Victoria Nile, which is a barrier to fish movement. Lake Victoria contains 12 fish families, and between 238 to 288 species (Lévêque, 1997), over three quarters of which are cichlids, most endemic, followed by cyprinids, clariids and mormyrids. As a footnote, many of these species have disappeared due to the introduction in the 1950s and 1960s of the large and piscivorous *Lates niloticus* (Pringle, 2005; Witte et al., 2000). Despite its indirect connection to the Nile, Lake Victoria's modern fauna is very dissimilar to that of the Nile. Its fauna is, however, similar taxonomically to that of both Lake Edward, with which it may have been connected in the Late Pleistocene (Bishop & Trendall, 1967) and/or earlier, and to Lake Kivu, a small lake to the south of Lake Edward but no longer connected with it. Recent DNA evidence indicates Lake Victoria's haplochromine cichlids derived from Lake Kivu possibly 100,000 years ago (Verheyen et al., 2003) when the two lakes were somehow connected.

Unfortunately Lake Victoria has a poor fossil record of both cichlids and non-cichlids, with fossils known only from Early Miocene deposits on Rusinga Island and from Kavirondo sites near present day Winam Gulf (Greenwood, 1951) (Fig. 1). These deposits contained taxa with widespread Miocene occurrence, including *Protopterus*, *Polypterus*, *Synodontis* and *Lates* (Table 1); *Lates* has only been recently introduced to the modern lake, while the other three genera are present in small numbers. The Miocene Victoria lake or series of lakes dried out, and, like Lake Albert, was traversed by westward flowing rivers. A Plio-Pleistocene cichlid recovered near Kanam – *Oreochromis spilurus* – is now only found in eastern flowing rivers, suggesting the watershed was further west than at present (Trewavas, 1937). The DNA evidence linking the modern Victoria cichlids with those from Lake Kivu suggests the two lakes were connected in some way in the late Middle Pleistocene until the Late Pleistocene (Verheyen et al., 2003). Little is then known about the morphology of the Victoria basin until the latest Pleistocene, when tectonic tilting led to overflow of the present basin indirectly into the White Nile (Talbot et al., 2000), although barriers prevent movement of fish. Fish faunas from Holocene sites located on inflowing rivers to Lake Victoria contain genera represented in the modern lake. The best documented of these is from the Middle Holocene site of Gogo Falls (Fig. 4), located on the Guja River (Robertshaw, 1991), containing mormyrids, *Barbus*, *Bagrus, Clarias*, *Synodontis* and indeterminate cichlids (Marshall & Stewart, 1995) (Table 4).

3.4 Lake Turkana

Lake Turkana was last connected to the White Nile via the Lotigipi Swamps, and the Sobat and Pibor Rivers in the humid early and middle Holocene (Adamson & Williams, 1980; Johnson, 2009), but subsequently drought has reduced the lake level so that overflow cannot occur. The mainly swampy ground and deserts between the modern lake and the Nile are a barrier to fish, leaving the Turkana fauna isolated from the Nile. The fauna of modern Lake Turkana reflects the recent Nile connection, as its 18 families are all shared with the Nile, as are about 35 of its 51 species (Lévêque, 1997).

The earliest remains from Turkana are from the early Miocene site of Loperot, and from a large and diverse late Miocene fauna from Lothagam, both in the western Turkana basin. The Lothagam fauna contains 11 extant genera, all present in the modern lake (Stewart, 1997, 2003a) (Fig. 1; Table 1). This taxa largely duplicates the taxa from other reported Miocene sites, especially Lake Albert, which has a very similar fauna. Lothagam contains the earliest confirmed record of *Lates niloticus*, which is subsequently widespread in Plio-Pleistocene sites.

While the extensive Turkana basin Pliocene and Pleistocene faunas contain much of the Miocene taxa (Figs. 2 and 3; Tables 2 and 3) new apparently endemic species (four new *Sindacharax* species and a new species of *Lates* [Stewart, 2003a, b; Stewart and Murray, 2008]) from the Lothagam, Kanapoi and Omo River sites suggest the early Pliocene lake (Feibel, 1988) was isolated for a period of time. The recovery of the widespread *Brycinus macrolepidotus* is its earliest record, and it also may have evolved in the isolated Pliocene lake (Stewart, 2003b). The appearance of *Sindacharax deserti* in the Pliocene Lothagam, Kanapoi and Ekora (a Pliocene-aged site near Kanapoi) deposits coincides with its appearance in Pliocene Nile River deposits (Wadi Natrun), and in Pliocene Lake Albert deposits. Evidence of expanded lakes and rivers in the early Pliocene (e.g., Lakes Turkana, Chad, Manonga [Feibel, 1988; Griffin, 2006; Harrison, 1997]) suggest that new in/outflows were probably created; additionally the newly strengthened Nile River had emerged. The distribution of *S. deserti* may signify an exchange of fauna between these basins. The brackish-water stingray *Dasyatis* is present in late Pliocene until early Pleistocene deposits, indicating a connection between the paleolake and the Indian Ocean. *Dasyatis* was apparently able to colonise the lake and maintain a breeding population during this period (Feibel, 1994). In the late Pleistocene, *Sindacharax* and *Semlikiichthys* disappear; the last evidence of Sindacharax is 700,000 years BP (Feibel, 1988). There is evidence of drought in the late Pleistocene, but it is not known how low the lake levels were, and lack of late Pleistocene sites to indicate which taxa survived.

Modern Lake Turkana may be a model of what happened during Pleistocene aridity. At present the lake level is declining, which concentrates the lake waters, making them highly saline (it has the highest salinity of the large Rift lakes). Several mormyrid species, which possess an electro-sensory system, were recorded in the lake in the early twentieth century, but are now rarely found in the lake and have apparently moved into the Omo delta area and river, where the water is fresher (discussion in Beadle, 1981). Unfortunately the fossil record is not extensive enough to test this model.

In the pluvial early and middle Holocene, three Turkana basin sites (Koobi Fora sites: Stewart,1989; Lowasera: Phillipson, 1977; Lothagam: Robbins, 1974) contain evidence of a diverse fauna – eleven genera plus mormyrids and cichlids – which are all in modern Lake Turkana and in the modern Nile (Hopson & Hopson, 1982) (Fig. 4; Table 4). The sites date between about 9,500 to 4,500 BP and suggest that the connection with the Nile had already been established. Surprising is the number of endemic species in the lake –10 (Hopson & Hopson, 1982) – probably due to its isolation from the Nile River since the early to middle Holocene. Two closely related species – *Lates macrophthalmus* and *L. longispinis* in Lakes Albert and Turkana respectively, are an example of the rapid rate of latid endemism in the Holocene lakes following connection to the Nile: both species are assumed to have evolved from *L. niloticus*, which entered the lakes from the Nile in the early to middle Holocene, meaning an evolution of only about 5,000 to 9,000 years (Greenwood, 1976c).

3.5 The Blue Nile and Lake Tana

Compared to the main and White Nile Rivers, there is a paucity of data on the Blue Nile River and its fauna. The modern fauna includes about 46 species, with most apparently downstream of Roseires. Most genera are shared with the modern Nile (Greenwood, 1976a). Lake Tana, from which the Blue Nile arises, has an interesting fauna quite different from the Blue Nile (Vijverberg et al., 2009). The lake has about 28 species of fish, of which 18 are endemic to the lake. It also has a well-studied *Barbus*/*Labeobarbus* species flock (De Graaf et al., 2007) and a genus, *Nemacheilus* (Greenwood, 1976a), known only in Europe and Asia. The endemism and species-flock reflect Lake Tana's isolation from the Blue Nile, due to a basalt flow 30 km downstream from its outflow.

I know of no reported pre-Holocene faunas for the Blue Nile or Lake Tana. The lack of a fossil record is unfortunate because the past history of Lake Tana's *Barbus* and *Labeobarbus* species flock would be of great evolutionary interest. DNA analysis suggested that the evolution of one *Barbus* species from another occurred <16,000 years ago, after the most recent formation of the lake (De Graaf et al., 2007).

A Holocene fauna was dug from the Sheikh Mustafa site on the Blue Nile, dating to about 7,930 BP. It consisted virtually completely of *Clarias* (Chaix, 2003; Fernandez, 2003), which is now present in the Blue Nile.

4 Conclusions

Differences in the modern fish faunas of the Nile River and its southern basins reflect their fossil history in conjunction with geomorphological changes. The fossil fish record essentially begins in the Eocene and Oligocene deposits of the Fayum, Egypt, where eight families including four endemics – Protopteridae, Polypteridae, Gymnarchidae, Alestidae, Clupeidae, Cichlidae, Latidae and Channidae – have some of their earliest records. All of these families and some genera are present in the modern Nile River, possibly suggesting continuity from the early/middle Cenozoic to the present.

Descendants of these families were part of a uniform Miocene fauna which was apparently widespread across northern, eastern and probably western Africa, including the present Nile valley area, and the Albert, Victoria and Turkana basins. This fauna was possibly dispersed by Miocene rivers flowing west across the present Sahara from the Red Sea mountains, with connections to inflows to the lake basins. The emergence of a strengthened Nile River in the latest Miocene provided a north/south waterway for the further movement of fish. The Nile Valley's Pliocene Wadi Natrun fauna shows continuity with the widespread Miocene taxa, which continues through the late Cenozoic.

In contrast, Pliocene and Pleistocene faunas from Lakes Albert, Edward and Turkana, and what little we know of Victoria and Tana, show ongoing disappearances and new immigration of taxa, resulting from tectonic and climatic events at this time. In the humid early Pliocene there is evidence of faunal exchanges with the appearance of the extinct *Sindacharax deserti, ?Hyperopisus* (not in Turkana) and *Semlikiichthys* at the Albert and Turkana basins and the Nile River. In this humid period Lake Albert may have acted as a conduit between the Congo and Nile systems for faunal exchange. In contrast, the aridity and drought of the early and late Pleistocene in many areas eliminated several taxa, including those now extinct, and probably forced others into refuges.

A period of humidity and extensive waterways in the early and middle Holocene allowed the movement of fish faunas between the Nile River and the saharan and sahelian zones. The Nile River and two of its large basins (Lakes Albert and Turkana) now have a fish fauna with a primarily ‘nilotic’ distribution, while three other basins (Lakes Edward, Victoria and Tana), whose faunas were isolated in the late Pleistocene and Holocene, have largely endemic faunas.

The fossil record for Nile River fish can be frustrating in its lack of fish identified to the species level. While it contributes to the history of modern Nile taxa at a generic level, it has little to offer on the evolution of the Nile’s endemic species, and has obvious limits to its inferences on biogeography. Nevertheless the fossil record is far richer than it was thirty years ago, and can answer more questions about evolution and biogeography than in the past.

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Birds of the Nile

Jim Green

Abstract The bird fauna of the Nile ranges from cosmopolitan species, such as the Osprey (*Pandion haliaetus*) and Moorhen (*Gallinula chloropus*), to endemic species with limited distributions, such as the Blue-winged Goose (*Cyanochen cyanopterus*), which is confined to the Ethiopian uplands. There are great differences in the status of birds of different families. The herons and egrets (Ardeidae) are mostly resident, while the 17 residential species of ducks and geese (Anatidae) are supplemented by 14 species of regular winter visitors, with the possibility of another 12 rare or vagrant species occurring, particularly in the Nile Delta. In the family Laridae (gulls and terns) only 1 of the 19 species is a residential breeder. Among the passerine birds there are about eight species, from four different families, that can be regarded as papyrus specialists. During historical times there have been retreats of various species from the Egyptian Nile, which may be related to the expansion of the human population, and a reduction in the area of papyrus.

1 Introduction

The Nile is unique among rivers in its range of latitude: from the source at 3° S to the mouth at 32° N. No other river flows through more than about 23° of latitude. The huge range of the Nile is reflected in the diversity of its habitats; including rocky upland streams, papyrus swamps, tropical forests, savannah and deserts. It flows out of the Afrotropical Region into the southern Palaearctic in Egypt, so that its avifauna can be expected to have elements from both regions.

Decisions about which birds to include as Nilotic are not always easy. Some groups, such as cormorants (Phalacrocoracidae) and ducks (Anatidae) are obviously aquatic, but in some families decisions have to be made on a more specific basis. The Burhinidae provide a good example: *Burhinus vermiculatus* (Water Thick-knee) and *B. senegalensis* (Senegal Thick-knee) are both closely associated with water,

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and have been included, but *B. oedicnemus* (Stone Curlew) and *B. capensis* (Spotted Thick-knee) prefer more arid areas. They have been excluded, even though they occur in countries through which the Nile flows. The Flamingos have been excluded because they are particularly associated with saline lakes (cf. Jenkin, 1957).

The tables forming the basis of this chapter have been compiled from the following sources: general – Snow (1978), Hall & Moreau (1970), Brown, Urban & Newman (1982) and the subsequent six volumes of The Birds of Africa (1986–2004). Uganda – Carswell et al. (2005); Kenya – Zimmerman, Turner & Pearson (1996), Stevenson & Fanshawe (2002); Ethiopia – Urban & Brown (1971); Sudan – Cave & Macdonald (1955); Nikolaus, 1987; Egypt – Goodman & Meininger (1989), and my own field notes from all five countries.

Table 1 lists the families of non-passerines with aquatic species on the Nile, and gives the numbers of resident species. About half the species are resident, but the proportion varies widely between families. In the Ardeidae 16 out of 17 species are resident, while in the Scolopacidae there is only one resident out of 23 recorded species; all the others being winter visitors.

Seven families are represented by single species, and six of these have only one species in Africa. The seventh family, the Strigidae (owls), has 30 species in Africa,

Table 1 Non-passerine bird families on the Nile

Family	Common name	No. spp. on Nile	Resident spp.
Podicipedidae	Grebes	3	3
Phalacrocoracidae	Cormorants	2	2
Anhingidae	Darter	1	1
Pelecanidae	Pelicans	3	2
Ardeidae	Herons, egrets	17	16
Scopidae	Hammerhead	1	1
Ciconiidae	Storks	8	5
Balaenicipitidae	Shoebill	1	1
Threskiornithidae	Ibises	8	6
Anatidae	Geese and ducks	43	17
Accipitridae	Birds of prey	5	3
Rallidae	Rails	17	12
Gruidae	Cranes	5	3
Heliornithidae	Finfoot	1	1
Jacanidae	Jacanas	2	2
Rostratulidae	Painted snipe	1	1
Recurvirostridae	Avocet and stilt	2	2
Burhinidae	Thick-knees	2	2
Glareolidae	Pratincoles	5	2
Charadriidae	Plovers	15	8
Scolopacidae	Waders	23	1
Laridae	Gulls and terns	19	1
Rhynchopidae	Skimmer	1	1
Strigidae	Owls	1	1
Meropidae	Bee-eaters	9	6
Alcedinidae	Kingfishers	10	8
	Total	205	108

and three of these are fishing owls (*Scotopelia*), one of which, *S. peli*, occurs on the Blue Nile and Atbara, and is widespread in other parts of Africa.

Tables 2–13 give the species included in the larger families. Indications of status are given as follows: Res – resident, WV – winter visitor; SV – summer visitor,

Table 2 Grebes to pelicans on the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Podicipedidae					
Tachybaptus ruficollis – Little Grebe	Res	Res	Res	Res	Res
Podiceps cristatus – Great-crested Grebe	(+)	+	Res	–	WV
P. nigricollis – Black-necked Grebe	(+)	Res?	Res	+	WV
Phalacrocoracidae					
Phalacrocorax carbo – Great Cormorant	Res	Res	Res	Res	WV
P. africanus – Reed Cormorant	Res	Res	Res	Res	–
Anhingidae					
Anhinga melanogaster – Darter	Res	Res	Res	Res	vagr
Pelecanidae					
Pelecanus onocrotalus – Great White Pelican	Res	Res	Res	WV	WV
P. rufescens – Pink-backed Pelican	Res	Res	Res	Res	SV
P. crispus – Dalmatian Pelican	–	–	–	–	(WV)

Table 3 Ardeidae of the Nile

	Status	Uganda	Kenya	Ethiopia	Sudan	Egypt
Ardea cinerea – Grey Heron	Res and migr	+	+	+	+	+
A. melanocephala – Black-headed Heron	Res	+	+	+	+	–
A. goliath – Goliath Heron	Res	+	+	+	+	(+)
A. purpurea – Purple Heron	Res	+	+	+	+	
Egretta alba – Great White Egret	Res and migr	+	+	+	+	(+)
E. ardesiaca – Black Heron	Res	+	+	+	+	–
E. intermedia – Intermediate Egret	Res	+	+	+	+	–
E. garzetta – Little Egret	Res	+	+	+	+	+
Bubulcus ibis – Cattle Egret	Res	+	+	+	+	+
Ardeola ralloides – Squacco Heron	Res	+	+	+	+	+
A. rufiventris – Rufous-bellied Heron	Res	+	+	–	–	–
Butorides striatus – Green-backed Heron	Res	+	+	+	+	+
Nycticorax nycticorax – Black-crowned Night Heron	Res	+	+	+	+	+
N. leuconotus – White-backed Night Heron	Res	+	+	(+)	(+)	–
Ixobrychus minutus – Little Bittern	Res	+	+	+	+	+
I. sturmii – African Dwarf Bittern	Res	+	+	+	+	–
Botaurus stellaris – Eurasian Bittern	WV	(+)	(+)	(+)	(+)	(+)[a]

[a] ( ) brackets indicate rare or vagrant.

Table 4 Ciconiidae of the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Mycteria ibis – Yellow-billed Stork	Res	Res	Res	Res	SV
Anastomus lamelligerus – African Openbill	Res	Res	Res	Res	–
Ciconia nigra – Black Stork	Migr	migr	migr	migr	migr
C. abdimi – Abdim's Stork	MB	MB	MB	MB	–
C. episcopus – Woolly-necked Stork	Res	Res	Res	Res	–
C. ciconia – White Stork	Migr	migr	migr	migr	migr
Ephippiorhynchus senegalensis – Saddle-billed Stork	Res	Res	Res	Res	–
Leptoptilus crumeniferus – Marabou	Res	Res	Res	Res	–

Table 5 Threskiornithidae of the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Plegadis falcinellus – Glossy Ibis	WV	WV	migr	WV	migr
Bostrychia hagedash – Hadada	Res	Res	Res	Res	–
B. carunculata – Wattled Ibis	–	–	Res	–	–
B. olivacea – Olive Ibis	(+)	(+)	–	–	–
B. rara – Spot-breasted Ibis	(+)	–	–	–	–
Threskiornis aethiopica – Sacred Ibis	Res	Res	Res	Res	extinct
Platalea leucorodia – Spoonbill	migr	migr	migr	migr	WV
P. alba – African Spoonbill	Res	Res	Res	Res	–

Table 6 Anatidae of the Nile

	Status	Uganda	Kenya	Ethiopia	Sudan	Egypt
Dendrocygna bicolor – Fulvous whistling Duck	Res	+	+	+	+	–
D. viduata – White-faced whistling Duck	Res	+	+	+	+	–
Thalassornis leuconotus – White-backed Duck	Res	+	+	+	+	–
Cygnus olor – Mute Swan	Rare WV	–	–	–	–	+
C. cygnus – Whooper Swan	Rare WV	–	–	–	–	+
Anser fabalis – Bean Goose	Rare WV	–	–	–	–	+
A. albifrons – White-fronted Goose	Rare WV	–	–	–	+	+
A. erythropus – Lesser White-fronted Goose	vagr	–	–	–	–	+
A. anser – Greylag Goose	vagr	–	–	–	–	+
Branta leucopsis – Barnacle Goose	vagr	–	–	–	–	+
B. bernicla – Brent Goose	vagr	–	–	–	–	+
B. ruficollis – Red-breasted Goose	vagr	–	–	–	–	+
Cyanochen cyanoptera – Blue-winged Goose	Res	–	–	+	–	–
Alopochen aegyptiacus – Egyptian Goose	Res	+	+	+	+	+

(continued)

Table 6 (continued)

	Status	Uganda	Kenya	Ethiopia	Sudan	Egypt
Tadorna ferruginea – Ruddy Shelduck	WV	–	–	+	+	+
T. tadorna – Common Shelduck	WV	–	–	–	–	+
Plectropterus gambensis – Spur-winged Goose	Res	+	+	+	+	vagr
Pteronetta hartlaubi – Hartlaub's Duck	Res	+	–	–	+	–
Sarkidiornis melanotus – African Comb Duck	Res	+	+	+	+	–
Nettapus auritus – African Pygmy Goose	Res	+	+	+	+	–
Anas penelope – Wigeon	WV	+	+	+	+	+
A. strepera – Gadwall	WV	–	+	+	+	+
A. crecca – Teal	WV	+	+	+	+	+
A. acuta – Pintail	WV	+	+	+	+	+
A. platyrhynchos – Mallard	WV	–	–	+	+	+
A. clypeata – Shoveller	WV	+	+	+	+	+
A. querquedula – Garganey	WV	+	+	+	+	+
A. capensis – Cape Teal	Res	(+)	+	+	(+)	–
A. undulate – Yellow-billed Duck	Res	+	+	+	–	–
A. sparsa – African Black Duck	Res	+	+	+	+	–
A. erythrorhyncha – Red-billed Duck	Res	+	+	+	+	–
A. hottentota – Hottentot Teal	Res	+	+	+	–	–
Marmaronetta angustirostris – Marbled Teal	Res	–	–	–	–	+
Netta rufina – Red-crested Pochard	WV	–	–	–	–	+
N. erythrophthalma – Southern Pochard	Res	+	+	+	+	–
Athya farina – Common Pochard	WV	+	+	+	+	+
A. nyroca – Ferrugineous Duck	WV	(+)	+	+	+	+
A. fuligula – Tufted Duck	WV	(+)	+	+	+	+
Mergus albellus – Smew	Rare WV	–	–	–	–	+
M. serrator – Red-breasted Merganser	WV	–	–	–	–	+
M. merganser – Goosander	Rare WV	–	–	–	–	+
Oxyura leucocephala – White-headed Duck	Rare WV	–	–	–	–	+
O. maccoa Maccoa – Duck	Res	+	+	+	–	–

Table 7 Accipitridae of the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Pandion haliaetus – Osprey	WV	WV	WV	WV	WV
Milvus migrans – Black Kite	Res	Res	Res	Res	Res
Haliaetus vocifer – African Fish Eagle	Res	Res	Res	Res	vagr
Circus aeruginosus – Marsh Harrier	WV	WV	WV	WV	WV
C. ranivorus – African Marsh Harrier	Res	Res	–	–	–

Table 8 Rallidae of the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Sarothrura pulchra – White-spotted Flufftail	Res	(Res)	–	(Res)	–
S. rufa – Red-chested Flufftail	Res	Res	Res	–	–
S. boehmi – Streaky-breasted Flufftail	Res	Res	–	–	–
Crex egregia – African Crake	Res	Res	–	–	–
Rougetius rougetii – Rouget's Rail	–	–	Res	–	–
Rallus caerulescens – African Water Rail	(Res)	Res	Res	–	–
R. aquaticus – Water Rail	–	–	–	–	Res
Porzana parva – Little Crake	(migr)	(migr)	migr	migr	migr
P. pusilla – Baillon's Crake	(Res)	Res	Res	–	migr
P. porzana – Spotted Crake	(migr)	migr	migr	migr	migr
Amaurornis flavirostris – Black Crake	Res	Res	Res	Res	–
Porphyrio alleni – Allen's Gallinule	Res	Res	Res	Res	–
P. porphyrio – Purple Swamphen	Res	Res	Res	–	Res
Gallinula chloropus – Common Moorhen	Res	Res	Res	migr	Res
G. angulata – Lesser Moorhen	Res	Res	Res	Res	–
Fulica atra – Eurasian Coot	–	–	WV	WV	Res +W
F. cristata – Red-knobbed Coot	Res	Res	Res	–	–

Table 9 Gruidae of the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Grus grus – Common Crane	–	–	WV	WV	WV
Bugeranus carunculatus – Wattled Crane	–	–	Res	–	–
Anthropoides virga – Demoiselle Crane	–	vagr	WV	WV	WV
Balearica pavonina – Black-crowned Crane	Res	(Res)	Res	Res	(vagr)
B. regulorum – Grey-crowned Crane	Res	Res	–	–	–

Table 10 Finfoot to pratincoles on the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Heliornithidae					
Podica senegalensis – African Finfoot	Res	Res	Res	–	–
Jacanidae					
Actophilornis africana – Jacana	Res	Res	Res	Res	–
Microparra capensis – Lesser Jacana	Res	Res	Res	Res	–
Rostratulidae					
Rostratula benghalensis – Painted Snipe	Res	Res	Res	Res	Res
Recurvirostridae					
Himantopus himantopus – Black-winged Stilt	Res	Res	Res	Res	MB
Recurvirostra avosetta – Eurasian Avocet	(Res)	WV	WV	WV	MB
Burhinidae					
Burhinus senegalensis – Senegal Thick-knee	Res	Res	Res	Res	Res
B. vermiculatus – Water Thick-knee	Res	Res	–	–	–

(continued)

Table 10 (continued)

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Glareolidae					
Pluvianus aegyptius – Egyptian Plover	(+)	(+)	Res	Res	(+)
Glareola pratincola – Common Pratincole	Res	Res	Res	Res ?	MB
G. nordmanni – Black-winged Pratincole	migr	migr	migr	migr	migr
G. nuchalis – Rock Pratincole	Res	Res	Res	+	–
G. ocularis – Madagascar Pratincole	–	(migr)	vagr	–	–

Table 11 Resident charadriidae and scolopacidae on the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Charadrius pecuarius – Kittlitz's Plover	+	+	+	+	+
C. tricollaris – Three-banded Plover	+	+	+	+	–
C. alexandrinus – Kentish Plover	vagr	WV	+	WV	+
C. marginatus – White-fronted Plover[a]	WV	(+)	+	–	–
Vanellus senegallus – Wattled Lapwing	+	+	+	+	–
V. albiceps – White-headed Plover[b]	–	–	–	+	–
V. spinosus – Spur-winged Plover	+	+	+	+	+
V. crassirostris – Long-toed Plover	+	+	+	+	–
Galinago nigripennis – African Snipe	+	+	+	+	–

[a] Predominantly coastal, but found on sandy beaches by large rivers.
[b] Mainly in Central and West Africa, but reaches the Bahr el Ghazal.

Table 12 Laridae of the Nile

	Status	Uganda	Kenya	Ethiopia	Sudan	Egypt
Larus ichthyaetus – Great Black-headed Gull	WV	(+)	(+)	+	(+)	+
L. cirrocephalus – Grey-headed Gull	Res	+	+	+	(+)	–
L. ridibundus – Black-headed Gull	WV	+		+	+	+
L. melanocephalus – Mediterranean Gull	WV	–	–	–	–	+
L. genei – Slender-billed Gull	WV	+	+	+	(+)	+
L. minutus – Little Gull	WV	–	(+)	–	–	+
L. audouinii – Audouin's Gull	WV	–	–	–	–	+
L. canus – Common Gull	WV	–	–	–	–	+
L. fuscus – Lesser Black-backed Gull	WV	+	+	+	+	+
L. cachinnans – Yellow-legged Gull[a]	WV	–	–	–	–	+
L. heuglini – Heuglin's Gull[a]	WV	+	+	+	+	+
Sterna nilotica – Gull-billed tern	WV	+	+	+	+	+
S. caspia – Caspian tern	WV	+	+	+	+	+
S. benghalensis – Lesser Crested Tern	vagr	+	+	+	+	+
S. hirundo – Common Tern	WV	+	+	(+)	(+)	+
S. albifrons – Little Tern[b]	MB	–	(+)	+	–	+
Chlidonias hybridus – Whiskered Tern	WV	+	+	+	+	+
C. niger – Black Tern	WV	–	+	+	+	+
C. leucopterus – White-winged Tern	WV	+	+	+	+	+

[a] Both species were included in *Larus argentatus* in older literature.
[b] Migrant breeder in the delta; passage migrant and winter visitor elsewhere.

Table 13 Alcedinidae of the Nile

	Uganda	Kenya	Ethiopia	Sudan	Egypt
Halcyon smyrnensis – White breasted Kingfisher	–	–	–	–	migr
Alcedo athis – European Kingfisher	–	–	–	vagr	migr
Alcedo semitorquata – Half-collared Kingfisher	–	vagr	Res	vagr	–
Alcedo quadribrachys – Shining Blue Kingfisher	Res	(Res)	–	(Res)	–
Corythornis leucogaster – White-bellied Kingfisher	Res	–	–	–	–
Corythornis cristata – Malachite Kingfisher	Res	Res	Res	Res	–
Megaceryle maxima – African Giant Kingfisher	Res	Res	Res	Res	–
Ceryle rudis – Pied Kingfisher	Res	Res	Res	Res	Res
Ceyx lecontei – African Dwarf Kingfisher[a]	Res	–	–	–	–
Ceyx picta – African Pygmy Kingfisher[a]	Res	Res	Res	Res	–

[a] These two species are more terrestrial that the others on this list, but do take aquatic insects.

MB – migrant breeder; migr – passage migrant; + – recorded, status uncertain; vagr – vagrant. The inclusion of any category in brackets indicates that the species is rare in that locality. Resident species may also have migratory populations which augment their numbers during the northern winter.

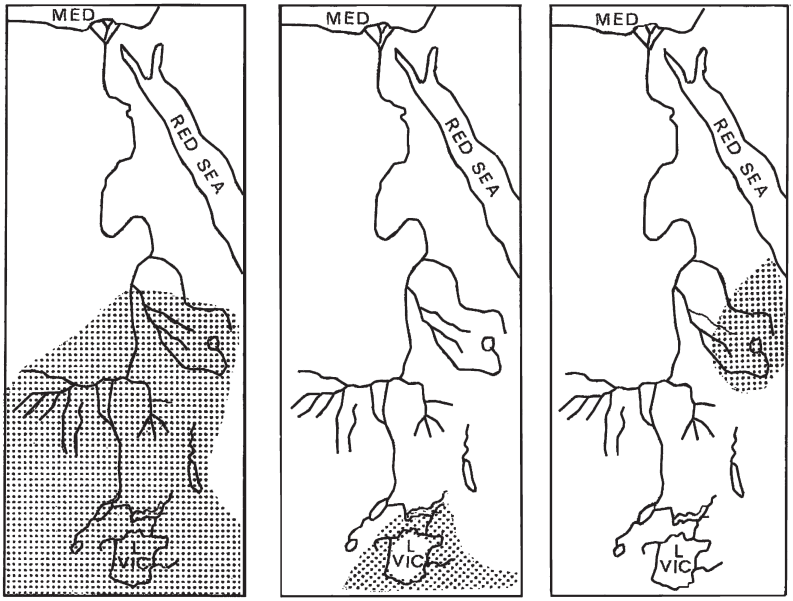
Some of the largest families merit further comment.

2 Family Ardeidae: Herons and Egrets

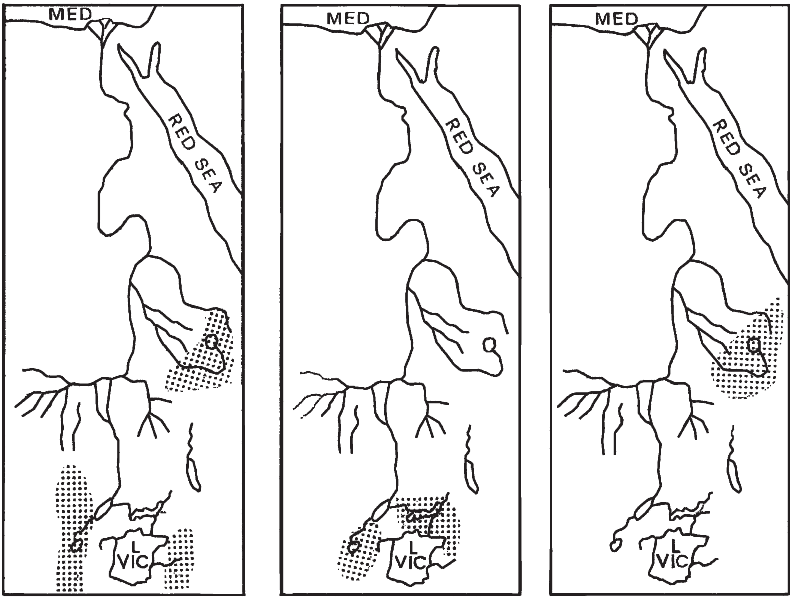
The Ardeidae form one of the most conspicuous elements in the avifauna of the Nile, and most of the species are resident, although they may have migratory populations in addition. One of the species, *Botaurus stellaris* (Eurasian Bittern), is known only as a scarce migrant. Table 3 shows that the Egyptian part of the Nile lacks some of the residential species occurring further south. One southern species, *Ardeola rufiventris* (Rufous-bellied Heron), has the most limited distribution on the Nile, occurring in Uganda and the far south of Kenya (Fig. 1).

3 Family Anatidae: Swans, Geese and Ducks

More species of the Anatidae have been recorded from Egypt than from the other countries in the Nile system (Table 6), but the records include nine rare winter migrants and vagrants. Most of the vagrants are swans and geese. Regular winter migrants, mostly in the genus *Anas*, extend well to the south of Egypt. The most abundant Palaearctic duck reaching Uganda is *Anas querquedula* (Garganey), which is mainly a passage migrant in Egypt. The resident species of *Anas*, such as *A. undulata* and *A. sparsa,* do not extend northwards into Egypt. This distribution is also found among residents in other genera, such as *Dendrocygna* (Whistling Ducks)



Corythornis cristata Ardeola rufiventris Alcedo semitorquata



Motacilla clara Serinus koliensis Cyanochen cyanopterus

Fig. 1 Examples of various distributions of birds on the Nile. *Corythornis cristatus* – a widespread African kingfisher, reaching its northern limit near Khartoum. *Ardeola rufiventris* – a resident heron of Central and Southern Africa, reaching its northern limit in Lake Kioga. *Alcedo semitorquata* – a kingfisher with a largely southern and eastern distribution, but with a separate population centered in Ethiopia. *Motacilla clara* – the Mountain Wagtail, inhabiting fast flowing headwaters. *Serinus koliensis* – the Papyrus Canary, a specialised swamp dweller. *Cyanochen cyanopterus* – the Blue-winged Goose, endemic to Ethiopia (orig.)

and *Thalassornis* (White-backed Duck). The Blue-winged Goose (*Cyanochen cyanopterus*) has a unique distribution, and is found only in the marshes and streams above 2,000 m in the headwaters of the Atbara and Blue Nile, where it feeds mainly by grazing short grasses.

4 Family Accipitridae: Birds of Prey

This family includes the African Fish Eagle, which is the top avian predator in the Nile system. Apart from fish, it also preys on water birds, including cormorants, darters and grebes (Brown, 1980), and it can wipe out breeding colonies of herons and egrets by raiding nests and eating the young. The population of adults along the eastern shore of Lake Albert in 1962 was estimated as 167 over a distance of 209 km (Green, 1964). These birds were estimated to consume less than 0.4% of the total annual catch by fishermen along the same stretch of coast.

Another study, by Eltringham (1975), along the Kazinga Channel showed a higher population density of about one pair per 0.6 km, but even at this density it was estimated that the eagles consumed less than 1% of the local fishery landings.

The Harriers (*Circus* spp.) take a high proportion of birds, up to the size of a duck (*Anas* spp.), but also include small mammals, frogs and lizards in their diet, so they are less directly dependent on the river for their food.

5 Family Charadriidae: Plovers

The members of this family vary in their relationships to water: some feed actively in shallow waters, while others are more terrestrial and feed in the floodplain. About 15 species are more or less aquatic in the region of the Nile, but only 8 species can be considered as residents (Table 11). The most abundant and widespread of the residents is the Spur-winged Plover (*Vanellus spinosus*). The Long-toed Lapwing (*V. crassirostris*) is associated particularly with swamps and floating aquatic plants, and may be found in the company of Jacanas (*Actophilornis africanus*).

6 Family Scolopacidae: Waders

Although 23 species of this family have been recorded along the Nile, only one, *Galinago nigripennis* (African Snipe) is a resident. The vast majority of species are Palaearctic winter visitors. Members of the genus *Tringa*, such as the Wood Sandpiper (*T. glareola*) and Greenshank (*T. nebularia*) are particularly widespread, from the delta down to the Kazinga Channel in Uganda.

7 Family Laridae: Gulls and Terns

About 46 species of this family have been recorded from African waters, but the majority are marine and coastal in distribution, and some have Atlantic or southern distributions. Of the 19 species that can, even remotely, be considered as occurring on the Nile, only one, *Larus cirrocephalus* (Grey headed Gull) is a resident breeder, with large colonies on Lake Victoria and Lake Turkana. It is also frequent around Lake Edward and the Kazinga Channel. Another species, *Sterna albifrons,* (Little Tern), is a migrant, breeding in the Nile Delta and Lake Qarun. The remaining 17 species are all winter visitors, penetrating to various extents along the Nile. Table 12 shows that four species winter only in Egypt, but others, such as *Larus ridibundus* (Black-headed Gull) and *Larus fuscus* (Lesser black-backed Gull) reach Uganda. Among the terns, *Chlidonias leucoptera* (White-winged Tern) is probably the most widespread and abundant.

8 Family Alcedinidae: Kingfishers

Of the 18 species of kingfishers in Africa 9 belong to the subfamily Daceloninae, the woodland kingfishers, which are not generally associated with inland waters. One species in this group, *Halcyon smyrnensis* (White-breasted Kingfisher), widespread in Asia, occurs in the Nile Delta, and includes fish in its diet. The other subfamily, Alcedininae, also includes nine African species, which occur in various parts of the Nile. Table 13 shows the three most widespread nilotic species are *Ceryle rudis* (Pied Kingfisher), *Megaceryle maxima* (Giant Kingfisher) and *Corythornis cristata* (Malachite Kingfisher).

The White-bellied Kingfisher (*Corythornis leucogaster*), mainly a West and Central African species, just gets into the nilotic fauna by dwelling in forest streams in western Uganda. *Alcedo quadribrachys* (Shining blue Kingfisher) is another West and Central African form occurring in Uganda and just reaching the west of Kenya and the extreme south of the Sudan. Its congenor, *A. semitorquata* (Halfcollared Kingfisher) does not occur on the White Nile, but is fairly common on the upper reaches of the Blue Nile and the Atbara. The third member of the genus, *A. atthis* (European Kingfisher) is only a winter visitor to the delta and a vagrant in Sudan. The two species of *Ceyx* are more terrestrial and insectivorous than the others in their subfamily, but both take aquatic insects. *Ceyx lecontei* spreads across from the Congo into the forested streams in the Ugandan headwaters, while *C. picta* is more widespread.

9 Family Meropidae: Bee-Eaters

The inclusion of this family is based on eight of the species in the Nile region including Odonata in their diet. The majority of species live up to their name and consume Hymenoptera whenever they are available, but they are very opportunistic feeders, and some species include hundreds of species of insects in their diet. Some have also been recorded taking small fish (Fry, 1984). Although they are by no means confined to riverine habitats, their local distributions are sometimes closely related to the channel of the Nile. The best example is *Merops orientalis* (Little Green Bee-eater) in Egypt, from Aswan to the Delta.

10 Passerine Birds on the Nile

The problem of which species to include is even more difficult for the passerines than for the non-passerines. Many species descend to the waters edge to drink, but otherwise play no part in the ecology of the river. The following account gives examples of the ways in which passerines can be considered as part of the Nile fauna, but no attempt is made to give a complete list.

The Mountain Wagtail (*Motacilla clara*) is a characteristic resident of fast flowing streams in the upper reaches of the White and Blue Niles. Its diet includes a wide range of aquatic insects, many of which are emerging adults (Tyler & Ormerod, 1986). In the winter this resident is joined by the migrant *M. cinerea* (Grey Wagtail), and both species may forage in the same stream.

Papyrus swamps are used by birds to varying extents. Relatively few species are papyrus specialists, others include papyrus as part of their range of habitats, and yet others dwell on the swamp edges. Briton (1978) made a detailed survey, including mist netting, of the Yala Swamp, on the north-eastern side of Lake Victoria. Excluding Palaearctic migrants he found the following passerines on at least four out of 15 monthly visits (numbers in parentheses). The names of the papyrus specialists are preceded by **P.**

Family Malaconotidae
  Tchraga minuta – Marsh Tchagra (4)
  P *Laniarius mufumbiri* – Papyrus Gonolek (15)

Family Pycnonotidae
  Pycnonotus barbatus – Common Bulbul (10)

Family Sylviidae
  Bradypterus baboecala – Little Rush Warbler (6)
  P *B. carpalis* – White-winged Warbler (15)
  P *Acrocephalus rufescens* – Greater Swamp Warbler (15)
  P *Chloropeta gracilirostris* – Papyrus Yellow warbler (9)
  P *Cisticola carruthersi* – Carruthers' Cisticola (15)
  Eminia lepida – Grey-capped Warbler (6)

Family Muscicapidae
  Muscicapa aquatica – Swamp Flycatcher (12)

Family Nectariniidae
  Cynnyris cuprea – Copper Sunbird (6)
  C. erythrocerca – Red-chested Sunbird (4)

Family Ploceidae
P *Ploceus pelzelni* – Slender-billed Weaver (10)
P *P. castanops* – Northern Brown-throated Weaver (14)
P. melanocephalus – Yellow-backed Weaver (11)
P. jacksoni – Golden-backed Weaver (4)
Euplectes axillaris – Fan-tailed Widowbird (8)

Family Estrildidae
Estrilda astrild – Common waxbill (6)

Family Fringillidae
P *Serinus koliensis* – Papyrus Canary (10)

A striking feature of this list is the importance of Warblers (Sylviidae) among papyrus specialists. This is a general feature of the avifauna along other heavily vegetated parts of the Nile. In just one genus, *Acrocephalus,* there are three resident species in southern Sudan and Uganda, another abundant resident, *A. stentorius* (Clamorous Reed Warbler) in the delta, and four Palaearctic migrants which overwinter on various parts of the Nile. All these species feed on insects, including emerging aquatic forms, and some have been recorded eating fish fry and small frogs. Overwintering Sedge Warblers (*A. schoenobaenus*) sometimes occur in hundreds when feeding on emerging lake flies (*Chaoborus*) on the shores of Lake Victoria (Pearson, 1982).

The Weavers (Ploceidae) are another important group along the Nile. They have a mixed diet, including insects, but also eat the seeds of aquatic plants. *Euplectes axillaris,* dwelling on swamp edges, eats the seeds of *Polygonum senegalense* and *Echinochloa colonum,* as well as caterpillars and termites.

11 Interactions

The river provides food for birds in the form of fish, invertebrates and plants. Overall about 70 species of birds take fish from the Nile, using various methods. Fish eagles and Ospreys swoop from the sky and use their claws to catch fish near the water surface. Cormorants and grebes can dive and swim to catch fish in deeper water, while herons and shoebills stalk or ambush fish in shallow water. Invertebrates are taken by a wide range of birds, especially the Palaearctic migrant waders, Lily-trotters (Jacanidae), rails and wagtails, feeding at the waters margin. Emergent insects provide food for aerial feeders such as swallows, martins, swifts and pratincoles, while the insects associated with emergent aquatic plants are eaten by a wide range of passerines, especially warblers (Sylviidae) and weavers (Ploceidae). Aquatic plants are eaten by various species of Anatidae Ducks, and their seeds are taken by a range of passerines, some of which are specialists, such as the Papyrus Canary (*Serinus koliensis*), while others take both seeds and insects in their diet. The birds of the Nile thus provide a spectrum of dependency on the river. The piscivores are totally dependent, as are some of the invertebrate eaters, the insect eaters are often less dependent, and feed on terrestrial as well as aquatic insects.

Most birds have characteristic patterns of behaviour, but occasionally an individual will behave in an unexpected manner. The Hooded Crow (*Corvus corone sardonius*) is widespread in Egypt, and although it is seen frequently along the Nile, it cannot be regarded as a riverine bird, however one crow was seen hovering like a Pied Kingfisher (*Ceryle rudis*), attempting to catch fish by plunging into the water. A second crow was observed behaving like a Skua (*Stercorarius* spp.), chasing a Black-headed Gull (*Larus ridibundus*) in an attempt to make it drop food it was carrying. This was almost certainly independently learned behaviour, but it is worth mentioning that in 1985 an Arctic Skua (*Stercorarius parasiticus*), ringed in Shetland, was found near Omduman, Sudan, and this species occurs frequently in winter along the Mediterranean and Red Sea coasts of Egypt (Goodman & Meininger, 1989). Piracy is quite common among the piscivorous birds of the Nile. If a relatively small species, such as a Hammerkop (*Scopus umbretta*) catches a fish which it cannot swallow immediately it is likely to be robbed by a predator such as the African Fish Eagle (*Haliaetus vocifer*). The Fish Eagle will even take small fish from the Pied Kingfisher (*Ceryle rudis*) (Brown, 1980), although it will also attack and rob much larger birds such as the Great White Pelican and Goliath Heron.

Black Kites (*Milvus migrans*) are widespread in non-aquatic habitats, but also frequently scavenge along riverbanks and lake shores. They can also behave as raptors. In December 1976, on the Nile near Lake Shambe, a group of six White-winged Terns (*Chlidonias leucopterus*) were following our boat, diving into the water disturbed by our passing. They formed a loose, widely spread group, without any marked coordination. Five Black Kites appeared, and began making stooping attacks on the terns. The behaviour of the terns then changed markedly. They formed a compact flock, flying in tight formation, wheeling and turning in unison. This made it very difficult for the Kites to single out an individual for attack, and the sudden coordinated twists and turns made it impossible to predict where the flock would be at any instant in time. The Kites had intervened in the ecology of the river, causing the terns to stop feeding.

Man has intervened in the ecology of Lake Victoria by introducing the Nile Perch. This large predator has changed the fish community by eliminating many of the endemic cichlids, and this has influenced the diet of the Pied Kingfisher. Small cyprinids, *Rastrineobola argentea*, were always a part of the diet of the kingfishers, but they now form a much higher percentage of the diet. The kingfishers have to catch more fish per day because the weight of the cyprinid is lower than that of a cichlid of the same length (Wanink & Goudswaard, 1994).

Finally, man's intervention on the Nile has eliminated some species from Egypt. It is ironic that probably the most famous of the birds of ancient Egypt, the Sacred Ibis (*Threskiornis aethiopicus*), which still bred there in the nineteenth century, no longer occurs in modern Egypt. In the Late Dynastic and Greco-Roman periods the Sacred Ibis was bred in sanctuaries associated with temples. They were sacrificed and mummified in enormous numbers. The sacred necropolis at North Saqqara contains an estimated 1.5 million mummified ibises (Martin, 1981). The surviving art from Ancient Egypt indicates that other birds may also have been more common at the time of the Pharaohs. The best known illustration, from the IV Dynasty mastaba of Atet at Meidum (ca 2,500 BC) shows three species of geese, including the Red-breasted Goose (*Branta ruficollis*), which is now known only as a rare vagrant to Egypt.

Houlihan & Goodman (1988) have made a detailed study of the birds depicted in Ancient Egyptian art. Aquatic species that are now rare or absent are often shown against a background of papyrus. The reduction in bird diversity and abundance is probably related to the increase in human population and the associated reduction of papyrus swamps.

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Part IV
Human Use

Fisheries in the Nile System

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Abstract The contribution to fishery by the River Nile itself is far less substantial than that of the Nilotic lakes. Especially during the past decades the fish landings from the lakes rose considerably. Concomitant with a decreased salinity between the 1920s and the1990s, fish landings in Lake Borullus and Lake Manzala in the Nile Delta rose from about 6,000 to 50,000 t y^{-1} and from 12,700 to 55,000 t y^{-1} respectively. In both lakes the dominance of mullets in the catches changed into a dominance of tilapiines. The estimated annual catch in Lake Albert rose from 24,800 t in 1991 to 182,000 t in 2007 and the catch composition changed towards small sized species. In Lake Victoria, Nile perch and Nile tilapia were introduced in the 1950s to improve the dwindling catches of native tilapiines. Subsequently, predation by Nile perch, fishery and ecological changes caused a decline of the endemic haplochromines and many other native fish species. However, the stocks of Nile perch, Nile tilapia and the indigenous

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zooplanktivore *Rastrineobola argentea* increased strongly. After the Nile perch boom at the end of the 1980s, the annual fish production increased tenfold to about 1,000,000 t in 2005. During the same period the fishing effort had tripled. Initially Nile perch made up more than 70% of the fish landings, but by 2005 this had changed to 53% *R. argentea* and 26% Nile perch. Lake Tana's subsistence fishery with reed boats and small gill nets changed after the introduction of motorised boats and modern nylon gill nets in 1986. The total landings of the motorised boats increased to a peak 388 t y^{-1} in 1993 and were 292 t in 2006. A decrease in abundance by about 75% of the riverine spawning *Labeobarbus* species and the collapse of juvenile *Labeobarbus* during the 1990s were observed. Possibly with the exception of the Sudd swamps, all studied areas of the Nile system show signs of overfishing.

1 Introduction

Fish has been an important and high quality food source to human beings since long, and the fish of the River Nile and the Nilotic lakes are no exception. Beside water and energy derived therefrom, it is also the most important renewable resource a river system has to offer to mankind (Dumont, 2009). Though the river itself is a source for fishery, the contribution to the inland fisheries of Africa by the Nilotic lakes, especially Lake Victoria, is far more substantial. In 1988, the yearly catch of inland fisheries in Africa amounted 1.8 million t (Lévêque, 1998) of which approximately half a million ton originated from Lake Victoria alone (Ligtvoet et al., 1995; van der Knaap et al., 2002; Matsuishi et al., 2006; Balirwa, 2007). In 2000, the nominal catch of fisheries in the inland waters of Africa produced 2.2 million t of freshwater and diadromous fish, and trends of the last decade indicate that further significant increases seem unlikely (Welcomme, 2005). Recent Catch Assessment Surveys (CAS) estimated the total annual catch from Lake Victoria at about 1 million t (LVFO CAS Report, 2006). According to Welcomme (2003), the knowledge base on African river fisheries is highly localized, largely out of date, and based mainly on short-term studies before 1990. As a consequence of the restricted knowledge on the riverine fishery and because of its low contribution to the annual catches compared to that of the Nilotic lakes, this chapter focuses to a large extent on its lakes and reservoirs (Table 1). The fish taxa mentioned in this chapter are further discussed in the chapter "Fish fauna of the Nile" and a list of species and their authors is given in the Appendix of that chapter.

2 Nile Fishery in Ancient Egypt

Remarkably, fishery in ancient Egypt (since the Old Kingdom some 4,500 years ago) did not differ much from modern fishery in the Nile. Paintings and models in Egyptian graves revealed fishing techniques used, and species caught by these techniques (Sahrhage, 1998). Spears and harpoons seem to have been used mainly in

Table 1 Main water bodies related to the Nile, their surface and their fish landings after the 1990s

Area	Surface (km^2)	Fish landings (t y^{-1})	Year	Main fish taxa	References
Egypt					
Lake Borullus	460	50,000	1990–2004	*Tilapiine cichlids*, *Clarias*	Dumont and El-Shabrawy, 2007
Lake Manzala	840	54,900	1989–1993	*Tilapiine cichlids*	Khalil, 1997
Lake Nasser	6,000	41,000	1999	*Oreochomis*, Cyprinids	Feidi, 2001
Sudan					
Lake Nubia	1,140	1,000	2003	?	A. I. El-Moghraby, unpublished
Gebel Aulia Reservoir	1,500	13,000	2003	?	A. I. El-Moghraby, unpublished
Sennar Reservoir	160	1,000	2003	?	A. I. El-Moghraby, unpublished
Roseires Reservoir	290	1,500	2003	?	A. I. El-Moghraby, unpublished
Sudd	30,000–40,000	30,000	2003	?	A. I. El-Moghraby, unpublished
East African Lakes					
Lake Albert	6,800	182,000	2007	*Brycinus*, *Neobola*; *Lates*, *Bagrus*	NaFIRRI FS and CAS Reports, 2007
Lake Edward/George	2,600	11,000		*Oreochromis Protopterus*, *Clarias*, haplochromines	NaFIRRI FS and CAS Reports, 2006
Lake Kyoga	2,700	34,700	2006	*Rastrineobola*, *Oreochromis*, *Lates*, *Protopterus*	NaFIRRI FS and CAS Reports, 2006
Lake Victoria	68,800	1,000,000	2005	*Rastrineobola*, *Lates*, *Oreochromis*, haplochromines	LVFO CAS Report, 2006
Ethiopia					
Lake Tana	3,100	1,000	1987–2006	*Oreochromis*, *Labeobarbus*, *Clarias*	Wudneh, 1998; De Graaf et al., 2006
Total	129,390	1,419,100			

sport fishery for Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*). Angling may have been used both for leisure and commercial purposes. Many species were depicted in angling catches, but the most common were catfishes from the genus *Synodontis* and *Clarias*, the puffer fish *Tetraodon* and barbs (*Barbus bynni*). Traps made from reed and used single or in groups, often in opposing rows, were common in papyrus documents, engravings, wall paintings and other tomb scenes of the Old Kingdom, but were rare in paintings of later periods. Apart from spearing of fish, the use of nets was the most common motif in pictures of fishery. Scoop nets were used for small fish. Large seine nets that are more productive were operated from the beach or from two boats. The main fish taxa depicted in seine catches were *O. niloticus*, *B. bynni* and species of the genera *Synodontis*, *Clarias*, *Mormyrus*, *Citharinus* and *Tetraodon* (Sahrhage, 1998). A kind of pair trawling with a net that was towed between two papyrus boats, propelled by men with paddles, was performed as well. Many of the fishing techniques used in Ancient Egypt are currently still used in the Nile drainage basin.

3 Nile Fishery in Egypt at Present

Especially the natural lagoons in the Nile Delta and man-made lakes higher upstream appear to be important for fishery. There are several littoral lagoons in the delta area of the Nile. Their total surface area is about 2,000 km^2; the two largest are Lake Manzala (840 km^2) and Lake Borullus (460 km^2) (Table 1; Khalil, 1997; Feidi, 2001; Dumont & El-Shabrawy, 2007). As a result of the changed water regime due to the Aswan Dam (see below) and other dams in the River Nile, Lake Borullus turned from brackish to almost fresh, and its fishery, formerly marine and mullet based, changed to one dominated by tilapiine cichlids and the catfish *Clarias gariepinus* (previously *C. lazera*; Dumont & El-Shabrawy, 2007). Between the 1930s and mid 1960s, fish landings from Lake Borullus fluctuated around 4,000–8,000 t y^{-1}, but since 1990 the landings are about 50,000 t y^{-1} (Table 1; Dumont & El-Shabrawy, 2007). Across the 1990s the average size of the tilapiines decreased by 30%, due to overfishing (Dumont & El-Shabrawy, 2007). A similar pattern was observed in Lake Manzala between 1920 and 1993; total annual catches increased from 12,700 to 55,000 t, and the contribution of mullets declined from 56% to 9%, whereas that of tilapiines increased from 20% to 70% (Khalil, 1997). Since the mid-1990s, Lake Borullus and Lake Manzala became heavily polluted by drainage water from nearby urban centers, such as Cairo, and from other industrial, domestic and agricultural sources (www.undp.org/gef/05; Thieme et al., 2005; Dumont & El-Shabrawy, 2007). A Global Environment Facility (GEF) project implemented by UNDP has set out to tackle the problem in Lake Manzala (www.undp.org/gef/05).

Around the mid-nineteenth century, damming of the Nile began, culminating with the high Aswan Dam in 1964. The finishing of the Aswan Dam resulted in Lake Nasser, called Lake Nubia in Sudan. In 1999 all inland water bodies of Egypt together produced some 250,000 t of fish, of which 41,000 t were landed from Lake Nasser (Table 1; Feidi, 2001). The inland fisheries in Egypt are mainly operated by fishermen with non-motorized boats. The main species landed comprise tilapiine cichlids and cyprinids (Feidi, 2001).

4 Nile Fishery in Sudan

Fishery research in Lake Nubia has been performed since 1967. During the early years of lake formation, species of the genera *Distichodus*, *Citharinus*, and *Bagrus* were commercially important, but by 1976 the main components of the commercial fish landings were tilapiine cichlids of the genus *Oreochromis* (previously *Sarotherodon*) and cyprinids of the genus *Labeo* (Ali, 1984). In 2003 the landings of Lake Nubia were 1,000 t (Table 1), while the potential yield was estimated at 5,100 t y^{-1} (A. I. El-Moghraby, unpublished). Of the other man-made reservoirs, Gebel Aulia in the White Nile and Sennar and Roseires in the Blue Nile, especially Gebel Aulia contributed significantly to the inland fisheries of Sudan (Table 1).

Further southwards, the Sudd swamps in southern Sudan produced about 30,000 t of fish in 2003 (Table 1). The potential yield of this wetland with a surface of 30,000–40,000 km^2 has been estimated at 75,000 t y^{-1} (A. I. El-Moghraby, unpublished). The prevailing fishing techniques are hook and line, long lines, gill nets, seine nets, cast nets, traps, and spear fishing. The recent information on the fisheries in Sudan is scarce, but the mesh size of the monofilament gill nets seems to become smaller and the twine thinner.

5 Fisheries in the Albert Nile, Lake Albert and Lake Edward/George (Uganda)

During the 1960s and 1970s the entire Albert Nile fishery between Pakwach and Moyo (a river stretch of about 200 km in northern Uganda), produced yields of some 1,000–2,000 t y^{-1} (FAO, 1989). Commercial fishery in the area had begun to develop in the first decades of the twentieth century after the introduction of synthetic gill nets. A one day survey in the area in August 1989 revealed that fishermen also used beach seines, cast nets and long lines (FAO, 1989). The main fish genera that were present at the markets during the short survey were: *Oreochromis*, *Labeo*, *Distichodus*, *Citharinus*, *Bagrus*, *Clarias*, *Mormyrus*, *Protopterus* and *Lates* (FAO, 1989).

In the past, the main fisheries in Lake Albert were for tilapias (*Oreochromis niloticus*, *O. leucostictus*, *Sarotherodon galilaeus* and *Tilapia zillii*) living around the margins of the lake, for *Citharinus citharus* in the southern river deltas, and for *Alestes baremoze* and *Lates niloticus* (Lowe-McConnell, 1987). In 1991 the estimated annual catch was 24,800 t, of which the main contributors were the genera *Hydrocynus* (32.2%), *Lates* (31.5%) *Alestes* (10.9%), the tilapiines (10.9%) and *Bagrus* (6.3%) (Coenen, 1991). In 2007, Catch Assessment Surveys conducted by the Uganda National Fisheries Resources Research Institute (NaFIRRI FS and CAS Reports, 2007) in Lake Albert estimated an annual catch of 182,000 t. At this time the catch was dominated by *Brycinus nurse*, which contributed 64% of the total catch. Other species landed were the small (<5 cm Total Length, TL) endemic cyprinid *Neobola bredoi* (19%), *L. niloticus* (8%), *Bagrus bayad* (4%), *O. niloticus* (2%). *Alestes baremoze* and *Hydrocynus forskalii* each contributed only about 1% to the catch. These data reveal a strong increase in the landings over the past 15 years and changes in catch composition towards the small sized species.

Lake Edward/George and the Kazinga Channel together produced 12,000 t of fish in 1976. In 1989 and 1991 the official annual landings were around 6,000 t. However, it was estimated that the catches should be raised by a factor 2 or 3 due to illegal fishing (Coenen, 1991).

6 Fishery in Lake Victoria before the Nile Perch Boom

Though artisanal fishing in the coastal areas of the Nilotic lakes must have been carried out since long, historical data on fishery in these lakes are scarce. In a report on a lake-wide expedition in 1928, Graham (1929) gives an extensive description of the fishery in Lake Victoria. Flax gill nets from Europe had been introduced in 1905, but traps, baskets and moving papyrus fences (operated as a kind of seines) were still frequently used in 1928, and even recently traps were still in use in some areas (Fig. 1a). Perhaps with the exception of scoop nets, netting material was not used in the traditional fishing techniques in Lake Victoria (Graham, 1929).

The most important food fish of the lake was the tilapiine cichlid *Oreochromis esculentus*, but other large fish species such as *O. variabilis*, the lungfish *Protopterus aethiopicus* and the catfishes *Clarias gariepinus* and *Bagrus docmak* were also fished (Graham, 1929). In shallow water, women caught the small (<8 cm TL) cyprinid *Rastrineobola argentea* by forming a circle, driving the fish to the centre and scooping them from the water with baskets.

Apart from the widely appreciated *O. esculentus*, the preference for other fish species in Lake Victoria differed locally (Graham, 1929; Witte et al., 1999). For instance, the lungfish that was disliked by most Wasukuma people, because of its snake-like appearance, was highly appreciated by the Wajuluo, living around the Nyanza Gulf. The Wahaya and Baganda on the western and northern side of the lake considered *B. docmak* a delicacy. Haplochromine cichlids were popular as food fish among the Wakerewe at Ukerewe Island.

The introduction of modern fishing gear, like gill nets and beach seines (Fig. 1b), and the increased demands for fish because of the growing human population and the opening of new markets, due to new roads and railway connections, had a strong impact on the fish catches in the first half of the twentieth century (e.g. Graham, 1929; Beverton, 1959; Fryer & Iles, 1972; Ogutu-Ohwayo, 1990; Balirwa et al., 2003; Pringle, 2005; Balirwa, 2007). Popular food fish such as *O. esculentus* and the cyprinid *Labeo victorianus* showed clear signs of overfishing (Fryer & Iles, 1972; Fryer, 1973; Cadwalladr, 1965; Ogutu-Ohwayo, 1990). The introduction of the more catch efficient and long lasting nylon gill nets and of outboard engines after the Second World War further increased the fishing pressure. The minimum mesh size of 127 mm (5 in.) for gill nets was repealed in 1958, which resulted in a short revival and subsequent further dwindling of the catches. By the 1970s the catches of *O. esculentus* had decreased from 50–100 fish in a 50-m long 127-mm mesh gill net to <0.5 fish in the same net (Fryer, 1973; Balirwa, 2007). The changes in the Lake Victoria fish stocks between 1950 and 1980 conform to the fishing down model, viz. a dramatic decline in tilapiine catches, followed by a decline in large catfishes and lung fish and an increase in smaller taxa including haplochromine cichlids (Balirwa et al., 2003; Welcomme, 2005).

Fishery for the small pelagic *R. argentea*, using lamps to attract the fish, developed in the 1960s and 1970s in Lake Victoria, and was derived from a similar

Fig. 1 Fisheries on Lake Victoria. (**a**) Local traps near papyrus. (**b**) Beach seine fishery. (**c**) *Rastrineobola argentea* caught with light and encircling nets operated from catamarans (at the back). (**d**) Bottom trawler fishing haplochromines for fishmeal factory. (**e**) Nile perch smoking. (Photos by F. Witte) (*see Color Plates)*

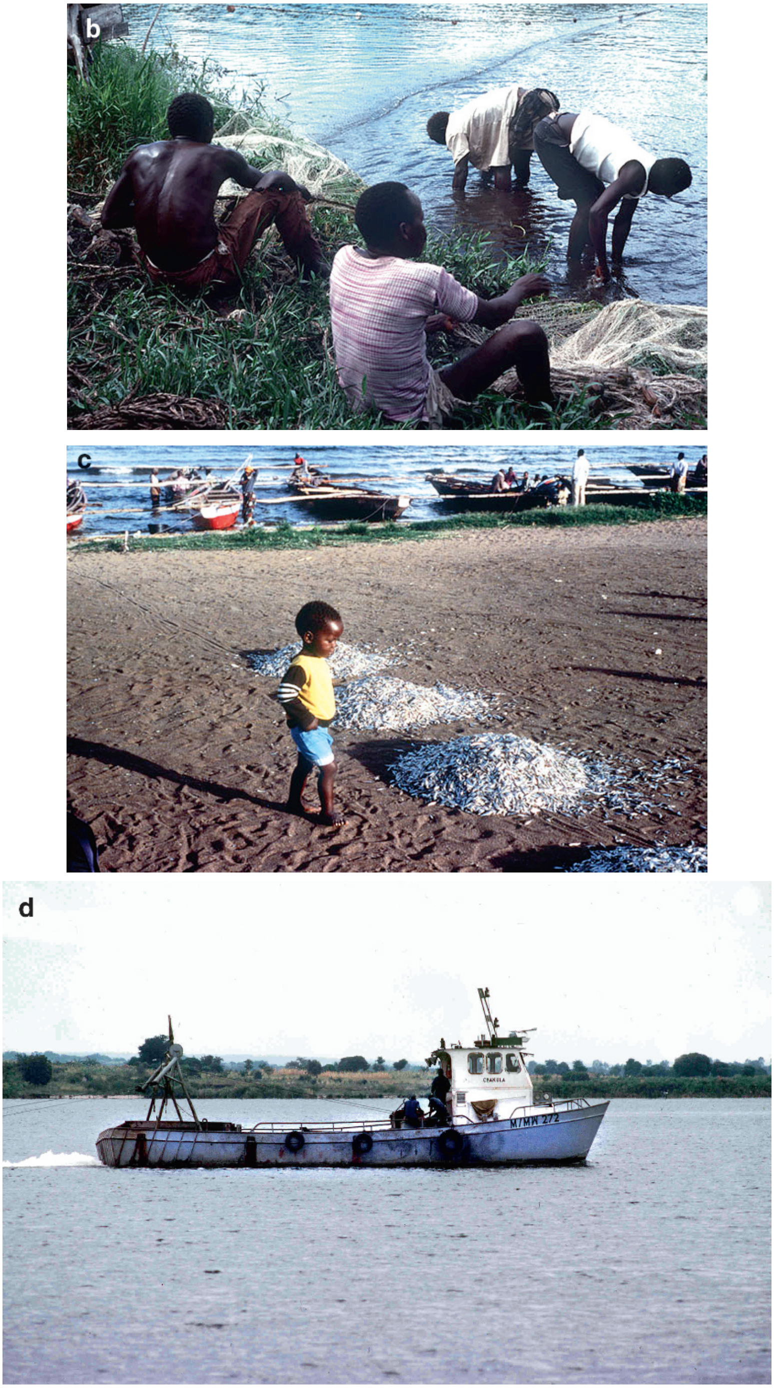

Fig. 1 (continued)

Fig. 1 (continued)

fishery in Lake Tanganyika aiming at clupeids (Okedi, 1981). Originally, fish were attracted by lamps attached to rafts that were hauled in slowly to the shore, where the fish were caught with small meshed beach seines. Since the end of the 1980s, lift nets and encircling nets, which could be operated offshore, were used to catch the fish that had been attracted by the lamps (Fig. 1c; Ligtvoet et al., 1995).

A lake wide trawl survey in 1969 estimated the standing stock of haplochromine cichlids at 600,000 t (80% of the demersal fish stock in the lake) and it was suggested that 200,000 t y^{-1} could be harvested (Kudhongania & Cordone, 1974). Ways were sought to exploit this major fish source. Bottom trawling for haplochromines for a fishmeal factory in Mwanza started in the Tanzanian waters in 1976 (Fig. 1d). This factory converted some 10–15 t of haplochromines per day into animal fodder, and signs of local over fishing of haplochromines in the Mwanza area were reported within a few years (Fig. 2b; Witte & Goudswaard, 1985).

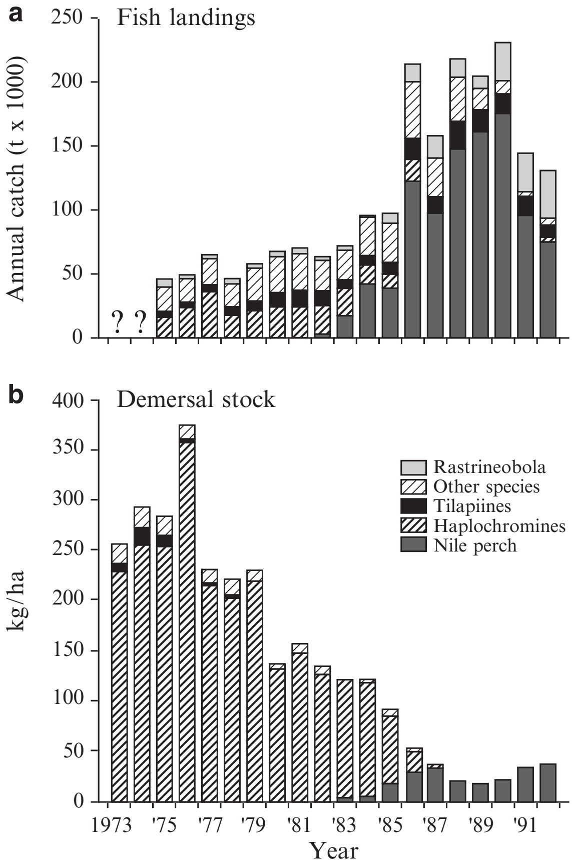

Fig. 2 Changes during the 1970s and 1980s in (**a**) total fish landings in the Tanzanian part of Lake Victoria. (**b**) Demersal fish stocks in the Mwanza Gulf (Tanzania) calculated from bottom trawl catches. The decline of haplochromines in the bottom trawl catches in the Mwanza Gulf in the period 1973–1984 was mainly due to trawl fishery; the subsequent further decline was caused by the Nile perch upsurge. Note that bottom trawls did not catch the small pelagic *Rastrineobola argentea*. After 1985, Nile tilapia dominated the tilapiine catches (redrawn from Witte et al., 1999)

7 Fishery in Lake Victoria after the Nile Perch Boom

To improve the dwindling catches, several fish species were introduced into Lake Victoria in the 1950s (Welcomme, 1988; Pringle, 2005). They comprised the Nile perch (*Lates niloticus*) and the tilapiines *Oreochromis niloticus* (Nile tilapia), *O. leucostictus*, *Tilapia zillii* and *T. rendalli*. In an earlier book on the Nile (Rzóska, 1976), Greenwood ends his chapter on the fish fauna with the note that due to these fish introductions and other human impacts "it is difficult to be optimistic" about the future of Lake Victoria. Indeed, in the 1980s Nile perch suddenly boomed in Lake Victoria and, concomitantly, the haplochromine cichlids in the sub-littoral and offshore areas vanished almost completely, also in areas where there was no fishery on haplochromines (Fig. 2; Barel et al., 1985, 1991; Ogutu-Ohwayo, 1990; Witte et al., 1992; Goudswaard et al., 2008). In the course of the 1980s frequent blooms of cyanobacteria also became a common feature. They were the result of eutrophication due to the increased human population density, deforestation, and bad agricultural practices (Hecky, 1993; Mugidde, 1993; Scheren et al., 2000; Verschuren et al., 2002). Eutrophication and algal blooms caused decreases in water transparency (Mugidde, 1993; Seehausen et al., 1997a; Witte et al., 2005) and in dissolved oxygen levels (Ochumba & Kibaara, 1989; Kaufman, 1992; Hecky et al., 1994; Wanink et al., 2001). Sudden up-welling of hypoxic water caused mass fish kills (Ochumba & Kibaara, 1989; Ochumba, 1990, 1995; Kaufman, 1992; Kudhongania & Chitamwebwa, 1995).

Nile perch predation, competition with introduced species, habitat deterioration and fishery also caused declines in other native species than haplochromines, e.g. the lung fish (*Protopterus aethiopicus*), catfishes (e.g. *Bagrus docmak*, *Xenoclarias eupogon*, *Synodontis victoria*), and the indigenous tilapiines *Oreochromis esculentus* and *O. variabilis* (Ogutu-Ohwayo, 1990; Goudswaard & Witte, 1997; Goudswaard et al., 2002 a, b). By the end of the 1980s only three species were common in sublittoral and offshore waters of Lake Victoria; these were the small indigenous cyprinid *Rastrineobola argentea*, and the introduced Nile perch and Nile tilapia (Figs. 2 and 3; Ogutu-Ohwayo, 1990; Wanink, 1999; Goudswaard et al., 2002b). Together, they dominated the fish landings by more than 80% (Figs. 2 and 3; Reynolds et al., 1995).

Though biodiversity decreased strongly and water quality deteriorated, fish production in Lake Victoria flourished after the Nile perch boom. In the 1960s and 1970s the total landings for the lake were approximately 100,000 t y^{-1}. In the late1980s and early 1990s, just after the Nile perch boom, the fisheries produced over 500,000 t of fish annually, an increase by a factor five (Fig. 3; Balirwa, 2007). Concomitantly, bottom trawl catches revealed that the standing stock of demersal fish decreased about five times (Fig. 2; Okaronon, 1994; Witte et al., 1999; Balirwa, 2007). This indicates

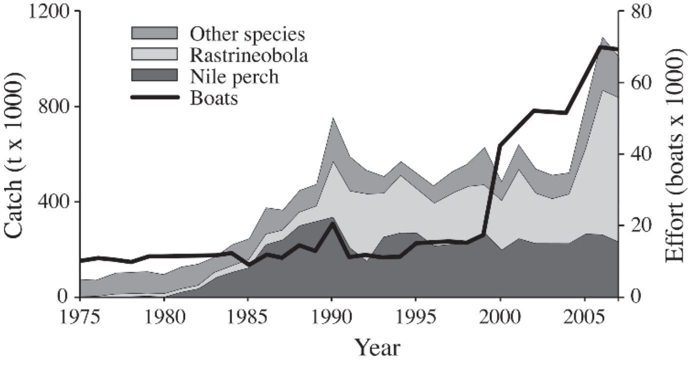

Fig. 3 Trends in total annual fish landings and total fishing effort in Lake Victoria during the period 1975–2005. Nile tilapia is included in "other species". Note that the increase in effort was mainly directed at Nile perch (effort data from LVFO Frame Survey Report, 2006; Catch data from LVFO FMP 2, 2008)

that the strong increase of fish landings was caused by an increase in fishing effort, which was indeed observed during the past decades (Geheb, 1995; Ogutu-Ohwayo, 2004; Matsuishi et al., 2006; Balirwa, 2007). The number of fishers and fishing boats tripled between 1990 and 2007 (Fig. 3; Ogutu-Ohwayo, 2004; Matsuishi et al., 2006; Mkumbo et al., 2007).

Since the beginning of the 1990s the total annual landings increased, but by the mid 1990s, the contribution of Nile perch showed some decline, whereas landings of *R. argentea* and *O. niloticus* increased (Matsuishi et al., 2006). Just after the boom, Nile perch made up more than 70% of the landings (Figs. 2 and 3; Van der Knaap et al., 2002), but between 1990 and 2000 the catch per unit effort for Nile perch dropped from about 80 to 45 kg per boat day (Matsuishi et al., 2006). By 2000 the total fish landings amounted to 657,000 t, 40% of which was made up by Nile perch, 41% by *R. argentea* and 8% by *O. niloticus* (calculated from Table 1 in Matsuishi et al., 2006). In the period 2005–2007, the annual landings were even estimated at 1 million t and the contribution of Nile perch was about 26%, while that of *R. argentea* had increased to about 53% (Fig. 3; LVFO, CAS Report, 2006). Apparently, the species composition in the fish landings have changed towards lower trophic level species (viz. *R. argentea* and Nile tilapia; Matsuishi et al., 2006), but hydroacoustic surveys between 1999 and 2007 suggested that over the studied period the overall fish biomass in Lake Victoria remained more or less constant (Fig. 4; Getabu et al., 2003; Mkumbo et al., 2005; LVFO, FMP 2, 2008; LVFO Hydroacoustic Survey Report, 2007). The foregoing seems to represent a second fishing down episode in Lake Victoria (Balirwa et al., 2003).

In the course of the 1990s, after the decline of the Nile perch catches, a slow resurgence of some haplochromine species was observed, mainly zooplanktivores and detritivores (Witte et al., 1995, 2000, 2007a, b, 2009; Seehausen et al., 1997b; Balirwa et al., 2003; Getabu et al., 2003). By 2000, the landings of haplochromine

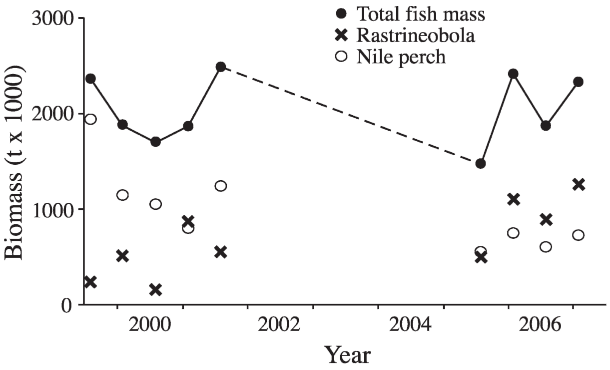

Fig. 4 Estimated fish biomass in Lake Victoria based on acoustic surveys in the periods 1999–2001 and 2005–2007. Note that both the equipment and analytical protocols differed between the periods 1999–2001 and the periods 2005–2007 (redrawn from LVFO Hydroacoustic Survey Report, 2007)

cichlids had increased from virtually 0 to 17,000 t y^{-1} in the Tanzanian waters and to 4,000 t y^{-1} in the Ugandan waters, whereas in Kenyan waters the catches were only 300 t y^{-1} (Matsuishi et al., 2006).

Originally, the fishermen did not like Nile perch, because they had problems with handling, processing and marketing the fish; the larger and relatively fat perches could not easily be dried or transported. However, in the years after the upsurge, people rapidly adjusted the processing and transporting techniques. The larger fishes were chopped into pieces and subsequently fried in the fat removed from the intestines (Ligtvoet et al., 1995). The smaller ones were dried in the sun or smoked (Fig. 1e). For frying and smoking firewood was needed, thus the Nile perch boom strongly exacerbated the ongoing deforestation along the lake shore. In the 1990s filleting factories arose which export Nile perch fillets to Europe and Asia (Ntiba et al., 2001). The total capacity of these factories is several hundred tons per day and they became the main buyers of Nile perch. Many of these fish processing plants operate below their installed capacity. Balirwa (2003) reports for Uganda alone, 15 factories with a total installed capacity of 420 t day^{-1}, but actually processing 185 t day^{-1}. Currently, about 1.2 million people are directly or indirectly dependent for livelihoods on the fishery in Lake Victoria (Matsuishi et al., 2006). In 2003 the estimated annual catch was worth at least US$ 540 million at the fish landings, whereas a further US$ 240 million was earned in fish exports (Balirwa, 2007).

Several observations, e.g. the decline in annual landings and the decline in size at first maturity, suggest that Nile perch is intensively fished, which may result in over exploitation and it has been suggested that, under the scenario of increased fishing effort, the Nile perch fishery is unsustainable (Pitcher & Bundy, 1995; Mkumbo, 2002; Matsuishi et al., 2006; Mkumbo et al., 2007; but see Kolding et al., 2008). In the past, the management measures governing Lake Victoria resources were different in each country (Ntiba et al., 2001). However, through the Lake Victoria Fisheries Organization (LVFO) that was formed in 1994 and support from the EU to implement a Management Plan, attempts to harmonize policies and regulations and also to develop standard operational procedures are continuing. Lake wide management regulations are established and co-management approach is adopted with Beach Management Units (BMUs) in place. Some 1069 BMUs are established around Lake Victoria to take an active role in management of the resources at beach level (LVFO Website – www.lvfo.org). The harmonized rules include banning of beach seines and bottom trawls, cast nets, gill nets below 13 cm (5 in.), and implementation of a slot size of 50–85 cm total length for Nile perch (Kizza et al., 2005).

8 Fishery in Lake Kyoga

Lake Kyoga and several satellite lakes of Lake Victoria (e.g. Lake Nabugabo), in which Nile perch were also introduced, showed patterns of changes in fish composition that were similar to those observed in Lake Victoria (Ogutu-Ohwayo, 1990, 1993, 1995; Chapman et al., 2003, 2008). In Lake Kyoga, where the Nile perch boom occurred about a decade earlier than in Lake Victoria, the total yield increased from 18,000 t in 1964 to 167,000 t in 1978, among others because of the rise in contribution of Nile perch from 700 to 71,000 t (Ogutu-Ohwayo, 2004). However, the yield of Nile perch in Lake Kyoga had decreased to 15,000 t y^{-1} again by 1989 (Ogutu-Ohwayo, 2004). In 2006, the National Fisheries Resources Research Institute of Uganda estimated a total annual catch of 34,700 t, of which Nile perch contributed 15%, *Rastrineobola argentea* 44% and *O. niloticus* 28%. Other species caught were *Protopterus aethiopicus* (6%), haplochromines (4%), *Clarias gariepinus* (2%). *Bagrus docmak* and other small species contributed less than 1% to the annual catch. The haplochromines that had almost disappeared showed some recovery (Mbabazi et al., 2004).

9 Lake Tana's Traditional Fisheries (Ethiopia)

Before 1986 Lake Tana fisheries was composed of a predominantly subsistence reedboat fishery (Fig. 5a), operated by the Woito people, an ethnic minority. This type of fishery is limited to the shore areas and targets the native *Oreochromis niloticus*, using locally made fish traps and small gill nets (length 15–20 m). In 1992–1993 in the Bahir Dar Gulf 113 reed boat fishermen (one per boat) were counted, fishing with a total of 374 gill nets of on average 18 m length, 8 cm stretched mesh (Wudneh, 1998). The overall mean CPUE (kg day^{-1}) for the reed boats was 12.3 kg (7.8 kg *O. niloticus*, 4.3 kg *Labeobarbus* spp. and 0.2 kg *Clarias*

Fig. 5 Fisheries on Lake Tana. (**a**) Fishermen building a tankwa. (**b**) Hundreds of fishermen catching migratory fish in a spawning river. (c) Ladies processing fish for the Fish Production and Marketing Enterprise in Bahir Dar. (Photos by F.A. Sibbing) (*see Color Plates)*

Fig. 5 (continued)

gariepinus; Wudneh, 1998). Over the past 20 years the total number of reed boat fishermen in the lake has remained stable at ca 400, landing around 800 t annually.

In addition to the reed boat fishery on the lake itself, seasonal fishermen (farmers) traditionally target *Labeobarbus* on the upstream spawning grounds between July and October each year. These seasonal fishermen use a variety of fishing techniques like barriers, basket traps, hooks, scoop nets and even poisoning of the shallow water upstream using the dried and crushed seeds of the berberra tree (*Milletia ferruginea*, Leguminosae; Fig. 5b; Nagelkerke and Sibbing, 1996). The seasonal fishing on migrating labeobarbs in the upstream spawning areas has taken place for at least 200 years, and most probably for hundreds of years more, as fishing with poison was already observed and described around 1,770 by the Scottish explorer James Bruce during his travels around Lake Tana. Unfortunately, limited data are available on the impact of this traditional, seasonal riverine fishery on the *Labeobarbus* stocks. According to Ameha and Assefa (2002) the number of fish sold on the local markets by these seasonal fishermen fluctuated during the 1990s between 2 (1992, 1998) and 11 (1993) to 19 t (1994). It is unclear if these fluctuations in marketed fish are due to differences in fishing effort by the seasonal fishermen or represent actual changes in the size of the spawning populations. In Lake Victoria a similar indigenous cyprinid fishery, using barriers and basket traps along the rivers, did not have a particular deleterious effect on the *Labeo* and *Barbus* stocks (Ogutu-Ohwayo, 1990). However, the introduction of more efficient gill nets at the mouths of the rivers during the spawning period damaged this cyprinid fishery (Cadwalladr, 1965; Ogutu-Ohwayo, 1990). Similar negative effects after the introduction of modern gill nets have also been reported for Lake Tana's cyprinid fishery (de Graaf et al., 2004, 2006). Obviously, preventing fishing activities both in the river mouths and on the upstream spawning grounds during the peak spawning period (August–September), is of imminent importance in order to keep the *Labeobarbus* fishery sustainable and to protect Lake Tana's unique cyprinid species flocks.

10 Modern Fisheries in Lake Tana

Fishing has never been an important activity in Ethiopian history. Fish is not highly valued as a source of cheap protein and is mainly eaten during religious fasting periods. On average, an Ethiopian eats only 0.1 kg of fish per year. However, the distribution of fish consumption is highly skewed towards areas close to the shores of lakes (8–10 kg y^{-1}) and also to the capital city Addis Ababa (1 kg y^{-1}). To fulfil the increasing demand for fish from Addis Ababa, largely created by foreigners (Reyntjes et al., 1998), motorised boats and modern, more efficient, nylon gill nets were introduced in Lake Tana in 1986.

The development of commercial motorised gill net fishery in Lake Tana has benefited considerably from assistance by Dutch NGOs and the EU sponsored Lake Fisheries Development Program. In the late 1980s the new motorised gill net fleet consisted of about 20 boats and was manned by a new group of around 100 inexperienced Amhara fishermen (ethnic majority). In the late 1980s and early 1990s effort, catch per unit effort (CPUE) and total landings increased (Fig. 6). Annual yield peaked in 1993 (388 t y^{-1}), but gradually decreased until 2003, with a minimum in 2000 (139 t y^{-1}). Since 2003 (148 t y^{-1}) the total annual catch has been increasing again, resulting in 292 t in 2006 (Fig. 6). Number of gill nets (20 per boat), mesh size (10 cm stretched mesh) and number of fishing days per month (20) did not change during the 1990s (de Graaf et al., 2003, 2006). The decrease in effort after 1997 contrasts with the general trend of many African lakes, like Lake Victoria (Fig. 3; Goudswaard et al., 2002b; Matsuishi et al., 2006) and Lake Mweru (Jul-Larsen et al., 2003), where the fishing effort increased during the past decades. However, the decrease in effort is in line with the collapse of many African industrial or commercial fisheries, both freshwater and marine, where investment driven growth in fishing efficiency dominated (Jul-Larsen et al., 2003). After the initial investments in Lake Tana's motorised gill net fisheries at the end of the 1980s, the number of operating boats (maximum 23) started to decrease rapidly due to mechanical failure and lack of spare parts and in 1993 only seven were still in use. The EU sponsored Lake Fisheries Development Program only enabled the fishermen to buy European outboard engines that, unfortunately, proved to be unreliable and for which spare parts were not available. In the first few years, motorised boats with outboard engines quickly ceased to operate. Only boats with an inboard diesel engine remained functional during the 1990s. Still the number of boats fishing per day continued to decrease from seven to five between 1993 and 2001. In 2003 a Dutch NGO donated five new fishing boats and one new collection boat to the fishermen in the small town of Zegi at the Bahir Dar Gulf. This increase

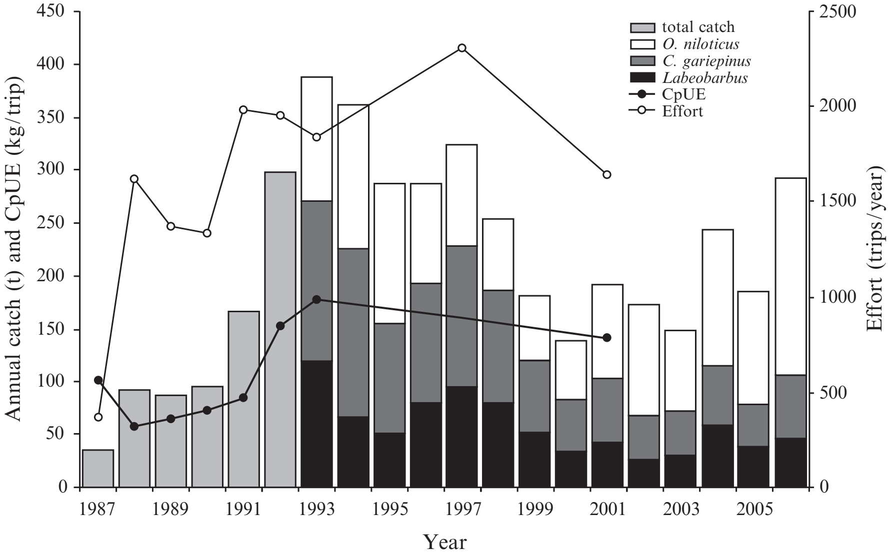

Fig. 6 Estimated total annual fish landings, total effort and CPUE of the motorised gill net fishery in Lake Tana. Data on annual fish landings from Fish Production and Marketing Enterprise. Note that the species composition of the annual catch data 1987–1992 is unknown (redrawn from de Graaf et al., 2006)

in capacity is the most likely cause for the increase in total landings of the gill net fishery since 2003 (Fig. 6).

During the 1990s significant changes occurred in effort allocation, species composition and abundance of fish stocks. In 1991–1993 the vast majority (71%) of fishing activity took place in the Bahir Dar Gulf and only 14% of the effort was allocated to the north-eastern shores of the lake. After 1991–1993 the gill net fishery moved in northern direction. In 2001 41% of the effort was allocated to the north-eastern shores of Lake Tana adjacent to the floodplains. During the 1990s *Oreochromis niloticus*, *Clarias gariepinus* and *Labeobarbus* each made up roughly one third of the total catch (Fig. 6) of the motorised gill net fishery. However, since 2001 the contribution of *O. niloticus* has increased to more than 50%, while the contribution of both *C. gariepinus* and *Labeobarbus* halved (Fig. 6). CPUE of *O. niloticus* almost doubled during the 1990s (Fig. 7a), without significantly affecting the abundance of tilapia as determined by fishery independent trawl surveys (Fig. 7b). In contrast CPUE and abundance of *Labeobarbus* decreased by respectively 50% and 75% during this period (Fig. 7).

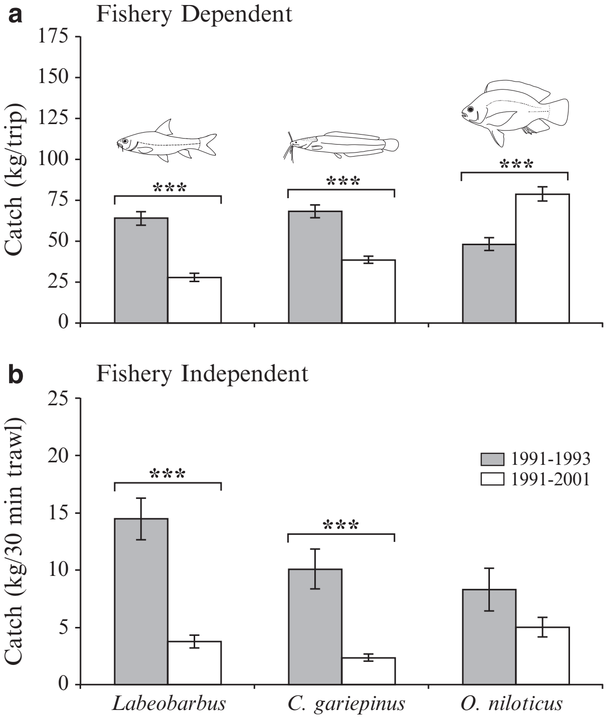

Fig. 7 Temporal variation in (**a**) CPUE of the commercial gill net fishery (Fishery Dependent). (**b**) CPUE of the experimental trawl surveys (Fishery Independent) for *Labeobarbus*, *C. gariepinus* and *O. niloticus* during 1991–1993 and 1999–2001. Error bars indicate 95% confidence interval; *** = P < 0.001 (redrawn from de Graaf et al., 2006)

The whole catch of traditional fishermen is sold on local markets and to restaurants around the lake. In contrast, almost all fish landed by the motorised gill net fishery, are purchased and processed (Fig. 5c) by the Fish Production and Marketing Enterprise (FPME) in Bahir Dar, and transported to Addis Ababa. Only recently the FPME started exporting Lake Tana fish to neighbouring Sudan. Prices paid to the operating fishermen are even too low to cover petrol and maintenance, let alone to save money and invest in new or better gear. To maximise their income, the fishermen specifically target *O. niloticus*, the most favoured fish for consumption among Ethiopians. *Labeobarbus* is less appreciated due to its intra-muscular bones and is therefore mainly used for soup or "wot", a spicy (chopped) fish sauce. The scale-less *C. gariepinus* is considered unclean according to the Ethiopian Orthodox Church and is almost exclusively eaten by Western and African foreigners in Addis Ababa.

Unlike other African lakes, Lake Tana's small sized (<10 cm) fish species are at present not harvested. The viability of developing a new fishery targeting the two common small *Barbus* species in Lake Tana, the pelagic *B. tanapelagius* and benthic *B. humilis* is currently being assessed. The standing stock of the small zooplanktivorous *B. tanapelagius* is the largest and this species could be exploited selectively by pelagic fishing (Dejen, 2003; Dejen et al., 2003).

11 Future of Lake Tana's Fisheries

In Lake Tana, the relatively unspecialised ecologically flexible species such as *O. niloticus* and *C. gariepinus*, which are adapted to fluctuating environments, can be categorised as resilient (de Graaf et al., 2006). The increase in fishing efforts after the introduction of the motorised commercial gill net fishery has had only limited effect on abundance, i.e. reduction of large *C. gariepinus*, and no effect on recruitment of both species between 1992 and 2001 (de Graaf et al., 2004, 2006).

In sharp contrast to *Oreochromis niloticus* and *Clarias gariepinus*, the *Labeobarbus* species are predicted to be by far the most susceptible to fisheries as the labeobarbs are: (a) long-lived (Wudneh, 1998), (b) form spawning aggregations (Nagelkerke and Sibbing, 1996; de Graaf et al., 2005), and (c) are predominantly ecologically highly specialised endemics (Sibbing & Nagelkerke, 2001; de Graaf, 2003; de Graaf et al., 2008). A drastic decrease in abundance by ca 75% of the migratory riverine spawning *Labeobarbus* species and the collapse of juvenile *Labeobarbus* (between 5 and 18 cm FL: by 90%) during the 1990s suggest recruitment-overfishing (de Graaf et al., 2004, 2006). The most likely cause for the dramatic decline in *Labeobarbus* stocks is the introduction of the motorised commercial gill net fishery as no changes were recorded in the traditional fisheries (de Graaf et al., 2006) and environment (de Graaf et al., 2004). *Labeobarbus* catchability varies highly during the year, more than 50% of the annual *Labeobarbus* yield is landed during the three months of peak spawning, July–September, when fishermen target the spawning aggregations in the river mouths.

The drastic and rapid consequences of an unregulated gill net fishery on spawning aggregations of large African cyprinid fishes repeatedly has become painfully clear with the collapses of *Labeo mesops* fisheries in lake Malawi (Skelton et al., 1991), *Labeo victorianus* and *Barbus altianalis* fisheries in Lake Victoria (Cadwalladr, 1965, Ogutu-Ohwayo, 1990; Ochumba & Manyala, 1992) and the virtual disappearance of *Labeo altivelis* from the Mweru-Luapula system within a period of 20 years (Gordon, 2003). The situation of the unique *Labeobarbus* species flock is critical. To prevent a total collapse of the *Labeobarbus* species dependent on riverine spawning, effort control regulations limiting the gill net fishery in the spawning season and/or in areas around the river mouths, as well as the seasonal fishery on the upstream spawning areas (Fig. 5b), are to be implemented immediately.

12 Conclusions

The fisheries in the Nile drainage system, especially in the Nilotic lakes, make a major contribution to the inland fish production of Africa. In several of these lakes the fish landings rose dramatically during the past decades. Most important is Lake Victoria, which with about 1,000,000 t y^{-1} is responsible for more than half of the fish production in the entire Nile system. Possibly with exception of the Sudd Swamps in southern Sudan, most of the studied areas are extremely heavily exploited and show signs of overfishing, such as declines in species diversity and shifts towards small species of a low trophic level in the fish landings.

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Nile Basin Asymmetries: A Closed Fresh Water Resource, Soil Water Potential, the Political Economy and Nile Transboundary Hydropolitics

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Abstract The Nile Basin is characterised by a number of *asymmetries*. First, the water endowments and use are asymmetrical. The eight upstream riparians provide all the *surface water* in the basin but they make negligible use of these surface waters. Downstream Egypt and the Sudan are arid but benefit from a notional total use of the *flowing surface waters*. A second asymmetry is that the upstream riparians are also well endowed with *soil water*. Soil water cannot be shared except in traded commodities and these non-shareable *soil waters* are probably twice the volume of the technically shareable surface waters. The third asymmetry is in adaptive capacity.

Egypt has adapted to its serious water deficits since the early 1970s by achieving water security by diversifying and strengthening its economy. Its diversified economy has enabled it to import food and embedded *virtual water*. The upstream riparians have achieved much lower levels of adaptive capacity. The fourth and most important asymmetry is a consequence of Egypt's adaptive capacity. There is a marked asymmetry in *power relations* in the Nile Basin. Egypt is the basin hegemon. A hegemon is a first amongst assumed equals. Its interests have been asserted in basin *hydropolitics* and are expressed in de facto allocations and in the existing Nile Water Agreements – 1929 and 1959 – between Egypt and the Sudan. Its interests continue to be influential across the basin in the initiatives that emerged in the 1990s as an organisation established in 1999 – *The Nile Basin Initiative*.

1 Introduction

The first purpose of the chapter is to highlight the driving forces that have shaped the current approaches to managing the water resources of the Nile Basin. The major driving force is demography. Population is rising rapidly in all the riparian economies. Each additional individual requires about 1,000 m^3 of water per year for food, livelihood and domestic water needs. Ninety per cent is for food. As a consequence of the rising

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populations all the economies have had to mobilise more water to meet the needs of the additional consumers. These additional demands have closed the *freshwater* Nile resources. The flowing freshwater of the Nile basin is used mainly in Egypt and the Sudan. Egypt has already reached the stage that the quality of its water environment is being impaired by the levels of water abstraction for irrigation and other economic and social uses. A second driving force arises from the additional consumption associated with the advancement of an economy and associated uses of water by society. As the incomes of riparian populations rise, their new consumption behaviour requires more water. This driving force is as yet weak in the Nile Basin as the GDP per head of the populations of the Nile Basin countries are not rising significantly – with the exception of those of Egypt and the Sudan. This driving force is not currently significant but it will be when the economies begin to develop more rapidly. A third, and related, driving force is the diversification of economies. This force has the very important potential to ameliorate the problems of water scarcity caused by population increase. A more advanced and diverse economy is strong and has options that weak economies do not. A diverse economy can generate revenue surpluses that enable the economy to import water intensive commodities such as staple foods. Egypt has already demonstrated that it is possible to cope with the challenges of a serious water deficit. Egypt has achieved food security by having the capacity to remedy its water scarcity in the global trading system by ‘importing’ virtual water. It will be shown that those Nile Basin riparians already experiencing water deficits revealed by their no longer being food self-sufficient can only achieve water and food security by engaging in international commodity trade. Internal trade amongst the riparians will be shown to be limited. It will also be shown that Egypt not only benefits from the freshwater in the Nile River, which is fed by rainfall in Ethiopia and in the East African Lakes Basin. It is also the major ‘importer’ in the basin of virtual water from the soil water surplus East Africa in its substantial imports of tea and coffee.

The chapter provides estimates of the water resources that contribute to water and food security of the Nile riparians. The *freshwater* in the Nile River and its tributaries – about 100 billion cubic metres annually (Zeitoun & Allan, 2007) – is important but is not the major water resource of the basin as a whole. The basin’s water resources also include the – usually ignored – *groundwater* in aquifers to which the respective riparians have access. Even more important – and *always* ignored until FAO began to make estimates of soil water use in the Nile Basin in 2005 – is the *soil water* in the rainfed soil profiles of the basin (FAO, 2008). Rainfed soil water produces crops and livestock products. The volume of soil water in the territories of the Nile riparians, an area much larger than the Nile Basin itself, has been estimated to be about 229 billion cubic metres (evaporation from crops only) annually (Zeitoun & Allan, 2007). The review of the Nile Basin’s water resource endowment will provide a perspective on the underlying fundamentals that should inform water policy makers and water users on water management options to achieve ecological and environmental sustainable outcomes.

Nile freshwater resources do not by any means provide water security for the Nile riparians. The chapter will provide an overview of the *water security* of the basin’s riparians by examining their *food trade* statistics.

The Nile surface waters are closed. That is, further use of them with current technologies, will seriously degrade the flowing water resources and also impact negatively ecological diversity more generally. Water security is an issue of growing significance. The nature of the conflictual relations over these shared water resources will be analysed. The agreements and institutions that have been established to buttress *prior use* approaches – that is *water integrity* – which serve the interests of downstream riparians will be discussed. The upstream riparians prefer the principle of *water sovereignty* – which especially serves the interests of upstream riparians that enjoy high levels of rainfall. There will also be a discussion of the attempts to introduce the notion of *equitable utilization* a principle of international customary water law. The idea of shared *socio-economic benefits* that could be gained from alternative approaches to managing scarce transboundary waters will also be reviewed.

It will be concluded that the Nile Basin is characterised by a number of *asymmetries*. First, water endowments are asymmetrical. The eight upstream riparians provide all the *surface water* in the basin but they have not used these surface waters. Downstream Egypt and the Sudan are extremely arid or semi-arid but benefit from a notional total use of the *flowing surface waters*. A second asymmetry is that the upstream riparians are also well endowed with *soil water*. Soil water cannot be shared and these non-shareable *soil waters* are probably twice the volume of the shared surface waters. The third asymmetry is in adaptive capacity. Egypt has adapted to its serious water deficits since the early 1970s by achieving water security by diversifying and strengthening its economy. Its diversified economy has enabled it to import food and embedded *virtual water*. The upstream riparians have achieved much lower levels of adaptive capacity. The fourth and most important asymmetry is a consequence of Egypt's adaptive capacity. There is a very marked asymmetry in *power relations* in the Nile Basin. Egypt is the basin hegemon. Its interests have been asserted in basin *hydropolitics* and are expressed in the existing Nile Water Agreements – 1929 and 1959 – between Egypt and the Sudan. Its interests continue to be very influential across the basin in the initiatives that emerged in the 1990s as an institution established in 1999 – *The Nile Basin Initiative*.

2 Asymmetric Hydrology

The orientation of the Nile river flow is from two relatively high rainfall regions in the south to a rainless desert region in the north. Egypt and the Sudan benefit from the summer rains that fall in the highlands of Ethiopia and in the relatively well-watered region in the Lakes Basin in East Africa. The East African basin includes most of Uganda, Rwanda and Burundi but only very small parts of Kenya, Tanzania, and the Democratic Republic of the Congo (DRC). Figure 1 shows the small proportion that the headwaters region of the Nile Basin occupies of the East African and Horn of Africa riparians.

Fig. 1 The Nile Basin and the areas covered by the territories of the riparians (London Water Research Group, 2007; map reproduced with permission of the FAO) (*see Color Plates)*

Table 1 provides the areas of the riparians and the proportions of their territory that lie within the Nile Basin. Table 2a shows quantities and proportions of the flowing Nile *freshwater*. Estimates are also shown in Table 2b of the *groundwater* resources of the ten riparians – mainly unutilised, and also estimates of the soil water being used currently based on the evapo-transpiration from the crops being raised. There are no estimates of the potential volumes of utilisable soil water in the basin countries.

Table 1 Base data on Nile Basin states in relation to the Nile Basin

	State Area (km²)	State Area in Nile Basin (km²)	Per cent of Area of Basin	Per cent of State Area inside Nile Basin
Egypt	1,001,450	326,751	10.5	32.6
Sudan	2,505,810	1,978,506	63.6	79.0
Ethiopia	1,100,010	365,117	11.7	33.2
Eritrea	121,890	24,921	0.8	20.4
Eastern Nile		2,695,295		
Uganda	235,880	231,366	7.4	98.1
Kenya	580,370	46,229	1.5	8.0
Tanzania	945,090	84,200	2.7	8.9
Burundi	27,834	13,260	0.4	47.6
Rwanda	26,340	19,876	0.6	75.5
DR Congo	2,344,860	22,143	0.7	0.9
Southern Nile		417,074		
Basin as a whole		3,112,369	100	

Source: based on Phillips et al. (2006: 67) (based on FAO AQUASTAT data).

Table 2a Freshwater flows of the Nile and its tributaries and precipitation in the ten riparians

	Average annual precipitation (mm)	Inflow ($Mm^3 y^{-1}$)	Outflow ($Mm^3 y^{-1}$)
DR Congo	1,245	0	1,500
Burundi	1,110	0	1,500
Rwanda	1,105	1,500	7,000
Tanzania	1,015	7,000	10,700
Kenya	1,260	0	8,400
Uganda	1,140	28,700	37,000
Eritrea	520	0	2,200
Ethiopia	1,125	0	80,100
Sudan	500	117,100	55,500
Egypt	15	55,500[a]	Less than 10 to sea

[a] Allocation to Egypt after deduction of evaporation from Lake Nasser, according to 1959 Sudan-Egypt Nile Basin Treaty. Evaporation from Lake Nasser is currently high because the level of the lake is high after almost two decades of above average rainfall in Ethiopia. Evaporation fell to between five and six cubic kilometres in the drought years of the mid-1980s (Stoner, 1995).

Source: Stoner, D., 1995. Future irrigation planning in Egypt, In Howell, P. P. & J. A. Allan, *The Nile: sharing a scarce resource*, Cambridge: Cambridge University Press, pp 281–298.

The asymmetric hydrology can be deduced from Tables 1 and 2a, b. They show that apart from some relatively minor surface flows derived from rainfall in southern Sudan almost all the Nile flows come from Ethiopia – about 85%. The rest comes from the East African Highlands. The East African water is subject to major evaporative losses in Lake Victoria and to high levels of evapo-transpiration in the wetlands of southern Sudan. These losses reduce the flow on the White Nile at Khartoum to 50% of the flow from Lake Victoria. The freshwater flows from Ethiopia that come down the Blue Nile and the Atbara flow fast into the Sudan and

Table 2b Freshwater flows of the Nile by riparian and showing the average annual precipitation, soil water consumption and groundwater production

	Average annual precipitation (mm)	Nile River Freshwater Flows*		Soil Water Consumption** (Mm3 y-1)	Groundwater Production*** (Mm3 y-1)
		Inflow (Mm3 y-1)	Outflow (Mm3 y-1)		
DR Congo	1,245	0	1,500	31,909	421,000
Burundi	1,110	0	1,500	6,132	2,100
Rwanda	1,105	1,500	7,000	11,000	3,600
Tanzania	1,015	7,000	10,700	31,583	30,000
Kenya	1,260	0	8,400	20,386	3,000
Uganda	1,140	28,700	37,000	45,504	29,000
Eritrea	520	0	2,200	843	
Ethiopia	1,125	0	80,100	31,075	40,000
Sudan	500	117,100	55,500	50,313	7,000
Egypt	15	55,500[a]	<10,000 (to sea)	0	1,3000
Total in System		approx, 100,000		approx, 229,000	

* Evaporation from natural & constructed storage not accounted.

** 2002 soil water data based on Nile Basin Dataset (FAO, 2006a – see also Appendix B). The figures do not include soil water used by natural vegetation.

*** Aquastat *production* figures. Groundwater *availability* data are not available. No production data available for Eritrea. Allocation to Egypt after deduction of evaporation from Lake Nasser, according to 1959 Sudan-Egypt Nile Basin Treaty. Precipitation and freshwater data from FAO (1997: Table 20). Evaporation from Lake Nasser is currently high because the level of the lake is high after almost two decades of above average rainfall in Ethiopia. Evaporation fell to between five and six cubic kilometres in the drought years of the mid-1980s (Stoner 1995).

Source: Stoner, D., 1995, Future irrigation planning in Egypt, In Howell, P. P. & J. A. Allan, *The Nile: sharing a scarce resource*, Cambridge: Cambridge University Press, pp 281–298.

Egypt. Flood waters reach Egypt within a few weeks of their entering the system in the highlands of Ethiopia and are much less subject to evaporation. Waters stored in Lake Nasser/Nubia are subject to evaporative losses at a rate of 3 m depth per year. Aswan has the highest evaporative rate on Earth. When the Lake was low in 1986 the losses were over five billion cubic metres per year. The Lake has been at a high level for almost two decades and the losses are currently about 13 cubic billion cubic metres per year, the level recorded in the late 1970s (Stoner, 1995).

The first hydrological asymmetry is the difference between the fresh water endowment of the southern basin compared with that of the north. The second asymmetry, is in soil water endowments – see Table 2b. This asymmetry comes about for the same reason as the freshwater asymmetry – the rainfall distribution in the basin. The southern basin is even more rich in soil water than it is in freshwater. Soil water is the infiltrated rainfall that remains in the soil profile long enough to sustain vegetation and crops. Table 2b shows estimates of soil water use in the ten riparians; there are no estimates of actual soil water resources that could potentially be utilised. The soil water used in the southern riparians is estimated to total

229 billion cubic metres (FAO, 2006a). This volume is more than twice the 100 billion cubic metres of fresh Nile water flows.

The significance of the southern soil waters had not been given any prominence until the mid-1990s when the author first raised the idea publicly at a Nile 2002 meeting in Addis Ababa (Allan, 2001). The scale of the soil water resources of the southern basin is very significant both economically and politically especially as Ethiopia and the riparians of the East African Highlands export almost all their Nile freshwater. Freshwater can be, and has been, captured. Soil water on the other hand cannot be shared unless it is incorporated in traded commodities. Soil water is not politically significant unless attention is drawn to it. It can become very political if it is suggested that it be taken into account in comparing the water endowments of competing riparians. As a silent water resource it underpins significantly the water security of the southern basin riparians. Flowing surface freshwater is already highly politicised as it is palpably shareable and quickly becomes the focus of conflict as the demands for water of competing riparians rise.

The prominence of the climate change science makes it necessary to check what climate scientists are saying about the future of the Nile Basin. The future climate scenarios are favourable for Nile basin riparians. Both surface freshwater and soil water resources will be higher although they may be more drought and flood impacted. In this case both the north and the south will benefit as the north will receive the higher river flows if the existing international allocations of waters continue. Since the low flows of the 1980s levels of seasonal monsoon precipitation in the south of region have been above the long-term average. The majority of climate change scientists suggest that future Nile flows will continue at current high levels rather than at the low levels of the early 1980s levels (Milly et al., 2005; Conway et al., 2007). The existence of extensive spillage from Lake Nasser-Nubia since the early 1990s (see maps at google.com) has created large flooded areas to the north west of Aswan confirming the higher flows. The southern riparians will benefit from the higher levels of soil water in the twenty-first century. Amongst the many uncertainties regarding climate change impact is the levels of future evaporation and evapo-transpiration.

3 Asymmetric Political Economies

The Nile riparians are also asymmetric vis-à-vis their development indicators. The extent to which an economy is developed is extremely important with respect to its capacity to deal with water scarcity. Table 3 shows that the downstream riparians, Egypt and the Sudan, have achieved much higher levels of GDP per head. This indicator, albeit crude, is helpful as a way of estimating the adaptive capacity of an economy. Egypt's higher GDP per head is consistent with its capacity to meet it seriously worsening water resource insecurity. Egypt's more diverse and relatively stronger economy has enabled it to achieve security – not by self-sufficiency in land and water – but through its capacity to trade its way to security by importing water intensive food commodities.

Table 3 Past and projected populations of Nile Basin States, 1960–205 in millions and GDP per head 2006 in US$ per head

	1960	1975	1990	2005	2020	2035	2050	Est Growth Rate[a] p.a.	GDP/ Head 2006 Indicator of adaptive capacity
Egypt	27.8	39.3	55.8	74.9	96.9	114.7	127.4	1.2%	1484
Sudan	11.4	16.7	24.9	35.0	44.5	53.3	60.1	1.2%	934
Ethiopia	24.1	35.2	52.0	74.2	104.8	138.3	171.0	2.0%	164
Eritrea	/	?	?	4.5	6.6	8.6	10.5	2.0%	249
Uganda	6.8	10.8	17.4	27.6	46.6	73.6	103.2	3.0%	842
Kenya	8.3	13.6	23.6	32.8	38.5	42.2	44.0	0.9%	650
Tanzania	10.2	16.2	26.1	38.4	49.8	60.2	69.1	1.4%	319
Rwanda	2.9	4.4	6.8	8.6	11.6	14.4	17.0	1.8%	242
Burundi	2.9	3.7	5.6	7.3	11.1	15.1	19.5	2.0%	114
DRCongo	15.4	23.9	37.4	56.1	84.4	118.6	151.6	2.2%	136
All Nile States	111.0	165.7	249.4	359.4	494.7	639.0	773.7	1.75%	

Based on FAOSTAT, FAO Statistics Division ("long-term series (quinqu.) tot./rural/urban" from FAOSTAT Classic view).

[a] Estimated growth rate derived from population figures. GDP data form UNDP and World Bank.

All the riparians face serious water resources challenges as a consequence of their rising populations. The current growth rate of Uganda is particularly significant when projected to mid-century. The population growth in north-east Africa as a whole is high by global standards. Egypt has begun on its demographic transition which will lead to a leveling off of the rising trend by mid-century. But a doubling of Egyptian population is still possible. The levels at which the populations of Ethiopia, of Uganda and of Kenya are growing place extreme burdens on the limited adaptive capacity of these economies as well as on their limited soil and freshwater water resources. That Egypt is at a more advanced stage in the demographic transition than the economies in the south of the basin is a major asymmetric feature of the political economy of the Nile Basin.

Egypt has demonstrated that it is possible to cope with the closure of its Nile water resource. Egypt has always been more dependent on Nile freshwaters than any of the other riparians. By the millennium, however, it had sufficiently diversified its economy to be able to access half its national food requirements via global trade in food commodities. Such trade freed the political leadership from the economic and political stress of mobilising non-existent water within its own economy. Egypt's achievements in the political economy are much less prominent in political discourse than the conventional emphasis which concerns the devotion of political energy and investment to developing the very unpromising and already over-utilised freshwater resources.

Adaptiveness as expressed by the capacity to diversify the economy is clearly *asymmetrically arranged* in the Nile Basin. Egypt is relatively adaptive. The other economies are much less so. Most are classified as fragile states. One of the reasons for the lack of adaptiveness in the southern political economies is that the southern riparians have endured and are currently experiencing high levels of internal and/or international conflict. Such conflict is also *asymmetric* across the basin with high levels in the south. Egypt is significantly less troubled by internal conflicts, especially by armed conflict. Although even Egypt is seriously divided internally, however, over the issue of how and at what pace it should modernise its society and economy. In the south in 2008 there were numerous examples of violent conflict; in the Sudan, in Uganda, in Kenya and in the DRC. There was an international violent intervention in Somalia in 2007, which was ongoing in 2008. If the 1990s are included all the Nile riparians except Egypt and Tanzania, have endured high levels of internal violent conflict. Only 9% of Tanzania's area lies in the Nile Basin.

4 Water, Food and Trade and Water Security and Sustainability Asymmetries

A further *asymmetry* is expressed in the levels of trade in food commodities both between riparians within the basin and especially with respect to trade between the Nile riparians and economies outside. The Nile Basin riparians can achieve water security either by increasing their crop and livestock productivity or by 'importing' virtual water. Virtual water is the water required to produce a crop or a livestock product. It requires about 1,000 tonnes (cubic meters of water) to produce a tonne of wheat. It requires about 16 times that volume of water to produce a tonne of beef. If an economy can avoid the economic and political stress of mobilising impossibly scarce local water to meet food needs the outcome can be favourable for a food importing economy such as Egypt. Or at least it was until 2006 when global food prices began to rise rapidly. Global food prices have been kept low by EU and US subsidies for most of the second half of the twentieth century. Egypt encountered its food deficit in the early 1970s at a point in economic history when wheat was on the world market at half its production cost. The end of Egypt's Nile waters based water security has been very effectively hidden by the wonderfully economically invisible and politically silent import of water intensive food commodities. The political leadership of Egypt was greatly assisted by the invisibility and silence of the solution of the politically embarrassing strategic problem of the absence of water and food self-sufficiency. No political elite or national leader wants to draw attention to an external solution over which they have no control that reveals extreme national insecurity.

There are two other political-economy related *asymmetries* between the north and the south of the Nile Basin. The first concerns the use of water resources in agriculture and livestock production. The second relates to the extent to which Egypt has become dependent for its water security on the global trading system to a much greater extent than any of the other riparians (see Tables 6.1–6.3).

There are three elements to the asymmetries in water resource use for crop and livestock production. First there is scarcely any irrigation in the south. Egypt's agriculture is 98% irrigated (Tables 4 and 5).

Secondly, crop and livestock productivity and are high in Egypt and low in the southern riparians. Thirdly, livestock production is a major element of the national economies of the southern riparians, of Ethiopia, of Kenya and of Tanzania and also of the southern Sudan. Livestock production is a relatively minor activity in Egypt as reflected in the respective contributions to national GDP.

High yields and high returns to agricultural water are associated with irrigated cropping in the north. Low yields per hectare everywhere obtain in the rain-fed tracts of the south where there are substantial volumes of under-utilised soil water. A major difference between the north and south is that the irrigation option has *not* been tried to a significant extent in the south. The southern riparians have been, and continue to be prevented, from using Nile waters by a combination of factors. First, the economies of the southern riparians are weak which prevents them mobilizing investment in water infrastructure. Secondly, their political weakness has to date prevented them from challenging the Egyptian hegemony on Nile freshwater allocation. At the same time they have not been given support to build dams and diversion structures by the international community. International agencies and international financial institutions (IFIs) and bilateral agencies have not wanted to intervene beyond the level of fostering cooperation over shared management of Nile freshwater resources through such initiatives as the Nile Basin Initiative.

A second element of the crop and livestock production asymmetry is that the southern riparians have the majority of the waters in the Nile Basin even when they export almost 100% of the Nile surface flows. To date these economies have not been able to take advantage of this potentially favourable *asymmetry*. Yields of staple grains from rainfed farming languish at under one tonne per hectare (Dorosh, 2008). That is at the levels of the past half millennium. The African tropical rainfed regions have not benefited from the green revolution experiences enjoyed by Asia in the second half of the twentieth century. The jury is out on what yields are possible for these rain-fed regions in tropical Africa. Food and Agriculture Organisation (FAO) scientists argue that the poor soils of tropical Africa and their drought prone rainfall regimes determine a low rain-fed yield scenario (Burke & Steduto, 2007). Others have argued that it is not only environmental factors that determine pre-modern levels of rain-fed yields. It has been shown that distance from urban markets has a marked impact on rained crop yields in upland East Africa suggesting that a more than doubling of productivity will be possible (Tiffen & Mortimore, 1994; Dorosh

Table 4 Rainfed and irrigated agriculture of all Nile Basin states

	Total	Rainfed	Irrigated
Area of Land Farmed (1,000 ha)	52,449	46,020 (87%)	6,429 (13%)
Crop Production (MT per annum)	172,107	96,811 (56%)	75,301 (44%)

The data include all of the agriculture in the DR Congo, 99% of which is understood to take place outside of the Nile Basin.

Table 5 Rainfed and irrigated cultivated land in Nile Basin states

	Rainfed Land		Irrigated Land		Total			
	Area (1000 ha)	Production (1000 MT)	Area (1000 ha)	Production (1000 MT)	Area (1000 ha)	Production (1000 MT)	Share of Irrigated Land	Share of Irrigated Production
Eastern Nile								
Egypt	0	0	4,432	57,714	4,432	57,714	100%	100%
Sudan	10,945	4,648	1,502	9,320	12,447	13,969	12%	67%
Ethiopia	9,796	14,422	187	2,243	9,984	16,662	2%	13%
Eritrea	529	445	20	83	548	526	4%	16%
Southern Nile								
Uganda	5,989	20,046	10	188	5,999	20,234	0%	1%
Kenya	3,552	8,629	68	3,511	3,621	12,139	2%	29%
Tanzania	6,455	15,082	108	1,776	6,562	16,858	2%	11%
Rwanda	1,271	4,494	4	21	1,275	4,515	0%	0%
Burundi	1,032	3,569	90	425	1,122	3,994	8%	11%
DR Congo	6,451	25,476	8	20	6,459	25,496	0%	0%
Nile Basin	46,020	96,811	6,429	75,301	52,449	172,107	12%	44%

NB. Values shown are state-wide, and not limited to crops produced within the basin itself.
Source: Modified from FAO Food Balance Sheets by FAO Land and Water Unit.

et al., 2008). The road connectivity factor is closely related to a large number of other input, infrastructure and management factors that when in place can increase the productivity of remote crop and livestock producers (Dorosh et al., 2008). The Egyptian farming systems could not be more different. The irrigated delta and alluvial river lowlands of Egypt are so densely settled that almost all farms are within five kilometers of an urban centre and connected by good roads and market services.

The oil price spike since 2005 has directly affected the costs of all sorts of production and transportation. It has also encouraged the production of biofuels, which compete for land and water. Egypt has useful oil and gas resources, which help its foreign exchange affairs. It exports natural gas. The Sudan is enjoying rising oil revenues and is able to attract the assistance of global players such as China to develop both its oil as well as its water infrastructure (Mohieldeen, 2008). Since 2000 the Sudan has been developing a dam on the main Nile just south of the Egyptian border. The Merowe (or Meroe) reservoir will generate hydropower and provide water for irrigation and other uses. The evaporation from the reservoir and the diversion of water for irrigation will bring the Sudan's utilisation to, or beyond, the 18.5 billion cubic metres per year – 25% of annual flow – which is the share agreed with Egypt in the1959 Nile Water Agreement between Egypt and the Sudan. Egypt has not opposed the construction of the dam because it wants the Sudan to be in the same position as Egypt itself with all the 1959 waters in use so that they are more difficult to negotiate (Mohieldeen, 2008). In brief, the southern Nile riparians face the additional asymmetry of being less well endowed with non-water natural resources. Only in soil water are they better endowed than the two downstream riparians.

4.1 Adapting to Water Scarcity

The extent to which the Nile basin economies have resorted to the international market for food to solve their water scarcity problem is also asymmetric. On this issue of global and Nile Basin market solutions it is extremely asymmetric. Egypt is a major importer of water intensive crop and livestock commodities from outside the Basin. (Table 5.3) It exports a relatively small proportion of its crop and livestock production to the rest of the world and an insignificant proportion to the other Nile Basin riparians. Some of the upstream East African Nile Basin economies - notably Kenya and Uganda – export significant volumes of rain-fed soil water intensive commodities such as tea and coffee to rest of the world and to Egypt (Fig. 2). The Sudan in normal circumstances is a major exporter of livestock products (Table 6.2) both within the Basin to Egypt and to markets beyond the basin especially to the Gulf economies.

Table 6.3 shows the virtual water 'imports' and 'exports' for crop and livestock products for the individual Nile Basin economies both within the basin and with the rest of the world. A number of things are evident. The proportion of the *in-basin* crop and livestock trade compared with the trade *with rest of the world* is trivial. Figure 3 also illustrates this difference. Egypt depends on the global system for

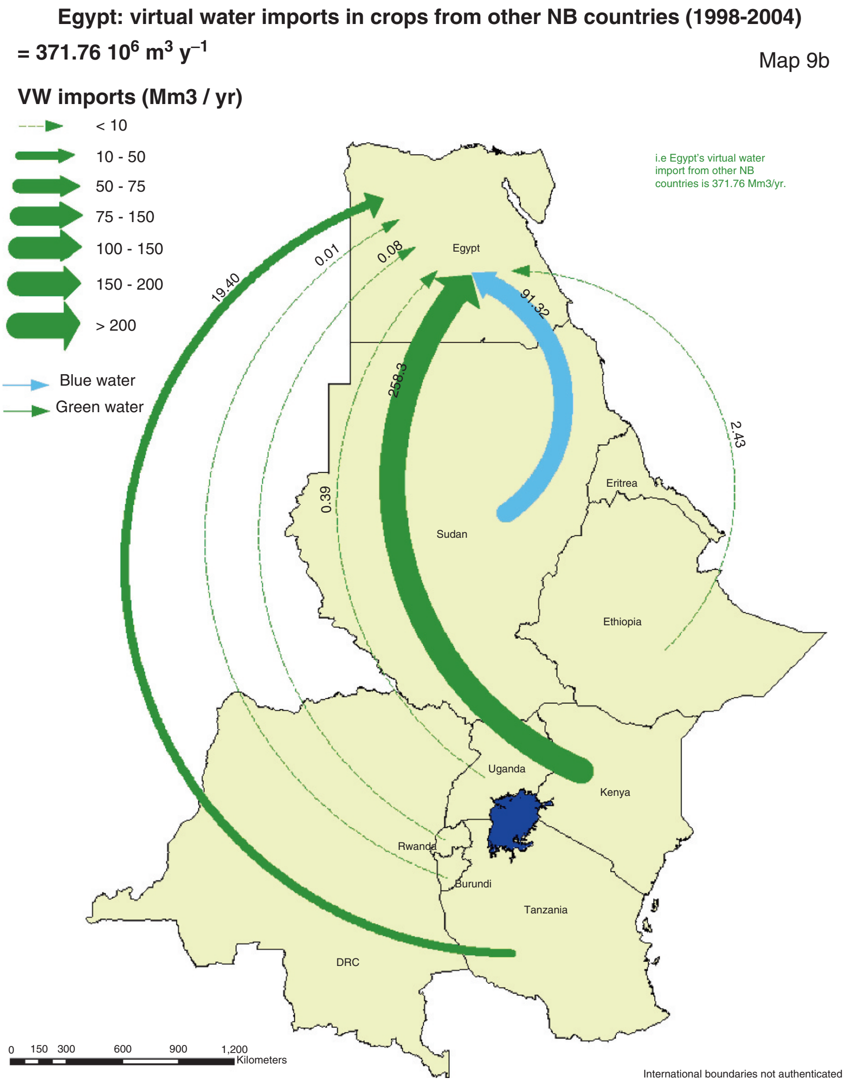

Fig. 2 Egypt's virtual water (vw) imports in crops from other Nile Basin countries (1998–2004) (source: London Water Research Group, 2007) (*see Color Plates)*

its food and water security to an extreme extent. The Nile Basin can provide neither the freshwater nor the soil water that Egypt requires now. It certainly cannot provide these waters for Egypt's future even higher requirements. Egypt's water security depends on its capacities to diversify and strengthen its economy.

Figure 3 also confirms a number of the other asymmetries identified in this analysis. Despite almost all the Nile freshwater flows being used in Egypt and the Sudan the main 'exports' of virtual water are generated in the southern riparians. Even

Table 6.1 Virtual water related CROP 'imports' and 'exports' within the Nile Basin between riparians and 'trade' with the rest of the world. Mm^3 of virtual water per year

	In Basin		With rest of world	
	'Imports'	'Exports'	'Imports'	'Exports'
Egypt	372.0	51.0	30195.0	1034.0
The Sudan	184.0	122.0	3565.0	652.0
Ethiopia	1.0	10.0	1061.0	1053.0
Eritrea	0.0	0.0	8.0	0.7
Uganda	41.0	169.0	682.0	2501.0
Kenya	197.0	403.0	1817.0	2909.0
Tanzania	31.0	132.0	1818.0	1888.0
Rwanda	48.0	1.0	56.0	400.0
Burundi	30.0	2.0	28.0	318.0
DRC	0.0	15.0	0.0	1.0
Total	905.0	905.0	30230.0	11321.0

Table 6.2 Virtual water related LIVESTOCK 'imports' and 'exports' within the Nile Basin between riparians and virtual water 'trade' with the rest of the world. Mm^3 of virtual water per year

	In Basin		With rest of world	
	'Imports'	'Exports'	'Imports'	'Exports'
Egypt	18.0	0.9	2041.0	28.0
The Sudan	0.2	18.0	93.0	2503.0
Ethiopia	0.0	0.0	0.2	29.0
Eritrea	0.0	0.0	0.0	34.0
Uganda	1.5	0.3	5.0	2.6
Kenya	0.2	4.0	0.9	5.6
Tanzania	3.3	0.3	10.0	0.3
Rwanda	0.1	0.0	0.3	0.2
Burundi	0.1	0.0	0.6	0.04
DRC	0.0	0.0	0.0	0.2
Total	24.0	24.0	2122.0	2062.0

Table 6.3 Virtual water related CROP & LIVESTOCK 'imports' & 'exports' within the Nile Basin between riparians & 'trade' with the rest of the world. Mm^3 of virtual water per year

	In Basin		With rest of world	
	'Imports'	'Exports'	'Imports'	'Exports'
Egypt	390.0	51.9	32236.0	1062.0
The Sudan	184.2	138.0	3668.0	3155.0
Ethiopia	1.0	10.0	1061.2	1082.0
Eritrea	0.0	0.0	8.0	34.7
Uganda	42.5	169.3	687.0	2503.6
Kenya	197.2	407.0	1817.9	2914.6
Tanzania	34.3	132.3	1828.0	1888.3
Rwanda	48.1	1.0	56.3	400.2
Burundi	30.1	2.0	28.6	318.0
DRC	0.0	15.0	0.0	1.2
Total	949.0	949.0	32352.0	13383.0

Source: All tables from Zeitoun and Allan (2007) based on FAO data for the Nile Basin.

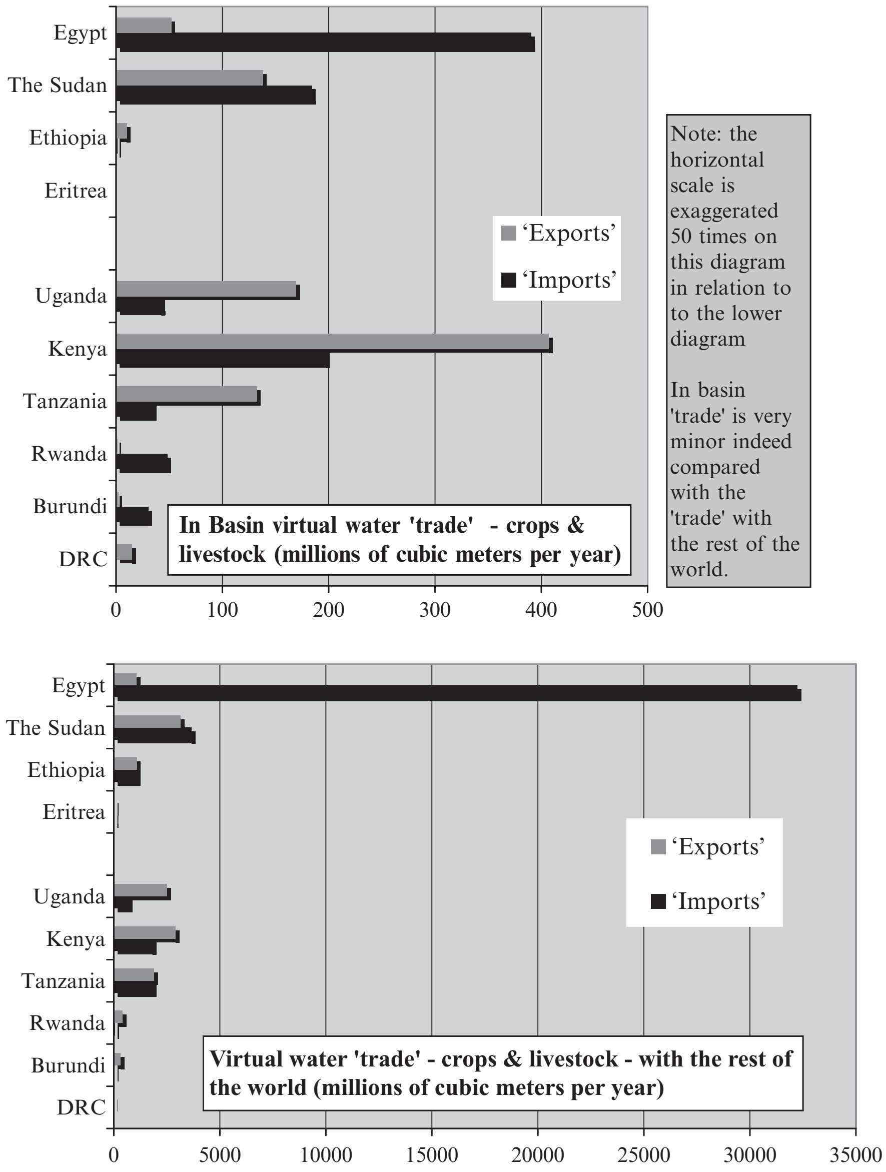

Fig. 3 Virtual water trade within the Nile Basin and between the Nile Basin and the rest of the world (1998–2004) (source: London Water Research Group, 2007)

the significant virtual water ‘exports’ of the Sudan derive from rain-fed soil water, mainly as livestock products from Darfur and Kordofan. Potential water surpluses – that is soil water surpluses – are in the south and not in the North. Adaptive capacity, however, is currently much stronger in Egypt than in the rest of the basin. Egypt has also diversified its irrigation sector by industrialising production of high value vegetables and fruits in its West Delta Project. During and since the 1990s this Egyptian private sector initiative has utilized groundwater to produce high value crops for export to Europe and the Middle East. As predicted the groundwater has been over-pumped and the venture needs Nile freshwater which has to be pumped up from the delta 'The proposed project will assist the Ministry of Water Resources and Irrigation (MWRI) to implement reforms for financial sustainability of irrigation infrastructure and for greater efficiency in the use of water resources and their conservation. The proposed project aims to achieve this by introducing full-cost recovery policies premised on a volumetric water usage charge with the expansion of surface water irrigation infrastructure to West Delta Area (project area); and to substantially involve key farmer stakeholders and the private sector in important aspects of system design and finance, construction and management through an appropriate sharing of the related risks with Government' (World Bank, 2006). The West Delta project with its hydrological, environmental and investment dilemmas faced by the Egyptian Government and its international backers highlights the predicament of Egypt. The West Delta Project makes sense in terms of export income, job creation and the high returns to water from industrialised farming. But it makes little sense from the point of view of the impacts on the already impaired delta water environment and relations over water with upstream partners who are being denied the option to develop their Nile freshwater resources.

Egypt has become dependent for its water security on the global trading system to a much greater extent than any of the other riparians. As Egypt's population grows its future water requirements will increasingly be met through its capacity to import food and the virtual water associated with such trade. Egypt's agricultural production could increase but not significantly.

5 Asymmetric Power Relations and Their Impact on Basin Water Agreements

The hydropolitics of the Nile are also extremely asymmetric. These asymmetric power relations have not mattered until the late twentieth century. Until then the demands on the water resources by the riparians were not beyond the capacities of the Nile Basin water resources – freshwater, groundwater and soil water. These water resources were sufficient to meet the needs of the populations of the mid-twentieth century. The population of the Basin has trebled since that time and continues to expand.

As a result the freshwater resources of the Basin are effectively closed. There is no freshwater to re-allocate. The downstream riparians – Egypt and the Sudan – have laid claim to 100% of the flows from both Ethiopia and from the East Africa highlands. They expressed their assumed entitlement to the total flow in the arrangements of the 1959 Nile Waters Agreement, which allocated 75% to the flow to Egypt and 25% to the Sudan. The assumption was in principle the same as that of the British-sponsored 1929 Nile Waters Agreement. In 1929 96% of flow was allocated to Egypt and 4% to the Sudan. The flow that could be managed with the limited infrastructures in place in 1929 was, however, less than half the flow that could be controlled and managed after 1959 with the High Dam at Aswan. The dam was operational from 1970. The 1959 agreement allocated 55.5 billion cubic metres per year to Egypt and 18.5 to the Sudan. It was estimated that ten billion cubic metres of water would be evaporated and leaked annually from Lake Nasser/Nubia out of the total long term assumed flow of 84 billion cubic meters per year. When the British were exerting colonial influence across almost all of the Basin – except Ethiopia – in the late nineteenth century and until the mid-twentieth century they were just as protective of the freshwater flows of the Nile to downstream Egypt and the Sudan. During this period British influence and imperial capacity established the practice that Egyptian engineers could monitor the flows of the Nile upstream in the Sudan and at Lake Victoria in Uganda.

Transboundary water flows are easily politicized. The natural flows of freshwater, unlike most groundwater and all soil water, can be re-allocated. Politics can be defined as the process that brings about the allocation of resources. Who gets, what when and how (Lasswell, 1956). The users who first need to use the natural flows capture the resource and assume henceforth that they have prior-rights to the utilisation of the water. Groundwaters can be transboundary but they are rarely politicized and never to date as much as freshwater flows have been in the Nile case. In other basins such as the Jordan Basin groundwater resources are highly politicized. For example, on the West Bank (Zeitoun, 2008) and to some extent in the case of the Disi aquifer between Jordan and Saudi Arabia (Greco, 2003).

Soil water resources cannot be politicized. They cannot be pumped or moved. Unfortunately, they are as a consequence ignored by everyone. By engineers who manage water, by economists who value water, and perhaps most importantly by water policy-makers and those at the most senior levels of national government who relate to their opposite numbers over transboundary waters. It has been shown in this chapter that the soil water resources of the Nile Basin riparians vastly exceed the freshwater resources. The freshwater resources are closed. The soil water resources have been significantly utilised but the productivity is so low that it will be possible to increase the returns to soil water in the southern basin riparians (Tiffen & Mortimore, 1994; Keijne et al., 2004; Molden, 2007; Dorosh et al., 2008). This information is not yet in currency in transboundary Nile waters international relations.

6 Hydropolitics, International Water and International Water Law

> ‘Upstream states use water to gain power. Downstream states use power to gain water’ (Warner, 2008).

Egypt’s power has been sufficient to establish for half a century its downstream preference for the principle of ‘prior use’ rights (Waterbury, 1979, 2002). No upstream has used significant volumes of Nile freshwaters that would impair Egypt's definition of its water resource security. The 1959 Nile Waters Agreement between Egypt and the Sudan allocated 75% of the *total Nile flow* to Egypt and 25% to the Sudan. The other riparians have followed the letter of the 1959 agreement without accepting its principles. This outcome is only partly because of Egyptian hegemony – that is the capacity of one partner to exert its power over partners that are nominally equal. It is also because the upstream riparians lack the resources to invest in and the capacities to develop their Nile waters. Here is yet another *asymmetry*. The northern riparians have the capacity to invest. The southern economies do not. This asymmetry is exacerbated by another. Egypt enjoys pivotal relations with the World Bank and other international agencies (IFIs). The southern economies do not. The southern riparians have strong *potential* relations with pivotal international financial institutions but their current levels of engagement in no way match those of Egypt. The long process of establishing the Nile Basin Initiative (NBI) since 1992, when cooperative basin-wide engagement started, is evidence that the fundamental impediment to significant water and benefit sharing over Nile waters is Egypt's sensitivity concerning water security (Cascao, 2008a, b).

The high levels of food imports by Egypt and the way that Egypt has participated in the establishment of the Nile Basin Initiative (NBI) and especially in the NBI Framework Agreement negotiations during 2007 suggests that Nile Basin water management options are limited. The riparians are still adopting classic upstream v. downstream positions. Transboundary waters are not regulated by international water law. Customary international water law exists. Customary international water law provides some norms of international bahaviour that tend to favour those who have already captured freshwater flows early in the history of water resource development in a basin.

The ancient civilizations of the Middle East first used the waters of such rivers as the Nile five thousand years ago in their lower reaches where simple technologies could provide partial control of floods and flows. This pattern has continued until the last decades of the twentieth century with the outcome that Egypt and the Sudan feel that they have acquired rights to the water by having developed economies dependent on the Nile freshwater flows.

There are three sets of principles that a riparian can reach for in taking a position on shared transboundary waters. First, that of *sovereignty*. Secondly, that of *integrity*. Thirdly that of *equitable utilization* (McCaffrey, 2002). The first two principles contradict each other. The third is a fair and reasonable approach but defining the idea so that it can be operationalised has proved to be impossible. *Sovereignty* is a simple concept. It appeals to upstream states which are often located in highlands which attract much of the precipitation that feeds the basin hydrology. The Nile is an extreme case as there is no recharge in Egypt, nor in the northern half of the Sudan; that is for over one third of the length of the system. Upstream Ethiopia exports almost all its Nile waters and contributes 85% of the flow at Khartoum. The East African riparians contribute the rest. Half of the East African water that leaves Uganda down the White Nile evaporates as it traverses the Sudd wetlands. Upstream riparians naturally adopt the *sovereignty* principle as it argues that all the water that falls on national territory can legitimately be utilised by an upstream riparian. In practice it is only upstream riparians with power and administrative, technical and financial capacities that can, at will, utilise such water resources. The United States, China and Turkey are examples of riparians that have been able to apply the principle of sovereignty.

The principle of *integrity* appeals to downstream riparians. It argues that prior utilization brings with it the entitlement to claim and use such flows in the future. This principle can be imposed by powerful downstream riparians such as Egypt and midstream riparians such as South Africa, India and Israel. In the Nile Basin Egypt has captured the surface flows of the Nile Basin and is reluctant to relinquish them. The evidence is the way that Egypt has participated in the establishment of the Nile Basin Initiative and especially in its unwillingness to agree the NBI Framework Agreement negotiated, but not agreed or ratified, during 2007. Egypt and the Sudan would not agree the article, which as far as they were concerned compromised their water security. They interpret their water security to be 100% of the freshwater resources of the Nile system.

The contradiction of sovereignty and integrity has been addressed by the UN International Law Commission. In the deliberations of the Commission since the early 1970s it was recognised that sovereignty and integrity were incompatible. Building on a long established principle of *equitable use* introduced into the 1896–1906 US-Mexico negotiations over the Rio Grande (McCaffrey, 2002) and the notion of equitable utilisation developed by the International Law Association (ILA, 1966) the principle of *equitable utilisation* has become the central organizing idea for future transboundary waters agreements. Unfortunately, equitable utilisation is very difficult indeed to operationalise and as a consequence the dominant riparian can easily ignore it and refuse to take it into account when engaged in negotiations. Hegemon riparians such as Egypt, Israel and India as downstream or mid-stream riparians have not recognised the 1997 UN Convention. Nor have the dominant upstream riparians – China and Turkey. ‘Upstream states use water to gain power. Downstream states use power to gain water’ (Warner, 2005). This insightful aphorism confirms another: ‘Water flows uphill to money and power’ (Reisner, 1984).

Power asymmetry is the most important of all the asymmetries identified in this analysis. Egypt does not have a monopoly of *hard power*. It does not need hard power which is in any event the least effective face of power (Lukes, 1974; Zeitoun, 2008). Egypt does have substantial *soft power*. One type of soft power is *bargaining power* – that is it can assert its interests to great effect. For example it has not agreed the key Article 39 of the draft 2007 NBI Framework Agreement as it would impair its continued assertion that it is entitled to 75% of the Nile flow. This delay is just a small increment in a process of delays in addressing the issue of re-allocation of Nile water. This tactic has been in place for decades and has been a low profile element in the Egyptian negotiating strategy since the inception of the Nile Basin 2002 process in 1992 and also during the process of establishing the Nile Basin Initiative since 1997. Such power is most effective in what is known as *ideational power*. Those who possess this type of power can set the agenda that determines what is accepted and even believed by other parties. Those with ideational power achieve their ends partly by knowing more than other participants and partly by having close relations with third parties – such as the International Financial Institutions (IFIs) that can finance the infrastructures in upstream states. In all these capacities Egypt is powerful and the other riparians are not. So powerful is Egypt that the strong commitment of the World Bank to reduce poverty in the upstream riparians by assisting them to install water infrastructures of all types has been successfully resisted.

7 Concluding Comments

Those managing Nile waters face extremely challenging water environments. The main purpose of the chapter has been to show that many asymmetries make ecological and economical sound and equitable utilization of the basin's waters – surface freshwater, groundwaters and soil waters – very difficult indeed. Surface waters are effectively closed to further major development without a new framework agreement enabling upstream surface water utilisation and the implied re-allocation that must accompany such new initiatives.

The asymmetries are environmental, economic, developmental and political. They concern water itself but mainly socio-economic capacity and power. And the most important of these is power. It has been shown that there are extreme asymmetries in water resource endowments, in the adaptive capacities to deal with differing endowments and in the capacity to establish the terms of engagement over water resources in the basin. The southern riparians enjoy relatively favourable rainfall regimes and as a consequence they have substantial surface freshwater resources. More importantly they have substantial soil water resources, which enable rainfed crop production. The soil water is important for the southern riparians as they export almost all their Nile surface waters. It has been shown that the asymmetries in levels of socio-economic development, in demographic trends, in adaptive capacity and the ability to set the terms of engagement are inter-related and pivotal. The ways that Nile freshwater flows are allocated are explained by these asymmetries as are the relative levels of development of the individual riparians.

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Human Impact on the Nile Basin: Past, Present, Future

Martin A.J. Williams

Abstract The gradual spread of plant and animal domestication throughout the Nile valley was associated with widespread deforestation, accelerated soil erosion and an exponential increase in the human population. The climate in the Nile basin during the first half of the Holocene was wetter than today. The advent of drier conditions began about 5,000 years ago and further accelerated the land degradation resulting from the spread of agriculture into the upland headwaters of the Blue and White Nile. A severe drought 4,200 years ago is evident in the strontium isotopic records from Lake Albert in Uganda as well as the Nile delta, and was associated with famine and severe social distress during Old Kingdom times. Deforestation in the Ethiopian highlands has led to accelerated soil loss from the Ethiopian headwaters of the Blue Nile/Abbai and Atbara/Tekezze rivers, with concomitant rapid rates of sedimentation in reservoirs downstream. By 1996, the capacity of the Roseires reservoir on the Blue Nile had been reduced by almost 60% through silt accumulation and that of the Khasm el Girba reservoir on the Atbara by nearly 40%. Historic fluctuations in Nile flood levels are in part related to El Niño Southern Oscillation (ENSO) events, with years of low flow often synchronous with years when the Southern Oscillation Index (SOI) is strongly negative. (The SOI is a measure of the surface atmospheric pressure difference between Darwin and Tahiti). Since over 300 million people will depend upon the waters of the Nile for their livelihood by the year 2020, a clear understanding of present land use and Nile flood history is essential for future planning.

1 Introduction

By the year 2020 over 300 million people will depend upon the waters of the Nile for their livelihood, so that a clear understanding of present land use and Nile flood history is essential for future planning (Hassan, 1981; Conway & Hulme, 1993;

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Fraedrich et al., 1997; De Putter et al., 1998; Ayoub, 1999; Schumm, 2007, pp. 518–521; Wolman & Giegengack, 2007; Woodward et al., 2007). The lower Nile valley was one of the cradles of urban civilisation, totally dependent on floods from the upper Nile, just as Egypt is today. This great civilisation was based upon sedentary agriculture and a complex social structure (Said, 1997), in strong contrast to the hunter-gatherer communities of the Later Stone Age who occupied the Nile valley before the advent of Neolithic farming some 8,000 and more years ago (Arkell, 1949, 1953; Adamson et al., 1974; Clark, 1989). An interesting question is how these prehistoric communities might have interacted with the ever changing environments in the Nile basin, and what light this might shed upon present-day and possible future impacts.

2 The Neolithic Revolution

With the advent of forest clearing from Neolithic times onwards, and the exponential increase in the human population as a result of plant and animal domestication (Williams et al., 1998, pp. 239–241), there is widespread evidence of accelerated soil erosion in many parts of North Africa (Williams, 1988), including the Nile basin. One point to be borne in mind is that an impressive body of well dated evidence shows that the climate in the Nile basin and the adjacent Sahara during the Later Stone Age and early Neolithic was, in general, far wetter than today (Williams et al., 1974; Ritchie et al., 1985; Pachur & Kröpelin, 1987; Haynes et al., 1989; Pachur & Hoelzmann, 1991; Ayliffe et al., 1996; Gasse, 2000; Haynes, 2001; Nicoll, 2001, 2003; Schild & Wendorf, 2001; Hoelzmann et al., 2004; Jousse, 2004; Linstädter & Kröpelin, 2004; Smith et al., 2004; Kuper & Kröpelin, 2006; Kröpelin et al., 2008). It is also worth stressing that the later Neolithic and its associated clearing of woodland for agricultural purposes coincided with the progressive desiccation which followed nearly 10,000 years of higher rainfall over much of North Africa. The past 4,000–5,000 years were thus a time when human impact aggravated and accelerated the effects of the processes of desertification that were already in train. One particular extreme drought took place about 4,200 years ago and is evident in the strontium isotopic record in the Ugandan headwaters of the Nile (Williams et al., 2006) as well as in the Nile delta 7,000 km downstream (Stanley et al., 2003) and caused severe social distress in Old Kingdom times in Egypt and further afield.

3 Deforestation

In the Ethiopian headwaters of the Blue Nile and Atbara/Tekazze rivers, the long-term rate of erosion in the forested highlands amounts to 10–15 m/Ma when averaged over the past 30 million years (McDougall et al., 1975; Talbot & Williams, this volume). The present rate is one to two orders of magnitude higher

(Hurni, 1999; Williams, 2000). A similar bleak picture is also true of the once densely forested uplands of Uganda, which have been extensively cleared for agriculture, construction and fuel, including charcoal burning. Indeed, land use change may now outweigh climate as a geomorphic agent in the more elevated parts of the Nile basin, especially the Ethiopian and Eritrean uplands (Nyssen et al., 2004).

Nevertheless, year-to-year variations in precipitation, and intermittent prolonged droughts, continue to exert a major influence upon plants, animals and human societies in the drier portions of the basin (Williams, 2003a, b). Seventeen years of monitoring vegetation cover along the southern margins of the Sahara using satellite imagery revealed considerable variation from year to year in response to annual variations in rainfall (Tucker & Nicholson, 1999). An earlier study by Tucker et al. (1991) extending from 1980 to 1990 concluded that at least 10 years of observations were needed to detect any possible trends in the vegetation cover in this region.

4 The Role of ENSO

We now recognise the role of El Niño Southern Oscillation (ENSO) events and of regional anomalies in sea surface temperature in controlling the incidence of major floods and droughts in widely scattered parts of the world (Adamson et al., 1987; Williams & Balling, 1996; Camberlin et al., 2001; Mo et al., 2001; Mo & Häkkinen, 2001; Giannini et al., 2003), including the Nile basin (Osman & Hastenrath, 1969; Whetton & Rutherfurd, 1994; Camberlin, 1997; Wang & Eltahir, 1999; Nicholson & Selato, 2000; Whetton et al., 2000; Osman & Shamseldin, 2002; Bergonzini et al., 2004).

Sir Gilbert Walker defined the Southern Oscillation in 1924 (Walker, 1924). The Southern Oscillation Index (SOI) is a measure of the surface atmospheric pressure difference between Darwin and Tahiti and, as noted above, is widely used today in predicting wet and dry years. Time series analysis shows a statistically significant correlation between years of low Nile flow, drought in Indonesia and years of weak summer monsoon rainfall in India and eastern China (Whetton et al., 1990; Whetton & Rutherfurd, 1994; Whitaker et al., 2001). The converse is equally true, with years of extreme flooding synchronous in each of these regions. Short periods of exceptionally heavy rainfall and flooding in the central Sudan (Hulme & Trilsbach, 1989; Davies & Walsh, 1997; Williams & Nottage, 2006) are often broadly synchronous with extreme downpours in regions outside the Nile basin, including Somalia and Inner Mongolia, as noted by Williams and Nottage (2006). On 16 August 1999, Khartoum received as much rain in 6 hours as it normally received in the entire year. In fact, the extreme rain that fell in only a few days in August 1999 filled the depressions between the dunes in the northern Gezira and created the tropical rain-pools so well described almost half a century ago by Julian Rzóska (1961). This extreme event also re-created the type of landscape familiar to the hunter-gatherer-fishing folk of the Early Khartoum Tradition (Williams & Nottage, 2006).

5 Erosion

Despite earlier claims to the contrary, overgrazing was not responsible for the prolonged drought that began in the Sahel region of western Africa and in the Sudan in 1968 (Williams, 1995, 2000, 2002; Williams & Balling, 1995; Zeng, 2003). However, drought can lead to local overgrazing which can in turn accelerate soil erosion by wind and water and re-activate previously stable vegetated dunes. The southern margins of the Sahara, including Kordofan Province west of the White Nile, are covered in sand dunes that have remained vegetated and relatively stable for the last 10,000 years. Recent severe droughts combined with tree clearing and over-stocking have led to remobilisation of the once stable desert dunes in this region. Aubréville (1949) documented the replacement of tropical African rainforest by secondary savanna and scrub as a result of tree clearing and burning associated with shifting cultivation and coined the term desertification to encapsulate this process. He concluded that humanly induced deserts were forming in Africa in areas receiving 750–1,500 mm of rain a year.

Removal of forest in tropical uplands can alter the local hydrological balance through increased runoff and reduced infiltration. Accelerated loss of soil from highland catchments can lead to sedimentation in reservoirs far downstream and not always within the same country. By 1996, the capacity of the Roseires reservoir on the Blue Nile had been reduced by almost 60% through silt accumulation and that of the Khasm el Girba reservoir on the Atbara by nearly 40% (Swain, 1997). The silt was from the Ethiopian highlands. Hurni (1999) has monitored accelerated soil erosion in the Ethiopian uplands. In one region in Gojjam Province the area cultivated increased from 40% in 1957 to 77% in 1995, while the area under natural forest decreased from 27% to 0.3%. Annual rates of soil loss amount to about 2 mm/a) on mountain slopes, but attain rates of over 15 mm/a during cultivation years, or some 5–10 times more than in non-mountainous areas (Hurni, 1999). However, as Nyssen et al. (2004) point out so clearly, deforestation in the Ethiopian highlands during the last several thousand years has not been a linear process, with intervals of forest regrowth alternating with periods of forest removal, a view endorsed by Williams (2003b, pp. 38–41), who also noted that gully erosion in Ethiopia was sometimes triggered by earthquake activity and had nothing to do with human impact (Williams, 2003b, pp. 41–45).

6 Salt Accumulation

Further examples of adverse human impacts upon landscapes in the Nile basin include the progressive accumulation of salt in agricultural soils as a result of clearing of the native vegetation, poor canal maintenance and inadequate soil drainage. Salt accumulation is now a major problem in parts of Egypt irrigated from the main Nile and in sporadic patches along the White Nile (Williams, 1968; Williams et al., 1982). Fortunately for the peasant farmers of the Gezira irrigation area watered from the Blue Nile, both the water and the sediments from the Blue Nile are non-saline, so that the long-term prospects for farming on soils derived from Blue Nile – by far the majority, as noted by Tothill (1946) as long ago as 1946 – are reassuring.

This latter point brings us to the issue of sustainable land use in the Nile basin. As a broad generalisation, sustainable use of all natural resources depends upon two key principles or prerequisites (Robèrt, 1992; Williams, 1999, 2000, 2003). First, materials should not systematically be removed from any natural or humanly modified system, at a rate faster than the capacity of that system to produce a surplus. Second, materials should not systematically be added to any natural or humanly modified system at a rate faster than the capacity of the system to absorb and recycle such materials. Accelerated soil erosion breaches the first condition; excessive use of fertilizer, pesticide or herbicide breaches the second condition. On planet earth the only source of any *net increase* in primary productivity is through photosynthesis. All else is simply recycling what is already present on earth. Hence, great care must be taken to avoid undue deforestation and removal of the plant cover.

7 Conclusion

With a world population in excess of 6.5 billion, and an exponential increase in greenhouse gases, it is highly probable that current global warming trends are primarily anthropogenic (Menon et al., 2002; Meehl & Tebaldi, 2004). Among predicted outcomes are more extreme rainfall events and an increase in tropical summer rainfall, and an increase in the magnitude and frequency of droughts in semi-arid areas. The geomorphic consequences are likely to be greater runoff and sediment yield from tropical rivers. The interactions between land, ice, ocean, atmosphere and biosphere are complex and involve lags, thresholds and feedback processes, both positive and negative. It is possible that dust mobilisation from the southern margins of the Sahara may be both a cause and a consequence of drought in the Sahel region of Africa (Prospero & Lamb, 2003; Zeng, 2003).

The frequency of El Niño events has decreased during the last 1,400 years (Moy et al., 2002), but we do not know what influence the general increase in global sea surface temperatures will have upon the magnitude and frequency of future El Niño events. In the Sudan – the largest country in the Nile basin and Africa – the distribution of tree species is closely allied to rainfall and soil type (Smith, 1949), so that any future changes in precipitation, if sustained, will have an as yet unforeseen effect upon animal habitats and human land use. It is too soon to argue that the severe drought that afflicted much of the Nile basin from 1968 onwards is linked to anthropogenic influences on climate, since there were, after all, prolonged historic droughts in East Africa (Verschuren et al., 2000) before the Industrial Revolution and its associated emissions of carbon dioxide, methane and nitrous oxides. However, we are entering uncertain times, where forecasting the impacts of future change is not easy. It is, for example, hard to predict the climatic consequences of the albedo changes linked to the decrease in polar ice, since the response may be non-linear. Human societies will need to learn to live with uncertainty in a time of rapid environmental change, just as our ancestors did in the past.

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Color Plates

Fig. 2.1 Dissimilar river sectors down the Nile: (**a**) savanna, southern Sudan; (**b**) floodplain swamps ('Sudd') (**c**) desert cataract (from Talling, 2006, with permission of the Freshwater Biological Association, Windermere)

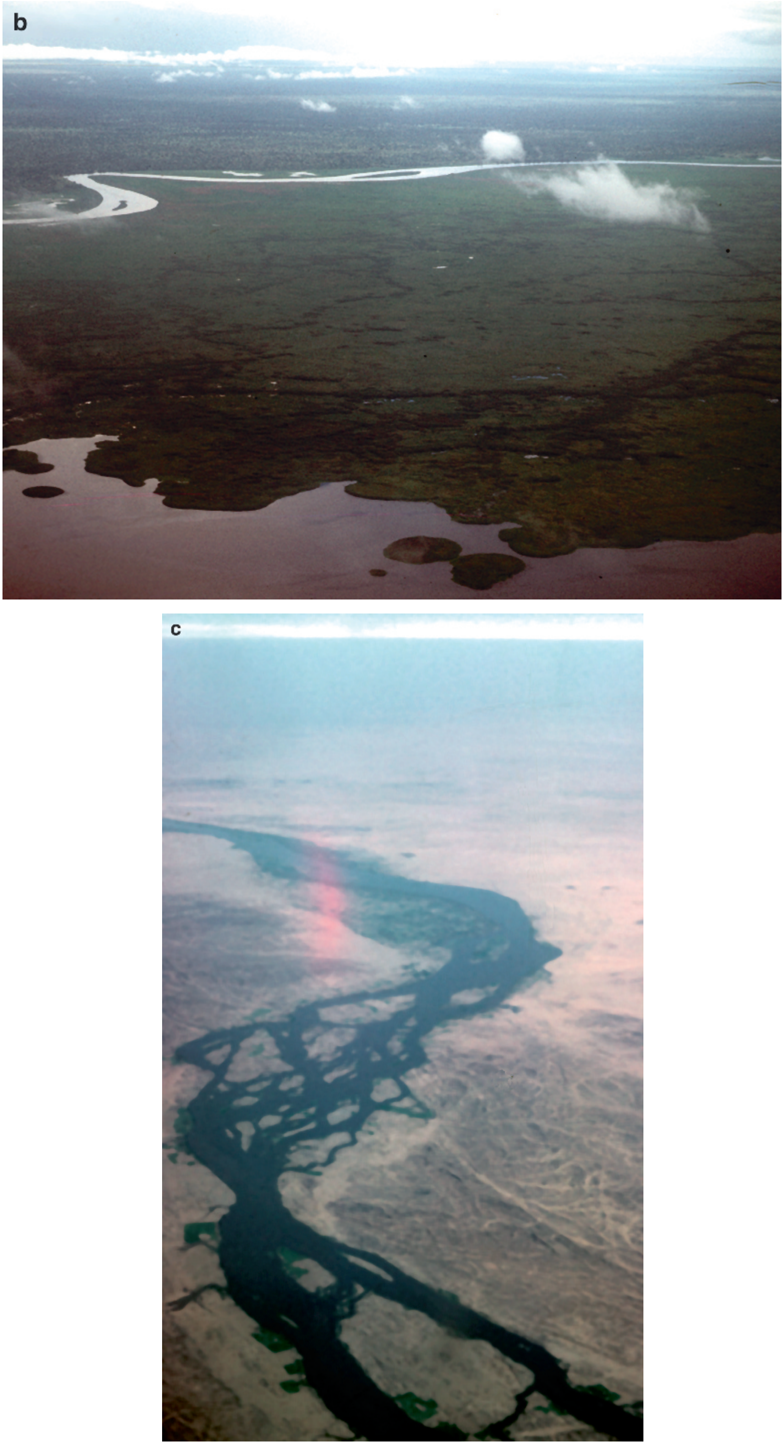

Fig. 2.1 (continued)

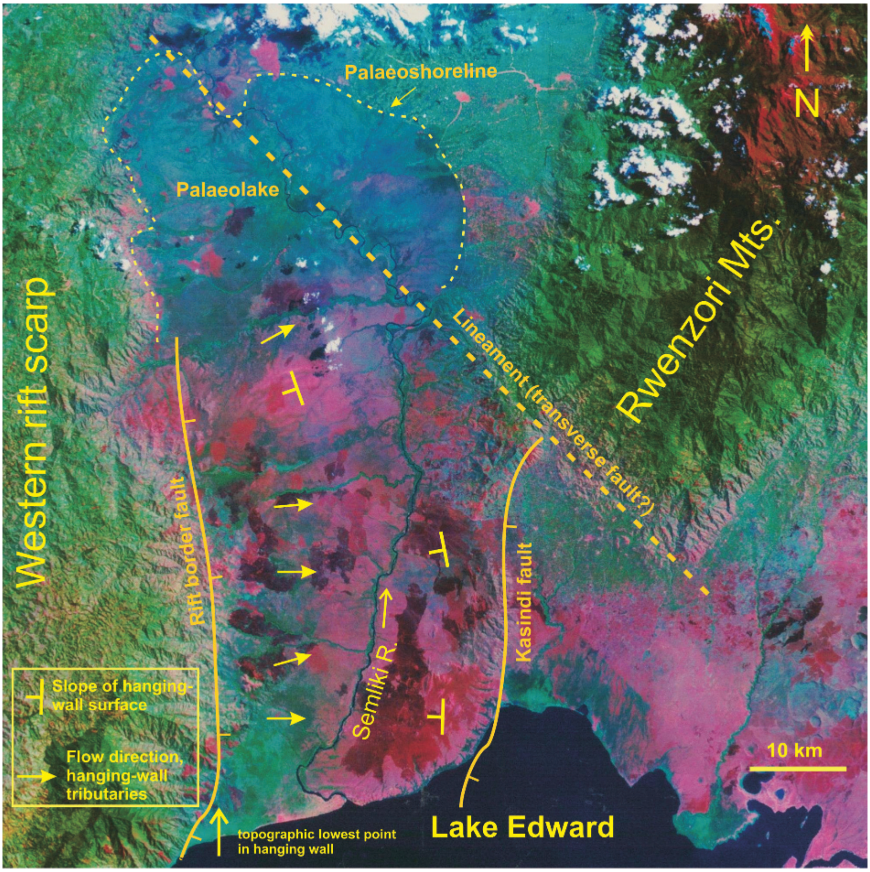

Fig. 3.5 Satellite image of the northern shore of Lake Edward and the upper Semliki valley. The proximal Semliki is incised into the hanging wall to the main rift-boundary fault. Evidence of recent rotation of the fault block is provided by the incised antecedent drainage from the western rift scarp. Further downstream there is geomorphological evidence of a palaeolake that formed between the northern edge of the hanging-wall fault block and the southern margin of a topographic high related to a rift transfer zone (satellite image courtesy of Amoco Norway)

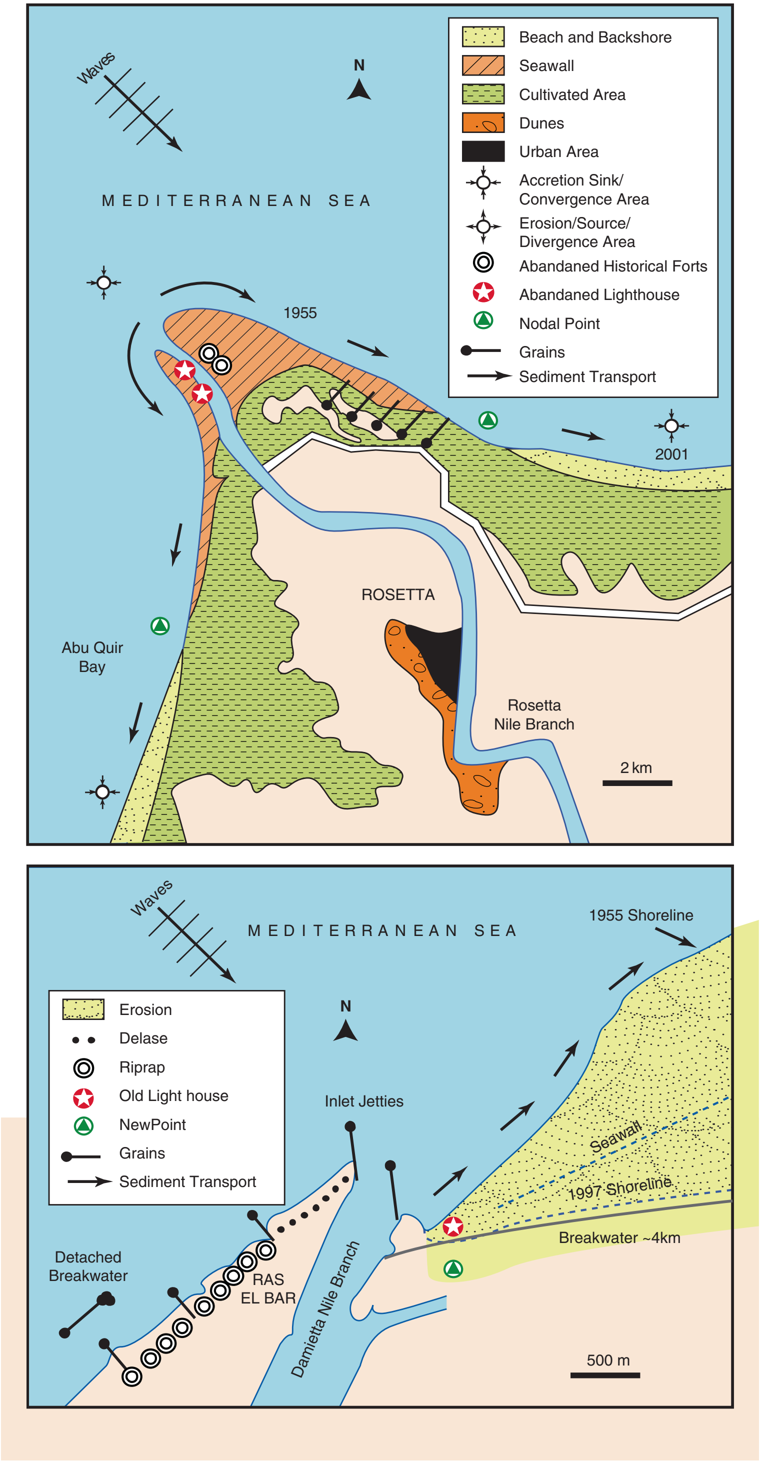

Fig. 5.3 Erosion and accretion features of the Rosetta (*upper*) and Damietta (*lower*) promontories and the developed protective measures (modified from Frihy et al., 1998 and 2001)

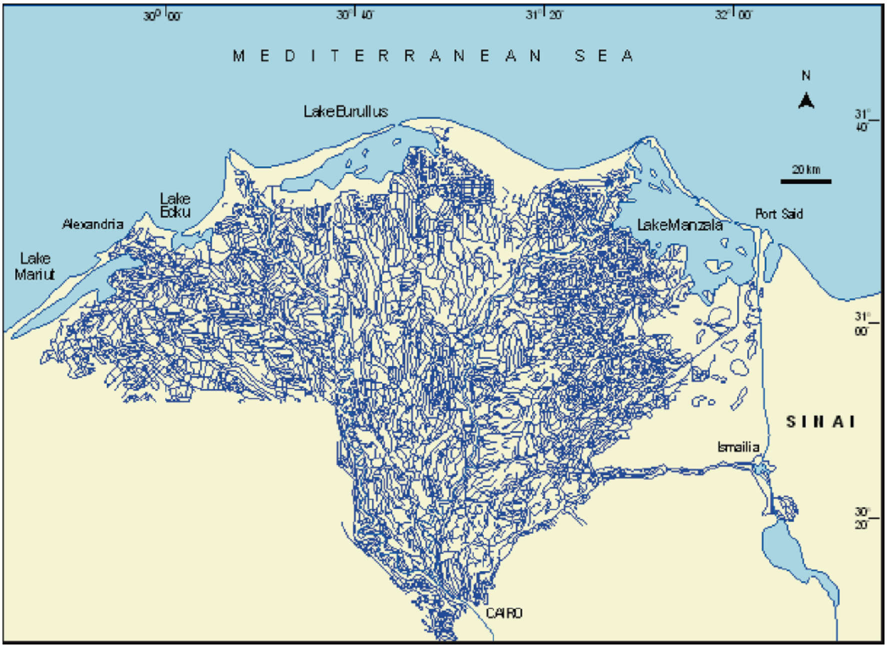

Fig. 5.5 Map showing >10,000 km of irrigation canals and drains forming the extensive waterway system in the Nile Delta (modified from Stanley, 1996)

Fig. 5.6 Eutrophication of Alexandria coast by sewage discharge from Lake Mariut (after Halim & Abu-Shouk, 2000)

Fig. 9.6 The high (40 m) Tissisat Falls ('The smoking waters falls'), 30 km downstream from the Blue Nile outflow. The falls effectively isolate the lake's fish community from the lower Nile basin. During the rainy season the waterfall is 400 m wide and is the second largest of Africa (photo by F.A. Sibbing)

Fig. 9.7 A large *Labeobarbus megastoma* caught by commercial fishermen (photo by F.A. Sibbing)

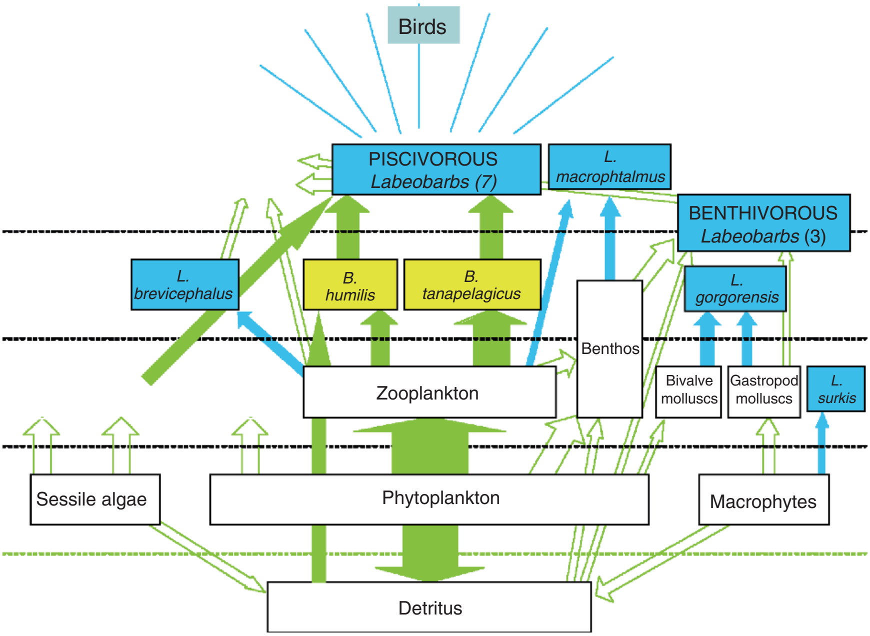

Fig. 9.8 Food web of L. Tana with emphasis on the fish community. Grey blocks represent fish species, white blocks food resources. Grey arrows indicate the systems main streams through zooplankton and benthos. Width of arrows reflects the contribution of a food type in the diet of a species. For benthivorous and piscivorous labeobarbs, number of species between brackets

Fig. 9.9 The ‘clumsy’ piscivorous labeobarbs of Lake Tana, showing lack of teeth on oral jaws and a narrow pharyngeal slit (*Labeobarbus megastoma*, photo by F.A. Sibbing)

Fig. 9.10 A traditional fisherman of L. Tana using a papyrus reed boat (tankwa) and a fish trap made from reeds (photo by F.A. Sibbing)

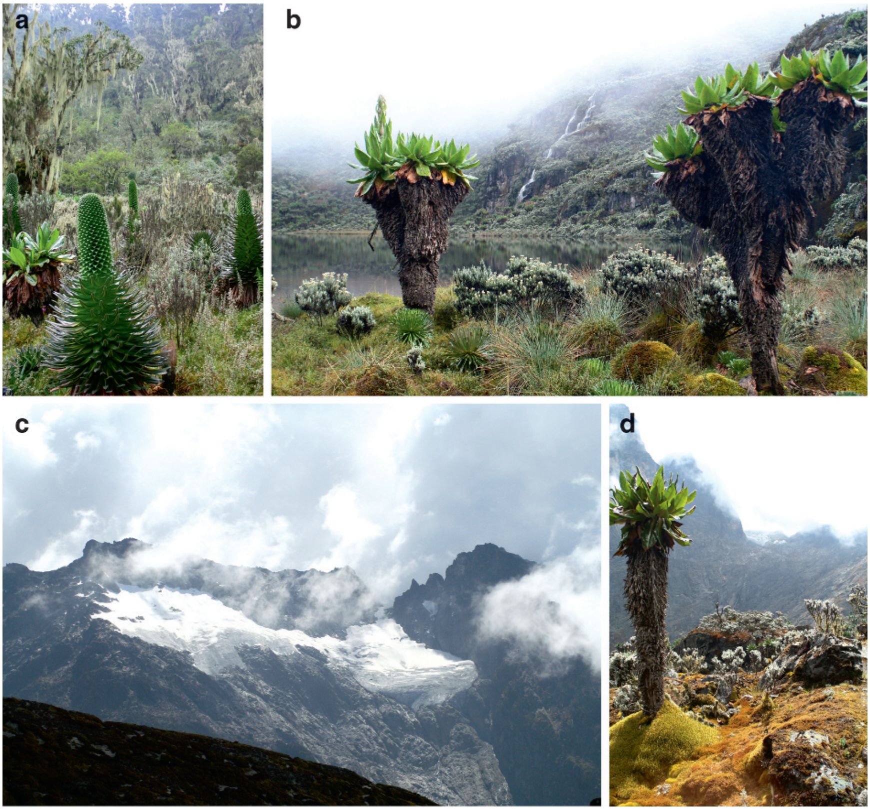

Fig. 13.2 Scenery and vegetation cover in the Rwenzori Mountains: (**a**) Ericaceous vegetation mixed with tree groundsel (*Senecio*) and *Lobelia* (Mutinda valley). (**b**) View on Lake Batoda, surrounded by tree groundsels, *Carex runssoroensis* tussocks and *Helichrysum stuhlmannii* (everlasting flowers) scrub. (**c**) Glacial retreat on Mt. Speke (picture taken from Lake Irene at 4,487 m elevation, July 2006). (**d**) Transition between Alpine and Nival zone, with tree groundsel and *Rhacocarpus humboldtii* forming bright orange carpets (photographs by H. Eggermont)

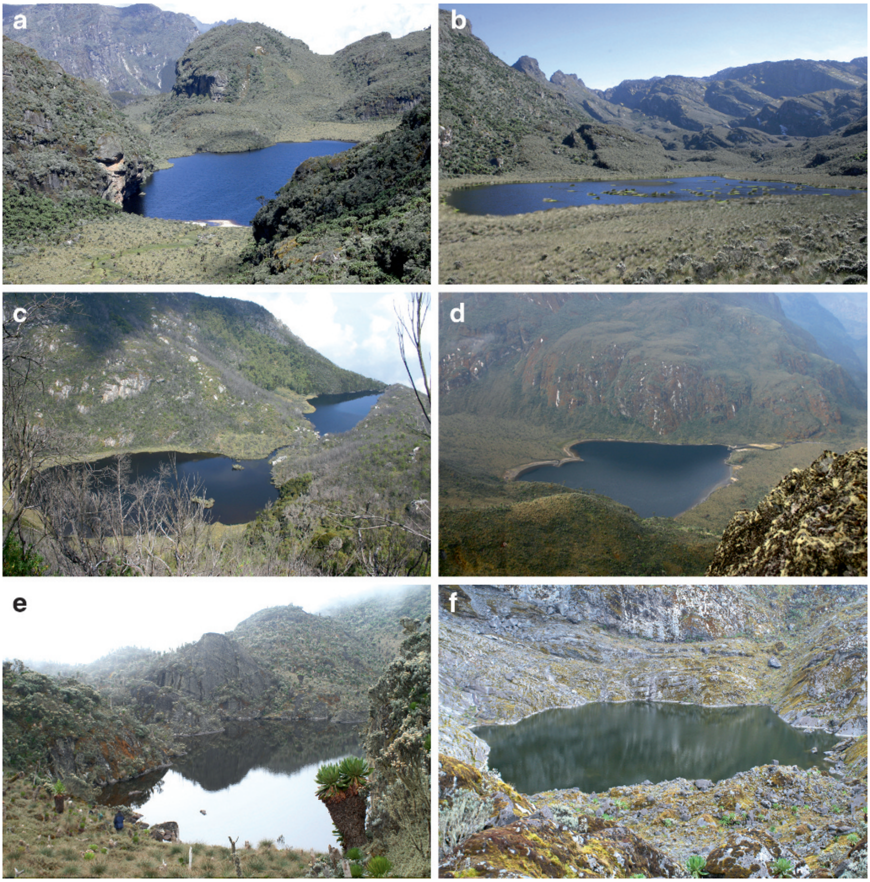

Fig. 13.3 Images of selected Rwenzori mountain lakes on the Ugandan side of the range: (**a**) Lake Batoda at 4,017 m asl in the Batoda valley. Tree groundsel forest covers most of the slopes, and *Carex runssoroensis* tussocks most of the bog surface. (**b**) Lake Bigata at 4,010 m asl in the Nyamugasani valley. The lake is surrounded by *C. runssoroensis* tussocks and *Helichrysum stuhlmannii* (everlasting flowers) scrub. Floating islands of tussocks dot the lake surface. (**c**) Middle (*left*) and Lower Kachope (*right*) at 3,840 m asl in the tributary valley of the Butawu. The slopes are covered with tree heathers, tangled undergrowth and scattered tree groundsel. Part of the vegetation is burned, likely caused by armed conflict in the area. (**d**) Lake Bujuku at 3,849 m asl in the Bujuku valley, with tree groundsel and *C. runssoroensis* covering the catchment. Streams from Speke glacier and former East Stanley Glacier have built a delta into the lake. (**e**) Lac du Speke at 3,822 m in the Luusilubi valley (DR Congo), surrounded by steep rocky cliffs and tree groundsel forest. (**f**) Lake Ruhandika at 4,341 m asl, where the terminus of the Speke glacier stood in the 1950s. Since then, the glacier has retreated about 600 m and greatly thinned, leaving this small lake in front of it. The lake is surrounded by bare rock, moss, liverworts and lichens (photographs by H. Eggermont)

Fig. 22.1 Dense growth of *Cyperus papyrus* on the bank of Damietta Branch, River Nile, Egypt

Fig. 23.2 (**a**) and (**b**) Two typical aerial views of the Sudd, with the Bahr El Jebel meandering through several swampy Lakes. The reeds *Typha*, Papyrus and *Phragmites* occupy the wetlands. The big lake is inhabited by floating, submerged and floating-leaved hydrophytes. In the foreground of Fig. 1b, woody trees occupy the relatively higher ground

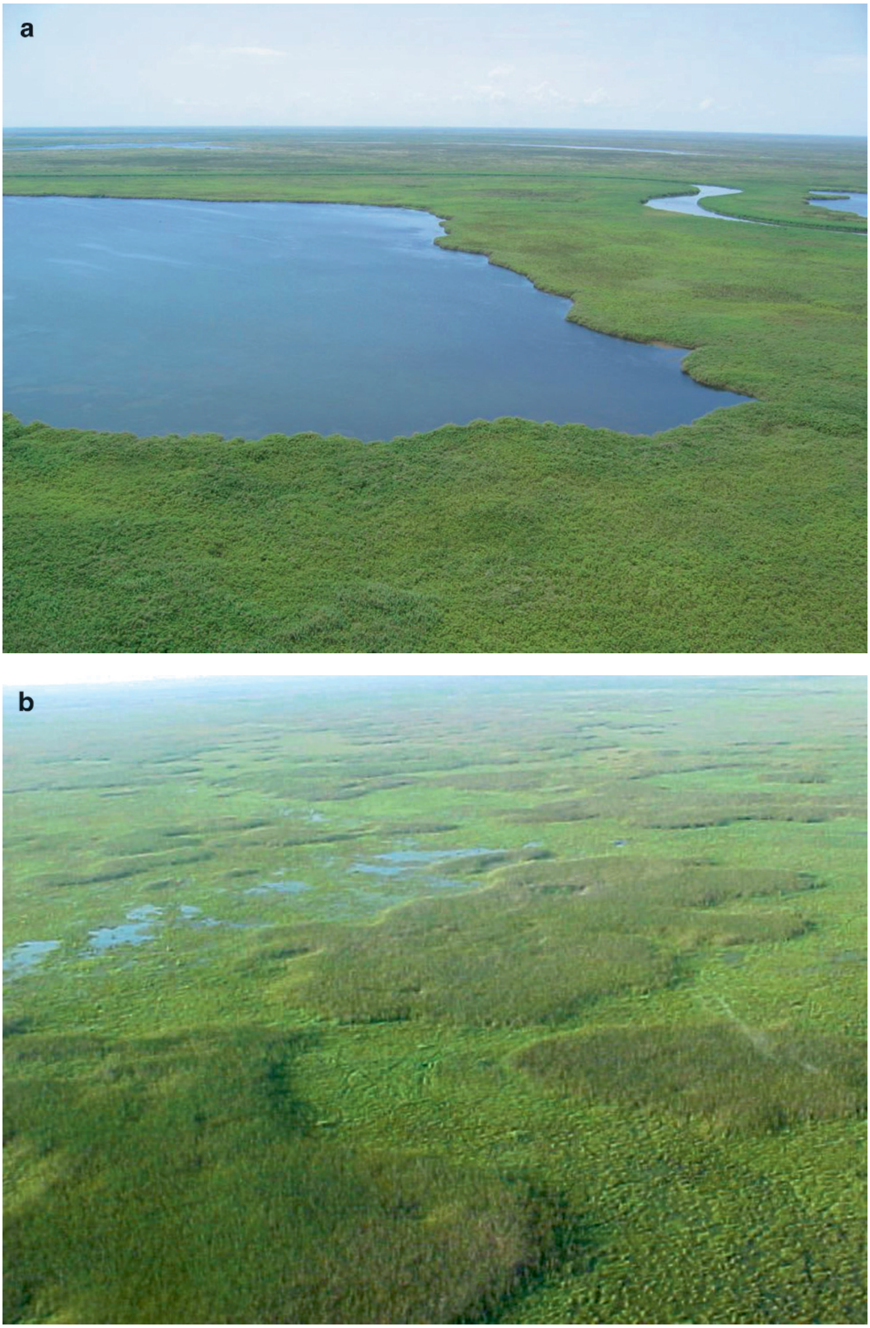

Fig. 23.3 (**a**) and (**b**) Vast swamps in the Sudd region occupied by *Typha domingensis* (*dark patches*) and *Cyperus papyrus* (*lighter green patches*). (**a**) Shows a large Sudd lake with the Bahr El Jebel in the background

Fig. 23.5 *Suddia sagitifolia*, the single higher plant presumed endemic of the Sudd swamps

Fig. 30.2 Massive eclosions of *Chaoborus* in the Great Lakes of Eastern Africa sometimes give the impression of smoke stacks (*top*) emerging from the lake water. When the swarms come on land to mate, they are actively chased by the local population and consumed fresh (*bottom*) (original pictures by H. J. Dumont)

Fig. 30.3 The two suborders of dragonflies. *Pseudagrion kersteni*, a zygopteran (*above*); *Trithemis furva*, an anisopteran (*below*). Both are Afrotropical species, but relicts exist in Yemen and in Jebel Marra, Darfur, Western Sudan, where these photographs were taken in 1985 (original pictures by H. J. Dumont)

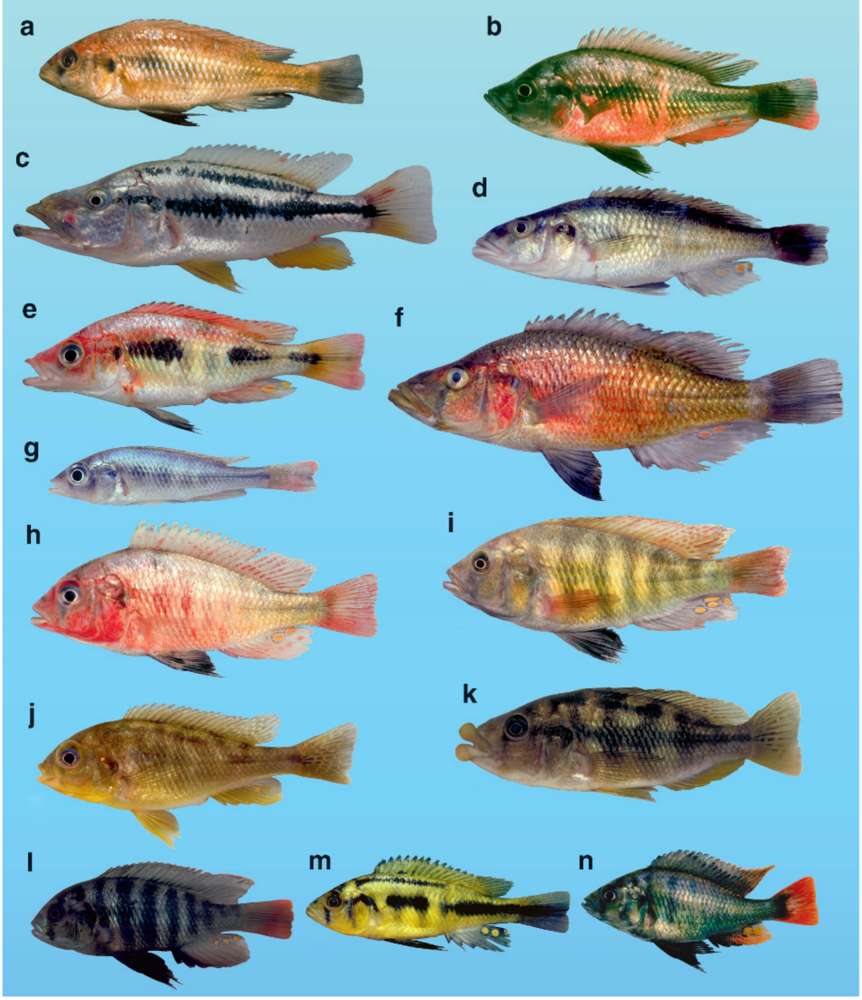

Fig. 31.5 Representatives of Lake Victoria haplochromine cichlids: (**a**) *H.* (*?*) *teunisrasi* (parasite eater); (**b**) *H.* (*Lipochromis*) *microdon* (paedophage); (**c**) *H.* (*Prognathochromis*) *macrognathus* (piscivore); (**d**) *H.* (*P.*) "dentex like" (piscivore); (**e**) *H.* (*P.*) "erythrocryptogramma" (prawn eater); (**f**) *H.* (*P.*) *argenteus* (piscivore); (**g**) *H.* (?) "argens" (zooplanktivore); (**h**) *H.* (*Labrochromis*) *teegelaari* (pharyngeal mollusc crusher); (**i**) *H.* (*Labrochromis*) *ishmaeli* (pharyngeal mollusc crusher); (**j**) *H.* (*Ptyochromis*) *sauvagei* (oral mollusc sheller); (**k**) *H.* (*Paralabidochromis*) *chilotes* (insectivore); (**l**) *H.* (*Neochromis*) *rufocaudalis* (algae grazer); (**m**) *H.* (*?*) "citrus" (phytoplanktivore); (**n**) *H.* (*Enterochromis*) "75" (detritivore/phytoplanktivore)

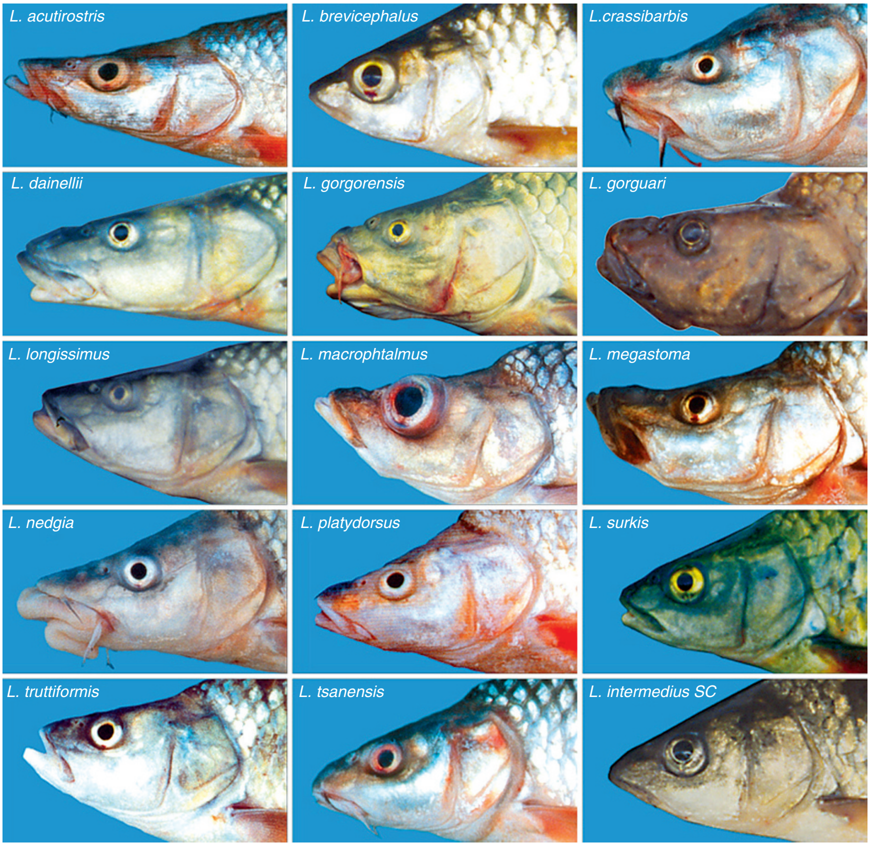

Fig. 31.7 Representatives of *Labeobarbus* species from Lake Tana. Obligatory piscivores (>80% fish): *L. acutirostris*, *L. truttiformis*, *L. longissimus*, *L. dainellii*, *L. megastoma*; facultative piscivores (>60% fish): *L. gorguari*, *L. platydorsus*; herbivores/molluscivores/detritivores: *L. surkis*, *L. gorgorensis*; polyphagous barbs: *L. brevicephalus*, *L. macrophthalmus*; benthivores: *L. nedgia*, *L. tsanensis*, *L. crassibarbis*, *L. intermedius* shore complex

Fig. 34.1 Fisheries on Lake Victoria. (**a**) Local traps near papyrus. (**b**) Beach seine fishery. (**c**) *Rastrineobola argentea* caught with light and encircling nets operated from catamarans (at the back). (**d**) Bottom trawler fishing haplochromines for fishmeal factory. (**e**) Nile perch smoking. (Photos by F. Witte)

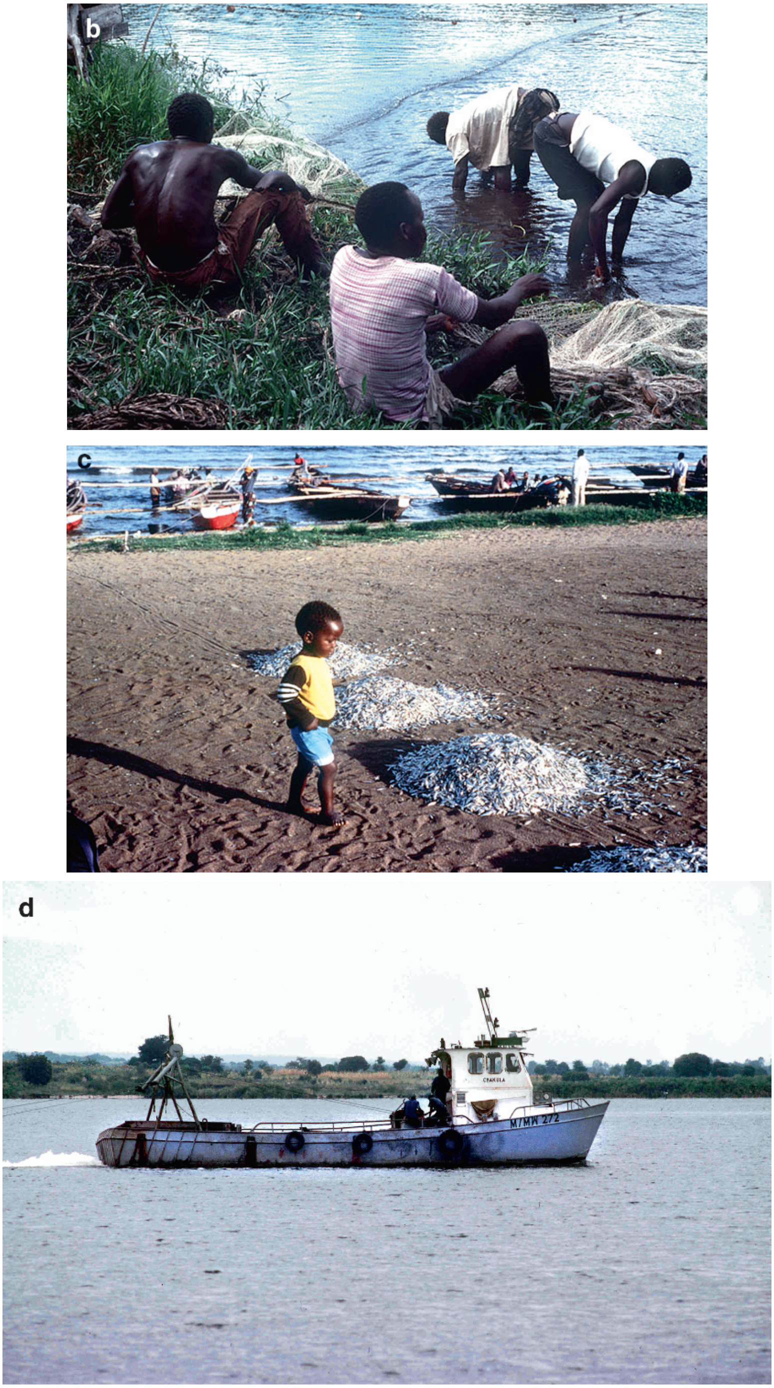

Fig. 34.1 (continued)

Fig. 34.1 (continued)

Fig. 34.5 Fisheries on Lake Tana. (**a**) Fishermen building a tankwa. (**b**) Hundreds of fishermen catching migratory fish in a spawning river. (c) Ladies processing fish for the Fish Production and Marketing Enterprise in Bahar Dar. (Photos by F.A. Sibbing)

Fig. 34.5 (continued)

Fig. 35.1 The Nile Basin and the areas covered by the territories of the riparians (London Water Research Group, 2007; map reproduced with permission of the FAO)

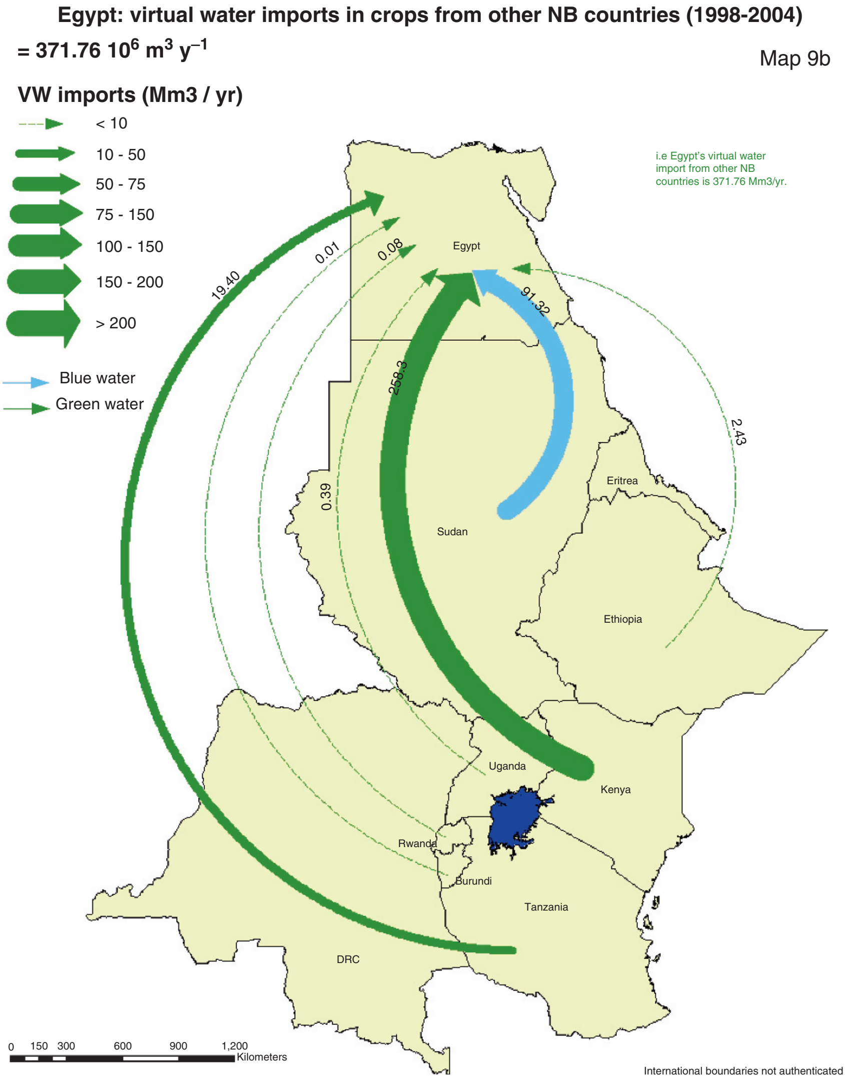

Fig. 35.2 Egypt's virtual water (vw) imports in crops from other Nile Basin countries (1998–2004) (source: London Water Research Group, 2007)

Index

Erratum

Chapter 7

Lake Nasser-Nubia

Gamal M. El-Shabrawy

Figures 7 and 8 have been interchanged
The figure appearing above the caption of fig. 7 is really fig. 8 and the figure appearing above the caption of fig. 8 is really fig. 7

The online version of the original article can be found at
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