Phytoplankton: Composition, Development and Productivity

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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.

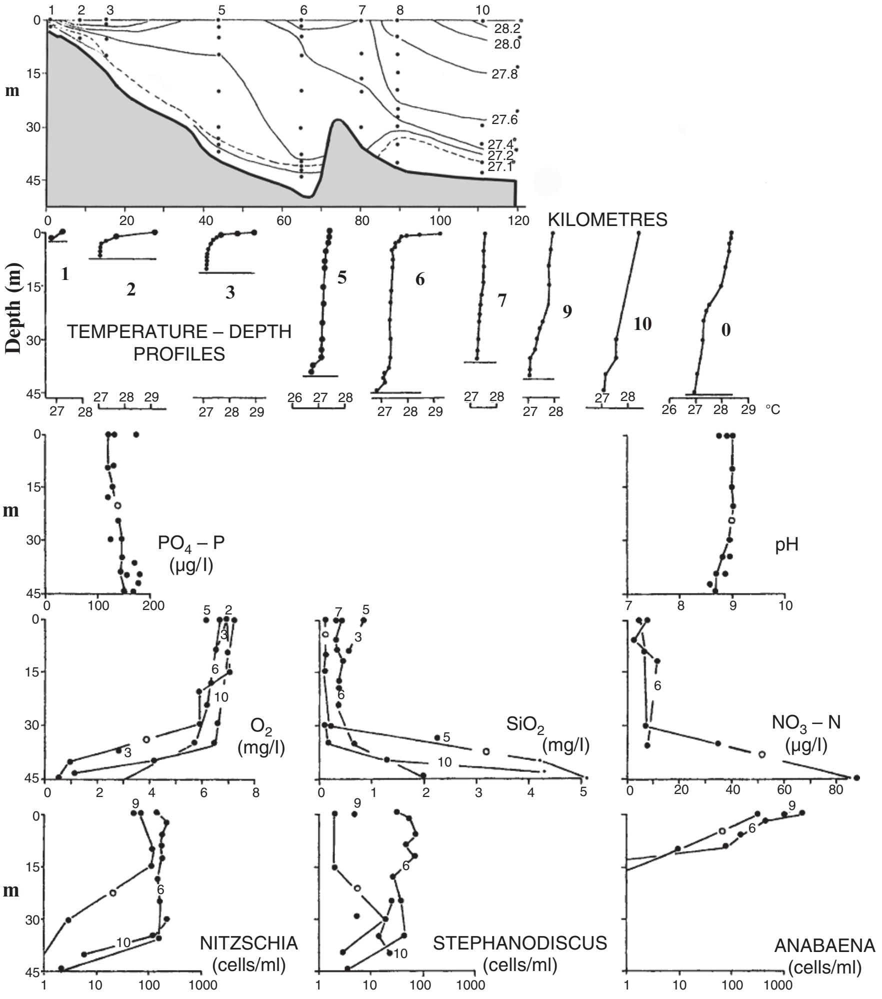

Fig. 1 Lake Albert: stratification patterns of temperature, some chemical components, and three species of planktonic algae, at numbered stations on a longitudinal section during 24–27 November 1960 (from Talling, 1963)

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 µg 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,

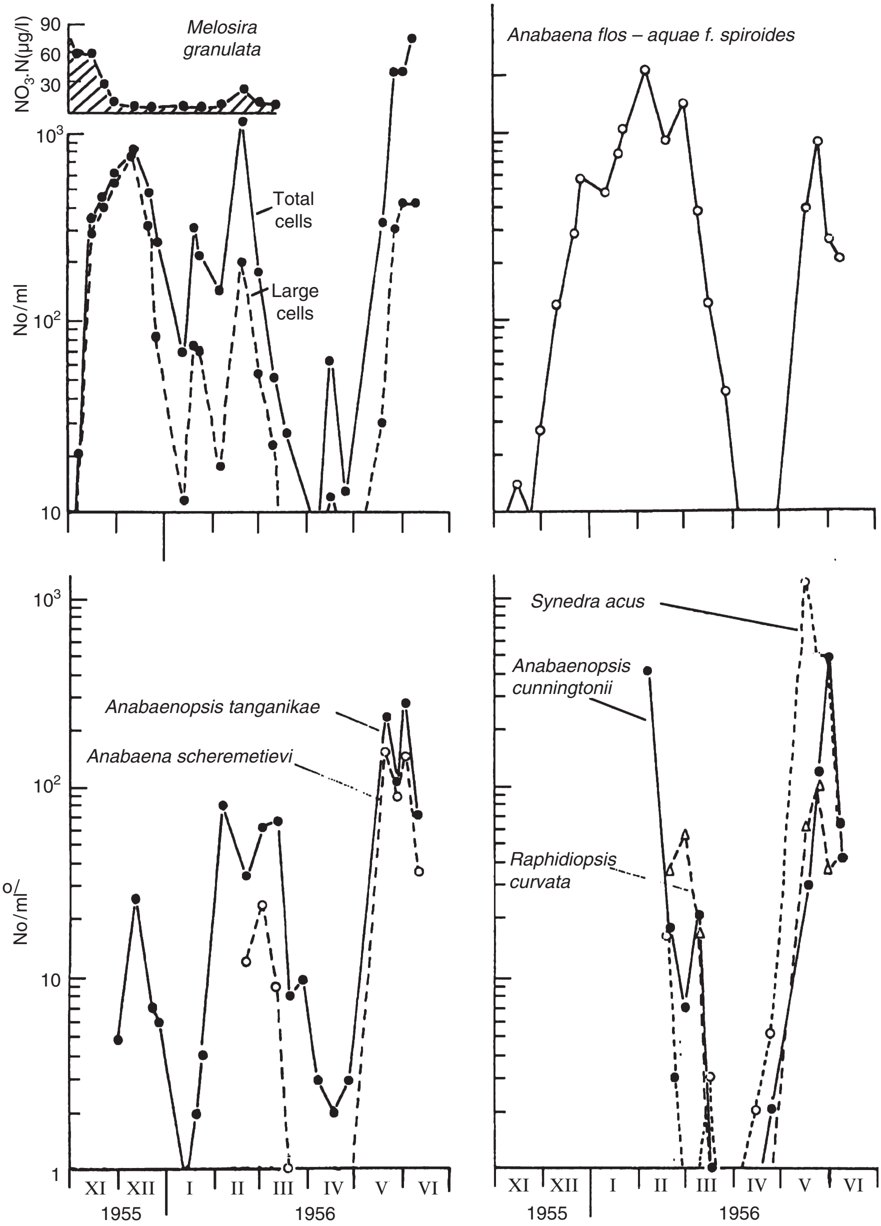

Fig. 2 Seasonal changes in the densities of phytoplankton species of the Blue Nile at Khartoum, 1955–1956. Units of population are cells (*Melosira*, *Synedra*, *Anabaena scheremetievi*), filaments (*Anabaenopsis*, *Raphidiopsis*), or coil turns of about 20 cells (*Anabaena flos-aquae* f. *spiroides*). 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 $mm^3\ l^{-1}$. 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).

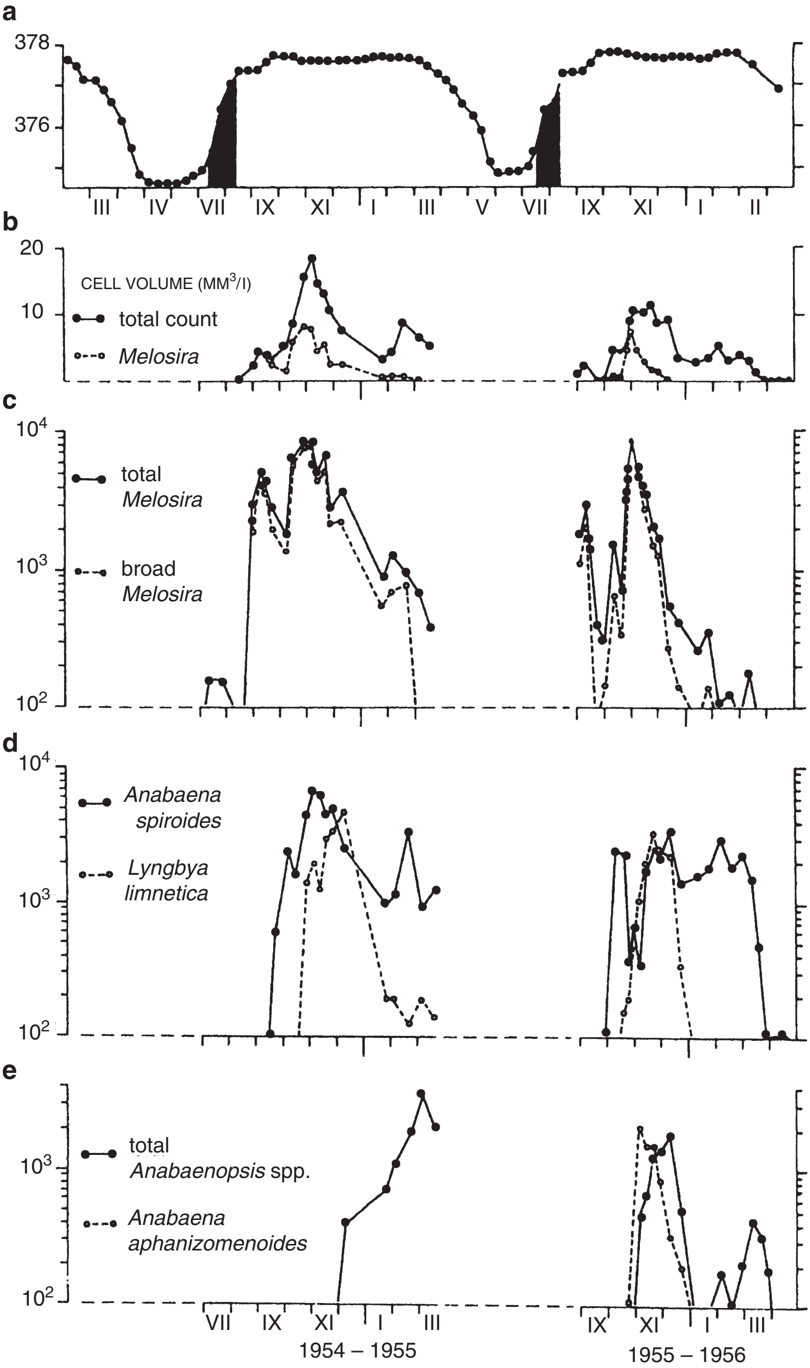

Fig. 3 Seasonal changes in the densities of phytoplankton species of the White Nile near Khartoum, 1954–1956 (**b**–**e**), shown in relation to water level in m (**a**) in the Gebel Aulia reservoir 40 km upstream. Full closure of the reservoir-dam is indicated by black columns. Units for *Aulacoseira* (*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* ($\mu g\ l^{-1} = mg\ m^{-3}$) 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 $\mu g\ l^{-1}$ in 1990, while the average minimum, ca 6.2 $\mu g\ l^{-1}$, 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 $\mu g\ l^{-1}$ at El-Allaqi in 1990, and a minimum value of 1.8 $\mu g\ l^{-1}$ at El-Ramla in 1994. Taha & Mageed (2002) stated that the lowest chlorophyll-*a* value, 0.6 $\mu g\ l^{-1}$, was recorded at the eastern side of Toshka. In contrast, near the western bank of Korosko, the maximum was 15 $\mu g\ l^{-1}$. In the Khors, they found a maximum of 7.4 $\mu g\ l^{-1}$ at Khor Allaqui, and a minimum of 0.90 $\mu g\ l^{-1}$ 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 $\mu g\ l^{-1}$, was recorded in April 1983, the lowest, 4.7 $\mu g\ l^{-1}$, in October 1982. Mean average chlorophyll-*a* showed a maximum of 10.8 $\mu g\ l^{-1}$ inside and a minimum of 9 $\mu g\ l^{-1}$ 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 μg l^{-1} (Shehata & Bader, 1985), with average 22.4 μg l^{-1} (Abdel-Hamid, 1991). The highest values, 41–108 μg 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

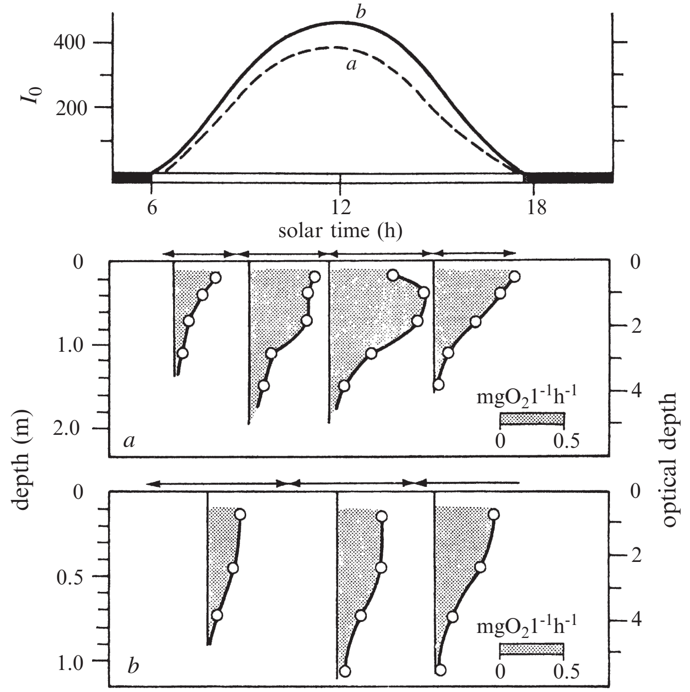

Fig. 4 Depth profiles of photosynthetic rate (*stippled areas*) in the Gebel Aulia reservoir for various periods during the day, during (**a**) 12 December 1954 and (**b**) 7 October 1955. The diurnal variation of incident solar irradiance I_o (in kerg cm^{-2} s^{-1} = W m^{-2}) is shown above (from 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}).

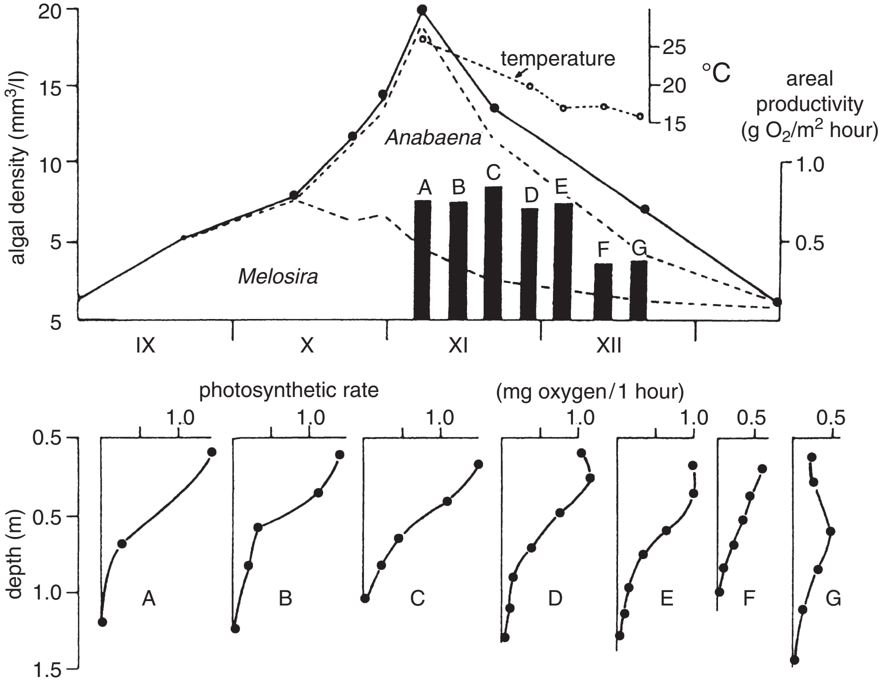

Fig. 5 Growth and decline of the 1953–1954 phytoplankton community in the White Nile at Gordon's Tree near Khartoum. Densities (in mm^3 cell volume l^{-1}) of two major components are shown, and associated rates of photosynthetic production per unit area (*histograms*). The latter are calculated from 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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