

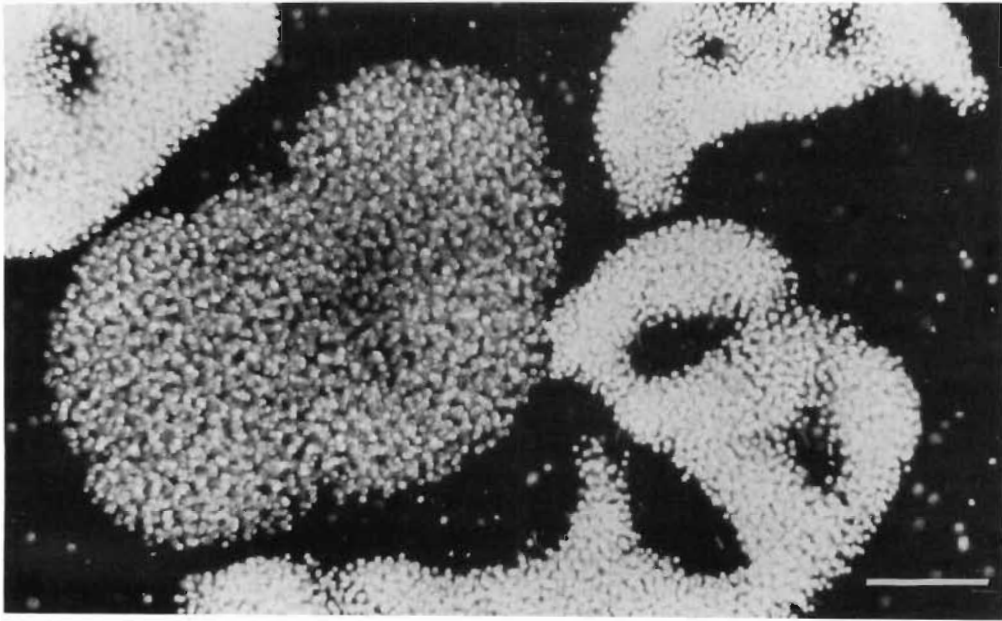
ON THE ECOLOGY
OF HYPERSCUM-FORMING
MICROCYSTIS AERUGINOSA
IN A
HYPERTROPHIC AFRICAN LAKE

by

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Microcystis aeruginosa Kütz. emend. Elenkin, natural populations. Bar = 0.1 mm.

PREFACE

The experimental work described in this thesis was carried out at the Limnology Division of the National Institute for Water Research (NIWR), Council for Scientific and Industrial Research (CSIR), Pretoria. The research work was supervised by Professor Charles M. Breen, Institute of Natural Resources, University of Natal, Pietermaritzburg, and Dr. Richard D. Robarts, NIWR.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of work of others it has been duly acknowledged in the text.

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Invaluable was the collaboration with Dr Richard D. Roberts. His scientific support, enthusiastic attitude, valuable suggestions and stimulating discussions were of paramount importance. I appreciated his encouragement along the way and I am much obliged for his contribution to many of my acquaintances with the local and international scientific communities.

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through Dr. Daan Toerien, and from NCRD made possible a joint project with Dr Yehuda Cohen from the Hebrew University of Jerusalem. Dr. Cohen brought microelectrodes and a stream of new ideas and methodologies from the frontier of microbial ecology.

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ABSTRACT

Light is the primary source of energy in most of earth's ecosystems. In freshwater ecosystems the major interacting factors that determine the abundance and species composition of planktonic phototrophs, the primary utilizers of light, are nutrients, temperature and light. With increasing eutrophication and declining geographical latitude, nutrient availability becomes in excess of the organisms' requirements, water temperature is more favourable for growth, and community structure depends to a greater extent on light availability.

This study focuses on the population dynamics of the bloom-forming cyanobacterium *Microcystis aeruginosa* Kütz. emend. Elenkin in subtropical Hartbeespoort Dam, South Africa. The objectives of the study were: to investigate the annual cycle, and the factors leading to the dominance and success of the cyanobacterium in this hypertrophic, warm monomictic lake, where light availability is the major factor limiting phytoplankton growth rates; to study the surface blooms and ultimately hyperscums that this species forms; and to assess the ecological significance of hyperscums.

A 4.5-years field study of phytoplankton abundance and species composition in relation to changes in the physical environment, was undertaken. The hypothesis was that *M. aeruginosa* dominated the phytoplankton population (> 80 % by volume) up to 10 months of every year because it maintained itself within shallow diurnal mixed layers and was thus ensured access to light. It was shown that wind speeds over Hartbeespoort Dam were strong enough to mix the epilimnion (7 - 18 m depth) through Langmuir circulations only 12 % of the time. At other times solar heating led to the formation of shallow (< 2 m) diurnal mixed layers (z_1) that were usually shallower than the euphotic zone (z_{eu} ; $x = 3.5$ m), while the seasonal mixed layer (z_m) was always deeper than z_{eu} . From the correspondence between vertical gradients of chlorophyll a concentrations and density gradients, when *M. aeruginosa* was dominant, it was implied that this species maintained the bulk of its population within z_1 . Under the same mixing conditions non-buoyant species sank into dark layers. These data point out the importance of distinguishing between z_m and z_1 , and show the profound effect that the daily pattern of z_1 , as opposed to the seasonal pattern of z_m , can have on phytoplankton species composition.

Adaptation to strong light intensities at the surface was implicated from low cellular chlorophyll a content ($0.132 \mu\text{g}$ per 10^6 cells) and high I_x (up to $1230 \mu\text{E m}^{-2} \text{s}^{-1}$). Ensured access to light, the post-maximum summer populations persisted throughout autumn and winter, despite suboptimal winter temperatures, by sustaining low losses. Sedimentation caused a sharp decline of the population at the end of winter each year and a short (2 - 3 months) successional episode followed, but by late spring *M. aeruginosa* was again dominant.

The mixing regime in Hartbeespoort Dam and the buoyancy mechanism of *M. aeruginosa* led to frequent formation of surface blooms and ultimately hyperscums. Hyperscums were defined as thick (decimeters), crusted, buoyant cyanobacterial mats, in which the organisms are so densely packed that free water is not evident. In Hartbeespoort Dam in winter *M. aeruginosa* formed hyperscums that measured up to 0.75 m in thickness, covered more than a hectare, contained up to 2 tonnes of chlorophyll a, and persisted for 2 - 3 months. Hyperscum formation was shown to depend upon the coincidence of the following preconditions: a large, pre-existing standing crop of positively buoyant cyanobacteria; turbulent mixing that is too weak to overcome the tendency of the cells to float, over prolonged periods (weeks); lake morphometry with wind-protected sites on lee shores; and high incident solar radiation. The infrequent occurrence of hyperscums can be attributed to the rare co-occurrence of these conditions.

Colonies in the hyperscum were arranged in a steep vertical gradient, where colony compaction increased exponentially with decreasing distance from the surface. This structure was caused by evaporative dehydration at the surface, and by the buoyancy regulation mechanism of *M. aeruginosa*, which results with cells being unable to lose buoyancy when deprived access to light from above. The mean chlorophyll a concentration and water content were 3.0 g l^{-1} and 14 % at the surface crust, 1.0 g l^{-1} and 77 % at a few mm depth, and 0.3 g l^{-1} and 94 % at 10 cm depth, where *M. aeruginosa* cell concentration exceeded 10^9 ml^{-1} .

A consequence of the high cell and pigment concentrations was that light penetrated only 3 mm or less, below which anaerobic, highly reduced conditions developed. Nutrient concentrations in hyperscum interstitial water, collected by dialysis, increased dramatically with time (phosphate: 30-fold over 3 months; ammonia: 260-fold). Volatile fatty acids, intermediate metabolites in anaerobic decomposition processes, were present. Gas bubbles trapped within the hyperscum

contained methane (28 %) and CO₂ (19 %), the major end products of anaerobic decomposition, and no oxygen.

The structure and function of *M. aeruginosa* in hyperscums was examined in relation to the vertical position of colonies and the duration of exposure to hyperscum condition. Colonies and cells collected from 10 cm depth in the hyperscum were similar in their morphology (light and fluorescent microscopy) and ultrastructure (transmission and scanning electron microscopy) to those of colonies from surface blooms in the main basin of the lake. With declining depth over the uppermost 10 mm of the hyperscum cells appeared increasingly dehydrated, decomposed and colonized by bacteria.

Studies employing microelectrode techniques demonstrated that photosynthetic activity of colonies at the surface of a newly accumulated hyperscum became rapidly photoinhibited, substrate-limited, and then ceased within hours of exposure to light intensities $> 625 \mu\text{E m}^{-2} \text{ s}^{-1}$. Photooxidative death followed. The dead cells dehydrated to form the dry crust, and space was thus created for colonies rising from underneath. Cells collected from 10 cm depth retained their photosynthetic capacity (¹⁴C-uptake experiments) throughout the hyperscum season, although a considerable decline in this capacity was noted over the last (third) month.

Altogether the data indicated that spatial separation developed within the hyperscum, between a zone at the surface of lethal physical conditions, a zone beneath the surface of stressful and probably lethal chemical conditions, and a deeper zone of more moderate conditions, which nevertheless, deteriorated after 2 - 3 months. A conceptual model describing the fate of a colony entering a hyperscum was then proposed. According to this model, a colony that arrives below a hyperscum and is not carried away by currents, becomes over-buoyant in the dark and floats into the bottom of the hyperscum. With time it migrates upwards, due to its own positive buoyancy, the buoyancy of colonies rising from underneath, and the collapse of cells at the top. It survives in the dark, anaerobic environment by maintaining low levels of basal metabolism while utilizing stored reserves. Depending on weather conditions, the colony may or may not remain within the hyperscum long enough to reach the zone of decomposition near the surface, where it would die. With the aging of the hyperscum and the accumulation of trapped decomposition products, the zone of decomposition expands. Thus, a hyperscum is essentially a site of a continuous cycle of death and dehydration at the surface and

upward migration of colonies from below to replace those that died, although not all colonies entering the hyperscum necessarily reach the lethal zone.

The formation of hyperscums was shown to have no major influence on the annual cycle of *M. aeruginosa* in Hartbeespoort Dam. The seasonality of increase and decline of the planktonic population was similar from year to year, irrespective of whether or not hyperscums formed. The phenomenon of hyperscums demonstrated that, as Reynolds and Walsby (1975) claimed, thick cyanobacterial water-blooms do form incidentally and have no vital function in the biology of the organism.

Water temperature did have a major effect on the annual cycle of this species in Hartbeespoort Dam. In temperate lakes the low water temperatures in autumn and winter ($< 10^{\circ}\text{C}$) cause *M. aeruginosa* to lose its ability to regain buoyancy in the dark, and consequently it sinks to bottom sediments. The higher ($> 12^{\circ}\text{C}$) minimum winter temperature in Hartbeespoort Dam leads to the maintenance of a relatively large residual planktonic population throughout the winter. Unlike the case in temperate lakes, the long-term survival of *M. aeruginosa* in warm-water lakes probably does not depend on winter benthic stocks for the provision of an inoculum for the following growth season.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Dominance of bloom-forming cyanobacteria

The shift in phytoplankton community structure towards an increased proportional abundance of bloom-forming cyanobacteria with increasing enrichment of freshwater systems is well documented (Fogg, 1969; reviews by Reynolds and Walsby, 1975; Reynolds, 1987). Bloom-forming cyanobacteria contain gas-vacuoles within their cells which allow them to float (Walsby, 1975). They are known for their sudden and striking appearance at the surface during conditions of low water turbulence. The mechanism of surface scum formation is well known: under calm-water conditions buoyant colonies from throughout the water column float to the surface and "telescope" into a thin, highly concentrated layer (Reynolds and Walsby, 1975). In contrast, the factors which allow cyanobacteria to grow to proportions where surface scums can occur, and to dominate the plankton populations of eutrophic lakes, are less well understood.

A large number of hypotheses have been advanced over the years to explain the dominance of cyanobacteria. These include superior nutrient-uptake kinetics of cyanobacteria (Hutchinson, 1967), in particular CO_2 (King, 1970; Shapiro, 1973); low N:P ratios (Smith, 1983); an ability to chelate iron (Murphy *et al.*, 1976); the production of toxic extracellular products (Keating, 1977); the ability to tolerate, if not flourish under, conditions of low oxygen tension and low redox potential (Sirenko, 1972); reduced population losses (Kalff and Knoechel, 1978) and reduced vulnerability to grazing (Arnold, 1971; Briand and McCauley 1978).

The hypotheses which have sustained most attention, however, are related to the ability of cyanobacteria to regulate their buoyancy. This capacity allows them to exploit spatial separations between nutrients in the hypolimnion and light in the epilimnion (Ganf and Oliver, 1982), and provides access to atmospheric CO_2 when supplies in the water column are limited, as in many enriched lakes (Paerl and Ustach, 1982). Reynolds and Walsby (1975) stressed the importance of positive buoyancy in keeping the cyanobacteria in the illuminated zones of optically shallow lakes (having a euphotic zone that is shal

lower than the mixed layer), and Humphries and Lyne (in press) hypothesized that positive buoyancy *per se* rendered cyanobacteria dominant by enhancing the average exposure to available light.

1.2 The biology of *Microcystis aeruginosa*

Microcystis aeruginosa Kütz. emend. Elenkin is one of the most successful and cosmopolitan species among the bloom-forming cyanobacteria, which is known for its late summer blooms in eutrophic waterbodies. It is a colonial prokaryote, of the order Chroococcales. Colonies are composed of spherical cells, 4 - 6 μm in diameter, that are embedded in a mucilaginous sheath. Colony shape is highly variable, and ranges from spherical or lense-shaped colonies (*M. aeruginosa* forma *flos aquae* according to Komarek, 1958) to irregular, net-shaped colonies (forma *aeruginosa*). Like most cyanobacteria this species is a photoautotroph (Stanier and Cohen-Bazire, 1977). Oxygenic photosynthesis is the predominant form of nutrition in cyanobacteria and is the only one known for *M. aeruginosa*.

The mechanism of buoyancy regulation in *M. aeruginosa* has attracted scientific interest in the last few years. Buoyancy regulation in cyanobacteria is achieved by varying the respective rates at which heavy cell materials (such as carbohydrates and protein) and intact gas vesicles are produced and destroyed (Walsby, 1970; 1972). Two mechanisms of light-mediated gas vacuole regulation were proposed by Walsby (1970): the collapse of gas vesicles by rising cell turgor pressure on exposure to increased light intensities, and the dilution of gas vesicles by cell growth. More recent studies (Kromkamp and Mur, 1984; van Rijn and Shilo, 1985) provided evidence that the strong gas vesicles of *M. aeruginosa* were able to resist the high turgor pressures shown to build up in the cells and that this species regulated its buoyancy by changing the intracellular carbohydrate content. In the dark the cells consumed their stored carbohydrates and became buoyant; in the light photosynthate was diverted into carbohydrates and their accumulation with time caused the cells to sink. The characteristic diel vertical migrations described for *Microcystis* (van Rijn and Shilo, 1985; Thomas and Walsby, 1986) were explained as a direct consequence of this buoyancy mechanism.

Reynolds *et al.* (1981) described the annual cycle of *M. aeruginosa* in the Blelham Tarn enclosures and postulated that their model applies generally to *Microcystis aeruginosa* populations in temperate and subtropical eutrophic lakes. According to their model, the main growth phase occurs in the plankton during spring and summer. The eventual

size of the standing crop is limited by nutrients or, if nutrients are available in excess of growth requirements, by the underwater light climate. Losses sustained by *M. aeruginosa* during its planktonic phase are small, as sinking colonies are mostly capable of upward migration and are not lost permanently, and only the smallest colonies (less than 60 μm in diameter) are grazed. They noticed that post-maximal populations may persist in the plankton for weeks or months due to the low loss rates. This 'stationary growth phase', as they named it, ends abruptly in autumn, by a rapid loss from suspension and mass migration to the sediments. They claimed this autumnal sedimentation to be an important transitional stage in the annual cycle. They proposed that although the benthic colonies retain their vegetative form, the cells become physiologically dormant. In this way a potentially viable stock is maintained as benthos over winter, when this cyanobacterium is absent in the water column, and provides a basis for growth in the following year. Colonies re-inoculating the water column the next spring are mostly new colonies that have arisen within the mucilage of the parent benthic colony following a short phase of cell division. The renewed physiological activity is apparently stimulated by low intensity irradiance, low oxygen concentrations and low redox potential of the bottom water. The water column is thus re-infected by a small inoculum of cells, which under the favorable spring growth conditions multiply to form the planktonic population of the following summer.

Indeed, many studies carried out in temperate eutrophic lakes worldwide serve to validate the model. Examples are: Sirenko *et al.* (1969); Topachevskiy *et al.* (1969); Reynolds and Rogers (1976); Kappers (1984); Fallon and Brock (1981); Takamura *et al.* (1984); Dokulil and Skolant (1986); Thomas and Walsby (1986); Bell and Ahlgren (1987), to name a few.

Recently, Thomas and Walsby (1986) showed that at temperatures below ca. 12°C the rates of breakdown of the carbohydrate ballast (through e.g. respiration, consumption or excretion) in the dark were so low that the cells could not regain buoyancy. They attributed the autumnal sinking of *M. aeruginosa* in temperate lakes to this mechanism. In tropical and subtropical lakes winter water temperature may not decline below 12°C. How would that affect the annual cycle of *Microcystis*?

The bulk of the studies on the population dynamics of *M. aeruginosa* were carried out in temperate lakes, whereas information from warm,

subtropical and tropical lakes is scarce. An exception is equatorial Lake George, Uganda (Ganf 1974; Ganf and Horne, 1975), where water temperature remains above 20°C throughout the year and where cyanobacteria, and particularly *M. aeruginosa*, dominate the plankton throughout the year. With daily variations in the mixing regime being more prominent than seasonal changes, a distinct diel pattern in the vertical distribution of phytoplankton was recorded, whereas the planktonic standing crop remained at a near steady-state over the annual cycle. Seasonal migration to the sediments did not occur. Another exception is subtropical Hartbeespoort Dam, South Africa, where *M. aeruginosa* was shown to dominate the phytoplankton populations during ten months of the year 1982/83 (Robarts and Zohary, 1984).

In order to further validate Thomas and Walsby's (1986) concept of the temperature-mediated autumnal sinking of *M. aeruginosa*, field data are required from subtropical, warm water lakes, which show characteristic annual cycles of the major physical variables, but where winter temperatures do not decline below the critical level for buoyancy regulation. This will also permit elaboration on the generality of the application of the annual cycle model of Reynolds *et al.* (1981). Published data from Hartbeespoort Dam (Robarts *et al.*, 1982; Robarts, 1984; Robarts, and Zohary, 1984) indicate that it is most suitable for addressing this issue.

Reynolds *et al.*'s (1981) model was based on observations of populations husbanded in artificial enclosures (Lund Tubes). Processes such as thick scum formation and beaching, that are typical of natural open water populations but did not occur in the enclosures, were excluded from their model. Topachevskiy *et al.* (1969) recognized scum formation to be an important phase (referred to as the 'neustonic phase') in the life cycle of *M. aeruginosa* in the Dnieper Reservoirs. They noted that thick, wind-driven blooms are thrown up on the shore, dehydrate and form dry crusts that later freeze. They claimed that in this form some of the cells retain their vitality for long periods, and when wet again return to the active state. Thus, in cold-water reservoirs with fluctuating water levels, the crusts represent an inexhaustible source of replenishment of the population, equivalent in its importance, they claim, to that of the overwintering benthic stocks.

While thick surface scums occur occasionally in many eutrophic lakes, the frequency of their occurrence and their persistence increase with increasing eutrophication, and they become a common eye-sore in hypertrophic waterbodies (Barica, 1981). Hartbeespoort Dam provides an

extreme case of hypertrophy, with primary production rates among the highest recorded for freshwater lakes (Robarts, 1984; 1985), and where thick surface scums, or 'hyperscums' (see below), which are the equivalent of the 'neustonic phase' of Topachevskiy *et al.* (1969), constitute an obvious phase in the annual cycle of *M. aeruginosa* (Zohary, 1985).

1.3 The contribution of this study

This study deals with the population dynamics of *M. aeruginosa* in Hartbeespoort Dam. In this warm monomictic, man-made lake the cyanobacterium was dominant not only in summer, but also in autumn and winter. During most of the period of its dominance it virtually excluded other species and comprised a practically unispecific natural population (Robarts and Zohary, 1984).

Whereas most previous studies of the annual cycle of *M. aeruginosa* were conducted in eutrophic lakes in which algal growth becomes limited by the availability of nutrients at the end of summer (e.g. Reynolds *et al.*, 1981; Kappers, 1984; Takamura *et al.*, 1984), Hartbeespoort Dam is hypertrophic, with nitrogen and phosphorus concentrations in excess of algal growth requirements throughout the year (Ashton, 1985; NIWR, 1985). The geographical location of Hartbeespoort Dam in subtropical Africa makes it a warm water lake with minimum winter temperatures of 10 - 12°C. Its semi-arid climate with summer rainfall, high incident solar radiation and low wind stress, together with its hypertrophic status, all contributed to a set of environmental conditions which led to the overwhelming success of *Microcystis*. The effects of the physical environment, and particularly that of temperature and low wind stress, on *Microcystis*, could be studied in this lake independent of interactions with nutrient limitation.

One consequence of the abundance of *M. aeruginosa* in Hartbeespoort Dam was the accumulation of surface blooms in wind-protected areas along lee-shores to form massive scums, or hyperscums. A hyperscum was defined to be a crusted buoyant cyanobacterial mat, often decimeters thick, in which the organisms are so densely packed that free water is not evident (Zohary, 1985). Depending on weather conditions, hyperscums could persist for weeks to months. Hyperscums differ from "scums" or "water blooms" in the magnitude of their spatial and temporal dimensions and of cell concentrations. While relevant dimensions for: "Scums" would usually be millimeters (for thickness),

hours (duration) and $10^2 - 10^3 \mu\text{g chl l}^{-1}$ (as an indicator of algal mass) those for hyperscums would be decimeters, weeks/months and $10^5 \mu\text{g chl l}^{-1}$. These differences justify the new term "hyperscum". It was felt that the use of the alternative term "neustonic mats", previously employed by Topachevskiy *et al.* (1969) and Seki *et al.* (1980) is unjustified. "Neuston" by definition refers to organisms adapted to living at the air-water interface (Wetzel, 1975). In hyperscums, however, the bulk of the population is below the surface while those cells at the interface die of photooxidation and dehydration (see chapter 6).

In comparison with the large volume of scientific literature dealing with cyanobacterial scums, little is known about hyperscums. A major reason is their infrequent occurrence (see later Table 4.2). Published accounts of hyperscums besides those from Hartbeespoort dam are limited to the "neustonic mats" from the Dnieper reservoirs, USSR (Topachevskiy *et al.*, 1969). Yet, unpublished observations indicate that hyperscums do occur elsewhere, e.g., in the King Talal Reservoir, Jordan (Dr. F. Hashwa, Univ. of Jordan, Amman, pers. comm.). The study of hyperscums in Hartbeespoort Dam therefore elucidates a new aspect in the ecology of *M. aeruginosa* under hypertrophic conditions.

The objectives of this study were: (1) to investigate new aspects relevant to the annual cycle, the dominance and success of *M. aeruginosa* in a hypertrophic, warm water lake, and (2) to study the hyperscum phenomenon and assess its role in the population dynamics of the cyanobacterium. The thesis thus addresses the following issues: (a) the relationship between the physical environment, intrinsic physiological adaptations and the abundance and success of *Microcystis* (Chapter 3). Particular emphasis is given to the role of vertical mixing patterns and the ability of *Microcystis* to maintain itself within shallow diurnal mixed layers; (b) hyperscums: the environmental factors that favor their formation (Chapter 4); the structural, physical and chemical characteristics of the hyperscum, how they develop with time and change with depth (Chapter 5); and the survival of *M. aeruginosa* in the dark, anaerobic hyperscum environment (Chapter 6). Finally, the role of hyperscums in the population dynamics of *M. aeruginosa* is assessed and a model of its annual cycle in Hartbeespoort Dam, including a hyperscum stage, is placed in context with existing models developed for temperate eutrophic lakes.

CHAPTER 2

METHODS

2.1 THE STUDY AREA

2.1.1 Location and topography

Hartbeespoort Dam is a warm monomictic man-made lake (Scott *et al.*, 1977; 1980; Robarts *et al.*, 1982; NIWR, 1985). It is situated 40 km north of Johannesburg in the Transvaal, South Africa (25° 43' S; 27° 51' E) at 1162 m above sea level (Fig. 2.1). The lake is fed by the Crocodile-Jukskei-Hennops River system, the Magalies River, and two minor streams. The Crocodile River system drains the urban and industrial areas of Northern Johannesburg and other cities on the Witwatersrand. It contributes approximately 90 % of the inflowing water and 99 % of the nutrient load (Toerien and Walmsley, 1978; Scott *et al.*, 1980; NIWR, 1985). The Magalies River drains a predominantly rural area used for grazing, nature reserves and agriculture (NIWR, 1985). The lake lies between parallel ranges of the Magaliesberg mountains and its dam wall is situated in a gorge (Fig. 2.2a). The four inflows contribute to the dendritic morphometry and bathymetry of the lake Fig. 2.2b).

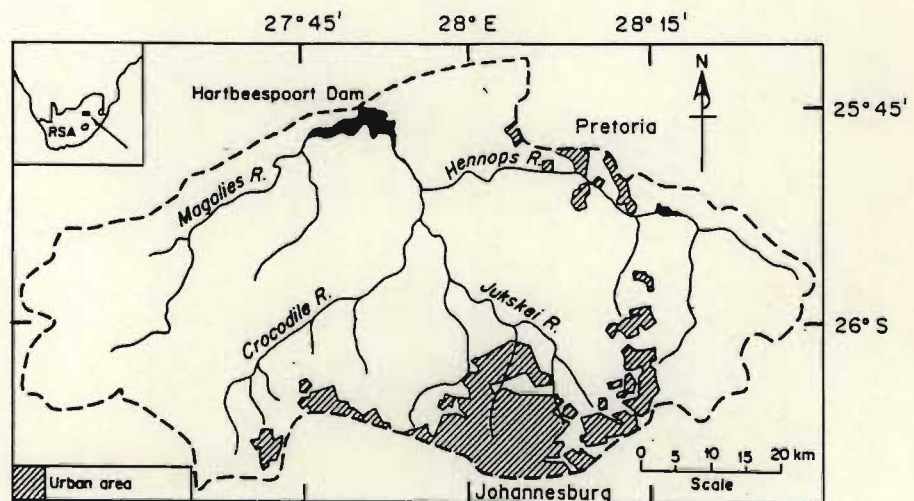


FIGURE 2.1 Hartbeespoort Dam catchment and its location in southern Africa.

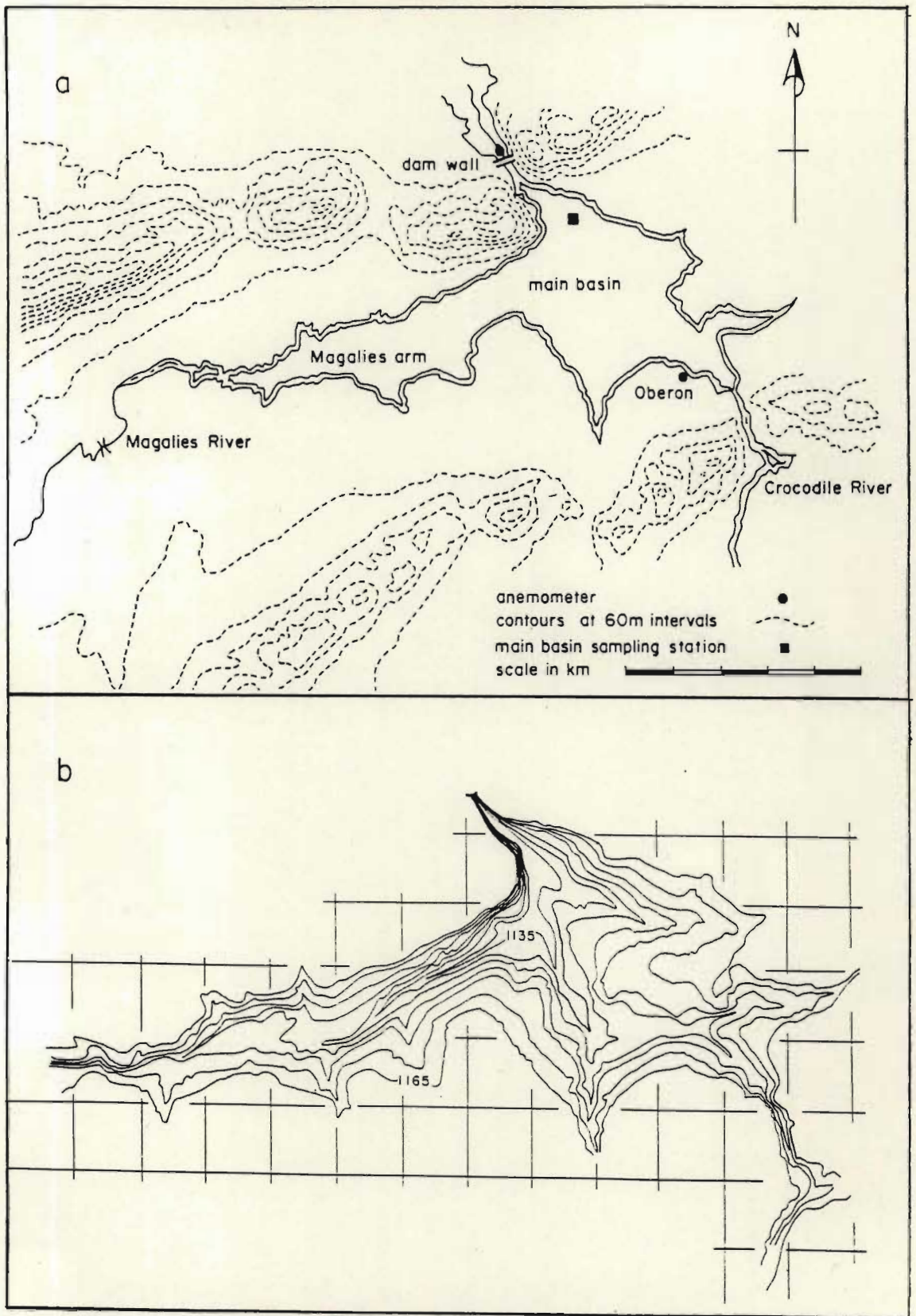


FIGURE 2.2 Hartbeespoort Dam, South Africa: a) topography, b) bathymetry (contour lines at 5 m depth intervals; depth in m above sea level, grid squares are 1 km x 1 km).

2.1.2 The climate

The lake lies in a semi-arid, summer rainfall (October to March) zone and is subject to an average annual rainfall of approximately 700 mm. During the study, however, a drought in southern Africa resulted with rainfall being only 500 - 600 mm each year (NIWR, 1985). Mean annual air temperature is about 19.5°C and ranges from about 2°C in winter to above 32°C in summer. Diel variations in air temperature are about 10 to 15°C year round. Solar radiation is high most of the year due to the subtropical latitude, high altitude, and the prevailing clear weather conditions, and commonly varies between 150 W m⁻² in winter and 290 W m⁻² in summer (NIWR, 1985). Wind speeds over the lake are generally low. The mean monthly wind speed varies seasonally between ca. 1 m s⁻¹ in May-June and ca. 2.5 m s⁻¹ in October-November. Winds in the gorge near the dam wall are stronger and may gust to over 10 m s⁻¹ (NIWR, 1985).

2.1.3 The lake: features and history

The dam was built in 1923 to impound water for irrigation (Steyn *et al.*, 1975; Scott *et al.*, 1980). The lake is currently used for irrigating approximately 130 km² of agricultural land downstream, as a drinking water source for the town of Brits, and as a major recreation site for the Johannesburg - Pretoria area (NIWR, 1985). When full, the impoundment has a surface area of 20 km², a full supply capacity of 195 x 10⁶ m³, mean depth of 9.6 m and maximum depth of 32.5 m (Table 2.1). The drought during this study led to a 12 m drop in water level and the lake volume decreased to 17% of full supply (Ashton, 1985).

TABLE 2.1 General characteristics of Hartbeespoort Dam at full supply level (after NIWR, 1985).

altitude	1162 m
capacity	195 x 10 ⁶ m ³
surface area	20 km ²
maximum depth	32.5 m
minimum depth	9.6 m
maximum length	12 km
width	5.6 km
catchment area	4144 km ²
mean annual water residence time	0.87 year
thermal stratification and anaerobic hypolimnion	present from September to April

Soon after the construction of the dam the lake was described by Hutchinson *et al.* (1932) as oligotrophic on the basis of its low phytoplankton content. However, with increasing urbanization and industrialization in its catchment nutrient loads to the lake have increased steadily (Allanson and Gieskes, 1961; Toerien and Steyn, 1975; Scott *et al.*, 1977; Ashton, 1985). Estimates of total annual loads to the lake during 1981 to 1984 ranged from 770 to 1700 tonnes N yr⁻¹ (Ashton, 1985) and 200 to 320 tonnes P yr⁻¹ (NIWR, 1985). Today, with total phosphorus concentrations of about 0.5 mg l⁻¹ and soluble inorganic nitrogen concentrations of 1 - 2 mg l⁻¹ (Table 2.2) that are maintained throughout the year, the lake is classified as hypertrophic (Robarts *et al.*, 1982; NIWR, 1985). Its phytoplankton primary productivity is among the highest measured in freshwater lakes, with hourly euphotic zone values exceeding 3 g C m⁻² h⁻¹ and annual production rates exceeding 2 kg C m⁻² (Robarts, 1984; 1985).

The chemical composition of Hartbeespoort Dam surface water (Table 2.2) is characteristic of a soft-water, alkaline lake.

TABLE 2.2 Mean annual values of some chemical components of Hartbeespoort Dam surface water (after NIWR, 1985).

Parameter	1982	1983	1984
nitrate-N, mg l ⁻¹	1.10	0.94	1.46
soluble reactive phosphorus, mg l ⁻¹	0.39	0.42	0.52
silica, mg l ⁻¹	5.2	4.7	4.4
pH	9.45	9.20	9.20
alkalinity (CaCO ₃), mEq l ⁻¹	160	135	138
conductivity, mS m ⁻¹	59	59	67
chloride, mg l ⁻¹	48	65	58
magnesium, mg l ⁻¹	23	21	21

2.1.4 The biota

Since the late fifties the phytoplankton populations were dominated in summer by the cyanobacterium *Microcystis aeruginosa* (Allanson and Gieskes, 1961). During 1976-77 a rapid population increase of the floating aquatic macrophyte *Eichhornia crassipes* (Mart.) Solms occurred and by October 1977 the plant covered up to 60 % of the lake's surface area and seriously impeded recreation (Scott *et al.*, 1980). It was brought under control by aerial spraying of a herbicide in 1977-78 (Scott *et al.*, 1980). Chemical spraying along the shoreline continues as a preventative measure.

In the absence of *Eichhornia*, dense populations of *Microcystis aeruginosa* dominate the phytoplankton and constitute the main primary producers of the lake (Robarts, 1984; Robarts and Zohary, 1984). Under calm weather conditions *M. aeruginosa* forms thick scums (Scott et al., 1980; Robarts and Zohary, 1984) which at times aggregate to form hyperscums (Zohary, 1985).

The zooplankton populations are dominated by the cladocerans *Daphnia pulex*, *D. longispina* and *Ceriodaphnia reticulata* (Jarvis, 1986). Secondary production in this lake is not concomitant with the extremely high primary production because colony size of *Microcystis* is usually too large to be grazed, and the zooplankton standing stock is limited by food availability (Jarvis, 1986).

Microcystis aeruginosa is a nutritionally inferior food for fish (Sorokin, 1968; De la Fuente et al., 1977; De Moor and Scott, 1985). The dominance of this cyanobacterium in Hartbeespoort Dam has led to an increase of detritus as food source for fish. Thus, the fish populations are dominated by the detritivorous/benthivorous *Cyprinus carpio*, the omnivorous *Clarias gariepinus* and the phytoplanktivore and detritivore *Oreochromis mossambicus* (Cochrane, 1984).

2.2 SAMPLING

2.2.1 Routine sampling at the main basin

Water samples for chemical and phytoplankton analyses were collected at weekly intervals from September 1982 to August 1986 between 10:00 and 12:00 h at a permanent station (depth 20.3 to 32.5 m, depending on the water level) in the main basin of Hartbeespoort Dam (Fig. 2.2). A 6 liter capacity opaque Van Dorn sampler was used to collect water samples from the surface and 0.5, 1, 2, 3, 4, 5, 6, 8, 10 m, and at 5 m intervals to the bottom. Surface samples were collected with the sampler held horizontally (internal diameter, 110 mm) because of frequent steep algal biomass gradients near the surface. The remaining samples were collected with the sampler held vertically (length, 56 cm). Dissolved oxygen, pH and chlorophyll a concentrations were determined on all samples. Filtered (Sartorius G/F filters) subsamples of the samples from 5 m depth intervals were collected for nutrient analyses. Equal volume aliquots of each of the surface to 8 m samples were combined to give an integrated phytoplankton sample. Half was immediately fixed with Lugol's iodine for cell enumeration

and the rest was kept fresh for algal identification and measurement of cell linear dimensions the following day.

The horizontal variability in chlorophyll concentrations in the upper 4 m was studied in 1985. Integrated 0-4 m water samples were collected at monthly intervals at 14 stations with depth greater than 4 m using a hosepipe designed by Zohary and Ashton (1985).

2.2.2 Sampling hyperscums

Field studies were restricted to those periods when hyperscums of considerable size and duration existed at the shelter of the dam wall. A preliminary field study was carried out in winter 1983 (9 May to 1 November), a more intensive study took place in winter 1984 (10 May to 4 September) and a complementary study in winter 1986 (1 June to 2 September). For brevity those study periods will be referred to as the 1983, 1984 or 1986 hyperscum seasons. Additional sampling was carried out in June 1987, when microelectrode studies were conducted.

During the 1983 and 1984 hyperscum seasons, 4 stations located 5 m, 50 m, 100 m and 170 m from the wall (Fig. 2.3) were sampled weekly or biweekly. A motor boat was forced through the hyperscum, which extended up to approximately 120 m from the dam wall, in order to reach these sampling stations. Due to excessive boat drives into and out of the hyperscum its middle zone near station 4 became increasingly vulnerable to breaking by NW winds. From 15 August 1984 onwards stations 2, 3 and 4 were replaced by stations 2A, 3A and 4A (Fig. 2.3) which were situated along a more protected transect line further east. Samples of the upper 1 m were collected between 10:00 and 12:00 using a 1 m length transparent perspex cylinder (44 mm internal diameter) that was inserted vertically into the hyperscum/water, sealed at the top with a rubber stopper and lifted carefully. The cylinder's base was closed underwater. The thickness of the hyperscum, taken to be the depth at which free water between colonies was first evident, was recorded. The core's contents were mixed in a bucket and subsampled (1 to 200 ml) for chlorophyll analysis.

The spatial variations in chlorophyll *a* and phaeophytin content of the hyperscum at 7 or 8 locations up to 50 m from the wall (Fig. 2.3) were compared on two occasions (Table 2.3). Spatial variations in the chlorophyll *a* content and the proportion of phaeophytins within this zone were small as indicated by the narrow ranges and small standard deviations from the means for these parameters (Table 2.3). The low phaeophytin content at all locations (maximum of 9.9 % of total

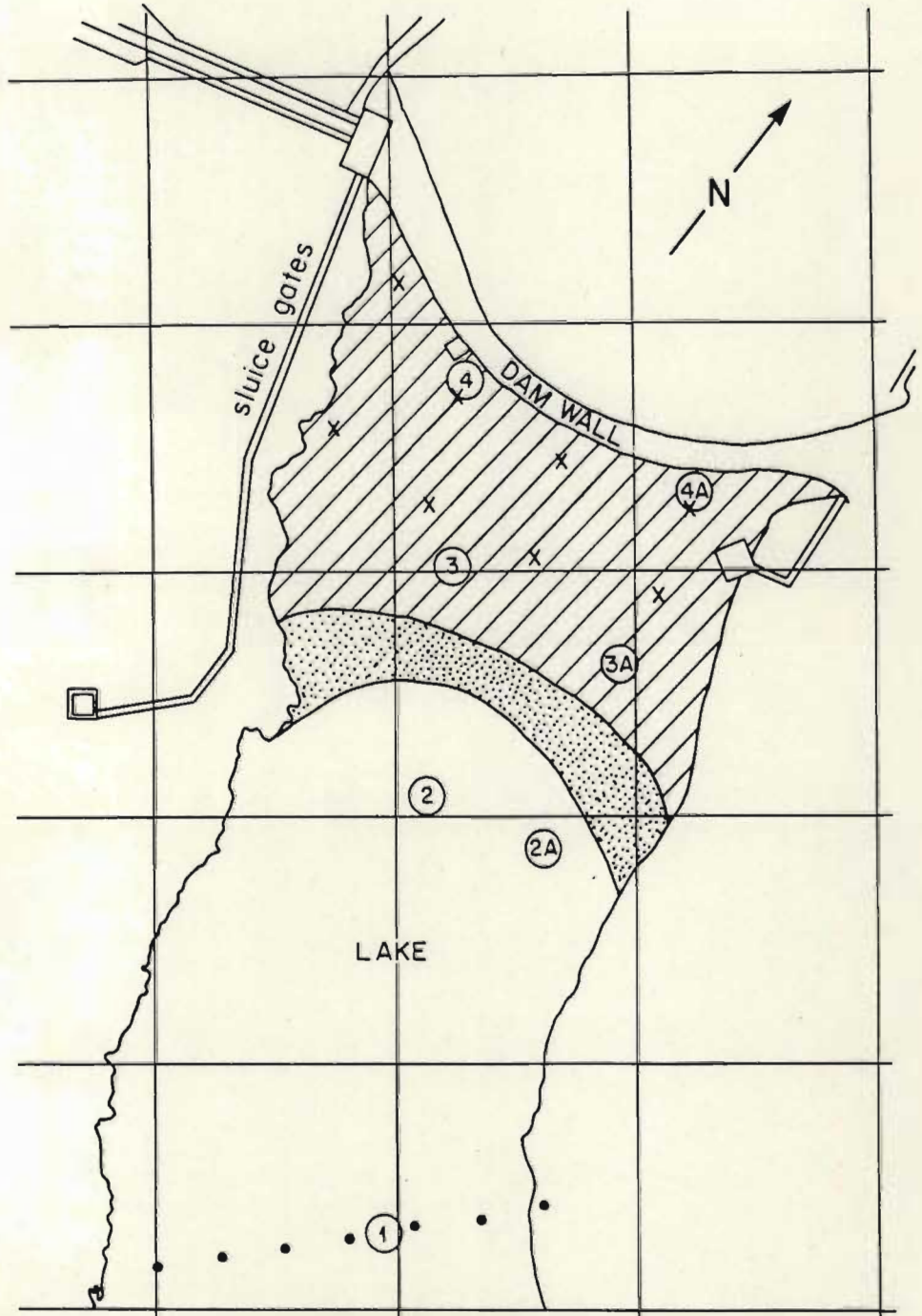


FIGURE 2.3 A map of the area near the wall of Hartbeespoort Dam showing sampling stations (numbered) during the hyperscum seasons. Grid squares are 50 m x 50 m. Dashed area - crusted hyperscum; dotted area - newly accumulated, non-crusted scum; crosses - sampling sites for estimation of the spatial variability in chlorophyll concentration.

chlorophyll derived pigments) indicated that decomposition was not significantly higher at one site compared with others. Thus, the horizontal distribution of photosynthetic pigments within the hyperscum was relatively homogeneous. All additional sampling was carried out at station 4 or 4A (Fig. 2.3).

TABLE 2.3 Spatial variability in the chlorophyll a and phaeophytin content of the hyperscum at several locations up to 50 m from the dam wall.

	date	mean \pm SD	n	range
chlorophyll a, mg l ⁻¹	6.6.84	66.9 \pm 9.8	8	51.3 - 78.3
	28.6.84	47.5 \pm 8.5	7	39.4 - 64.8
phaeophytins, %	6.6.84	7.3 \pm 0.3	8	5.6 - 8.5
	28.6.84	6.1 \pm 0.8	7	3.2 - 9.9

In 1984 the research was aimed at elucidating processes taking place within the hyperscum. Samples from discrete depths were collected from undisturbed cores by inserting a syringe fitted with a 16 G needle into holes drilled a 2 cm intervals and sealed externally with tape. Immediately upon retrieval the core was placed upright in a darkened box because the sudden exposure to light caused the colonies to float and compact. Samples were collected within 5 minutes and kept in the dark. Chlorophyll a, phaeophytin and carotenoid concentrations, pH, alkalinity and redox potential were determined on aliquots of the hyperscum samples from 10, 20, 40 and 80 cm depth. Cell counts were carried out on duplicate subsamples from 10 cm depth, preserved in Lugol's iodine.

Filtered water from various depths below the hyperscum was obtained by incubating dialysis tubings filled with distilled water for 20 to 24 h *in situ*. The tubing (45 mm inflated diameter) was cut into 1 m lengths, filled and knotted on both ends so that no air bubbles were trapped inside, and incubated horizontally at 10, 20, 40 and 80 cm depth by clipping the ends to the opposite sides of a submerged frame attached to floats. Following incubation water from each bag was carefully siphoned into triplicate glass reagent bottles, allowing it to overflow 2-3 times the volume of the bottle. Samples were analysed for dissolved oxygen, H₂S, inorganic-N species, and soluble reactive phosphorus (SRP). On 2 July 1986 triplicate dialysis bag samples from 10 cm depth were collected for determination of volatile fatty acids.

In the 1986 hyperscum season sampling was aimed at elucidating processes taking place at and near the top crust. For this purpose three structurally different zones within the hyperscum were identified and sampled: (1) the crust, comprising of the top 1-2 mm dry layer; (2) the compact algal layer of ca 5 - 10 mm thickness under the crust; and (3) the less compact layer from ca 1 cm depth to the bottom of the hyperscum comprising the bulk of the hyperscum. From each of the layers samples for pigment analyses and cell counts were taken as follows.

The crust was sampled by randomly collecting dry crust pieces. A few pieces were hydrated for 3 h in a 10 ml graduated cylinder containing 7 ml of filter-sterilized (0.2 μ m Sartorius membrane filters) lake water. The addition in volume due to the crust particles was noted, and the contents pored into a 20 ml vial. The mixture was shaken vigorously and 0.5 ml subsamples taken.

It was noted that when hyperscum samples were taken with a syringe the small aperture caused enrichment of the samples with inter-colony water. To prevent this the nozzle of a 1 ml plastic syringe was cut off, giving an aperture diameter of 4 mm, which was greater than the largest *Microcystis* colony. The nozzle-less syringe was used for all small volume sampling in the hyperscum.

The compact layer was sampled by scraping off the material adhering to the bottom of the crust with a glass microscope slide. Samples were diluted with filter-sterilized lake water prior to subsampling with the nozzle-less syringe.

The bulk of the hyperscum samples were collected from 10 cm depth with a hand-held transparent perspex cylinder (25 cm length; 20 mm diameter) that was used as a corer. It was inserted vertically to 11 cm depth and then pushed to a horizontal position so that its midline was at 10 cm depth. The core was then moved horizontally so that its contents were replaced by a sample from 10 cm depth and lifted in that position. Due to the thick consistency of the hyperscum the contents did not pore out. The sample was transferred into a glass jar, vigorously mixed and subsampled with the nozzle-less syringe. Filtered (Sartorius G/F filters) subsamples for chemical analyses were prepared by 100 fold dilution with deoxygenated (by bubbling N₂) distilled water. Samples were kept in full glass stoppered reagent bottles at 4°C.

2.3.2 Temperature

Water temperature was measured at about midday with a Cole-Parmer 8502-20 thermistor at the surface, 0.5 m and from then at 1 m depth intervals to the bottom. In the hyperscum the thermistor probe did not sink. It was therefore taped to a plastic rod that was pushed through the algal mat. Temperature was recorded at 10 cm intervals over the upper 1.2 m and then at 1 m intervals to the bottom.

2.3.3 Density gradients

Density (ρ), uncorrected for solute concentration, and its gradient with depth ($d\rho/dz$), were derived directly from water temperatures using Ruttner's equation as cited by Reynolds (1984). The depth of water subject to turbulent mixing was taken as the point beneath the surface at which the density gradient first exceeded $20 \text{ g m}^{-3} \text{ m}^{-1}$ (Reynolds, 1984). Due to diurnal heating this depth (designated z_1) was often only 1-2 m; the seasonal mixing depth (z_m) was therefore taken to be the depth of maximum density gradient $> 20 \text{ g m}^{-3} \text{ m}^{-1}$, excluding the gradients over the top few meters.

2.3.4 Stability

Stability is the amount of energy (in Newton m^{-1} or $\text{kg m}^2 \text{ s}^{-2}$) required to mix a thermally stratified column of water to isothermy. It was calculated as in the formula given in Viner (1984), using a hypsographic curve derived from a bathymetric map.

2.3.5 Light attenuation

The attenuation of photosynthetically available radiation (PAR; 400-700 nm) was measured with a quantum sensor (Lambda Instruments, LI-185; sensor, LI-125; precision $\pm 0.01 \mu\text{E m}^{-2} \text{ s}^{-1}$). Readings were taken from just below the surface and at 25 - 50 cm intervals to the depth of 1 % of the subsurface value. The attenuation coefficient, ϵ (ln units m^{-1}) and the depth at which 1 % of the subsurface radiation remained ($z_{0.01}$) were calculated for PAR by linear regression (Kirk, 1977).

2.4 CHEMICAL ANALYSES

2.4.1 Oxygen

Dissolved oxygen was measured by the azide modification of the Winkler technique (APHA, 1980) and determined spectrophotometrically (Ashton and Twinch, 1985).

2.4.2 pH, alkalinity and redox potential

pH was measured with an E444 Metrohm meter and total alkalinity was determined by titration with 0.1 N HCl to pH 4.5. Redox potential was measured on the same instrument with a platinum electrode against a standard electrolyte solution and then corrected for pH 7.

2.4.3 Nutrients

Technicon Autoanalysers were used to analyse ammonium-N, nitrate-N, nitrite-N, Kjeldahl-N, total phosphorus, soluble reactive phosphorus, and sulfate. Hydrogen sulfide was determined by the iodometric method described by the American Public Health Association (1980) and dissolved organic carbon as described by Van Steenderen and Lin (1981).

2.4.4 Volatile fatty acids

Volatile fatty acid concentrations were determined on a Water's Associates High Performance Liquid Chromatograph. The acids were separated on a Biograd fast acid column at 65°C with 0.001 M aqueous sulfuric acid as mobile phase and determined with a UV detector at 214 nm.

2.4.5 Gas chromatography

Gas samples were collected into a water-filled test tube held inverted over a funnel that was kept under the surface of the hyperscum. After the test tube's headspace filled with gas it was stoppered hermetically. Gases present in the headspace were analysed with a Perkin Elmer 881 gas chromatograph equipped with a thermal conductivity detector.

2.4.6 Photosynthetic pigments

Immediately upon collection of the water samples 50 - 2000 ml sub

samples were drawn through Sartorius G/F filters, placed in blackened vials containing 6 ml of 90 % ethanol and transported to the laboratory. In hyperscums 5 - 10 ml samples collected in a graduated cylinder were diluted x1000 times with filtered lake water prior to filtration, or alternatively, 0.5 ml samples collected by a nozzle-less syringe were directly injected into the ethanol-containing vials. The vials were suspended for 5 min in a water bath at 78°C and then kept overnight in the dark at room temperature. Absorbance of the extract was measured on a Hitachi 100-60 spectrophotometer at 750, 665 and 480 nm. The extract was then acidified for 1 - 3 min with 0.3 N HCl and absorbance at 750 and 665 nm re-read. Chlorophyll a and phaeopigment concentration were calculated according to Nusch (1980), and carotenoid pigment concentration according to Strickland and Parsons (1968). All chlorophyll values were corrected for phaeophytins. Mean chlorophyll a concentrations for the euphotic zone or 0 - 8 m water column were derived by planimetric integration of the depth profiles.

Phycocyanin was extracted following breakage of the cells by osmotic shock, caused by suspending the cells in glycerol and then rapidly adding distilled water (Wyman and Fay, 1986). Cell debris was separated from the water-soluble pigments by ultra-centrifugation (40 000 rpm). Phycocyanin in the supernatant was determined spectrophotometrically at 620 nm.

2.4.7 Dry weight

Dry masses were determined by oven drying samples at 105°C to a constant mass.

2.5 MEASUREMENTS ON NATURAL POPULATIONS

2.5.1 Phytoplankton cell numbers

Phytoplankton cell numbers were enumerated with an inverted microscope at x500 magnification after sedimenting 1 - 10 ml subsample of the Lugol-Preserved sample or a known dilution thereof in glass sedimentation chambers (Lund *et al.*, 1958).

In order to quantify the populations of *M. aeruginosa* individual cells, rather than colonies, had to be enumerated: *M. aeruginosa* colonies are often of irregular shape (see Reynolds *et al.*, 1981); their size is highly variable (Reynolds, 1973; Reynolds and Rogers,

1976; Box, 1981; Robarts and Zohary, 1984) and changes with the degree of turbulence (Robarts and Zohary, 1984); cell densities within the colony also vary considerably (Reynolds *et al.*, 1981). Consequently, estimates of the volume of *M. aeruginosa* per unit volume of water based on colony numbers cannot be compared with volumes of other species.

Methods for the disruption of *Microcystis* colonies to unicellular suspensions have been proposed by Reynolds and Jarworski (1978) and by Humphries and Widjaja (1979). Box (1981) compared the above methods and recommended the heating technique of Humphries and Widjaja (1979). An alternative, simple and quick method to disrupt *Microcystis* colonies to single cells was tried in our laboratory. The samples were subject to 30 s of high speed blending (20 000 rpm) by an Ultra-Turrax homogenizer (Janke Kunkel-Saufen, W. Germany). Microscopic examination demonstrated that the treatment resulted with unicellular suspensions. In order to ensure that *Microcystis* cells were not broken and lost by this treatment, cell counts of homogenized subsamples were compared with counts obtained for heat-treated (Humphries and Widjaja, 1979) subsamples of the same sample.

The data from 5 replicate counts for each treatment were tested graphically for normal distribution, using normal probability plots (Zar, 1974) and were found not to deviate significantly. The differences between the means and the variances of the cell number estimates were tested using the variance-ratio and the two-sample *t* tests (Zar, 1974). Cell counts of *M. aeruginosa* obtained using the two methods were not significantly different (Table 2.4). The means differed only by 2 %, the coefficients of variations were small in both cases (10 and 16 %) and the variances were not significantly different at the 10 % level.

TABLE 2.4 A comparison of the effect of high speed blending and heating (see text) on cell counts of *M. aeruginosa*. Data are: means (\bar{x}), no. of replicates (*n*), coefficients of variation (*cv*), and variances (s^2). At least 500 cells were counted in each replicate.

treatment	\bar{x} cells ml ⁻¹	<i>n</i>	<i>cv</i> %	s^2
blending	8.86 x 10 ⁶	5	10	8.48
heating	8.68 x 10 ⁶	5	16	1.86

difference between means: $t = 0.249, p > 0.2$
difference between variances: $F = 4.56, p > 0.1$

The effect of high-speed blending on cell counts of other phytoplankton species was examined by comparing cell counts of homogenized and hand-shaken (control) samples. The details of these experiments are given elsewhere (Zohary and Pais Madeira, 1987) and only the conclusions are summarized here. The high-speed blending resulted in significantly lower cell counts of some species (e.g. *Chroomonas* sp. and *Pediastrum boryanum*), whereas other species were unaffected (e.g. *Melosira granulata* and *Carteria* sp.). An exception was found for *Pseudanabaena* sp., a small cyanobacterium whose short filaments are usually embedded in the mucilaginous sheath of *M. aeruginosa*. Cell counts of this species were significantly higher in the homogenized samples. An explanation was that in the control samples the small filaments were hidden by the much larger *Microcystis* colonies.

Based on these experiments, high-speed blending was used routinely for preparation of subsamples for counts of *M. aeruginosa* and *Pseudanabaena* sp.; other species were counted on aliquots of the original, untreated samples.

From May 1982 till October 1983 five fields of vision and a total of at least 400 cells per sample were counted, giving precision of 10-20 % for the dominant species (Lund *et al.*, 1958). In order to obtain reliable counts of the less common species the counting method was modified according to Lewis (1978). From November 1983 onwards 100 cells of each species or 100 fields of vision, whichever came first, were counted. After each field counting was discontinued for species whose counts exceeded 100 cells. Counting was thus focused on increasingly rare species as the count proceeded, to a limit of 100 fields.

Algal species were identified according to Geitler (1932), Prescott (1954), Bold and Wynne (1978), Rippka *et al.* (1979), Greeson (1982), Komarek and Fott (1983), and W.E. Scott, F.R. Schoeman and R.E.M. Archibald (personal communication).

Cell volumes were estimated from the linear dimensions of living cells, assuming their forms correspond to simple geometric shapes. A minimum of 20 individuals of each species were measured in each sample. Cell volume of each individual was computed from its geometric shape using the formulae given in Rott (1981). The median cell volume for each species was used for conversion of cell numbers to volumes, as recommended by Rott (1981).

2.5.2 Bacterial cell counts

Bacteria in the hyperscum were enumerated and photographed under an epifluorescent microscope equipped with a camera using the DAPI staining technique (Robarts and Sephton, 1981). Bacteria were counted differentially according to morphological types. The biovolume of each type was estimated from linear dimensions measured under the fluorescence microscope or from photographs of the DAPI-stained bacteria.

2.5.3 Primary production

Primary productivity throughout the euphotic zone of the main basin was measured weekly using the ^{14}C uptake method described by Robarts (1984).

2.5.4 Potential photosynthetic capacity of hyperscum *M. aeruginosa*

The potential photosynthetic capacity of the dark adapted hyperscum *M. aeruginosa* was measured weekly between 10 May and 28 August 1984 using the ^{14}C uptake method as modified by Robarts (1984). Prior to each experiment *M. aeruginosa* from the hyperscum was acclimatized for 24 h to the light conditions in the lake. This was done by incubation of a hyperscum sample diluted 1000-fold with filtered (Sartorius G/F) lake water, in a dialysis bag (inflated diameter, 212 mm) tied at 50 cm depth to a raft at the main basin station. A control, using lake phytoplankton from the main basin, was treated similarly. On the following day the water from each bag was used to fill a series of duplicate light and single dark 125 ml glass bottles, keeping aliquots for chlorophyll, pH and alkalinity determinations. Each bottle was injected with 1.5 to 2.0 $\mu\text{Ci NaH}^{14}\text{CO}_3$ and incubated horizontally *in situ* at depths of 0, 0.5, 1, 2, 3, 4 and 5 m for 2 to 3 h between 11:00 h and 14:00 h. The procedure then followed that of Robarts (1984). Production rates were calculated using the mean light bottle counts minus the dark bottle counts. Photosynthetic capacity, the maximum production rate in the depth profile per unit chlorophyll (P_{max}), expressed as $\text{mg C (mg chl)}^{-1} \text{ h}^{-1}$, was computed for both the hyperscum and control (lake) populations.

2.5.5 Phytoplankton sedimentation rates

From November 1983 to October 1984 sediment traps were deployed at the main basin station. Traps were constructed according to Reynolds

(1979) design, using 565 ml glass screw-cap jars. Each cap had a hole bored out centrally, into which a 10 cm long plastic tubing (internal cross section area, 5.52 cm^2) was inserted so that about 2 cm projected. Performance characteristics of this design have been evaluated by Reynolds (1979). The traps were secured in triplets inside a wire basket attached to a weighted rope. Tension was provided by a submerged float and the location was marked by a surface buoy. During operation the apertures of the traps were located 1 m above the lake bed and facing upwards. The traps were emptied weekly and replaced by clean jars containing distilled water with 4 % formalin. Reynolds and Wiseman (1982) have shown that the fixative was effective for more than 2 weeks in preserving algae entering the traps and prevented possible growth within the traps.

Between 28 May and 4 September 1984 an additional set of sediment traps was deployed at 5 m depth below the hyperscum, near station 4 or 4A (Fig. 3.2), and was operated in the same manner as above. In order to get new traps into position under the hyperscum they were filled, assembled and lowered into the incubation depth outside of the hyperscum and then slowly towed behind the boat to their incubation site. Removal of incubated traps was done in the same manner.

Aliquots of the well mixed, combined trap contents were sedimented for enumeration of major algal species as described above. The trap catches were expressed as daily areal rates of sedimented algal cells $\text{cm}^{-2} \text{ d}^{-1}$.

2.5.6 Microelectrode studies

Oxygen (Revsbech, 1983) and pH (Thomas, 1978) microelectrodes with sensing tips of 5 μm and 55 μm , respectively, were inserted into core samples by means of a micromanipulator. Oxygen electrodes were calibrated with standards determined by the azide modification of the Winkler method (APHA, 1980) and pH electrodes with standard buffer solutions. Gradients of oxygen and pH over the uppermost 2 - 3 mm of the core samples were measured at 0.1 mm depth intervals in the dark and in the light after steady-state has been established (usually 1 to 3 min after light conditions were altered). Oxygenic photosynthesis rates were measured as the initial slope of oxygen depletion after the light was turned off (Revsbech *et al.*, 1981). All measurements were carried out at room temperature (ca. 19°C) and at light intensities ($625 - 1725 \mu\text{E m}^{-2} \text{ s}^{-1}$) resembling natural conditions in Hartbeespoort Dam at midday in winter.

2.5.7 Electron microscopy

Samples were prepared for transmission electron microscopy following a modification of the method of Cmiech *et al.*, (1984). Fresh samples were placed in Reichert 'flo-thru' capsules, prefixed in the field for 2 h in 2.5% glutaraldehyde in 0.05% phosphate buffer (pH 7.2), washed twice in phosphate buffer and left overnight at 4°C. The following day the samples were fixed for 1 h in 1% OsO₄ in 0.05 % phosphate buffer in the dark. Thorough washing with deionized water followed, thereafter samples were dehydrated through an ethanol series (50 %, 70 %, 90 % and 100 % x3 changes) and rinsed in 3 x 5 min changes of propylene oxide. The material was embedded in Spurr's (1969) soft resin, polymerized overnight at 70°C in a Reichert KT100 embedding oven, sectioned on an LKB Ultratome III, collected on copper viewing grids, double stained with methanol saturated uranyl-acetate and lead citrate (Reynolds, 1963), and viewed and photographed on a Phillips EM301 transmission electron microscope at 60 or 80 kW.

Samples for scanning electron microscopy were prepared according to Paerl and Shimp (1973). Fresh samples were collected on a nucleopore filter that was secured in aluminum foil, fixed in 2 % glutaraldehyde in cacodylate buffer (pH 7.2) for 1 h, dehydrated through an ethanol series and then critical-point dried in a pressure bomb apparatus. The filters were mounted on studs, coated with gold and viewed on a JEOL scanning electron microscope.

2.6 DATA ANALYSIS AND CALCULATIONS

2.6.1 Total chlorophyll content of hyperscums

The approximate area covered by the hyperscum at about 10:00 h on sampling days was traced on a map and later measured by planimetry. Assuming that the lateral distribution of chlorophyll concentrations was homogeneous (Table 3.1) the total amount of chlorophyll contained in the hyperscum was estimated by extrapolation from the area and the chlorophyll content of the top 1 m at stations 1 to 4 or 1A to 4A (Fig. 2.3).

2.6.2 Total chlorophyll content of the lake

Mean monthly values of total lake chlorophyll a content were derived from the weekly depth profiles of chlorophyll concentrations, using

the data available from all stations. The average concentration at each depth was weighted by the corresponding volume of water in a horizontal "slice" of the lake, calculated from a hypsographic curve for Hartbeespoort Dam. Data for shore stations were volume weighted separately. The total chlorophyll content was the cumulative sum for all the "slices". When hyperscums existed their monthly mean chlorophyll content was added to the total. However, due to the characteristic heterogeneous spatial distribution of chlorophyll in Hartbeespoort Dam (section 3.2.4) the resultant total lake chlorophyll content estimates should be regarded cautiously, as being only an indication of the real values.

2.6.3 Statistical analyses

Statistical analyses of the data were carried out on an Olivetti M24 Personal Computer using STATGRAPHICS version 2.1 (STSC, Inc.) or on a CDC Cyber 750 computer using the SPSS software package (Nie *et al.*, 1975).

CHAPTER 3

THE DOMINANCE OF *MICROCYSTIS AERUGINOSA* IN HARTBEESPOORT DAM

3.1 INTRODUCTION

According to the model of Reynolds *et al.* (1981) planktonic populations of *Microcystis aeruginosa* develop in spring or early summer, bloom and become dominant for 2-3 months in summer, then disappear from the water column to over-winter on the bottom sediments. Reynolds *et al.* (1981) proposed that their model may be generally applicable in temperate and subtropical eutrophic lakes. Indeed, the annual cycle of *M. aeruginosa* in many eutrophic temperate lakes conforms to this model: large planktonic summer populations that decline in autumn and are replaced by a benthic phase in winter have been reported by Sirenko *et al.* (1969); Topachevskiy *et al.* (1969); Reynolds and Rogers (1976); Kappers (1984); Fallon and Brock (1981); Takamura *et al.* (1984); Bell and Ahlgren (1987), to name a few.

Data from Hartbeespoort Dam indicated a different annual pattern, where *Microcystis* was the dominant phytoplankton species (>90% by volume) throughout the summer, autumn and winter of 1982/83 (Robarts and Zohary, 1984). Frequent surface blooms which accumulated at lee shores to form semi-permanent hyperscums occurred mostly in winter (Zohary, 1985).

With *M. aeruginosa* being a cosmopolitan species in eutrophic systems, it is important to understand the environmental conditions that favour its dominance over extended periods of the year. In this chapter the abundance, distribution and dominance of *Microcystis* in Hartbeespoort Dam are examined over a period of 4.5 years. The effect of the external environment and of intrinsic (physiological) characteristics on the abundance and on the annual cycle of *Microcystis* are assessed. The hypothesis was that in hypertrophic Hartbeespoort Dam *M. aeruginosa* remained the dominant phytoplankton species up to 10 months each year because by maintaining itself within shallow diurnal mixed layers it successfully competed for light, the major limiting resource (Robarts and Zohary, 1984). At the same time it was physiologically adapted to a high light environment. In addition, during periods of suboptimal temperatures, pre-existing populations could remain within the illuminated layers and suffered low loss rates.

3.2 RESULTS

3.2.1 The physical/chemical environment: an overview

Over the 4 year study mean 0-8 m water temperature in the main basin of Hartbeespoort Dam ranged between winter minima of 11.7 - 12.3 °C in July and summer maxima of 25.0 - 25.7 °C in January or February (Fig. 3.1a). Changes in temperature with time, depth and water levels, are shown in Fig. 3.2. Overturn occurred in March or April and stratification in late August or early September. The thermocline was not well defined, and in many cases the metalimnetic temperature gradient was spread over about 10 m; an anaerobic hypolimnion developed every year (Fig. 3.2).

Water column stability (S, the amount of energy required to mix a thermally stratified water column to isothermy) increased as the epilimnion heated following thermal stratification to a maximum in mid-summer. After overturn S declined to low values ($<10 \text{ kg m}^2 \text{ s}^{-2}$), which were maintained until the water column started to warm again (Fig. 3.1b). The extent of the stability maxima varied with the changes in water level: S was highest ($220 \text{ kg m}^2 \text{ s}^{-2}$) in September to October 1982 (Fig. 3.1b), when the lake was 27 - 30 m deep (Fig. 3.2). In the following years when maximum depth remained below 25 m stability did not exceed $135 \text{ kg m}^2 \text{ s}^{-2}$.

Solar radiation was characteristically high throughout the year, due to the subtropical latitude (26° S), the high elevation (1162 m), and the climate with winter days being mostly cloudless. It ranged between summer maxima of 26 to 34 $\text{MJ m}^{-2} \text{ d}^{-1}$ and winter minima of 11 to 12 $\text{MJ m}^{-2} \text{ d}^{-1}$ (Fig. 3.1c). In winter midday photosynthetically available radiation (PAR) usually exceeded $1000 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 3.1c), comparable with mid-summer PAR levels in many northern hemisphere temperate lakes.

Wind speeds recorded at Oberon (south-eastern shore; (Fig. 2.2a) were characteristically low (Figs 3.1d, 3.3). Lowest mean weekly speeds of 1 to 1.5 m s^{-1} were recorded between May and July each year, coinciding with the period of minimum stability and low winter temperatures (Fig. 3.1). Mean weekly wind speed increased between August and September, the time of the onset of stratification, and was highest (up to 2.5 m s^{-1}) in September or October. The seasonal pattern of diel cycles of shore wind speeds are shown in Fig. 3.3b. Typically, the night and early morning hours (20:00 to 08:00) were calm (wind

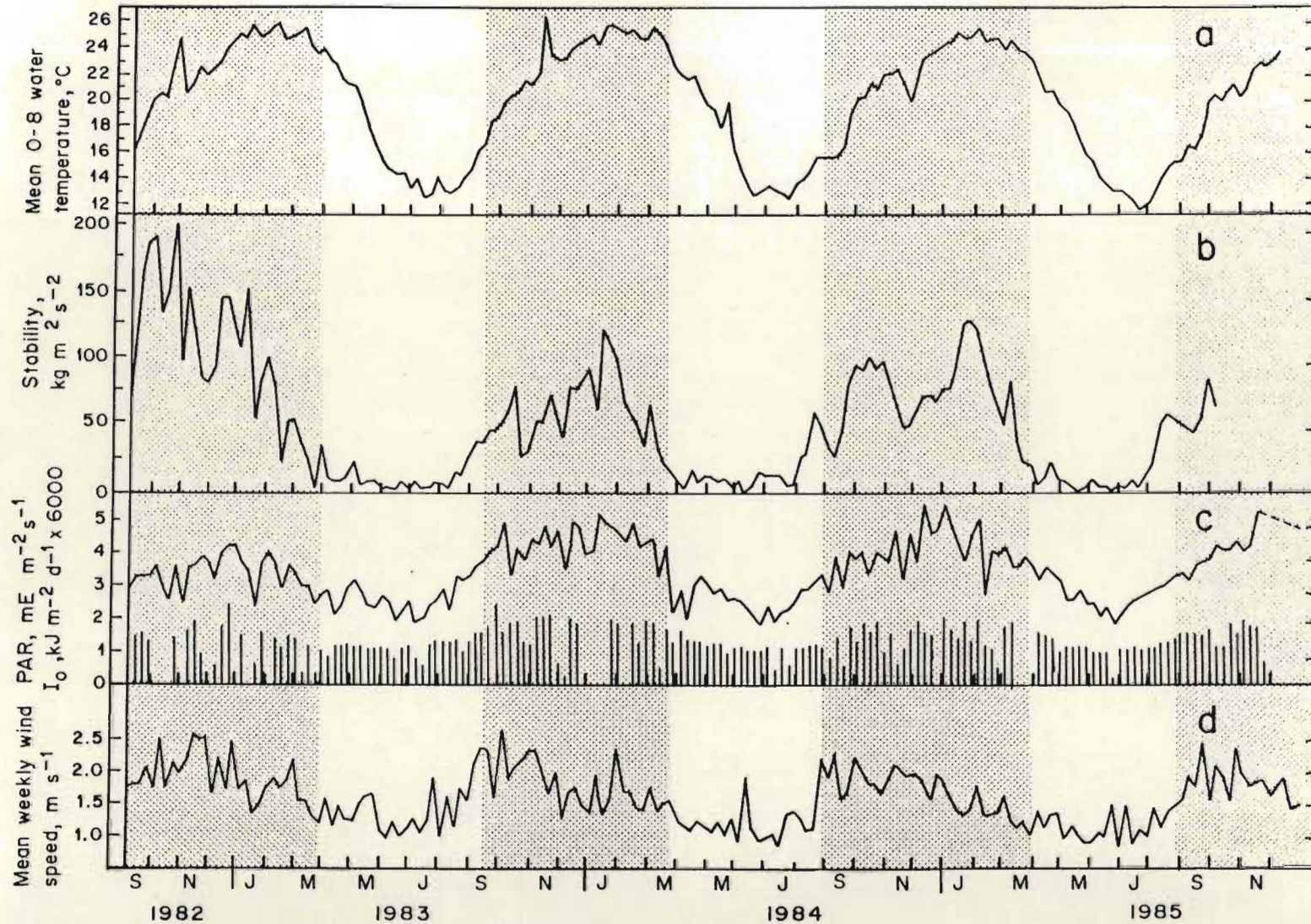


FIGURE 3.1 The seasonal cycles in Hartbeespoort Dam, South Africa of (a) mean 0-8 m water temperature, (b) water column stability for the main basin, (c) solar irradiance (solid line) and the weekly midday irradiance (PAR, histogram) and (d) the mean weekly wind speed measured on the southeastern shore of the main basin. Periods of lake stratification are indicated by shading.

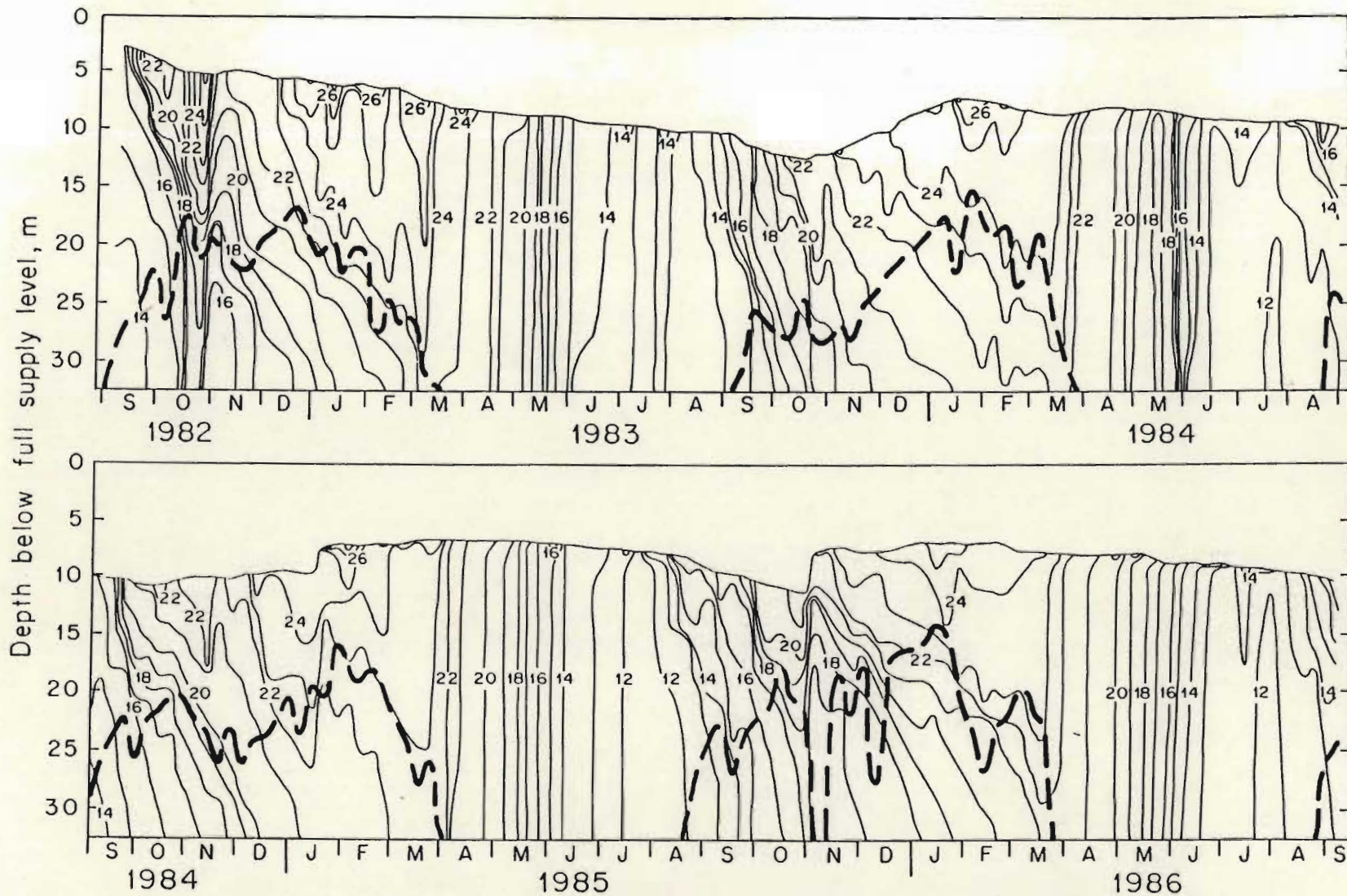


FIGURE 3.2 Isotherms for Hartbeespoort Dam, 1982-1986. Thick line marks the depth of 1% oxygen saturation.

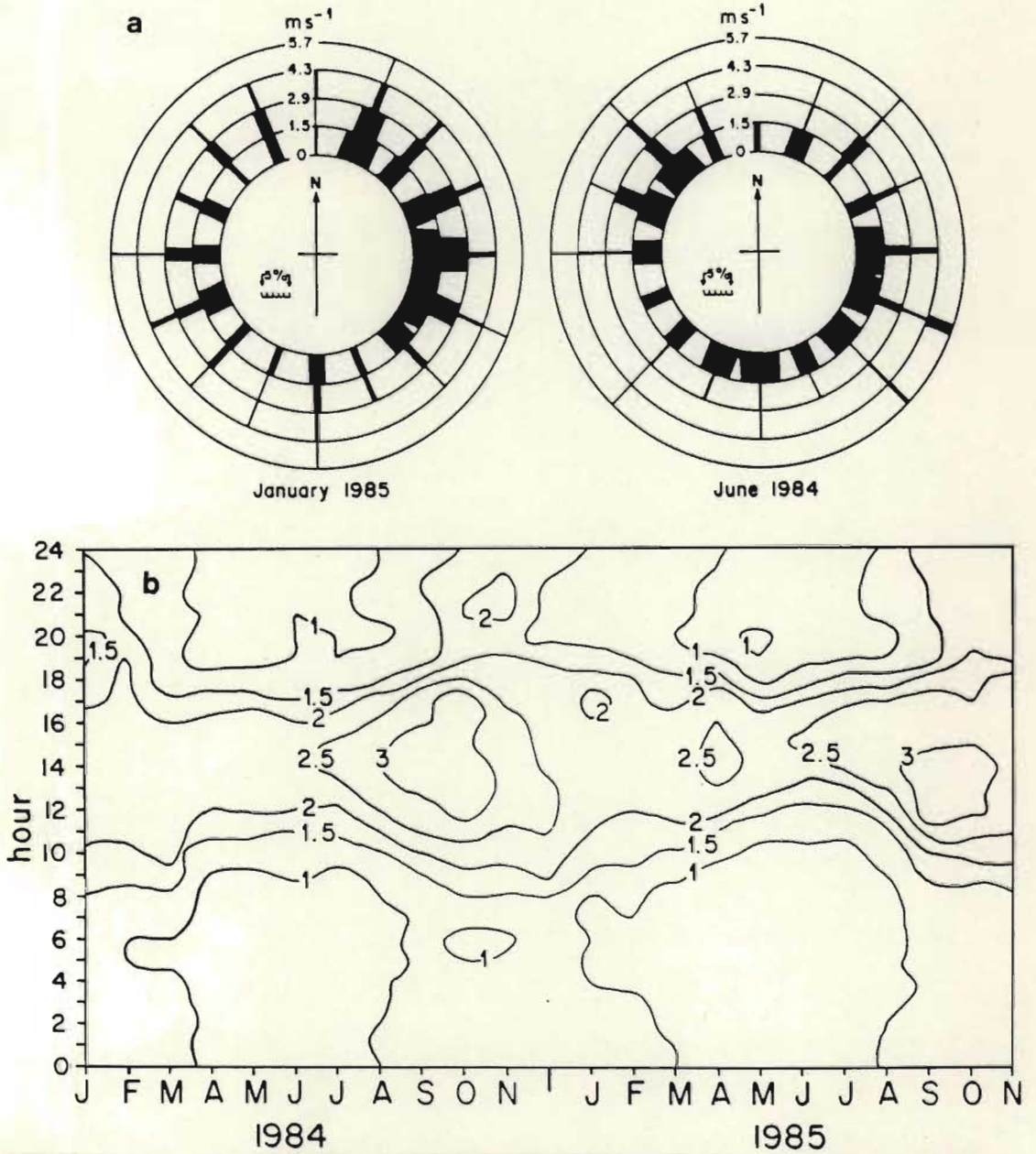


FIGURE 3.3 The wind regime at Oberon (Fig. 2.2a), on the southeastern shore of Hartbeespoort Dam: (a) Representative wind roses for summer (January) and winter (June) and (b) the seasonal and diel patterns of monthly mean hourly wind speeds.

speed ($<1.5 \text{ m s}^{-1}$). Wind speeds peaked between 13:00 to 14:00 and then declined again. Yet, as demonstrated in a wind rose for June 1984 (Fig. 3a), the maximum afternoon speeds on most days in winter and spring rarely exceeded 2.9 m s^{-1} .

Throughout the study period epilimnetic phosphorus (as SRP) and combined inorganic nitrogen (as $\text{NO}_3 + \text{NO}_2$ and NH_4) were never depleted to concentrations that would limit phytoplankton growth rates: the lowest concentrations recorded were $129 \mu\text{g l}^{-1}$ $\text{NO}_3 + \text{NO}_2\text{-N}$, $50 \mu\text{g l}^{-1}$ $\text{NH}_4\text{-N}$ and $227 \mu\text{g l}^{-1}$ SRP in February or March 1983 (Fig. 3.4). Rates of primary production and the size of the standing stock (as chlorophyll a) were not significantly related to epilimnetic concentrations of inorganic N or P ($p>0.1$) confirming that these key nutrients did not determine phytoplankton growth rates.

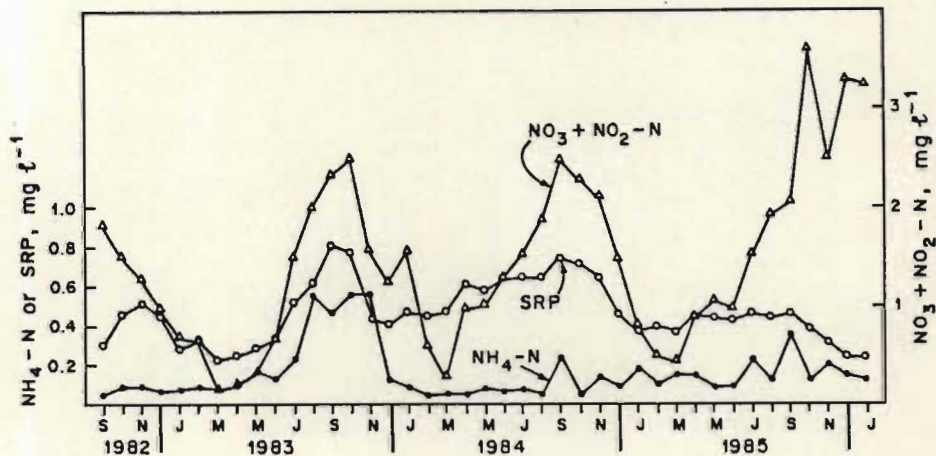


FIGURE 3.4 Seasonal variations in monthly mean concentrations of dissolved nitrogen and phosphorus (SRP = soluble reactive phosphorus) in the upper 5 m in the main basin of Hartbeespoort Dam.

3.2.2 The seasonal cycles of *Microcystis aeruginosa*

The temporal changes in the abundance of *M. aeruginosa* in the upper 8 m of the main basin of Hartbeespoort Dam, expressed as cell volumes per unit volume of water, are shown in Fig. 3.5a. The large week to week fluctuations in *Microcystis* abundance masked the seasonal pattern of growth and decline. As will be demonstrated later, these fluctuations were attributed primarily to horizontal shifts of buoyant, existing populations. Thus, examination of a running mean for the weekly data was justified. On 4 occasions when thick drifting surface

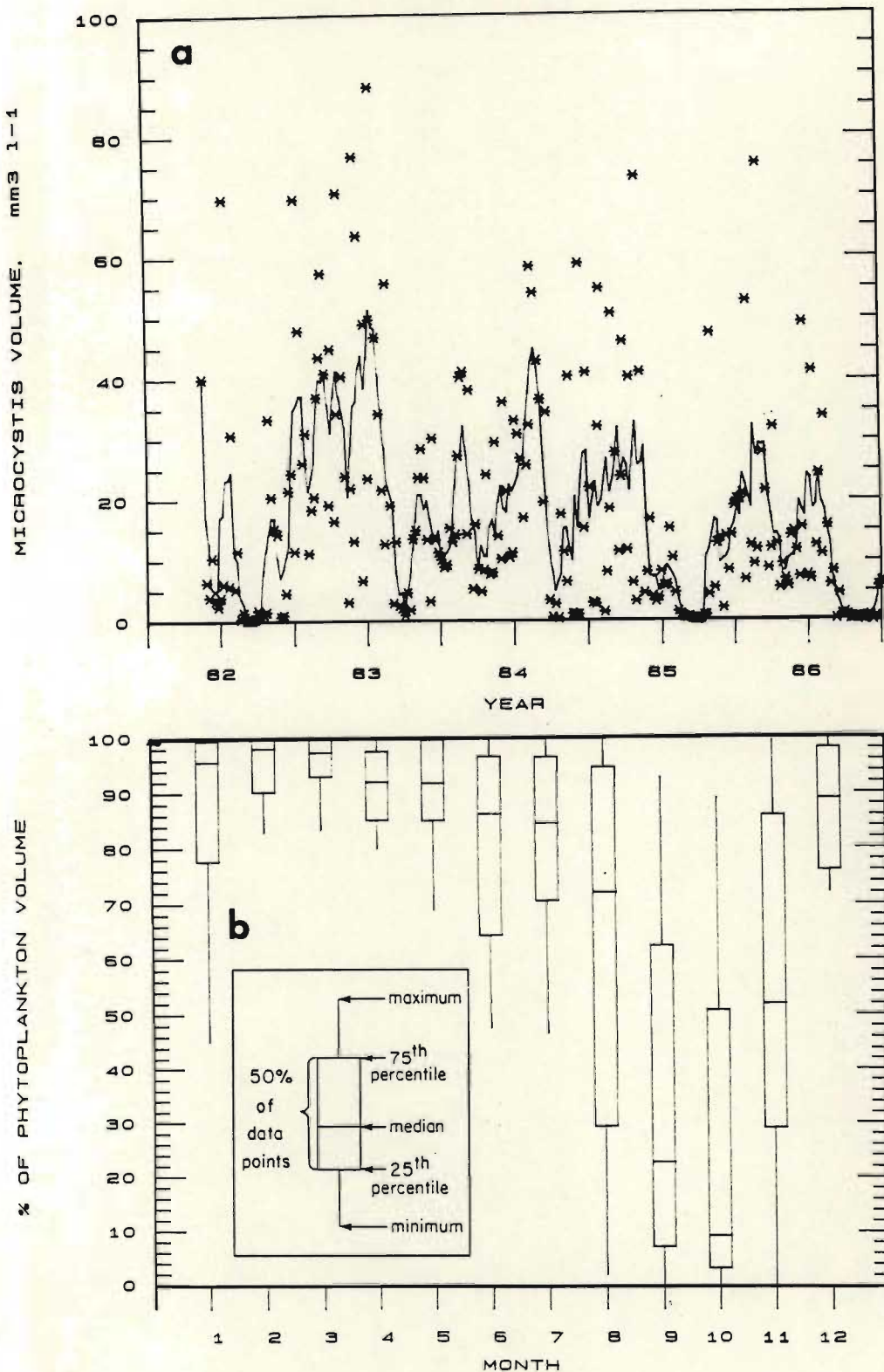


FIGURE 3.5 Seasonal variations in the abundance of *Microcystis aeruginosa* in the 0-8 m layer of the main basin of Hartbeespoort Dam, (a) changes in *Microcystis* volume plotted as a running mean for 5 consecutive weeks (individual data points are marked) and (b) the monthly changes in percentage contribution of *Microcystis* to the total phytoplankton population volume, summarizing 4½ years of weekly data (n=230).

blooms and not actual growth caused exceptionally high volume values ($>100 \text{ mm}^3 \text{ l}^{-1}$), these values were replaced by the mean for the preceding and following weeks. When a running mean for five consecutive weeks was then plotted a characteristic annual pattern emerged, although the timing, the rate of increase and the eventual standing crop varied from one year to another.

Lowest concentrations of *M. aeruginosa* were recorded in August and September each year (Fig. 3.5a), coinciding approximately with the onset of thermal stratification (Fig. 3.2). The period of low concentrations lasted only 2 to 3 months, and by October or November the population was rapidly increasing. Usually by the end of November *M. aeruginosa* was the dominant species, comprising $>80\%$ of the total phytoplankton volume in the upper 8 m (Figs 3.5b, 3.6). The population continued to increase in summer and reached maximum standing crops around January to February. The large standing crops and the

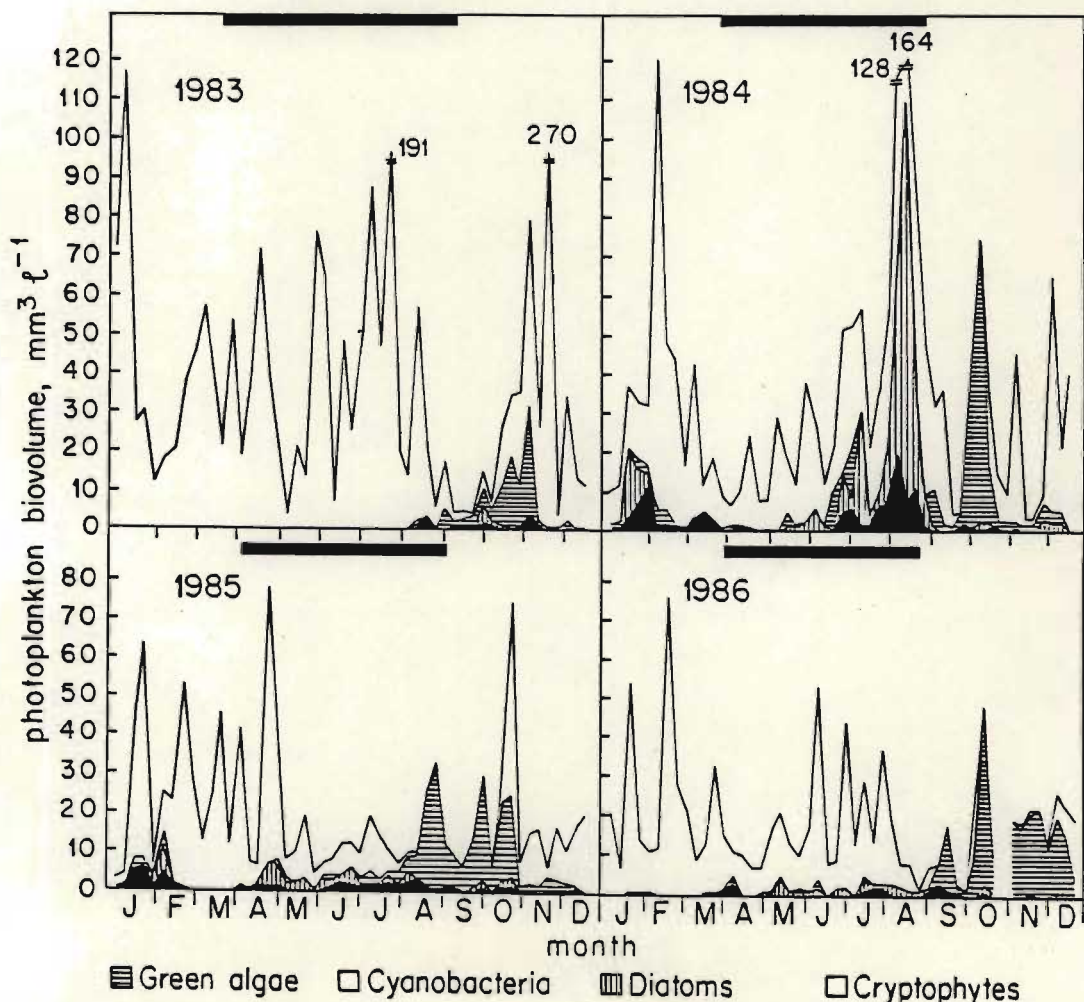


FIGURE 3.6 The seasonal changes in the composition and abundance of phytoplankton in the main basin of Hartbeespoort Dam. Black bars indicate periods of lake holomixis.

dominance of *M. aeruginosa* were then maintained all autumn and most of the winter (Figs 3.5, 3.6), and *Microcystis* abundance in July was similar to that in January and February. An important characteristic of the ultrastructure of the winter surface populations was the high gas vacuole content (50 to 70 % of section area) of the cells (see later, plate 6.3b). An abrupt decline of the population occurred each year in August, except in 1985 when the population gradually declined from April to August (Fig. 3.5).

Diatoms (mainly *Melosira granulata* (Ehrenb.) Ralfs), accompanied by cryptophytes (*Chroomonas* sp. and *Cryptomonas* sp.), and 2 to 3 weeks later *Oocystis* sp. (chlorophyceae), became dominant (Fig. 3.6). Other chlorophyceae, such as *Pediastrum boryanum* (Turpin) Meneghini, *P. duplex* Meyen, *Coelastrum* sp., *Scenedesmus* spp. and *Ankistrodesmus* sp. accompanied *Oocystis*. Over the short periods when other species were dominant, *M. aeruginosa* was still present in the water column, usually comprising 1 to 30% of the phytoplankton volume. The lowest recorded concentration of *M. aeruginosa* was 1900 cells ml⁻¹ or 0.12 mm³ l⁻¹ on 17 September 1985.

3.2.3 Sedimentation

The temporal changes in the concentration of *Microcystis aeruginosa* cells in the upper 0 - 8 m water column and in the recoveries of this species from sediment traps having apertures facing upwards are shown in Fig. 3.7. Trap recoveries were low during the main growth season

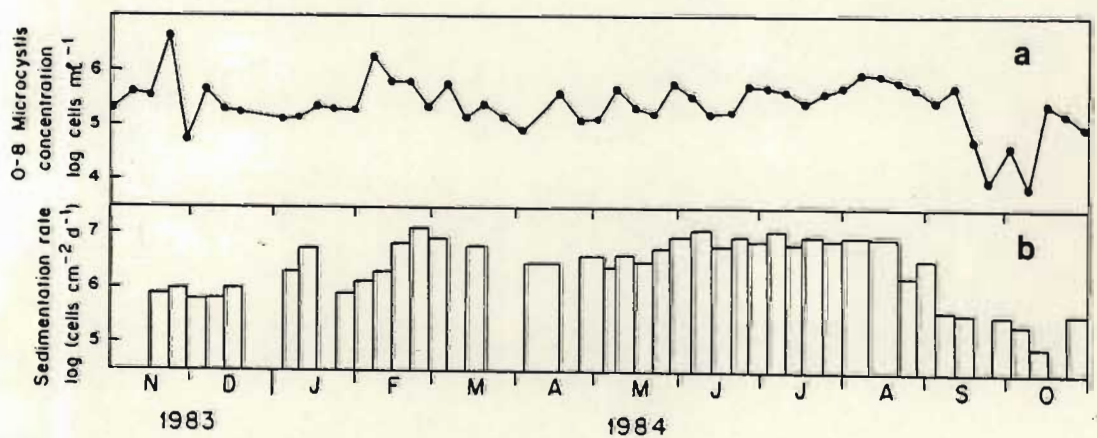


FIGURE 3.7 Temporal changes in *Microcystis aeruginosa* cell concentration in the upper 8 m of the water column in the main basin of Hartbeespoort Dam (a) and in catches in sediment traps (b). Histogram widths are proportional to the duration of trap exposure and their heights to the rate of *Microcystis* sedimentation. Periods without bars indicate missing data.

of this species from mid-November to mid-February, and then again in September - October when the planktonic standing stock was at its annual low (Fig. 3.6). Highest trap recoveries occurred in winter between June and August, preceding the major *M. aeruginosa* population decline.

3.2.4 Spatial variations in chlorophyll a distribution

As with phytoplankton volume (Fig. 3.6), week to week fluctuations in chlorophyll a concentration in the upper part of the water column were large. Surface (top 11 cm) chlorophyll a concentrations ranged over 3 orders of magnitude, e.g. from 4.2 mg m⁻³ in September 1983 to 2 970 mg m⁻³ in November that year (data not shown). When *Microcystis aeruginosa* was dominant the distribution of chlorophyll a with depth was characteristically uneven, with highest concentrations near the surface (Fig. 3.8a). This occurred at most times of the year, irrespective of whether the lake was stratified or non-stratified. The infrequent incidents of homogeneous distribution of chlorophyll a throughout the epilimnion usually coincided with periods of chlorophyceae dominance (Fig. 3.8b), or with strong winds as on 12 June 1984 (see Fig. 3.11).

Horizontal variations in chlorophyll a concentrations were as striking. The chlorophyll a concentrations of surface to 4 m integrated (hosepipe) samples collected at 14 pelagic stations over one and a half hours often ranged over 2 orders of magnitude (Table 3.1). When *M. aeruginosa* was dominant the coefficient of variation (CV) of the chlorophyll a concentrations ranged between 64.7 % and 163 % of the mean. However, when non-buoyant species (such as *Oocystis*) were dominant the horizontal variations in chlorophyll a were smaller, as indicated by the CV of 14.2 - 22.3 % (Table 3.1).

TABLE 3.1 Variability in the chlorophyll a concentration of the upper 4 m layer (hosepipe samples) among 14 pelagic (depth >4 m) stations in Hartbeespoort Dam. CV - coefficient of variation, % of SD.

Date	dominant species at main basin	chlorophyll a concentration, mg m ⁻³			
		n	mean	CV	range
19.02.85	<i>M. aeruginosa</i>	14	84.63	86.4	11.55 - 273.66
12.03.85	<i>M. aeruginosa</i>	14	92.86	66.1	21.83 - 245.92
21.05.85	<i>M. aeruginosa</i>	14	32.54	86.9	6.70 - 108.22
20.08.85	<i>Oocystis</i> sp.	14	39.23	22.3	28.33 - 59.46
17.09.85	<i>Oocystis</i> sp.	13	13.28	14.2	9.15 - 16.01
19.11.85	<i>M. aeruginosa</i>	14	57.36	163.1	16.22 - 375.76
21.01.86	<i>M. aeruginosa</i>	14	94.07	140.0	21.49 - 536.90
19.02.86	<i>M. aeruginosa</i>	14	73.03	64.7	17.54 - 158.58

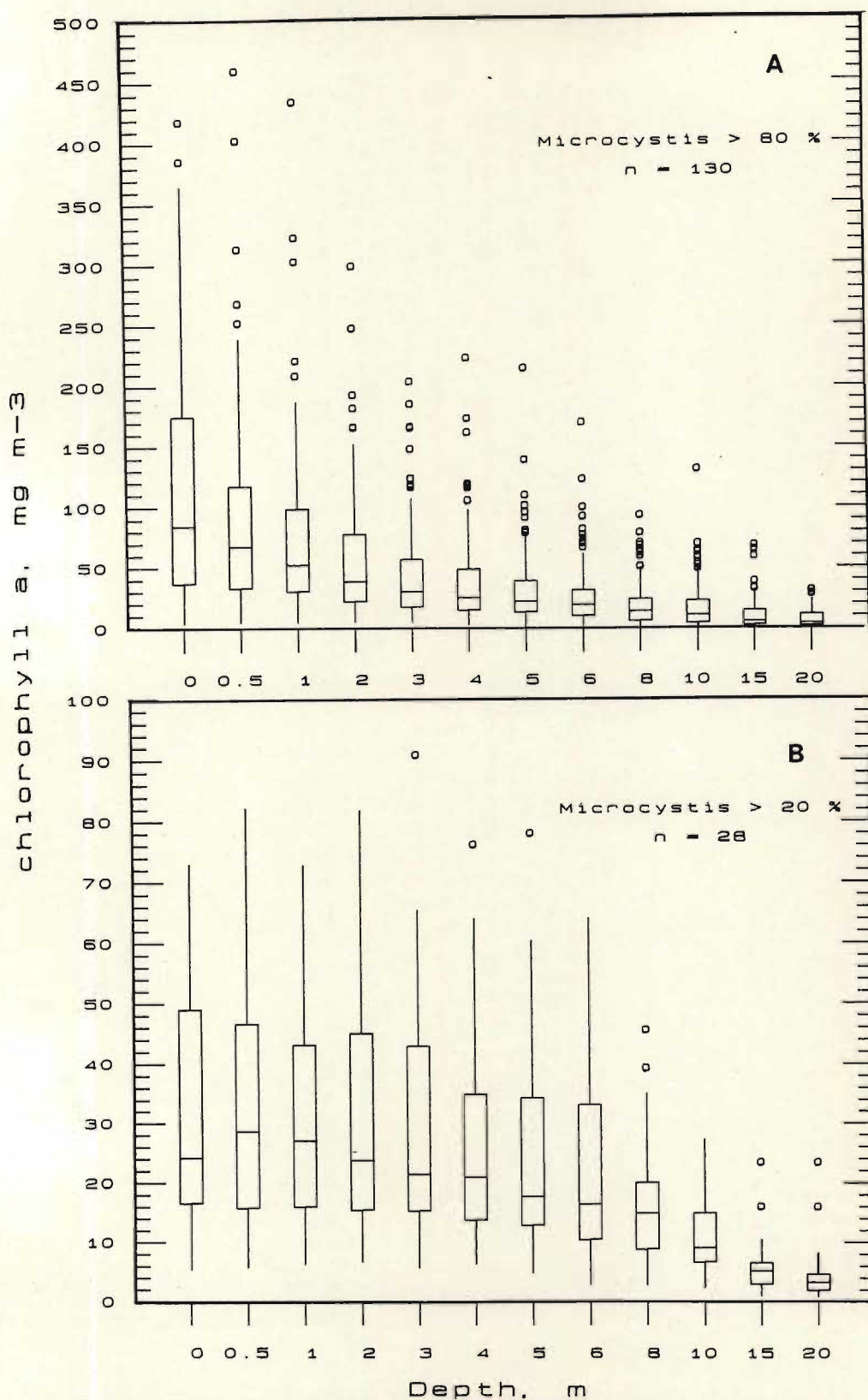


FIGURE 3.8 Depth-distribution of chlorophyll a concentration in the main basin of Hartbeespoort Dam, 1982 - 1986, (a) when *Microcystis* was > 80% by volume of the total biomass and (b) when *Microcystis* was < 20% of the total biomass. Box-plot components are as in Fig. 3.5b. Outlier points (> 1.5 the interquartile range) are marked individually, except 5 points in Fig. a, 0 m depth, which exceed 500 mg m⁻³ and range up to 3800 mg m⁻³. n = number of weekly samples for each depth.

3.2.5 Vertical mixing and vertical distribution of *Microcystis*

At winds exceeding a critical speed of 3.7 m s^{-1} turbulent mixing in the form of Langmuir cells begins (Scott *et al.*, 1969; George and Edwards, 1976). Using the linear relationship established between wind speeds over the main basin and at the southeast shore-based station (see methods), speeds of 3.7 m s^{-1} over the main basin corresponded to 2.9 m s^{-1} recorded on shore. The predicted proportion of the time each month that actual wind speeds in the main basin exceeded the critical value of 3.7 m s^{-1} are given in Table 3.2. The proportion was characteristically lower between March and July (autumn and early winter) and higher between September and December (spring and early summer), but throughout the year it did not exceed 25% (Table 3.2). Thus, on-lake winds were most of the time insufficient to cause vertical mixing over the epilimnion by Langmuir circulations.

TABLE 3.2 Proportion (%) of the time each month of wind speed exceeding 3.7 m s^{-1} in the main basin, as predicted from the data recorded at Oberon (see text).

Month	1984	1985	Month	1984	1985
January	14.8	8.3	July	8.2	6.3
February	11.7	8.8	August	12.5	9.6
March	5.7	no data	September	20.4	11.4
April	6.1	7.5	October	24.8	22.5
May	7.2	7.6	November	19.3	21.0
June	9.2	5.5	December	17.9	20.0

The depth of the bottom of the epilimnion, or of the seasonal mixed layer, z_m , was taken as the region in the depth profile over which the maximum density gradient was recorded, when this gradient was $> 20 \text{ g m}^{-3} \text{ m}^{-1}$ (or g m^{-4}), and excluding near-surface stratification. z_m , which reflected the gross thermal structure of the lake, ranged between 7 m and 18 m (Table 3.3). However, when short (daily) time scales were considered, a different mixing pattern emerged. The characteristic low speed winds (Fig. 3.3) and high incident solar radiation (Fig. 3.1c) caused heating of the uppermost part of the water column during the day (Fig. 3.9). Heating led to the formation of one or more shallow diurnally mixed layers (designated z_1 , z_2 , etc.), which were separated from the rest of the water column by density gradients $> 20 \text{ g m}^{-4}$. Such gradients over the top 2 m developed

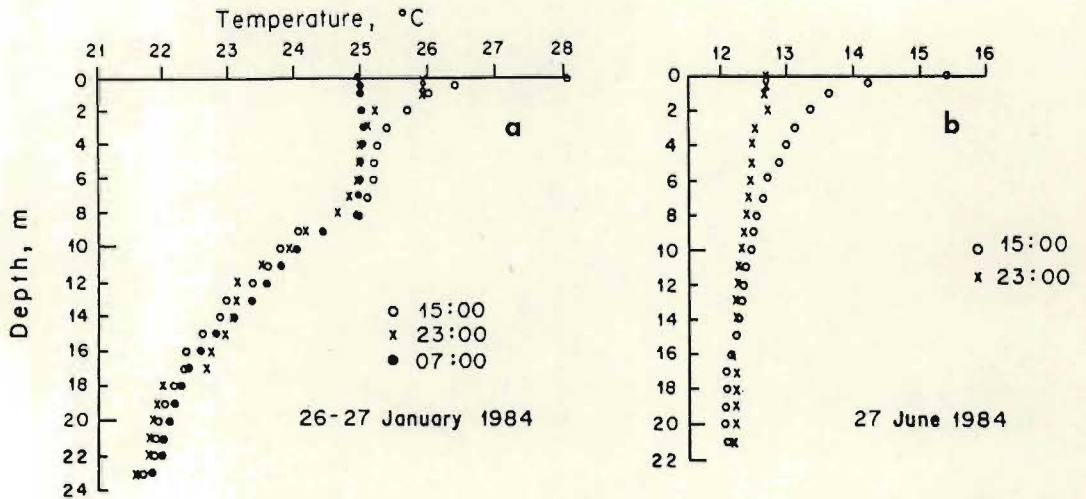


FIGURE 3.9 Diel changes in depth profiles of water temperature in the main basin of Hartbeespoort Dam during stratification (a) and during the winter holomixis period (b) showing the formation of a shallow diurnal mixed layer.

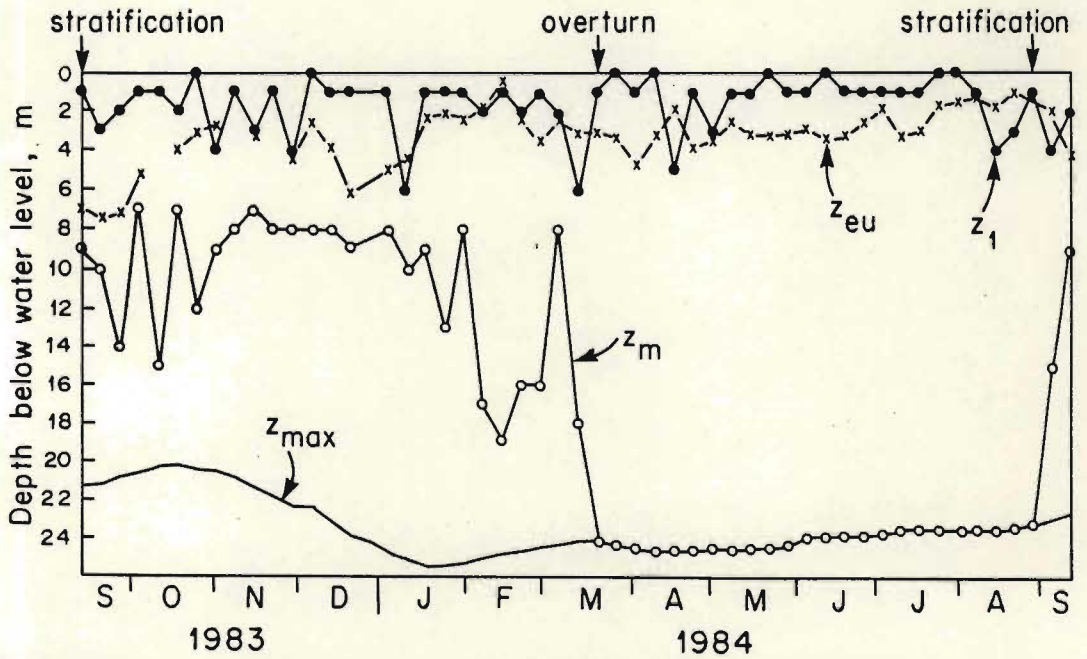


FIGURE 3.10 Temporal changes in the maximal lake depth (z_{max}), the depth of the seasonal mixed layer (z_m), the depth of the shallowest (see text) diurnal mixed layer (z_1) and the depth of the euphotic zone (z_{eu}) in the main basin of Hartbeespoort Dam.

on 79 to 85 % of the sampling days during stratification and on 56 to 75 % of the days during the non-stratified periods (Fig. 3.10, Table 3.4). The wind speed necessary to deepen the mixed layer through a given density gradient depends not only on the density gradient but also on the depth of the mixed layer overlying the gradient, i.e. on the potential energy of the water column. Wind speeds $> 4 \text{ m s}^{-1}$ are required to break a gradient of 20 g m^{-4} at 1 m depth, and $> 8 - 9 \text{ m s}^{-1}$ at 2 m depth or more (Reynolds, 1984). On many occasions in Hartbeespoort Dam the gradient was $> 100 \text{ g m}^{-4}$ (Table 3.4). Heat loss by conduction at night eliminated the density gradients, as indicated by the isothermal nature of the upper part of the water column in the night and early morning temperature depth profiles in Fig. 3.9.

TABLE 3.3 The means and ranges (in brackets) of weekly measurements of the euphotic zone depth (z_{eu}), mixing depth (z_m), and their ratios (z_{eu}/z_m during stratification and z_{eu}/z_{max} during the non-stratified periods) in Hartbeespoort Dam. Data for 1985/86 not available.

Year	z_{eu} , m	z_m , m	z_{eu}/z_m	z_{eu}/z_{max}
1982/83	3.4 (0.60-8.4)	14.2 (7-18)	0.24 (0.04-0.50)	0.14 (0.05-0.37)
1983/84	3.5 (0.45-6.2)	10.4 (7-18)	0.45 (0.02-0.82)	0.11 (0.04-0.19)
1984/85	3.5 (1.10-6.5)	12.0 (8-18)	0.28 (0.08-0.69)	0.16 (0.09-0.27)

TABLE 3.4 The proportion of the time during the stratified and the non-stratified periods that a shallow (surface - 2 m depth) diurnal mixed layer, recognized by a density gradient ($d\rho/dz$) $> 20 \text{ g m}^{-4}$ or $> 100 \text{ g m}^{-4}$, was recorded in the main basin of Hartbeespoort Dam.

year	$d\rho/dz > 20 \text{ g m}^{-4}$		$d\rho/dz > 100 \text{ g m}^{-4}$	
	stratified	non-strat.	stratified	non-strat.
1982/83	79 %	75 %	54 %	30 %
1983/84	85 %	56 %	56 %	12 %
1984/85	83 %	68 %	60 %	36 %
1985/86	no data	67 %	no data	43 %

Figure 3.11 shows representative depth profiles of temperature, density gradients, chlorophyll a and primary production. Near surface peaks in density gradients $>20 \text{ g m}^{-4}$ resulting from diurnal warming of the near surface water are evident in 4 out of 5 given cases. When *M. aeruginosa* was dominant the near-surface peak in density gradient was accompanied by peaks in chlorophyll a and primary production, whether this was during stratification (e.g. Fig. 3.11-I, II) or during the non-stratified period (Fig. 3.11-III). When, however, chlorophyceae were dominant, near-surface peaks in density gradient were not accompanied by chlorophyll a peaks while the primary production peak was small and caused by light attenuation (e.g. Fig. 3.11-V). On occasions of stronger winds, resulting in an isothermal column and density gradients $<10 \text{ g m}^{-4}$ that were insufficient to support a shallow diurnal mixed layer (Fig. 3.11-IV), chlorophyll was evenly distributed with depth, irrespective of the dominant species. These data demonstrate that, in the absence of turbulent mixing, buoyant *Microcystis* floated into the shallow diurnal mixed layers while non-buoyant species remained evenly distributed with depth, and were subject to sinking losses.

3.2.6 Light attenuation and *Microcystis*

The relationship between the vertical extinction coefficient of green light, ϵ_{min} (ln units m^{-1}) and the mean euphotic chlorophyll a concentration, B (mg m^{-3}), for the period April 1981 to January 1986 is given by equation (1):

$$(1) \quad \epsilon_{\text{min}} = 0.74 + 0.011 B \quad (r = 0.84, \quad n = 209, \quad p < 0.001).$$

This relationship accounted for 70 % of the variance in ϵ_{min} , suggesting that chlorophyll was the dominant factor in regulating the underwater light climate but that other factors were also influential. One of these factors was *Microcystis* colony size. A logarithmic relationship, similar to that reported by Robarts and Zohary (1984), between decreasing colony size and increasing light attenuation was found ($r = 0.88, n = 16, p < 0.01$).

The depth of the euphotic zone (z_{eu} , the depth to which 1 % of PAR penetrated) varied between 0.45 and 8.4 m with a mean of 3.4 - 3.5 m (Table 3.3). Since z_{eu} is a function of ϵ_{min} , the dominant factor controlling z_{eu} was the phytoplankton standing stock. The depth of the euphotic zone never exceeded z_m or z_{max} so that the ratios z_{eu}/z_m and $z_{\text{eu}}/z_{\text{max}}$ were always less than unity (Table 3.3, Fig. 3.8). When, however, shallow diurnal mixed layers existed, z_1 was nearly always shallower than z_{eu} (Fig. 3.10). Thus cells remaining within z_1 were ensured access to light.

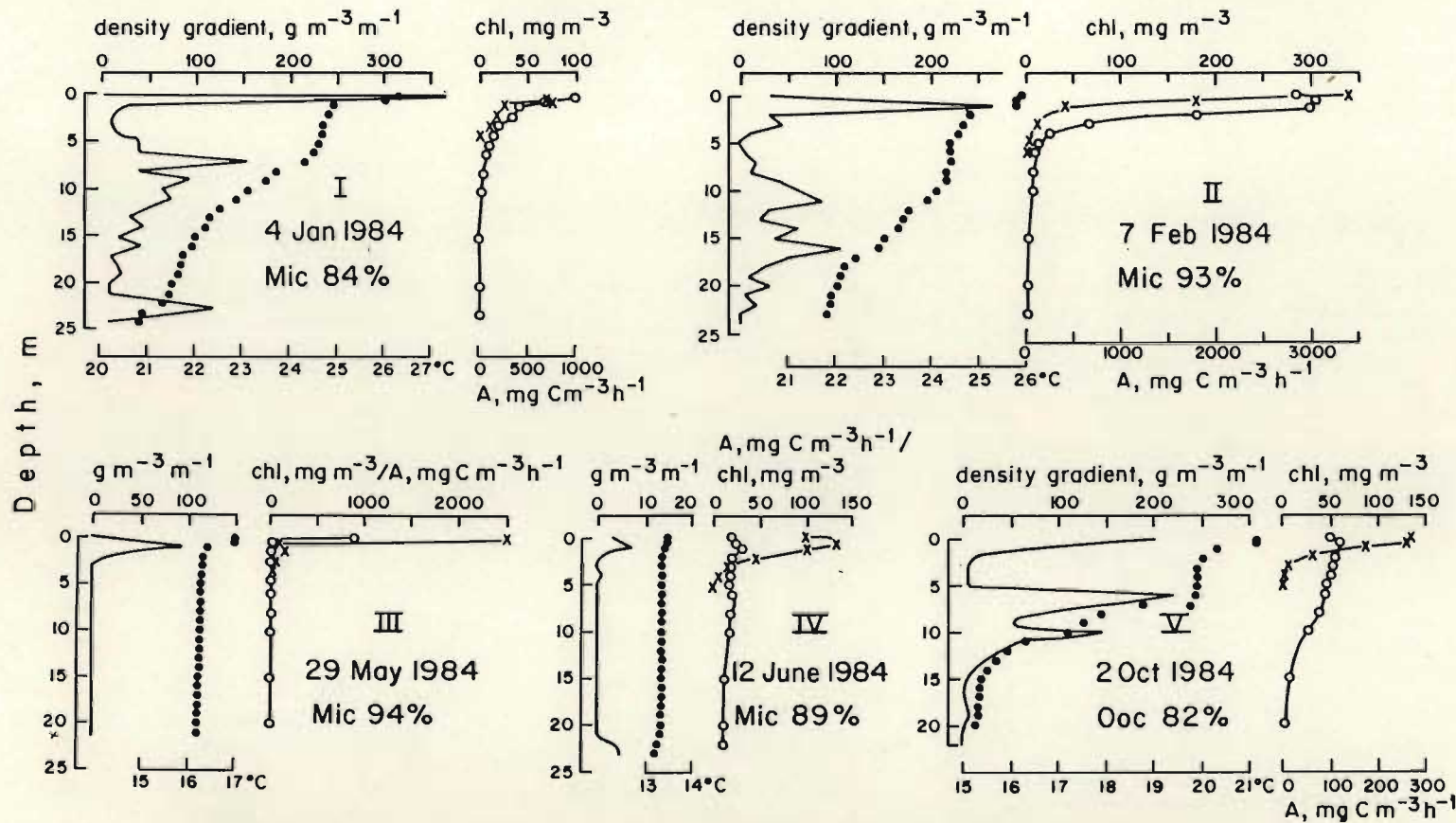


FIGURE 3.11 Representative depth profiles in 1984 of density gradients (continuous line), water temperature (\bullet), chlorophyll a concentration (chl, \circ) and ^{14}C uptake rates (A, \times) in the main basin of Hartbeespoort Dam. Also indicated is the dominant phytoplankton species (Mic = *Microcystis*, Ooc = *Oocystis*) and the proportion (%) it comprised of the total phytoplankton volume.

3.3 DISCUSSION

For four consecutive years *M. aeruginosa* dominated the phytoplankton populations of hypertrophic Hartbeespoort Dam not only in summer, as in many eutrophic temperate lakes, but also in autumn and winter. This occurred despite characteristic seasonality in the physical environment (water temperature, solar radiation, water column stability and stratification; Figs 3.1, 3.2). Nitrogen and phosphorus were available in excess of phytoplankton growth requirements throughout the annual cycle. In 3 out of 4 years the *M. aeruginosa* population was as large in July (mid-winter: 12-14°C; midday PAR of ca 1000 $\mu\text{E m}^{-2} \text{s}^{-1}$; mixed water column) as in January-February (mid-summer; 22-25°C; ca 2000 $\mu\text{E m}^{-2} \text{s}^{-1}$; stratified water column) (Figs 3.5, 3.6).

Several studies have demonstrated that the growth rate of *M. aeruginosa* declines sharply below a critical temperature of about 15°C (Konopka and Brock, 1978a; Kruger and Eloff, 1978; Kappers, 1984; Reynolds, 1984; Robarts and Zohary, 1987). Thus, dominance of this cyanobacterium in Hartbeespoort Dam under suboptimal winter temperatures depended on: (1) maintenance of planktonic populations that developed in summer and autumn, and (2) success in competition for light, the limiting resource in this lake (Robarts and Zohary, 1984), against other phytoplankton groups with physiological optima at lower temperatures.

Persistence into winter of summer populations implies the ability to remain in suspension and, concomitantly, maintain low losses through grazing, outflow, death and decomposition. Recent studies on buoyancy regulation of *M. aeruginosa* (Kromkamp and Mur, 1984; van Rijn and Shilo, 1985) have demonstrated that colonies in the illuminated zone become heavy as intracellular carbohydrate ballast is accumulated during the day and sink. They regain buoyancy after the stored carbohydrate is respired and utilized in the dark. Data on the changes in macromolecular synthesis of *M. aeruginosa* over diel periods is not available for Hartbeespoort Dam, but it is well established that the diel changes described by Kromkamp and Mur (1984) are characteristic of this species (Thomas and Walsby, 1985; 1986; Olesen and Ganf, 1986; Hama and Handa, 1987).

Thomas and Walsby (1986) have shown that below a critical temperature of about 12°C the rates of enzymatic breakdown of intracellular carbohydrate slow down to levels at which colonies cannot regain their buoyancy in the dark. They proposed that the autumnal sinking of *M.*

aeruginosa to the bottom sediments in temperate lakes is due to the decline of water temperature. In Hartbeespoort Dam winter temperature did not decline below 12°C. Also, the planktonic populations of *M. aeruginosa* did not disappear in autumn or winter as a consequence of sinking. Thus, water temperature may explain the apparent deviation of Hartbeespoort Dam from the annual cycle model for *M. aeruginosa* in temperate lakes (Reynolds *et al.*, 1981). However, the field data from Hartbeespoort Dam indicate that the ability of *M. aeruginosa* to remain buoyant under winter temperatures of 12 - 14°C (Figs 3.1a, 3.6) was linked to low wind activity (Figs 3.1d, 3.3) and the consequent weak turbulent mixing (Figs 3.1b, 3.10). Shallow diurnal mixed layers that formed on most days, irrespective of the seasonal stratification pattern (Figs 3.9, 3.10), facilitated the maintenance of *M. aeruginosa* in the near-surface illuminated zone (Figs 3.8, 3.11). The eventual decline of the population in August-September (Fig. 3.5a) coincided with increasing wind activity as well as water temperature (Figs 3.1a,d, 3.3), and not with minimal water temperatures. Further studies of the interactions between buoyancy and turbulence at low temperatures are needed.

The gas vacuole content of the winter *M. aeruginosa* in Hartbeespoort Dam was high in comparison with that reported for growing populations by Reynolds *et al.* (1981). The high gas vacuole content of the population in Hartbeespoort Dam contributed to its being buoyant during winter, and may have been related to the cessation of growth and senescence (cf. Smith and Peat, 1967; Lehmann and Jost, 1971; Reynolds, 1972; 1987).

High sedimentation rates of *M. aeruginosa* in winter (Fig. 3.8), preceding the major decline of the planktonic population, could not be compensated for by plankton growth as in summer, so that sedimentation was probably the major cause for the decline. The decline, however, occurred in August while sediment trap catches were already high in June. It is possible that sedimented colonies (those that were caught in the upward-facing sediment traps) in early winter were still capable of upward migration and only those that sank in late-winter were permanently lost. By employing upward- and downward-facing sediment traps Reynolds *et al.* (1981) were able to demonstrate that this indeed happened in Blelham Tarn. Other studies similarly concluded that sinking caused the seasonal decline of *M. aeruginosa* (Reynolds and Rogers, 1976; Livingstone and Reynolds, 1981; Reynolds *et al.*, 1981; Reynolds and Wiseman, 1982; Thomas and Walsby, 1986), but in

Hartbeespoort Dam the decline was postponed to late winter and did not occur in autumn as in these other studies.

Other losses to the *M. aeruginosa* populations in Hartbeespoort Dam were relatively small. Washout losses were low, as overflow did not occur due to the prolonged drought; compensation outflow was drawn from 8 m or deeper, where *M. aeruginosa* concentrations were usually low (Fig. 3.8).

Grazing losses of this cyanobacterium were also small. Due to its large colony size *M. aeruginosa* in Hartbeespoort Dam was not ingested by crustaceans, except very small colonies (Jarvis, 1986). The predominantly calm weather in Hartbeespoort Dam enhanced the aggregation of *M. aeruginosa* into large, inedible colonies (Robarts and Zohary, 1984). In a study of zooplankton grazing in Hartbeespoort Dam Jarvis (1986) has demonstrated that large cladocerans, such as *Daphnia*, depended on the chlorophyceae and cryptophyceae species as food sources and thus zooplankton population maxima were restricted to spring, when these species were abundant. During periods of *M. aeruginosa* dominance the smaller *Ceriodaphnia* dominated the zooplankton populations. This species depended to a greater extent on bacteria and detritus as food sources (Jarvis *et al.*, 1987) Thus not only were grazing losses of *M. aeruginosa* low, but high grazing pressure on other phytoplankton species was also influential to its dominance in Hartbeespoort Dam.

Population losses through decomposition did occur. While planktonic *Microcystis* in Hartbeespoort Dam is rarely found to be colonized by bacteria (Robarts and Sephton, 1981), it was suggested that its decomposition occurred mainly in the bottom sediments (Robarts and Ashton, in press) or in hyperscums (Zohary, 1988; see later chapter 6). Yet, colonies decomposing on bottom sediments were already lost to the planktonic populations, and decomposition in hyperscums was mostly of populations that would have otherwise sedimented (see later, chapter 7).

Microcystis aeruginosa not only remained in suspension throughout summer, autumn and winter, but also succeeded in competing against other species to their near exclusion over the greater part of the year. The buoyancy mechanism advantaged *M. aeruginosa* under the prevailing low-turbulence conditions in Hartbeespoort Dam. During the particularly calm winter nights (Fig. 3.3) *M. aeruginosa* floated to the surface so that it could utilize the available light from the

early morning hours. Nocturnal migration of *M. aeruginosa* and accumulation at the surface in the early morning hours was noted by others (Reynolds, 1973; Okino, 1973; Ganf, 1974; Takamura and Yasuno, 1984; van Rijn and Shilo, 1985; Thomas and Walsby, 1986). In the absence of vertical mixing strong enough to overcome its tendency to float, *M. aeruginosa* in Hartbeespoort Dam could maintain itself within the shallow diurnal mixed layers as they formed. The euphotic zone was usually deeper than z_1 , but it was always shallower than z_m (Fig. 3.10, Table 3.3). By remaining within the shallow mixed layers *M. aeruginosa* was ensured access to light. Thus, the time spent by this cyanobacterium in the euphotic zone approached the actual day length, except during irregular periods of wind activity strong enough to destroy the diurnal mixed layers.

In contrast, non-buoyant cells depended on turbulent mixing to return them to the euphotic zone. A suitable wind regime (winds $> 3.7 \text{ m s}^{-1}$) occurred less than 10% of the time in winter (Table 3.2), and even then these cells spent only the equivalent of z_{mix}/z_m in the illuminated zone. During the rest of the time negatively buoyant cells sank out of the euphotic zone at their intrinsic rates for the *in situ* temperatures (Reynolds, 1984). Humphries and Lyne (in press) noted the advantage incurred by the ability of *M. aeruginosa* to "track" diurnal mixed layers. They demonstrated in a mathematical model that when z_{mix} was shallower than z_m positive buoyancy gave a substantial growth advantage over negatively buoyant species thereby allowing buoyant species to form blooms. The data from Hartbeespoort Dam demonstrate that the advantage of positive buoyancy extends beyond the growth season and allows *Microcystis* to dominate even in winter when it can not grow. These data, therefore, point out the importance of distinguishing between the depth of the seasonal thermocline, z_m , and the depth of the diurnal thermocline, z_1 , and show the profound influence that the daily pattern of z_1 , as opposed to z_m , can have on the phytoplankton population composition.

An additional advantage of *M. aeruginosa* in Hartbeespoort Dam was its moderation of light attenuation through increasing colony size under calm conditions, thereby reducing population self-shading (Robarts and Zohary, 1984). Lake McIlwaine, Zimbabwe is a reservoir of similar physical proportions to Hartbeespoort Dam. Its phytoplankton is dominated by *M. aeruginosa* but unlike the typical situation in Hartbeespoort Dam, the phytoplankton of Lake McIlwaine were relatively evenly distributed over the euphotic zone (Robarts, 1979).

The difference in the phytoplankton biomass distribution in the two reservoirs can be mainly ascribed to the higher wind speeds ($\bar{x} = 2.6 \text{ m s}^{-1}$) at Lake McIlwaine (Ward, 1982) than at Hartbeespoort Dam ($\bar{x} = 1.6 \text{ m s}^{-1}$; Fig. 1d, Robarts and Zohary, 1984). This difference had further consequences for the *M. aeruginosa* population of Lake McIlwaine. The windier conditions maintained small *M. aeruginosa* colonies (cf. Robarts and Zohary, 1984) with the result that the light attenuation per unit chlorophyll ($0.021 \text{ m}^2 \text{ mg}^{-1}$; Robarts, 1979) was almost twice as high as found for *M. aeruginosa* in Hartbeespoort Dam ($0.011 \text{ m}^2 \text{ mg}^{-1}$, the slope in equation (1)). Consequently, the maximum measured euphotic zone chlorophyll a concentration in Lake McIlwaine was only 138 mg m^{-2} (Robarts, 1979) compared with 926 mg m^{-2} in Hartbeespoort Dam.

The advantage of being at or near the surface may be offset by the potential damage of photooxidation, a lethal condition in a variety of cyanobacteria (Abeliovich and Shilo, 1972; Eloff *et al.*, 1976). Yet, some strains of *M. aeruginosa* have been shown to be well adapted to high light intensities (Raps *et al.*, 1983; Paerl *et al.*, 1985). Adaptation of *M. aeruginosa* from Hartbeespoort Dam to strong light intensities is indicated by values as high as $1234 \mu\text{E m}^{-2} \text{ s}^{-1}$ (mean = $238 \mu\text{E m}^{-2} \text{ s}^{-1}$, $n = 220$) for the light intensity (I_{κ}) at which photosynthesis became light saturated. Lake McIlwaine *M. aeruginosa* had a maximum measured I_{κ} of $204 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Robarts, 1979) further indicating that it was subjected to a lower light environment than the *M. aeruginosa* from Hartbeespoort Dam. Another indication of the adaptation to high light intensities in *M. aeruginosa* from Hartbeespoort Dam was the atypically low cellular chlorophyll content (see Harris, 1978). An average value of $0.132 \mu\text{g chl per } 10^6 \text{ cells}$ was calculated for the data when *M. aeruginosa* comprised >90% of the phytoplankton volume. In comparison, the cellular chlorophyll content of natural *M. aeruginosa* populations from Blelham Tarn and Rostherne Mere in the English lake district, where incident irradiance levels are lower than upon Hartbeespoort Dam, were $0.302\text{-}0.455$ and $0.357 \mu\text{g per } 10^6 \text{ cells}$, respectively (Reynolds *et al.*, 1981).

3.4 CONCLUSIONS

Viner (1985) argued that the critical relationship between thermal stability patterns and phytoplankton operates primarily via the underwater light climate through which phytoplankton are moved or to which

they are allowed to adapt. While others have predicted and demonstrated that a buoyancy mechanism confers a major growth advantage by allowing some phytoplankton species to remain in the diurnal mixed layer and to bloom (Imberger, 1985; Humphries and Lyne, in press), this study has demonstrated that this advantage is potentially stronger, allowing a single species to dominate a population for almost an entire year and for several successive years, including seasons when growth is retarded due to low water temperatures. Indeed, the importance of the formation of shallow diurnal mixed layers is such that *Microcystis aeruginosa* may form blooms under low wind speed conditions even in oligotrophic, inorganically turbid systems, such as Lake Le Roux, South Africa (Hart *et al.*, 1983).

Nutrient concentrations are widely recognized as a major resource regulating phytoplankton succession in lakes. But, in optically shallow, warm-water lakes, where nutrient concentrations are always in excess of phytoplankton needs, the dominant factor leading to the dominance by *Microcystis aeruginosa* can be ascribed to low turbulence. The data from Hartbeespoort Dam have demonstrated that, by maintaining itself within diurnal mixed layers shallower than the euphotic zone, and aggregating into large colonies, *Microcystis aeruginosa* successfully competed for light, the major factor regulating autotrophic production. At the same time it maintained losses, such as grazing, at a minimum. Furthermore, physiological adaptation to the high light environment attained ensured the overwhelming success of *Microcystis aeruginosa* in Hartbeespoort Dam.

According to resource competition theory, different relative supply rates of two or more limiting resources should result in phytoplankton communities dominated by different species (Titman, 1976). The data from Hartbeespoort Dam support the theory of resource competition since for most of the year competition was for a single resource, i. e. light. Succession was suppressed to a short period when competition was being regulated by both light and water temperature.

Finally, it is possible that the effect of temperature could be dominant to that of turbulence in regulating the buoyancy of *M. aeruginosa*. In lakes where water temperatures fall below 10 - 12°C, colonies may sink out of suspension even under low turbulence conditions. The interactions between buoyancy regulation and turbulence under low temperatures require further investigation.

CHAPTER 4

ENVIRONMENTAL FACTORS FAVOURING THE FORMATIONS OF HYPERSCUMS

4.1 INTRODUCTION

In the previous chapter the long term dominance of *M. aeruginosa* was attributed to the combination of abundance of nutrients throughout the year, winter water temperatures above 12°C, predominantly low turbulence and formation of shallow diurnal mixed layers, coupled with the buoyancy mechanism and the adaptation of *M. aeruginosa* to high light intensities. Its abundance in winter, when wind stress was lowest, led to accumulation at the surface and hyperscum formation.

Preliminary observations on hyperscums from Hartbeespoort Dam (Zohary, 1985) showed that ca. 10 - 50 % of the lake's total chlorophyll was contained in a hyperscum that extended over less than 0.1 % of the lake surface area. It was suggested that hyperscums may play an important role in the population dynamics of *Microcystis aeruginosa*, the dominant cyanobacterium in this hypertrophic lake. However, in order to understand this role it is necessary to first establish how and under which conditions hyperscums form and break.

Reynolds and Walsby (1975) suggested that bloom-formation depended on the coincidence of three preconditions: a pre-existing population, a significant proportion of the organisms containing sufficient gas vacuoles to render them buoyant, and stability of the water column. It is proposed here that Reynolds and Walsby's preconditions are essential but not sufficient for hyperscum formation. In order to identify additional necessary preconditions, the dynamics of hyperscum formation and breakdown are examined in relation to changes in the wind regime, the shoreline morphometry and the standing stocks of buoyant *M. aeruginosa*.

4.2 RESULTS

4.2.1 The occurrence of hyperscums in Hartbeespoort Dam

The location and spatial dimensions of the major hyperscums during 1982 - 1987 are shown in Table 4.1. Figure 4.1a shows estimates of the total chlorophyll a content of Hartbeespoort Dam and the proportion of the total that was contained in the hyperscums over a period of three years. In 1983 and 1984 hyperscums started forming at the wind-sheltered area by the dam wall in May when mean wind speeds over the main basin were declining, reached maximum size and mass in July when wind speeds were lowest, and broke down in August - September when wind speeds were increasing (Fig. 4.1). In winter 1982 a 2 km long hyperscum covered the surface of the inflowing Crocodile River. In winter 1983 a hyperscum at the dam wall (plate 4.1a) covered up to 1.8 hectares (Table 4.1) and contained up to 2 tons of chlorophyll a, some 50% of the total chlorophyll a in the lake (Fig. 4.1). In winter 1984 a smaller hyperscum (up to 1.5 ha) formed at the dam wall. It contained up to 1.3 tons of chlorophyll a which was 30% of the total lake chlorophyll content at that time. A hyperscum did not form in the winter of 1985 but large hyperscums (up to 1.9 ha) formed again at

TABLE 4.1 Dimensions and location of the major hyperscums in Hartbeespoort Dam, South Africa, 1982-1987 in relation to changes in water levels.

% of Year	Period	lake	h y p e r s c u m		
		maximum full supply	maximum location	area, ha	thickness, cm
1982	May - July	90-80	Crocodile River inflow	(2-3) ¹	no data
1983	1 May - 11 Sept.	34-31	Dam wall	(1.8)	75
1984	8 May - 26 Aug.	37-35	Dam wall	(1.5)	50
1985	winter	44-40	no hyperscum	-	-
1986	15 May -30 Aug.	36-33	Dam wall	(1.9)	no data
1987	26 March -25 May ²	75-87	Dam wall	(1.8)	no data

¹estimated after hyperscum dispersed.

²when hyperscum was broken artificially by opening of sluice gates.

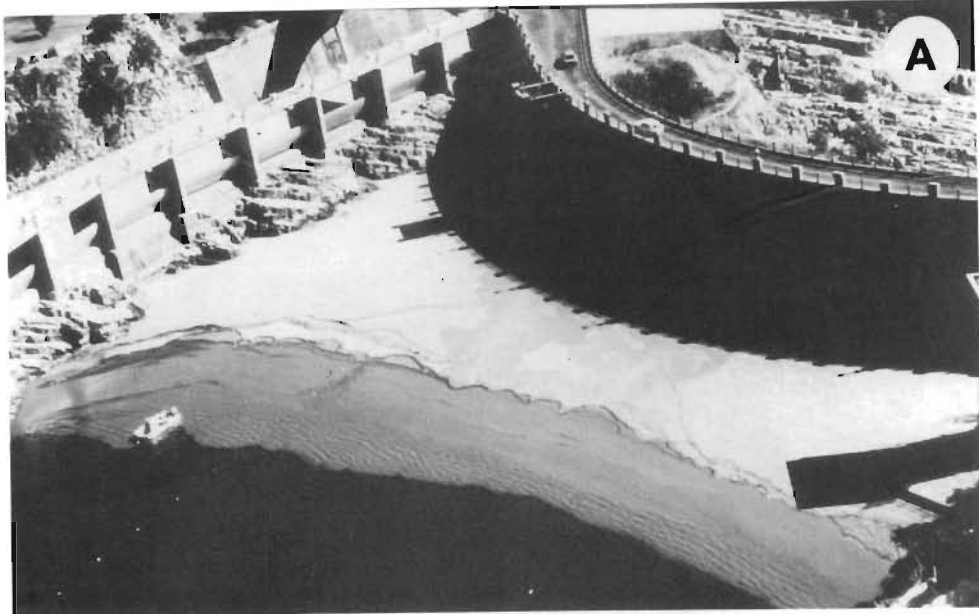


PLATE 4.1 (A) *M. aeruginosa* hyperscum in the shelter of the dam wall in Hartbeespoort Dam, South Africa, 27 June 1984. Whitish area - photooxidized crust covering the hyperscum; grey area - newly accumulated cyanobacteria; dark area at foreside - lake water. Boat length, 6 m. (B) Large portions of the hyperscum detached on 5 August 1984 by NW winds and transported as 'islands' up to 30 m long to the main basin, 1 km away. Boat length, 6 m.

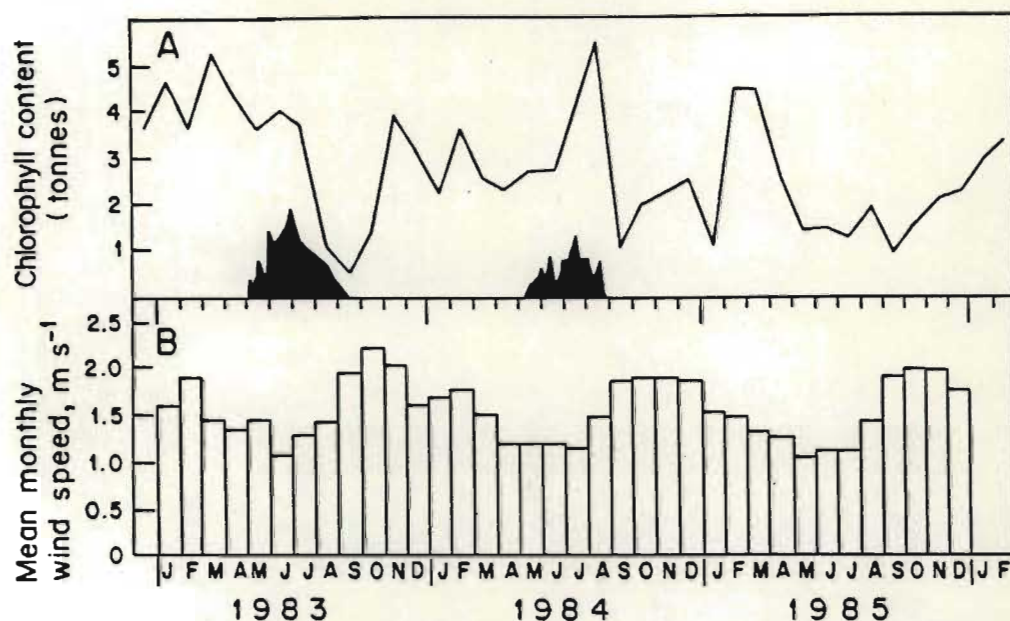


FIGURE 4.1 (A) Seasonal variations in estimates of total lake chlorophyll a content computed from weekly measurements at seven stations (1983 - 1984) or from monthly measurements at 14 stations (1985), and the proportion of the total that was contained in cyanobacterial hyperscums (blackened areas). (B) Seasonal changes in mean monthly wind speeds on the southeastern shore.

the dam wall in the winter of 1986 and autumn of 1987 (Table 4.1). Small hyperscums, covering several hundred square meters and persisting for short periods (days to 1-2 weeks) formed at other times of the year in wind-protected bays and among inundated terrestrial vegetation but, due to their unpredictable occurrence, they were not studied.

4.2.2 The wind regime

The seasonal changes in the monthly mean wind speed at Oberon (Fig. 2.2a) are shown in Fig. 4.1. The diel patterns of wind speeds and the distribution of wind speeds and directions for two representative months were shown earlier (Fig. 3.3). Winds at Oberon were demonstrated to be good indicators of the winds over the main basin (section 2.3.1). Highest speeds occurred each year in the afternoon hours in September - October and very low speeds, particularly at night, between April and July. Overall, wind speeds over the main basin were low, rarely exceeding 3 m s^{-1} , and variable in direction (Fig. 3.3).

In the gorge near the dam wall (Fig. 2.2a) the winds were channeled by mountains in two major directions: from the east-southeast (ESE) towards the dam wall, and from the northwest (NW) or west-northwest (WNW) towards the main basin (Fig. 4.2). On-lake winds recorded 200 m from the wall are compared with those recorded continuously on the dam wall about 20 m above the water in Fig. 4.3. The similarity in the diel wind pattern at the two locations is evident. East-southeast winds at night reached $7 - 8 \text{ m s}^{-1}$ but calmed abruptly after sunrise. On most days the wind changed direction and gentle ($< 2 \text{ m s}^{-1}$) NW winds prevailed for 2 - 4 h in the afternoon. A second reversal of wind direction occurred at night. The recorded speeds at the two stations were, however, somewhat different: SE wind speeds on the water were on the average 80% of those on the wall ($Y = 0.79 X + 0.08 \text{ km h}^{-1}$; $r = 0.96$, $n=65$, where $Y = \text{ESE wind speed over the water}$ and $X = \text{ESE wind speed on the wall}$). Northwest winds tended to be stronger on the water (Fig. 4.3). The similar pattern of winds at the two locations permitted the assumption that the wind regime recorded on the wall reflected the events in the gorge.

The diel cycle of winds illustrated in Fig. 4.3, with ESE winds dominating but NW or WNW winds blowing for several hours in the afternoons, repeated itself over most of the year in the gorge, but the duration and strength of these winds varied seasonally (Fig. 4.2). Generally, the gorge was exposed to much higher wind speeds than the main basin (Figs 3.3, 4.2).

4.2.3 Hyperscum formation and breakdown: the winter 1984 example

Autumn overturn was completed by the end of March 1984 (Fig. 3.2), the water column was isothermal and the summer population of *Microcystis aeruginosa* had not yet declined (Figs 4.1, 3.5a). The estimated total lake chlorophyll a in April and May 1984 exceeded 2.5 tons (Fig. 4.1a). In the main basin mean euphotic zone chlorophyll a concentration ranged between 16 and 368 mg m^{-3} and surface concentration reached a maximum of 1890 mg m^{-3} on 8 May. April and May were characterized by windless nights (mean hourly wind speeds below 1 m s^{-1}) and gentle morning winds of $1 - 2 \text{ m s}^{-1}$ over the main basin (Fig. 3.3). Under the calm conditions and moderate late autumn insolation levels *M. aeruginosa* colonies floated to the surface at night and were transported across the lake by the gentle morning winds. Surface currents carrying the blooms towards the dam wall along the west bank of the gorge were recorded on film (Zohary and Robarts, 1987). The blooms were typically mixed into the water column when wind speeds in the main basin increased towards noon (Fig. 3.3).

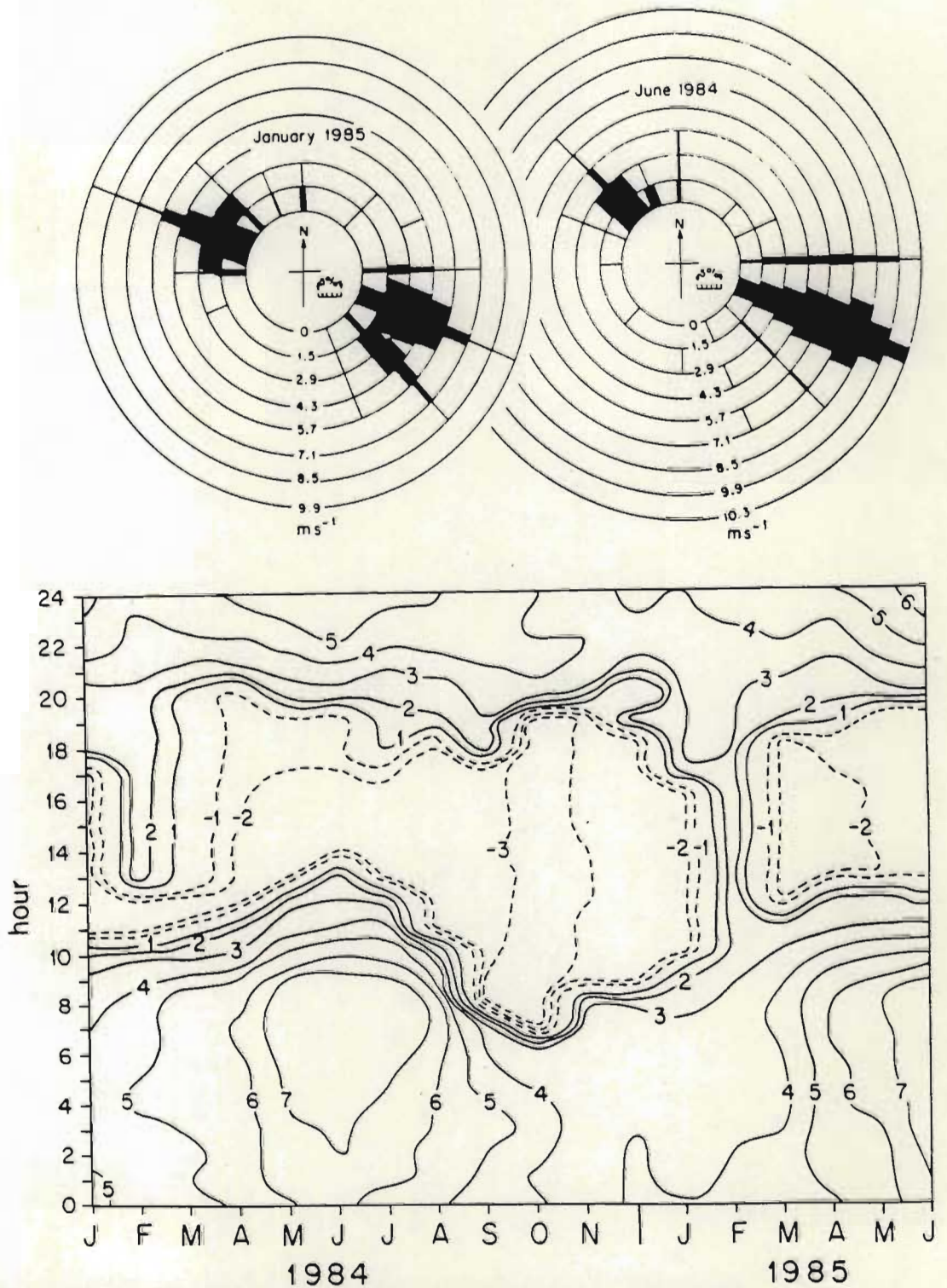


FIGURE 4.2 The wind regime on the wall of Hartbeespoort Dam. Top: representative wind roses for summer (January) and winter (June) wind showing the frequency distribution of wind speeds in 16 directions. Wind speed (m s^{-1}) is indicated by distance from the innermost circle. Radius breadth is the proportion of the time at a specific speed and direction. Bottom: seasonal changes in average hourly wind speed (m s^{-1}) in 2 major directions. Solid line, positive values - SE and ESE winds (towards the dam wall). Broken lines, negative values - NW and WNW winds (away from wall).

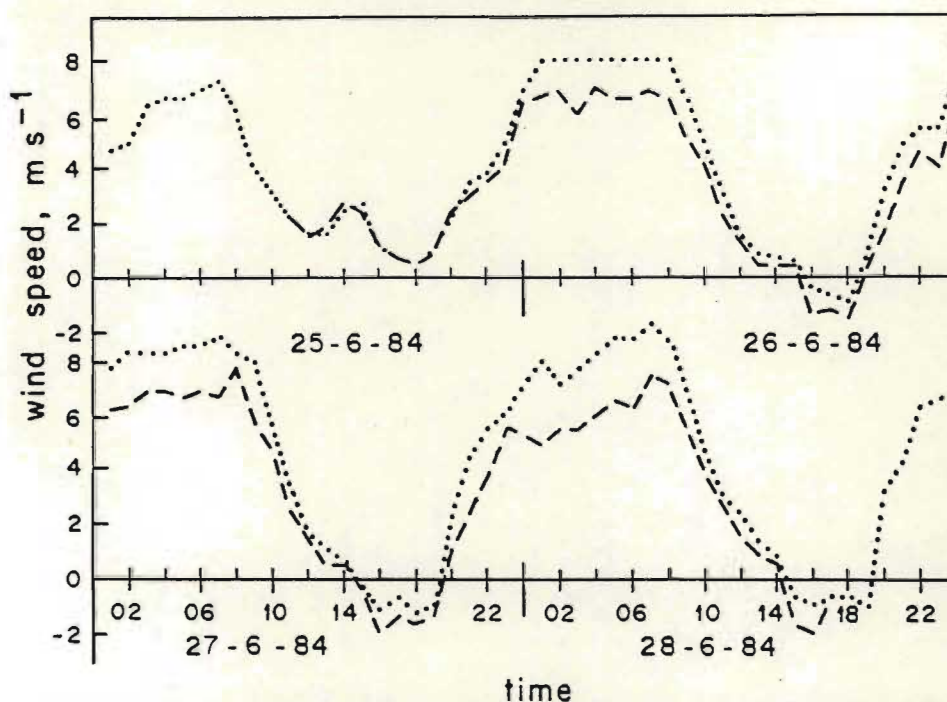


FIGURE 4.3 The diel pattern of wind speeds in 2 major directions as recorded on the dam wall of Hartbeespoort Dam about 20 m above the water (dotted line) and on the lake approximately 200 m away from the wall and 1 m above the water (broken line) over 4 days. Positive values - SE winds; negative values - NW winds.

The dam wall stood perpendicular to the major wind directions in the gorge, and in May 1984 it extended approximately 15 m above the water. When winds blow over a perpendicular barrier, a re-circulation zone forms in the lee of the barrier in which wind eddies in the reverse direction and of lower speed predominate (Sachs, 1972; Fig. 4.4). The distance from the wall that is protected from the full force of the wind by such eddies is proportional to the wind speed and to ca 6 times the height of the wall above the water (Sachs, 1972; Fig. 4.4). No direct measurements of these eddies were made, though wind stress on the water surface adjacent to the dam wall was consistently observed to be much weaker than even at 200 m away from the wall. The location of the wall at the lee of the prevailing winds and the protection it provided from NW winds made the re-circulation zone an accumulation site, where buoyant cyanobacteria were trapped until winds blowing in the opposite direction (NW) were strong enough to blow the algae away (Robarts & Zohary, 1986).

Depth profiles of chlorophyll a concentrations over the top 1 m near the wall on 3 sampling occasions in May 1984 are shown in Fig. 4.5. These data demonstrate a dramatic, 3 orders of magnitude increase in the chlorophyll a concentration near the surface, between 1 and 8 May.

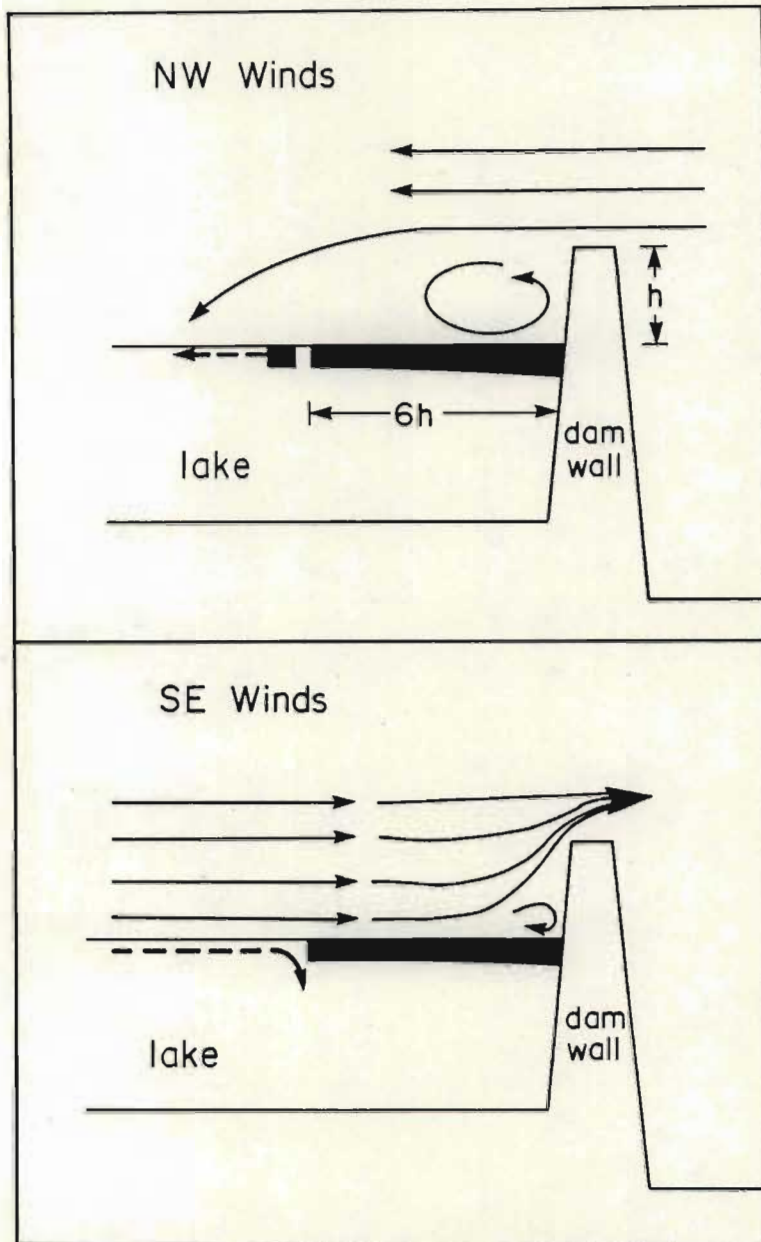


FIGURE 4.4 Schematic diagram drawn according to Sachs (1972) showing the theoretical pattern of winds (full arrows) near the dam wall, their effects on currents (dashed arrows) and the extent of the wind protected area next to the wall. A hyperscum is indicated by a black block. When NW winds blow a re-circulation zone, proportional to 6 times the height h , forms in the lake side of the wall. Within it wind eddies blow in the opposite direction. Parts of the hyperscum outside this zone are blown away from the bulk of the hyperscum (small black block).

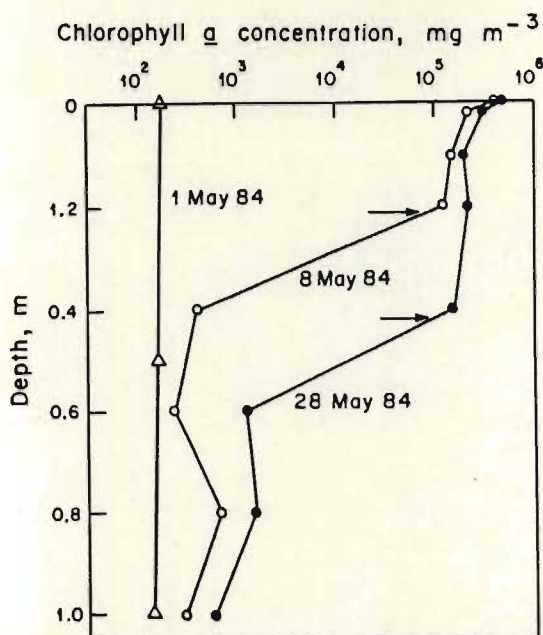


FIGURE 4.5 Depth profiles of chlorophyll a concentrations (note log scale) 5 m away from the dam wall on three occasions during the initial period of hyperscum buildup. Arrows indicate the recorded bottom of the hyperscum, or the shallowest depth at which free water between colonies could be seen.

On 1 May the near surface concentration was 185 mg m^{-3} . By 8 May *Microcystis aeruginosa* colonies at the top 20 cm were so densely packed that chlorophyll a exceeded $100\,000 \text{ mg m}^{-3}$ and free water was not visible between colonies. At the surface the chlorophyll concentration exceeded $500\,000 \text{ mg m}^{-3}$. A steep vertical gradient in chlorophyll a concentration (2-3 orders of magnitude) was recorded at the depth where free water between colonies could first be seen. This depth was taken as the bottom of the hyperscum.

Changes with time in the extent and thickness of the hyperscum and in the chlorophyll a content of the top 0-1 m layer 5 m, 50 m and 100 m from the wall are illustrated in Fig. 4.6. At 5 m and 50 m from the wall, both within the protected re-circulation zone, the two parameters increased from May to mid-July and then declined when wind speeds increased in August. The hyperscum extended as far as 100 m from the wall only in July.

Once accumulated at the surface at such densities, colonies rising underneath the hyperscum forced those at the surface out of the water, subjecting them to lethal photooxidizing conditions (see section 6.2) and causing them to dehydrate and desiccate. Within a few days the

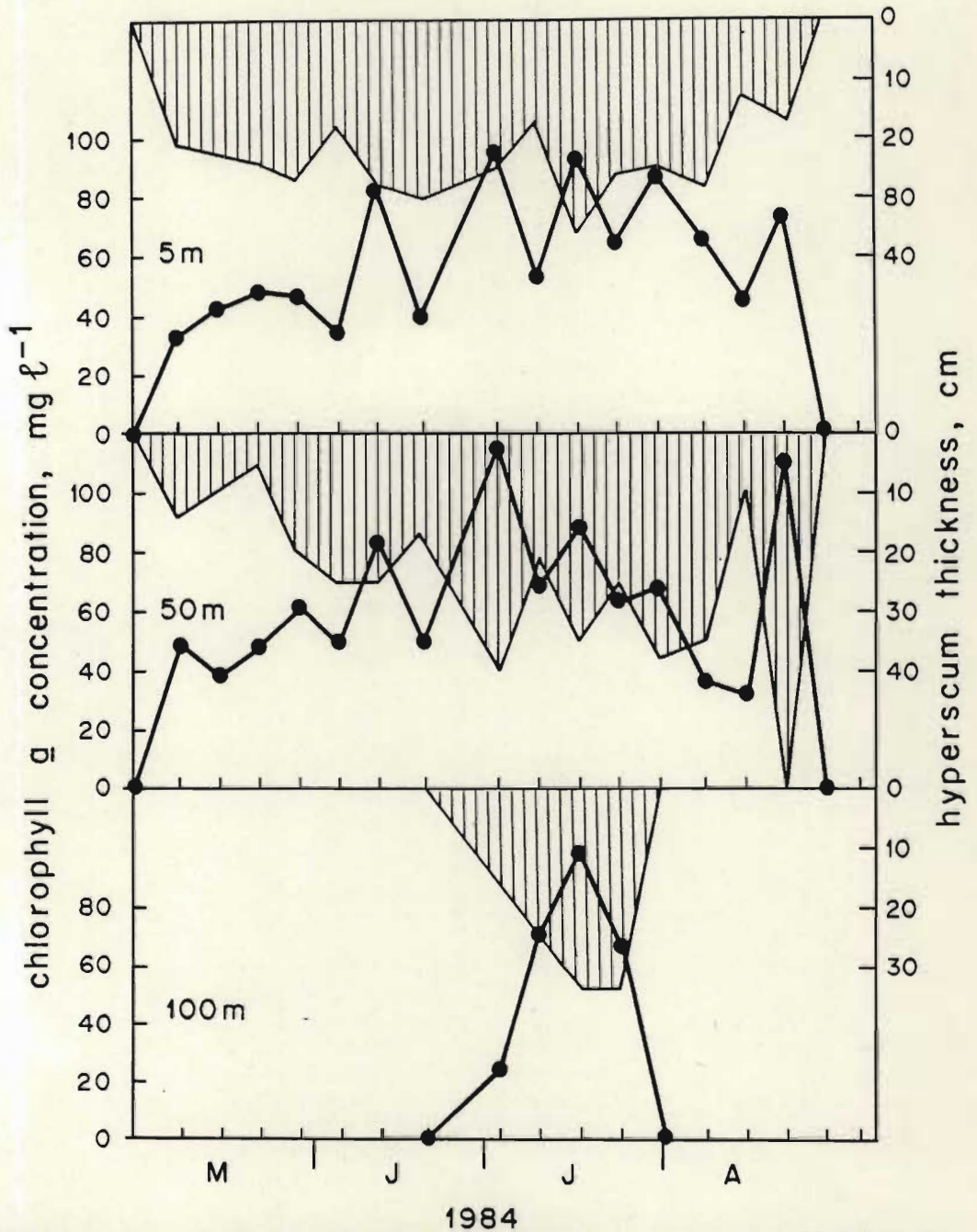


FIGURE 4.6 Changes with time in hyperscum thickness (shaded areas) and the chlorophyll a content of the top 0 - 1 m layer (thick line) at stations 2, 3, and 4 of Fig. 2.3. Distances of stations from the wall are indicated.

desiccated cells formed a dry, 1 to 3 mm crust on the hyperscum. The development of the crust is described with more detail in chapter 6.

Northwest winds $> 5 \text{ m s}^{-1}$ in the gorge were rare during May and June 1984 (Fig. 4.7a). They blew for 5 h on 16 May 1984 but from then until 30 May only moderate ($2.5 - 5.0 \text{ m s}^{-1}$) NW winds occurred and for less than 4 h a day (Fig. 4.7a,b). The windless nights and gentle morning winds in the main basin (Fig. 3.3) and predominant SE winds in the gorge (Fig. 4.2) caused a steady increase with time in the algal mass that accumulated at the dam wall shelter (Fig. 4.7c). The $6 - 8 \text{ m s}^{-1}$ SE winds at night in the gorge (Fig. 4.2) compacted the hyperscum against the wall. Occasional periods of increased NW wind activity (4 and then 12-13 June) transported large segments of the compacted algal mass back into the lake resulting in major declines in the hyperscum biomass (Fig. 4.7c). Thereafter, for a full month between 14 June and 15 July NW winds did not exceed 5 m s^{-1} (Fig. 4.7a) and the hyperscum steadily increased (Fig. 4.7c). Following several days without NW winds between 6 and 15 July (Fig. 4.7 a,b) the crusted hyperscum extended beyond the limits of the protected zone. It was estimated that a maximum of 1250 kg chlorophyll a was contained in the hyperscum on 17 July (Fig. 4.7c).

After 15 July the action of NW winds in the gorge increased progressively (Figs 4.2, 4.7) and consequently the wind-protected area declined. A typical diel pattern developed: morning SE winds caused new colonies to accumulate at the periphery of the crusted hyperscum, but they did not persist for long enough to form a crust. As NW winds started blowing around noon first the peripheral, non-crustrated portions would be dispersed within minutes. After about an hour of continuous NW winds the hyperscum, held as one piece by the crust, started to crack. The winds then impinged on the water-filled cracks and widened them. Eventually, large 'islands' (ca. $10 - 100 \text{ m}^2$) broke away and were blown into the main basin (plate 4.1b). On many occasions the 'islands' were transported 100 - 200 metres to the east shore of the gorge. The evening reversal of wind direction brought them back towards the wall. This daily pattern resulted in a gradual but progressive decline in the hyperscum size. The back and forth transport caused erosion from the bottom, and the hyperscum thinned with time (Fig. 4.6). Once the drifting 'islands' reached the main basin, they did not return, probably because the August winds in the main basin were sufficiently strong (Fig. 3.3) to disperse the colonies in the water column. Stormy weather on 26 August with NW winds of up to 7 m s^{-1} (Fig. 4.7) caused the final dispersal of the hyperscum.

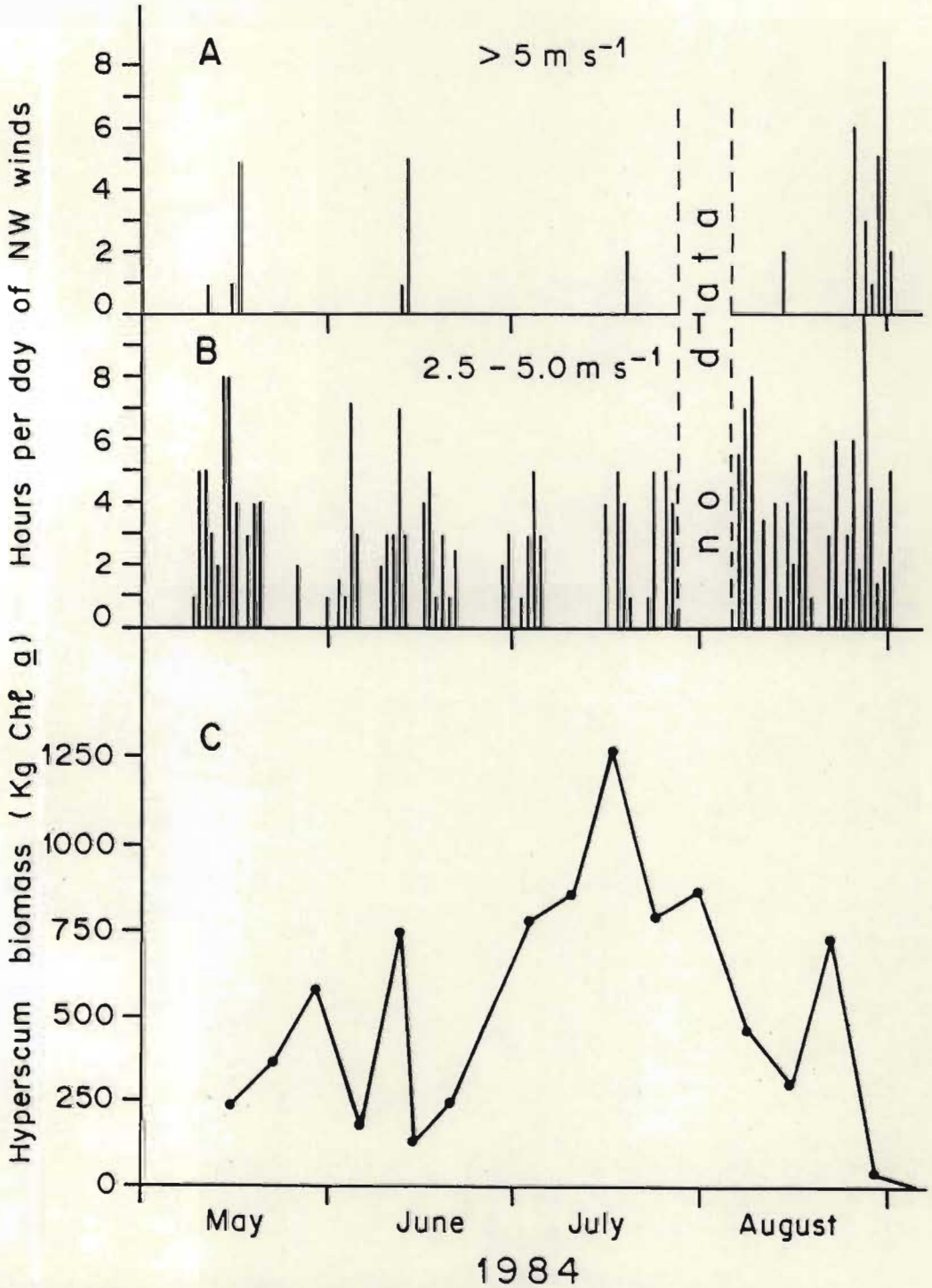


FIGURE 4.7 (A) The number of hours per day of strong (>5 m s⁻¹) NW winds and (B) of moderate (2.5 - 5.0 m s⁻¹) NW winds measured on the dam wall of Hartbeespoort Dam during winter 1984. (C) Weekly changes in the total cyanobacterial biomass (as chlorophyll a) contained in the hyperscum.

4.2.4 Shoreline morphometry and hyperscum occurrence

At full supply level (f.s.l.) the shoreline of Hartbeespoort Dam is rich in small bays and inlets, most of which disappear with declining water levels. The largest recorded hyperscum formed in the winter of 1982 when the water level was high (80 - 90% of f.s.l.; Table 1) at a section of the inflowing Crocodile River. This site was protected from winds by hills on both sides and from losses of hyperscum 'islands' by a 90° bend further downstream (Fig. 2.2). A hyperscum could not form at the dam wall that year because surface water was frequently released downstream through the sluice gates.

A major decline in water level between May 1982 and October 1983 caused by drought, led to the drying up of the sheltered site in the Crocodile River and of other small sheltered bays. During the low water level years that followed (1983 - 1986; Table 4.1) the only wind-protected site of any extent was at the wall. Small differences in water levels between the winters of these years would have resulted in six fold differences in the area protected from winds near the wall (Fig. 4.4). Indeed, an increase of ca 0.5 m in water level from winter 1983 to winter 1984 (Fig. 4.8), coincided with a 22% decline in the mean area of the hyperscum, from 1.4 hectare for June - July 1983 to 1.1 hectare for June - July 1984. The further decline of the sheltered area, due to a further 1 to 1.5 m increase in water level in

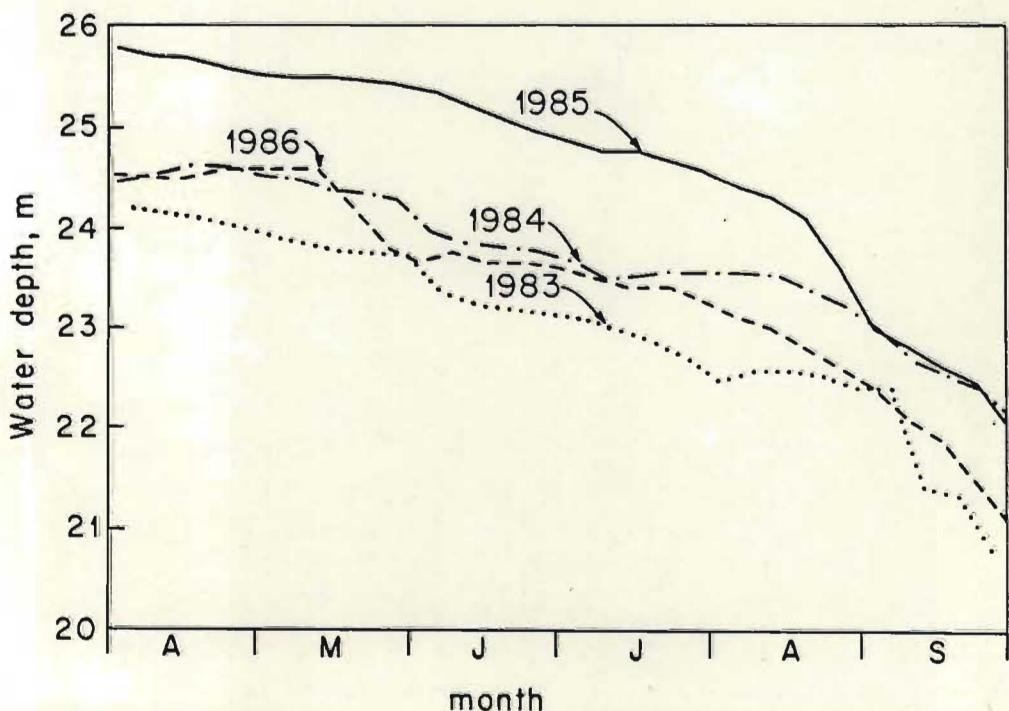


FIGURE 4.8 Changes in water levels during the winter months in Hartbeespoort Dam, South Africa, expressed as maximum depths.

winter 1985 (Fig. 4.8), may have been one of the factors that prevented hyperscum formation that year. Another important factor was the smaller *M. aeruginosa* standing crop that year (Fig. 4.1). When in winter 1986 the water level was close to that of 1983 (Fig. 4.8) a hyperscum of a similar size formed again at the dam wall (Table 4.1).

4.3 DISCUSSION

4.3.1 Conditions for hyperscum development

Based on the Hartbeespoort Dam data it appears that the preconditions for bloom formation recognized by Reynolds and Walsby (1975) (pre-existing population, buoyant cells and stability of the water column) are necessary but not sufficient for hyperscum development. I propose that hyperscums can form only when the following conditions coincide:

- (a) the pre-existence of a large standing stock of cyanobacteria,
- (b) that these cyanobacteria are buoyant,
- (c) low-speed winds over long periods of time (weeks),
- (d) shore morphometry with wind-protected accumulation sites,
- (e) high incident solar radiation.

(a) large pre-existing standing stocks

Reynolds and Walsby (1975) claimed that surface blooms resulted from accumulation at the surface of pre-existing populations because the alternative possibility of rapid multiplication of the algae at the surface would require a shorter doubling time than attained by any cyanobacteria in culture. In addition, the nitrogen and phosphorus requirements to maintain such growth rates were improbably high for natural conditions. The same logic applies to hyperscums. *In situ* growth cannot explain the observed rapid increase in chlorophyll *a* concentration (as demonstrated in Fig. 4.5). Moreover, the dark, anaerobic conditions within hyperscums (Zohary, 1985) are not favorable for growth of photoautotrophs.

Hyperscums that contain tons of chlorophyll *a* (Fig. 4.1) can only form in a water body that can sustain such large standing stocks. The latter can be maintained when conditions favour high growth rates (abundance of nutrients, high water temperatures and saturating light intensities) or low loss rates or both, and when the surface area of the water body is sufficiently large.

The fact that in Hartbeespoort Dam hyperscums formed in winter but not in summer, despite the larger or similar size standing crops in summer (Fig. 4.1) indicated that other factors interacted to enable or prevent hyperscum formation.

(b) buoyancy

In Hartbeespoort Dam *M. aeruginosa* accumulated at the surface only occasionally in summer whereas in late autumn and winter blooms formed nearly every morning. Several reasons could have contributed to these seasonal differences in the buoyant nature of *M. aeruginosa*. First, the summer months were generally more windy (Figs 4.1, 3.3) and vertical mixing may have prevented surface bloom formation. This could not have been the only explanation because days with many hours of low wind speeds frequently occurred in summer.

Second, it is documented that *M. aeruginosa* is capable of regulating its buoyancy in response to light intensity (Thomas and Walsby, 1985). It is possible that in summer *M. aeruginosa* regulated its buoyancy to avoid the high light levels ($>2000 \mu\text{E m}^{-2}\text{s}^{-1}$) at the surface, whereas in autumn and winter it floated to utilize the more moderate insolation levels ($>1000 \mu\text{E m}^{-2}\text{s}^{-1}$). These "moderate" light intensities are comparable with the maximum summer values in temperate lakes, but it was argued in chapter 4 that the Hartbeespoort Dam *M. aeruginosa* strain may be adapted to high light levels.

Finally, it is possible that the winter populations were senescent and lost their ability to regulate their buoyancy (Reynolds and Walsby, 1975). The growth rate of *Microcystis aeruginosa* is greatly reduced below a critical temperature of about 15°C (Krüger and Eloff, 1978; Nicklisch and Kohl, 1983; Kappers, 1984; Reynolds, 1984; Robarts and Zohary, 1987). In Hartbeespoort Dam, water temperature in winter declined below 15°C so that growth rate of *M. aeruginosa* must have been very low. Therefore, its ability to regulate excess buoyancy by dilution of gas vacuoles through cell division was practically lost. The gas vacuole content of *Microcystis aeruginosa* cells from a surface bloom in the main basin in winter was about 50 - 70 % of the cell section area (see later, section 6.2.1). This was high in comparison with the proportions reported for growing populations by Reynolds *et al.*, (1981). Other studies also indicated that cessation of growth and senescence were accompanied by increases in the relative gas vacuole content of the cells (Smith and Peat, 1967; Lehmann and Jost, 1971; Reynolds, 1972; 1987).

It is likely that, despite the relative abundance of light, the winter *M. aeruginosa* populations from Hartbeespoort Dam could not produce sufficient carbohydrate ballast to negate the excess buoyancy (Kromkamp and Mur, 1984; van Rijn and Shilo, 1985) caused by the high gas vacuole content. These populations thus became constitutionally buoyant, explaining why hyperscums typically formed in winter and not in summer.

The winter water temperatures in Hartbeespoort Dam did not decline below 12°C. In temperate lakes, however, water temperature in winter reach or get close to freezing. Thomas and Walsby (1986) have shown that below about 12°C *Microcystis aeruginosa* loses its buoyancy regulation capacity. Indeed, in temperate lakes this cyanobacterium loses buoyancy and sinks to the sediments in autumn (Reynolds, 1987 and references therein).

(c) winds

A factor overriding the surface accumulation of buoyant cyanobacteria is vertical mixing. Buoyant cyanobacteria become mixed into the water column only when on-lake wind speeds exceed about 3.7 m s^{-1} (Scott *et al.*, 1969; George and Edwards, 1976; Harris, 1980). When turbulent transport is sufficiently weak, blooms will form within several hours (Reynolds and Walsby, 1975). Yet, hyperscums develop over longer time scales, and continuous low speed winds over several weeks are necessary to maintain them.

In reality, a complex wind regime may be necessary. In Hartbeespoort Dam the interplay between the low wind speeds in the main basin and the strong night SE winds in the gorge (Figs 3.3, 4.2) seemed important. The main basin comprised 60 % of the lake's surface area and therefore constituted the origin for most of the *Microcystis* blooms that later formed the hyperscums. The role of the strong night SE winds in the vicinity of the wall (Fig. 4.2) was to compact the hyperscum. Possibly, without this compaction effect the same algal mass would have been spread more loosely over a larger area. The proportion of the algae inside the wind-protected zone would have then been smaller, and the resistance of the thinner scum to NW winds weaker.

(d) wind-protected accumulation site

When conditions (a), (b) and (c) coexist it is likely that thick sur

face blooms will form and that they will be transported by surface currents and accumulate at the lee shores. In order for a hyperscum to develop, however, the algae must accumulate where they will not be dispersed upon a reversal in wind direction. The Hartbeespoort Dam data have demonstrated the importance of the morphometric characteristics of the accumulation site. Small differences in water levels changed a large wind protected site to an unprotected one. In addition, the morphometry of the site determined the size of the protected area and therefore also dictated the maximum area a hyperscum could cover.

(e) high insolation levels

Strong light intensities enhance crust formation through two processes: photooxidation and dehydration (see later, section 6.2.2). The crust had greater resistance to wind activity than water, or even thick, non-crusted scums, and played an important role in maintaining the hyperscum as one unit under moderate winds.

4.3.2 Occurrence of hyperscums

Reports of intense cyanobacterial blooms with chlorophyll *a* concentrations of several mg l^{-1} are available from many parts of the world ranging from the tropics to temperate climates, and from a wide range of types and sizes of brackish and freshwater bodies (Table 2). Common determinants in all these records are enrichment of the water and calm weather conditions. Hyperscums occur more rarely (Table 4.2). The only definite published account of crusted hyperscums other than in South Africa is from the Dnieper reservoirs (Table 4.2). But there are published records about cyanobacterial scums that may have been hyperscums, although the data provided is insufficient for this kind of classification, and there are unpublished observations of hyperscums (Table 4.2).

While the coincidence of Reynolds and Walsby's (1975) three preconditions for bloom formation (pre-existing standing stocks, buoyancy and low turbulence) is common, as can be judged from the frequent occurrence of cyanobacterial blooms, the coexistence of the additional requirements for hyperscum formation is rare. The requirement of a large pre-existing cyanobacterial standing stock rules out highly eutrophic water bodies that sustain high concentrations of non-buoyant species as well as small hypertrophic water-bodies that sustain high

TABLE 4.2 Records of the occurrence of hyperscums in various eutrophic waterbodies where cyanobacterial blooms occur regularly.

Water Body	Trophic status	Surface area, km ²	Mean Depth, m	Dominant bloom genera	Mention of crusted hyperscum	Reference
Fish ponds, Israel	Eutrophic	0.035	1.2	<i>Microcystis</i> <i>Oscillatoria</i> <i>Spirulina</i>	No - surface blooms in early mornings disperse in afternoons	van Rijn & Shilo, 1985
King Talal Reservoir, Jordan	Hypertrophic	2.6	21.5	<i>Microcystis</i>	Yes - hyperscum, ca. 40 cm thick persisted for 4 months in summer 1986	F. Hashwa, pers. comm.
Lake Brielle, The Netherlands	Hypertrophic	4.0	5.5	<i>Microcystis</i>	? - "drijfslagen" (or "floating layers")	Meijer & van der Honing,
Lake Akersvatn, Norway	Eutrophic	2.4	6	<i>Microcystis</i>	No - but 5-10 g algal dry wt l ⁻¹ in lee shore aggregates	Berg <i>et al</i> , 1987
Kremenchug Reservoir, USSR	Hypertrophic	NS	NS	<i>Microcystis</i> <i>Anabaena</i>	Yes - "dry crusts", "neuston mats", "neustonic phase"	Topachevskiy <i>et al</i> , 1969
Lake Mendota, Wisconsin USA	Eutrophic	39.1	12.4	<i>Aphanizomenon</i>	No - but "massive blooms" do occur	Brock, 1985
Potomac River, Washington DC USA	Eutrophic			<i>Microcystis</i> <i>Oscillatoria</i>	No - but scums of "green paste" are common	Kroegmann <i>et al</i> , 1986
Lake George, Uganda	Eutrophic	250	2.4	<i>Microcystis</i>	No - surface accumulations in early mornings disperse in afternoons	Ganf, 1974
Hartbeespoort Dam, South Africa	Hypertrophic	20	9.6	<i>Microcystis</i>	Yes - hyperscums persist 3-4 months most winters	Zohary, 1985; Robarts & Zohary, 1986; This study.
Lake Suwa, Japan	Eutrophic	14.5	4.1	<i>Microcystis</i>	No - but 95 mg Chl l ⁻¹ recorded	Yamagishi & Aoyama, 1972
Lake Kasumigaura, Japan	Hypertrophic	178	4	<i>Microcystis</i> <i>Anabaena</i>	? - "heavy neuston mats of decimeters thickness"	Seki <i>et al</i> , 1980
Ciénaga Grande Lagoon, Columbia	Eutrophic	450	1.8	<i>Microcystis</i>	No "mass accumulation"	Hoppe <i>et al</i> , 1983

concentrations of cyanobacteria but where the total standing stock is not sufficiently large. Loss of *M. aeruginosa* buoyancy due to low winter water temperatures in temperate lakes (Thomas and Walsby, 1986) may contribute to the scarcity of hyperscums at high latitudes. The requirements of the continuous prevalence of low wind speeds over weeks, and of a complex interaction between the wind regime at various parts of the lake and its morphometry, eliminate many others. Thus, lakes with a typical diurnal cycle of e.g. calm mornings but windy afternoons, should not form hyperscums. This view gains support from observations at Lake George, Uganda, which maintains one of the largest recorded standing stock of cyanobacteria (ca 600 mg Chl m^{-2}) throughout the year (Ganf, 1974). This warm shallow lake undergoes diel alterations of destratification and restratification. Surface blooms that typically form during the early morning hours are mixed into the water column in the afternoon and hyperscums were not reported to occur there (Table 4.2). The additional constraints on shore morphometry and a requirement for strong incident light, all coinciding, result with the hyperscum phenomenon being rare (Table 4.2). Yet, hyperscums probably occur more often than recorded in the scientific literature, and with increasing hypertrophy in the third world (Robarts, 1985) it can be expected that the frequency and distribution of their occurrence will increase.

CHAPTER 5

THE HYPERSCUM ENVIRONMENT

5.1 INTRODUCTION

In the previous chapters hyperscums were shown to exist for several months and to contain ca. 10 - 50 % of the lake's chlorophyll a (Fig. 4.1A). It was also suggested that *Microcystis aeruginosa* colonies arriving at the hyperscum were mostly overbuoyant and senescent, belonging to post-maximal populations that maintained themselves from the previous summer. Eventually hyperscums broke and the colonies comprising them were dispersed in the lake. The fate of the colonies trapped in the hyperscum for two or three months is thus crucial to the understanding of the population dynamics of the cyanobacterium in hypertrophic Hartbeespoort Dam.

A characterization of the hyperscum environment is the first step towards the elucidation of the fate of *Microcystis aeruginosa* trapped in the hyperscum. The hypothesis was that conditions developing in the hyperscum were stressful for survival of photoautotrophic organisms and that prolonged exposure to these conditions was lethal. The following chapter is aimed at elucidating the structural, physical and chemical characteristics of the hyperscum, how they develop with time and change with depth. Chapter 6 then examines the response of *M. aeruginosa* to conditions within the hyperscum.

5.2 RESULTS

5.2.1 The hyperscum community

The hyperscum community was a cyanobacterial - bacterial association in which *Microcystis aeruginosa* was the dominant component, usually comprising >99% of the algal volume (Table 5.1) and >95% of the bacterial + algal volume (Table 5.2). The filamentous cyanobacterium *Pseudanabaena* sp. (identified according to Rippke *et al.*, 1979) often

TABLE 5.1 Median linear dimensions (μm), volume ($\text{mm}^3 \text{L}^{-1}$) and % contribution to the total algal volume of the species found in replicate 10 cm hyperscum samples.

Date	<i>Microcystis aeruginosa</i>				<i>Pseudanabaena</i> sp.			Other species		
	cells $\text{ml}^{-1} \times 10^6$	diam. μm	$\text{mm}^3 \text{L}^{-1}$	%	$\text{mm}^3 \text{L}^{-1}$	%	length μm	$\text{mm}^3 \text{L}^{-1}$	%	species
25.5.84	1.40	5	86 800	97.71	39.51	0.05	4	1 990	2.24	Oo
	1.49	5	92 400	93.79				131.4	0.13	4
5.6.84	0.90	5	55 600	97.99	91.8	0.16	3	1 049	1.85	Ni
	2.06	5	127 700	100				P	-	P
12.6.84	1.83	5	113 500	98.22				2 060	1.78	Oo
	3.11	5	192 800	100				P		P
20.6.84	1.50	5	93 000	100	P			P		Me
	1.76	5	109 000	97.66				2 613	2.34	Me
4.7.84	1.33	5	82 500	100	87.5	0.12	3	125	0.16	Ch
	1.22	5	75 600	99.72				P	P	
10.7.84	2.35	5	145 700	100			5	129 600	100	
	2.09	5	129 600	100						
17.7.84	2.05	5	127 100	98.66	177.3	0.14	4	155.37	1.20	Me
	2.84	5	176 100	99.94				112.5		0.06
24.7.84	2.70	5	167 400	99.95	80.64	0.05	4	P		Ni
	2.25	5	139 500	100				P	P	
31.7.84	2.06	5	115 300	100	P			P		Ni
	1.89	5	127 700	100					P	
8.8.84	2.20	5	136 400	100	P					
15.8.84	1.62	5	81 200	100				P		Me, Cy
	1.31	5	100 400	100						
22.8.84	1.83	5	113 500	100	128.7	0.08	4			
	2.55	5	158 100	99.92						
29.8.84	1.80	5	111 600	100	77.49	0.11	4			
	1.12	5	69 400	99.89						
4.9.84	0.0003	5	17.2	99.36	0.11	0.64	4	P		Cy

Abbreviations used: Ch - *Chroomonas* sp.; Cy - *Cyclotella menengiana*; Me - *Melosira granulata*; Ni - *Nitzschia* sp.; Oo - *Oocystis* sp.; P - present in sample but not in the counted fields.

TABLE 5.2 Bacterial numbers and volumes (based on linear dimensions of the different morphological types) from Hartbeespoort Dam hyperscum at 10 cm depth.

Date	Morphological type	mean diam. μm	mean length μm	cell volume μm^3	cells ml^{-1} $\times 10^9$	volume, $\mu\text{m}^3 \text{ml}^{-1}$ $\times 10^6$	% total bacteria volume	% total (algae + bac.) volume
4.7.84	coccoid	0.3	-	0.008	5.5	43.9	6.1	
	small rods	0.4	1.4	0.176	1.1	189.1	26.4	
	large rods A	1.0	1.4	1.10	0.37	377.1	52.7	
	large rods B	1.4	3	4.62	0.02	105.6	14.8	
	Total				6.9	715.7	100	0.09
8.8.84	Coccoid	0.3		0.008	4.0	43.1	3.3	
	small rods	0.4	1.4	0.176	2.4	554.9	42.5	
	large rods	1.4	3	4.62	0.1	706.9	54.2	
	Total				8.7	130.5	100	0.95
28.8.84	Coccioids	0.3		0.008	5.6	45.1	1.5	
	small rods	0.4	1.4	0.176	1.4	242.5	7.8	
	large rods A	1.0	1.4	1.10	0.4	183.9	59.3	
	large rods B	1.4	3	4.62	0.8	9.76	31.5	
	Total				8.4	310.2	100	3.3

inhabited the mucilaginous sheath around *M. aeruginosa* colonies but its contribution to the algal volume was always less than 0.2 % (Table 5.1). Eukaryotic algae (*Oocystis* sp., *Melosira granulata* var. *angustissima*; *Nitzschia* sp.) occurred only during the initial build-up phase and their contribution to the total algal volume was negligible (Table 5.1).

On three occasions in 1984 bacteria at 10 cm were enumerated and their sizes estimated (Table 5.2). They reached concentrations of 7×10^9 to 9×10^9 cells ml^{-1} or 2 to 3 orders of magnitude higher than their concentrations in the main basin epilimnion (Robarts, 1987). Sizes ranged from 0.3 μm diameter coccoids to 3 μm length rods (Table 5.2) which were much larger than the typical 0.1 - 0.2 μm diameter coccoids of the main basin (Robarts and Sephton, 1984). Yet, because of the small volume of even the largest bacteria compared with that of *M. aeruginosa*, bacteria at 10 cm depth in the hyperscum comprised only a small fraction of the total biovolume, ranging between 0.9% on 4 July and 3.3% on 28 August (Table 5.2).

5.2.2. The hyperscum structure

As soon as a crust started developing over a newly accumulated scum a distinct pattern in the vertical distribution of *M. aeruginosa* within it became evident: the highly buoyant colonies (section 4.3.1b) tended to float and compacted as they got closer to the surface, as was evident from the depth distribution of chlorophyll a and phycocyanin concentrations and of the proportion of the volume taken up by interstitial water in a newly accumulated scum (Fig. 5.1). The resulting structure is represented schematically in Fig. 5.2.

In 1986 the mean chlorophyll a concentration in the 1-2 mm crust layer was 3.07 g l^{-1} (Table 5.3). A few millimeters deeper the concentration was only one third of that, and at 10 cm depth it was one third of the later (Table 5.3). In 1984 the concentration at 10 cm depth was generally $> 200 \text{ mg l}^{-1}$, declining with depth to about 100 mg l^{-1} . Below the hyperscum (i.e. where water between colonies was evident) the concentration declined over about 20 cm to 5 mg l^{-1} (Fig. 5.3).

Based on these observations the hyperscum was treated as three structurally different but continuous zones: the crust, comprising the top 1-2 mm dry layer; the compact algal layer (ca. 5 mm) just below the crust; and a less compact layer from about 1 cm depth to the bottom, incorporating the bulk of the hyperscum (Fig. 5.2).

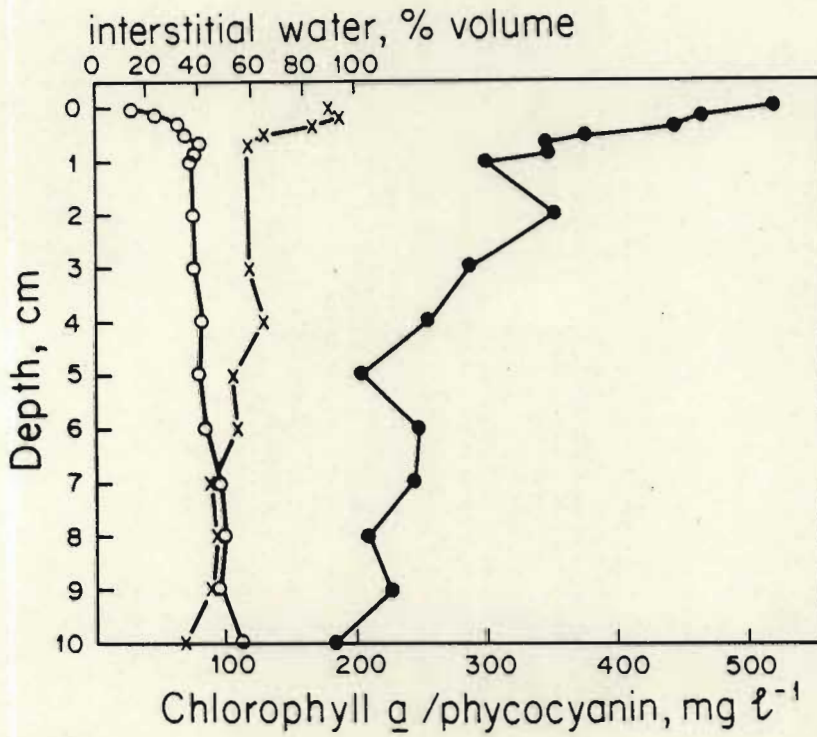


FIGURE 5.1 Depth profiles of chlorophyll a (●), phycocyanin (x), and the proportion of interstitial water (o) in a newly formed hyperscum.

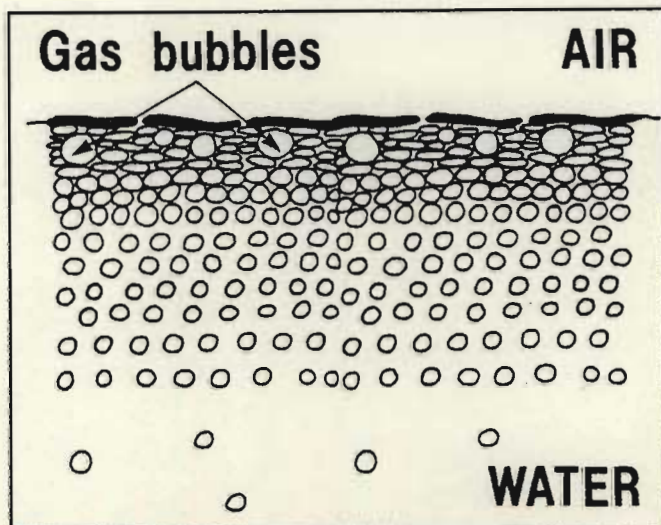


FIGURE 5.2 A schematic representation of a depth profile through a hyperscum of *M. aeruginosa*. Not to scale.

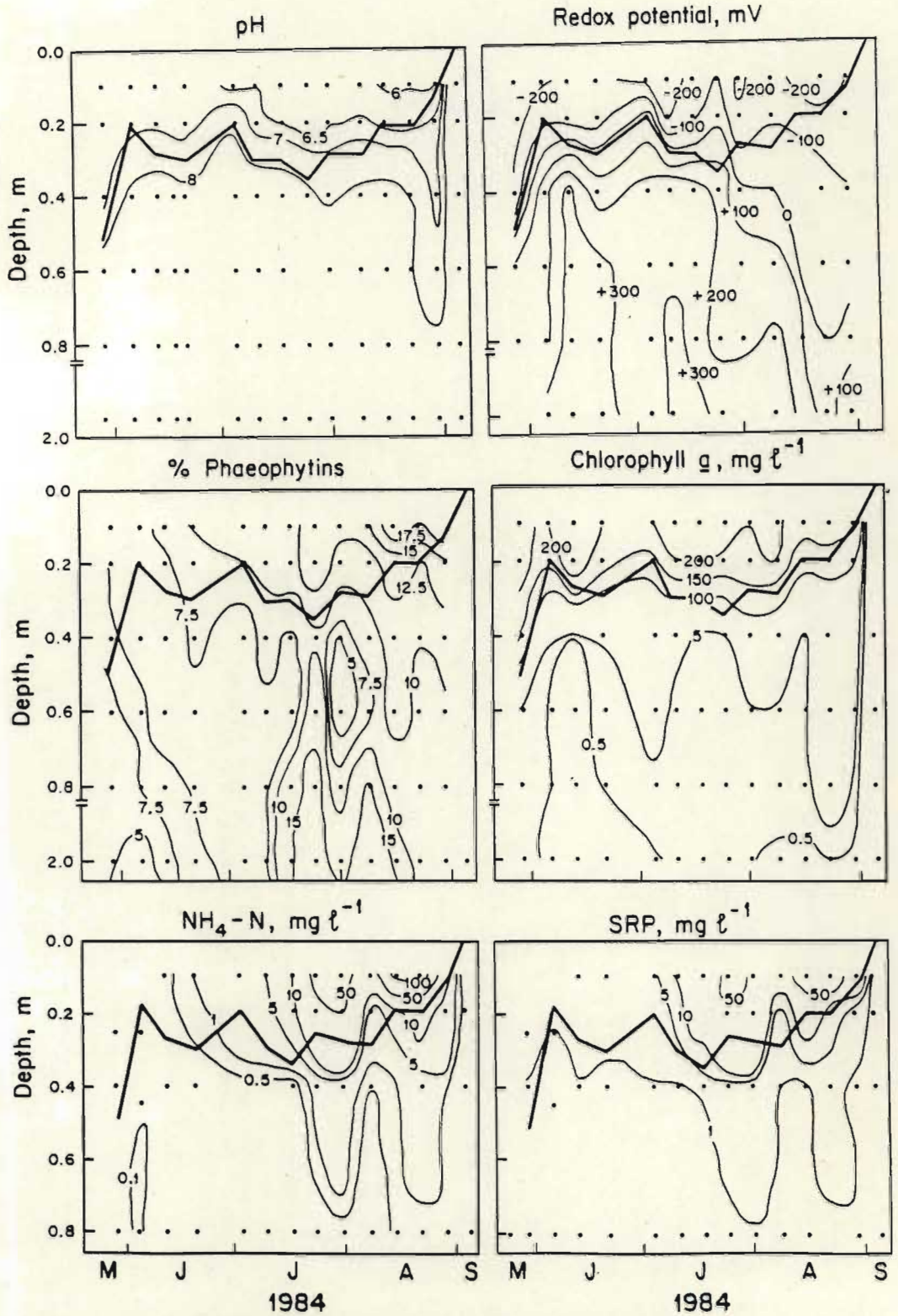


FIGURE 5.3 Isopleths of several chemical parameters within and below the hyperscum in winter 1984. Thick line marks the bottom of the hyperscum, dots mark sampling points.

TABLE 5.3 Chlorophyll a concentrations (Chl) and the water content ([total weight - dry weight]/total weight, expressed as percentage) of the different hyperscum zones, June - August 1986. CV = SD expressed as percentage of the mean.

Layer and depth	range	mean \pm CV	(n)
<u>I. Chl, g l⁻¹</u>			
crust, 0 - 2 mm	1.14 - 4.33	3.07 \pm 33 %	(9)
compact layer, 2 - 20 mm	0.53 - 1.63	1.00 \pm 31 %	(10)
bulk of hyperscum, 10 cm	0.22 - 0.52	0.33 \pm 27 %	(10)
<u>II. water content, % (inter- + intra-cellular)</u>			
crust, 0 - 2 mm	11.5 - 18.8	14.1 \pm 24 %	(4)
compact layer, 2 - 10 mm	62.5 - 84.6	77.2 \pm 11 %	(5)
bulk of hyperscum, 10 cm			
unfiltered	94.9 - 96.4	95.7 \pm 0.5 %	(7)
filtered	86.4 - 96.0	94.1 \pm 3.0 %	

The number of *M. aeruginosa* cells per unit volume of hyperscum at 10 cm depth ranged between 1.4×10^9 and 2.5×10^9 cells ml⁻¹ (Table 5.1), corresponding with volumes (assuming *Microcystis* cells to be spherical) ranging from 79 to 153 cm³ l⁻¹, or 8 to 15% of the hyperscum (algae + water) volume. These estimates excluded the volume contributed by the mucilage sheath in which *Microcystis* cells in natural populations are embedded (Reynolds *et al.*, 1981). The presence of a mucilaginous sheath surrounding *Microcystis* cells in the bulk of the hyperscum was evident from light and electron microscopy. Measurements of cell volume/colony volume ratio by Reynolds *et al.*, (1981) showed that cells rarely occupied more than 20% of the colony volume and in some populations the fraction was <5%. Applying a ratio of 20% to the hyperscum population implied that at 10 cm depth *Microcystis* colonies occupied between 40 to 75% of the hyperscum (algae + water) volume. This is in agreement with the thick consistency of these scums. Indeed, interstitial water (collected by centrifugation of thin core slices after gas vacuoles had been collapsed) comprised 40 - 56 % of the hyperscum volume between 4 and 10 cm depth (Fig. 5.1).

Samples collected from the compact layer under the crust contained so little inter-colony water that they had to be diluted before a subsample could be taken volumetrically. Chlorophyll a concentration in this layer ranged between 0.5 and 1.6 g l⁻¹ (Table 5.3). Cells could not be counted with accuracy in this material because of the abundance of decomposing cells. Converting chlorophyll a to cell numbers using

a mean cellular content of $0.11 \text{ pg Chl cell}^{-1}$ (see later, Table 6.2) and to volume using a mean cell diameter of 4μ (Table 6.1) the above range was equivalent to $146 - 500 \text{ cm}^3 \text{ l}^{-1}$. The sheath in this layer was attacked by bacteria, as indicated by electron microscopy (Plate 6.2C) and only a small proportion of it remained. It was therefore excluded from the above calculation. Still, space for very little inter-colony water remained, in agreement with the small amount of water (20 - 40 %) that could be separated by centrifugation from the 0.2 - 1.0 cm layer in a newly formed hyperscum (Fig. 5.1).

The maximum recorded chlorophyll a concentration in the crust, 4.3 g l^{-1} (Table 5.3) was equivalent to the improbable $1310 \text{ cm}^3 \text{ l}^{-1}$. But, as mentioned earlier, the crust was composed of dehydrated cells of reduced volume, and the conversion factors could not apply. Indeed, water comprised only 14 % of the total crust weight (Table 5.3), which justifies regarding it as a solid. The chlorophyll concentrations demonstrated that cells in the crust were at least ten times more compact than in the bulk of the hyperscum.

5.2.3 The hyperscum physical and chemical characteristics

Due to light attenuation by photosynthetic pigments surface blooms with chlorophyll a concentration (top 2.5 cm) of 13 mg m^{-3} attenuated most of the light and only 1.5 % of the incident irradiance was measured under a 5 mm algal film (Table 5.4). Under thicker surface scums of $152 \text{ mg chl m}^{-3}$ only 0.05 % of the incident light could be detected.

A consequence of the compact nature of the top hyperscum layer was attenuation of all the incident light within the upper few millimeters, and light intensity at about 5 mm depth was always below detection limit of the light sensor, i.e., less than $0.01 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Table 5.4). It was impossible to measure with the available light meter the exact euphotic zone depth but circumstantial evidence from microprofiles of photosynthetic activity measured with microelectrodes (see later, section 6.2.1) indicated that light did not penetrate more than 2-3 mm of a new (non-crust) scum. It could be inferred that light could not penetrate the crust.

The moderating effect of the high heat content of pure water on temperature did not apply to the dry crust and the compact algal layer beneath it. Indeed, temperature at the hyperscum surface fluctuated with the diel cycle of air temperature and with exposure to

TABLE 5.4 Incident (I) and subsurface (ca. 5 mm depth; I_0) light intensities under a range of natural surface *M. aeruginosa* blooms from Hartbeespoort Dam. Chlorophyll a concentrations (Chl) are for the top 2.5 cm layer.

Date	Description	Chl mg l ⁻¹	I μE m ⁻² s ⁻¹	I_0 μE m ⁻² s ⁻¹	I_0/I %
17.6.86	thin surface film of cyanobacteria	13	2200	34	1.5
26.5.86	surface scum	37	2240	20	0.9
26.5.86	very thick surface scum	52	2400	1.2	0.05
2.7.86	20 cm thick, non-crusted scum	188	2210	0	0
2.7.86	crusted hyperscum	>500	2430	0	0

illuminated/shaded conditions. For example, on 23.7.84 at 12:00 h the surface temperature at a shaded station (4; Fig. 2.3) was 9.2°C, but 10 m away in the sun it was 13.9°C. The temperature at the bottom of the hyperscum was, however, moderated by the underlying lake water. Thus, extreme vertical temperature gradients developed over several decimeters within the hyperscum, and the closer to the drier surface, the steeper the gradient. When on 23 August 1984 at 12:00 h station 4A (Fig. 2.3) was exposed to direct sunlight, a gradient of 5 °C over the top 10 cm was measured (Fig. 5.4A). After cold nights reversed temperature profiles were recorded. Air temperature declined to 0°C before sunrise on 28 May 1984. At 10:00 h the temperature just below the crust, at the shaded station 4 was 7.9 °C while at 0.5 m it was 17.3 °C (Fig. 5.4). A similar reversed temperature gradient was often noted during the 1983 hyperscum season. For example, on 23 June a reversed gradient of 6°C over 75 cm was recorded (Fig. 5.4B).

The lakeward margin of the hyperscum was marked by a sharp horizontal temperature gradient (Fig. 5.4B) which implied an irregularity in water movement. Drift cards indicated that incoming surface currents plunged when they hit the hyperscum boundary (see Fig. 4.4). When strong NW winds caused the surface current to travel away from the hyperscum an upwelling current may have developed at the boundary, as suggested in Fig. 5.4B.

With *Microcystis* colonies comprising 40 - 70 % of the total volume at 10 cm depth, free water movement took place around and under the hyperscum, but within it water movement was restricted to diffusion.

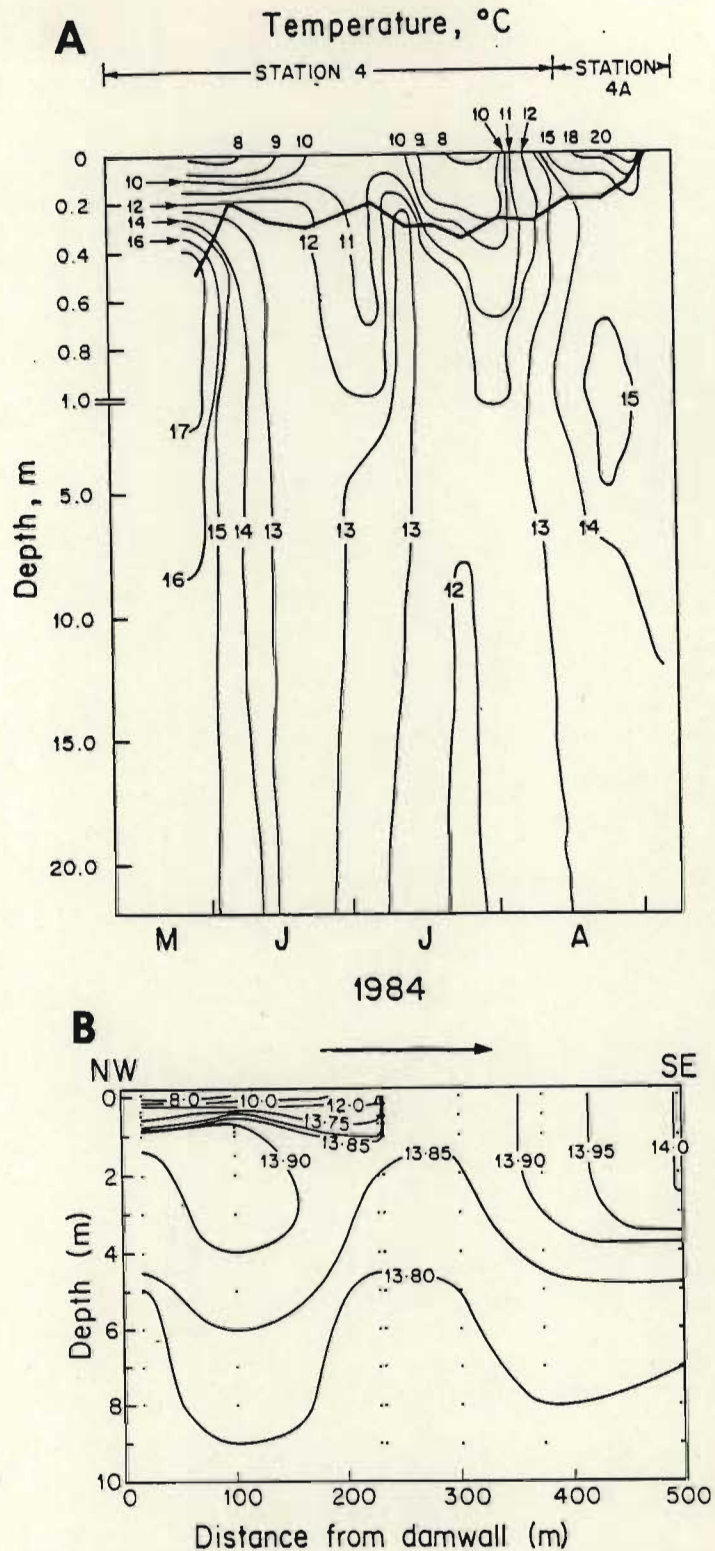


FIGURE 5.4 (A) Isotherms within and below a hyperscum at the dam wall of Hartbeespoort Dam, South Africa, 1984. Thick line marks the bottom of the hyperscum. Station 4 was shaded during measurements; station 4A was exposed to direct sunlight. (B) Isotherms along a 500 m transect from the dam wall towards the main basin at 10:00 h, 23 June 1983. The shaded area near the wall contained a 75 cm thick hyperscum thermally distinguishable by a steep reversed gradient. Arrow indicates wind direction.

This conclusion is supported by the chemical data (see below): while the water under the hyperscum was chemically similar to the main basin water, the chemical composition inside the hyperscum was significantly different (Table 5.5, Fig. 5.3), implying little or no inter-mixing. Also, the steep vertical temperature gradients of up to 10°C over 50 cm described above could not have existed if water movement was not restricted to diffusion.

TABLE 5.5 Comparison of several chemical characteristics of the hyperscum and the main basin near surface water for the period 28 May to 30 August 1984. Data are given as means of 12 or 13 weekly observations \pm standard deviations with ranges in brackets. hyperscum measurements are from 10 cm depth; main basin measurements are from 0.5 m depth.

Parameter	Hyperscum	Main basin
Dissolved oxygen, % saturation	0	97.3 \pm 30.0 (67 - 174)
Redox potential, mV	-203 \pm -5.14 (-278) - (-97))	250 \pm 102 * (61 - 350)
pH	6.3 \pm 0.3 (5.9 - 6.8)	8.5 \pm 0.2 (8.2 - 9.1)
Dissolved organic C, mg l ⁻¹	- (280 - 660)**	8.13 \pm 1.3 (6.0 - 10.2)
SRP, mg l ⁻¹	29.0 \pm 30.3 (0.54 - 83.3)	0.53 \pm 0.09 (0.31 - 0.83)
NH ₄ -N, mg l ⁻¹	35.1 \pm 43.9 (0.12 - 118.8)	0.12 \pm 0.07 (0.04 - 0.20)
(NO ₃ + NO ₂) - N, mg l ⁻¹	0.12 \pm 0.09 (0.02 - 0.29)	1.59 \pm 0.53 (1.26 - 2.41)
Inorganic N:P ratio	0.9 \pm 0.5 (0.04 - 1.5)	3.3 \pm 0.5 (2.2 - 4.6)
H ₂ S, mg l ⁻¹	(1.3 - 7.1)	0

*recorded in the lake water underlying the hyperscum at 2 m depth

**July-August only

Diffusion of atmospheric oxygen and other gases into the hyperscum was restricted. In the absence of light photosynthetic O_2 production stopped but respiratory oxygen consumption probably continued. With the high concentration of respiring organisms oxygen consumption most likely exceeded the available supplies, causing anoxia. Throughout the hyperscum season oxygen was never detected at 10 cm depth (Table 5.5). Anoxia was also indicated by continuously negative redox potentials which at 10 cm depth ranged between -278 and -166 mV (corrected for pH 7), except on one occasion when the redox was -97 mV (Table 5.5, Fig. 5.3). With increasing depth the redox increased to about zero at the bottom of the hyperscum and became positive ($>+200$ mV) in the underlying lake water (Fig. 5.3).

The pH in the hyperscum also exhibited a steep vertical gradient, being lowest (6 - 6.5) a few mm beneath the surface and increasing with depth to >8 below the hyperscum (Fig. 5.3). The low pH was probably another consequence of the lack of photosynthesis, and of the presence of metabolic processes which released organic acids (see below).

Steep vertical gradients similar to those of chlorophyll *a*, redox and pH were evident with other chemical parameters, e.g. concentrations of dissolved ammonia-N and soluble reactive phosphorus (SRP) (Fig. 5.3), with values being highest near the surface. At any given depth, concentrations typically increased with time as the hyperscum aged, but finally declined abruptly when the hyperscum broke down (Fig. 5.5). For example, at 10 cm depth the pH continuously declined (i.e. H^+ concentration increased) from 6.6 on 28 May to 5.9 on 29 August 1984 (Fig. 5.3). Changes with time in the concentrations of dissolved nutrients (in samples collected by dialysis from 10 cm depth) were dramatic (Fig. 5.5). Ammonia-N concentration increased approximately 260 fold over 3 months, from 0.45 mg l^{-1} on 28 May to 119 mg l^{-1} on 22 August. Soluble organic nitrogen in the same samples increased over the same period 48 fold, from 0.27 to 12.7 mg l^{-1} and SRP 30 fold, from 2.8 to 83.3 mg l^{-1} . From the steep vertical gradients in the isopleths of ammonia -N and SRP (Fig. 5.3) it seems likely that their concentrations reached even higher values closer to the surface. Then, during the final breakdown of the hyperscum in late August these concentrations declined rapidly to ambient lake concentrations (Fig. 5.3, 5.5).

Nitrite and nitrate concentrations remained low and did not exceed 0.2 mg l^{-1} (Table 5.5). This is not surprising: under the low redox

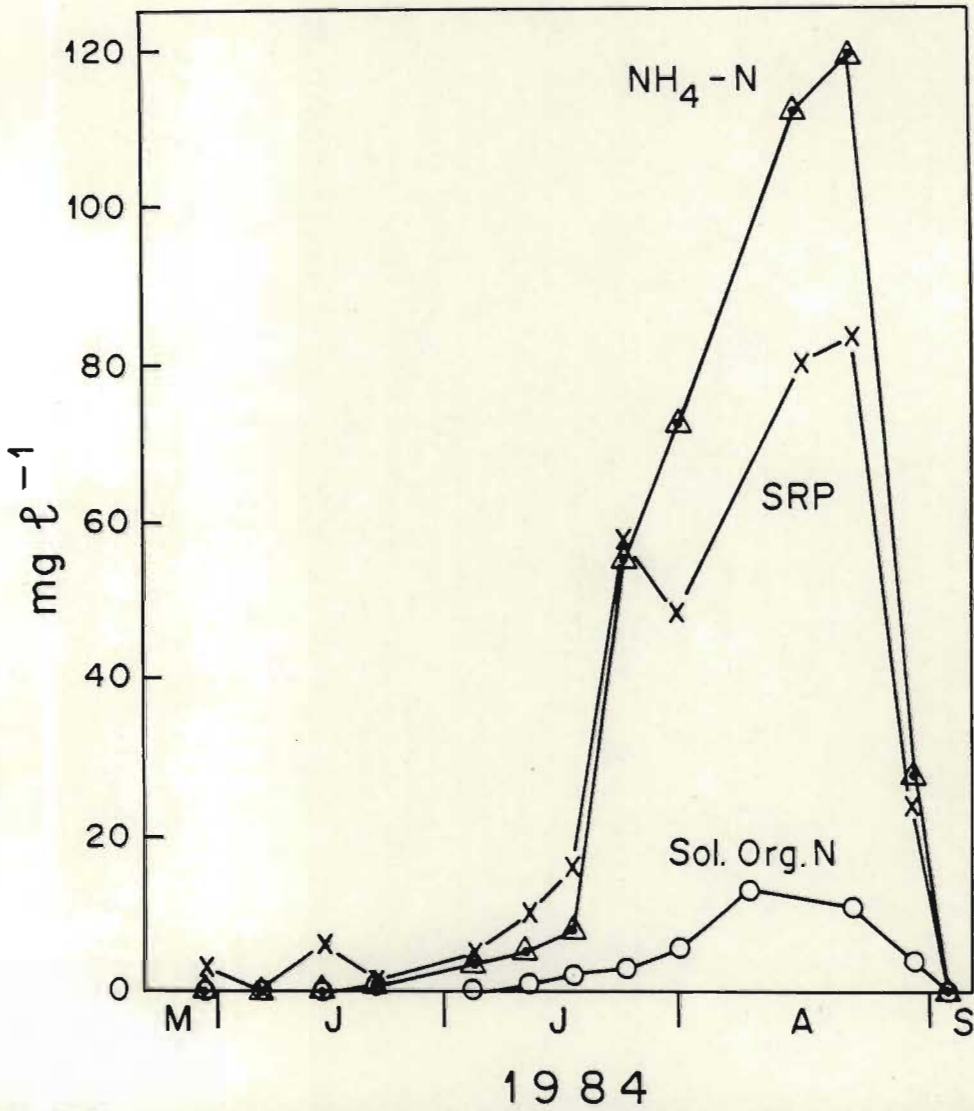


FIGURE 5.5 Changes with time in the concentrations of ammonia-N (NH₄-N), soluble reactive phosphorus (SRP) and soluble organic-N (Sol. Org. N) in the hypericum interstitial water at 10 cm depth.

potentials chemical and biological reduction processes were favoured and nutrients were converted to their reduced forms. Sulfide concentrations also increased with time to a maximum of 7.1 mg l^{-1} (Table 5.5). Dissolved organic carbon (DOC) concentrations in the hyperscum reached a maximum of 660 mg l^{-1} , or about 80 times higher than in the main basin (Table 5.5).

Another characteristic of the hyperscum environment was the production of gases that either escaped through cracks in the crust, releasing strong foul odours, or became trapped as large bubbles (up to 1 cm diameter) in the compact layer beneath the crust (Fig. 5.2). The bubbles were composed of 28 % methane, 19 % CO_2 , trace amounts of H_2 and no oxygen (Table 5.6). Methane and CO_2 are typical end products of anaerobic decomposition (Ward *et al.*, 1984). In addition, volatile fatty acids, the intermediate products of bacteria-mediated anaerobic decomposition, were present in the interstitial water (Table 5.7). Various short-chain fatty acids (C2 to C5) were present, with acetic acid at the highest concentration ($> 1 \text{ mmol l}^{-1}$; Table 5.7). The maximum theoretic acetic acid concentrations in the main basin of Hartbeespoort Dam are measured in $\mu\text{mol l}^{-1}$ (Robarts, 1986).

TABLE 5.6 Hyperscum gas-bubble composition.

methane	28 %
CO_2	19 %
N_2	51 %
H_2	traces
Total	100 %

TABLE 5.7 Volatile fatty acids (VFA) found in the interstitial water of a newly developed hyperscum collected 29 May 1987 (new) and in a mature hyperscum collected 2 July 1986 (mature). Concentrations in mmol l^{-1} are means for 3 to 10 samples from 0 - 10 cm depth.

Acid	new	old
Acetic acid	1.40	1.03
Propionic acid	0.51	0.05
Butyric acid	0.05	0.08
Isobutyric acid	0.03	0.06
Valeric acid	0.03	0.14
Isovaleric acid	0.03	0.07
total VFA	2.04	1.43

5.3 DISCUSSION

The structural, physical and chemical characteristics of the hyperscum, how they evolved, and how they changed with the aging of the hyperscum were described. The hyperscum was seen as one continuum of densely packed buoyant *M. aeruginosa* colonies, arranged in a steep vertical gradient, where colony compaction increased exponentially with declining distance from the surface. This spatial distribution of colonies was a direct result of the mechanism of buoyancy regulation operating in concert with evaporative dehydration. The cyanobacterial mechanism of buoyancy regulation is an adaptation for life in an environment where light is above and darkness below, and where by floating the cells can return to the light. In a hyperscum, however, with the exception of the uppermost 1 - 3 m it is dark from above. In the darkness *M. aeruginosa* utilized its stored carbohydrate that provided ballast and floated. However, deprived access to light at the top it could not replenish its carbohydrate and therefore could not lose buoyancy. The overbuoyant colonies became trapped, and only external turbulence could return them to the illuminated water. Overbuoyancy was therefore a consequence of the inadequacy of the buoyancy regulation mechanism under conditions where it is dark at the top. Colonies at the surface were subject to evaporative dehydration, which caused the increasing colony compaction with declining depth.

Changes with depth in the physical and chemical environment resulted from differences in colony compaction and in distance from direct contact with the atmosphere. The closer to the surface, the more compact the colonies and the more harsh the physical and chemical conditions.

With the exception of the uppermost few millimeters, the hyperscum environment was continuously dark, anaerobic and highly reduced. In the dark obligate phototrophs cannot photosynthesize and grow. Cyanobacteria, however, are known to withstand long periods of dark anaerobic conditions while maintaining their photosynthetic apparatus intact (Sirenko, 1972; Sentzova *et al.*, 1975). *Microcystis aeruginosa* survives throughout winter in the dark hypolimnetic sediments of temperate lakes (Reynolds *et al.*, 1987 and references therein). Some cyanobacteria are capable of heterotrophic growth in the dark (Raboy *et al.*, 1976; Stanier and Cohen-Bazire, 1977) but *Microcystis aeruginosa* was not proven to be one of them and is considered to be an obligate phototroph (Stanier *et al.*, 1971).

Other conditions within the hyperscum were potentially more harmful to *Microcystis aeruginosa*. Organisms at or near the surface would be subject to the potentially lethal effects of dehydration and photooxidation through exposure to direct radiation; ammonia (Fig. 5.5) and sulfide concentrations increased with time to potentially toxic concentrations (Abeliovich and Azov, 1976; Knobloch, 1969; Oren *et al.*, 1979); diel variations in temperature were greater than in the lake and at the hyperscum surface the temperature ranged between near freezing at night to above 20°C during the day. These diel variations may have placed an additional stress on an organism that usually thrives under more moderate temperature regimes.

According to Cole (1982) at the onset of cell death there is a large release of soluble materials from the cells, amounting to 20 - 50 % of the organic content. The soluble material which escapes the cells is rapidly metabolized by bacteria. The rapid increases of dissolved ammonia, phosphate (Fig. 5.3, 5.5) and DOC (Table 5.5), in the hyperscum are indicative of such processes. In addition, the presence of short chain volatile fatty acids and gas bubbles containing CO₂ and methane (Tables 5.6, 5.7), the decline in pH (Fig. 5.3), together point to the prevalence of decomposition within the hyperscum.

In order to roughly estimate the rate of decomposition the following theoretical calculation was made: using a mean cellular chlorophyll content of 0.11 pg cell⁻¹ (see later, Fig. 6.6) and cellular Chl/P ratio of 0.6 (NIWR, 1985), the maximum SRP concentration measured at 10 cm depth of 80 mg l⁻¹ (Fig. 6.4) would originate from 0.6 x 0.11 x Z cells l⁻¹; Z = 1.2 x 10¹² cells l⁻¹. This was about 60 % of the mean cell concentration over July and August (2.06 x 10¹² cells l⁻¹; Fig. 6.6). Possible explanations were that 60 % of the cells at 10 cm depth died, or that the phosphorus was transported from elsewhere. The only likely source would have been the crust and compact layer beneath it, where conditions were even more stressful than deeper in the hyperscum and where cells were about ten times more concentrated.

This chapter has thus raised the following questions: How did *M. aeruginosa* respond to the hyperscum conditions, and how did the response vary with time and with position? What were the implications for the population dynamics of *M. aeruginosa* and for the ecosystem as a whole?

These questions are addressed in the following chapters.

CHAPTER 6

MICROCYSTIS STRUCTURE AND FUNCTION WITHIN HYPERSCUMS

6.1 INTRODUCTION

The previous chapter has demonstrated that conditions in the hyperscum were unfavourable for growth of obligate phototrophs. It was suggested that decay and decomposition processes could explain the temporal changes in the chemical composition of the interstitial water. These conclusions seem contradictory to an earlier report (Zohary, 1985) and field observations, which showed that in the bulk of the hyperscum *Microcystis aeruginosa* survived for more than 2 months, retaining its photosynthetic capacity. The crust and compact layer beneath it were, however, excluded from these earlier investigations. A possible explanation for the apparent contradiction would be that death and decomposition occurred mainly at the top layers while deeper in the hyperscum the cells survived. Accordingly, it was postulated that conditions in the hyperscum were lethal to *M. aeruginosa* only at or near the surface. The positive buoyancy continuously forced colonies upwards, while dehydration at the surface caused shrinkage of dead colonies and space for more colonies from below. Released contents of dead cells at the surface gradually diffused downwards along concentration gradients, explaining the apparent increases with time in decomposition products deeper in the hyperscum.

The study was set to examine the relationships between the position of colonies within the hyperscum, the duration of exposure to the hyperscum environment and the structure and function of *M. aeruginosa*. Field observations provided hints about processes taking place at the surface. Light, fluorescent and electron microscopy were employed to investigate the morphological and ultrastructural characteristics of the cells. The changes with time in cell numbers and pigment concentrations were followed. The potential photosynthetic capacity of the dark-adapted cells from the bulk of the hyperscum provided a measure of the physiological state of the cells. The actual photosynthetic activity of cells within the narrow euphotic zone at the surface was examined, in an attempt to understand the processes leading

to crust formation. In addition, it was considered necessary to check whether sedimentation constituted a major loss from the hyperscum, because sinking losses of *M. aeruginosa* in the main basin were shown to be higher in winter than at other times of the year (Fig. 3.7).

Measuring photosynthetic activity in a euphotic zone of only a few millimeters depth was possible with an oxygen microelectrode. With a tip of 5 μm and spatial resolution of 50 μm the electrode measurements were relevant to the vertical gradients and distances within the hyperscum upper layers. Introduced only over the last few years to microbial ecology (Revsbech and Jørgensen, 1986) and not yet commercially available, the technology was employed in this study only at the "last moment" in June 1987.

6.2 RESULTS

6.2.1 Position in the hyperscum

(a) morphology

Morphological characteristics of *M. aeruginosa* from the various hyperscum layers (as defined in section 5.2.2) and from planktonic populations, during the early hyperscum season (May-June), are compared in Table 6.1. The planktonic colonies were always green. Both formae, *M. aeruginosa* forma *flos aquae* (spherical or lens-shaped colonies) and forma *aeruginosa* (net-shaped colonies; Komarék, 1958) coexisted. Colonization by bacteria was evident in samples collected from thick surface blooms but not in samples from 3 m depth. Individual cells were spherical, with a mean diameter of 5 μm .

During the early hyperscum season colonies within the bulk of the hyperscum (ca 1 cm depth to the bottom) were mostly green, of both formae, and similar in their general appearance to the planktonic bloom colonies. Colonization by bacteria was distinct (Plate 6.1; Table 6.1). Occasionally yellow colonies that were heavily colonized by bacteria occurred. Decomposition of parts of these yellow colonies was at times evident: under the light microscope decomposed regions were those where colourless or black remains of *M. aeruginosa* cells were heavily infested by bacteria.

Colony and cellular structure deteriorated with declining distance

TABLE 6.1 Morphological characteristics of *M. aeruginosa* from the main basin and from various positions within the hyperscum during May-June 1986.

	Main basin 3 m depth	Main basin thick surface bloom	hyperscum 10 cm depth	hyperscum compact layer 2 mm depth	hyperscum crust
Cells:					
Shape	spherical	spherical	spherical	'squashed' spheres	irregular
mean diameter	5 μm	5 μm	5 μm	4 μm	2-3 μm
Colonies:					
Shape	intact colonies	intact colonies	mostly intact colonies, some partially disintegrated	often "black holes" in colonies, where bacteria infest remnants of disintegrated cells	Only single cells after rehydration
colour	green	green	green, yellow	green, yellow, brown	yellow, brown, black
Bacteria:					
cells ml ⁻¹	10 ⁶ - 10 ⁷	10 ⁷ - 10 ⁸	3 x 10 ⁹	3 x 10 ¹⁰	10 ¹¹
attachment to <i>Microcystis</i>	rare	abundant	abundant	heavy	heavy

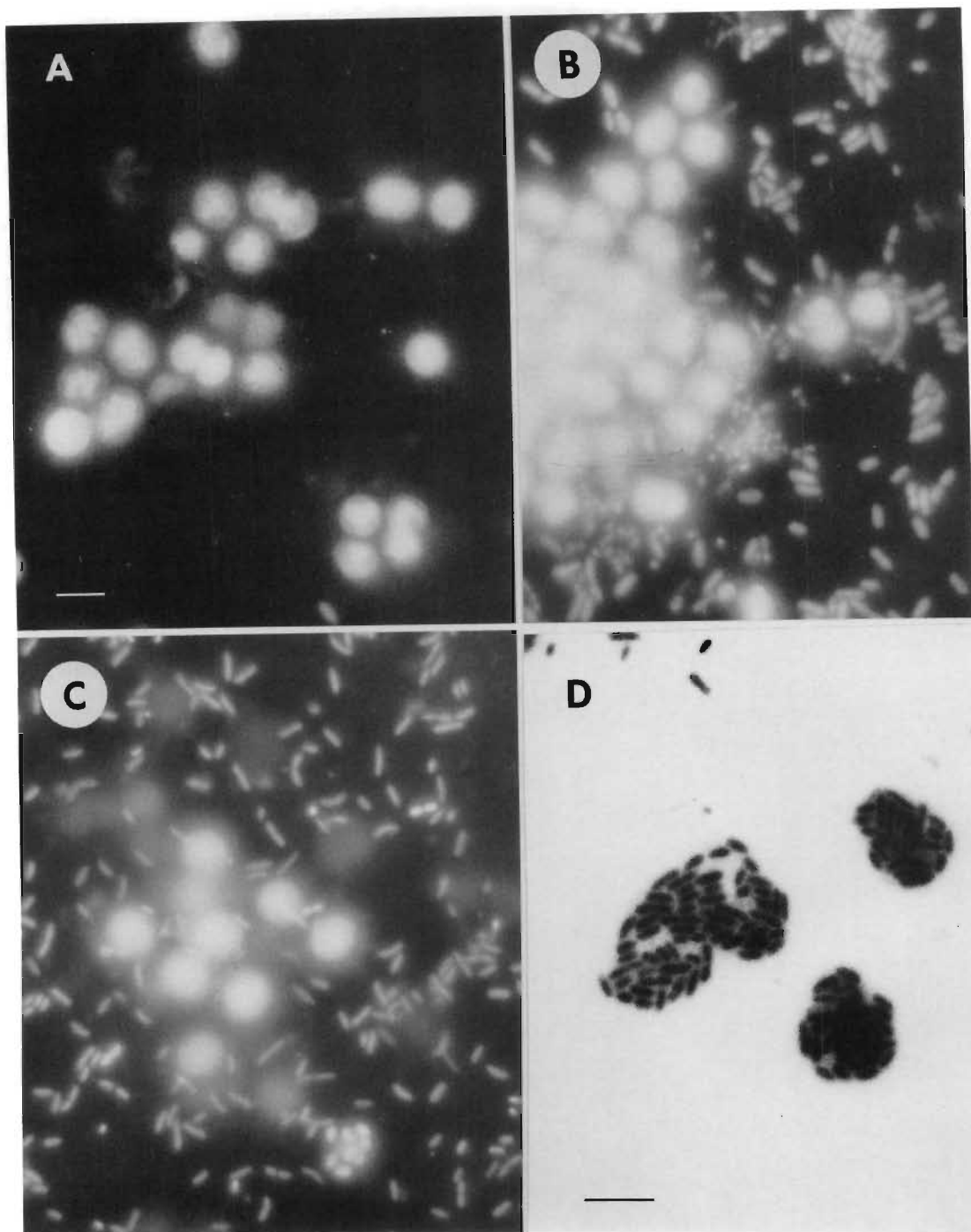


PLATE 6.1 Epi-fluorescent microscope photographs of *M. aeruginosa* (large round cells) and associated bacteria (small rods or cocci) stained with the DNA-specific fluorescent dye, DAPI. (A) main basin, planktonic populations from 3 m depth; (B) hyperscum, 10 cm depth; (C) hyperscum, compact layer; (D) crust, (negative). Scale bars are 5 μm . Black scale bar is for (B), (C) and (D).

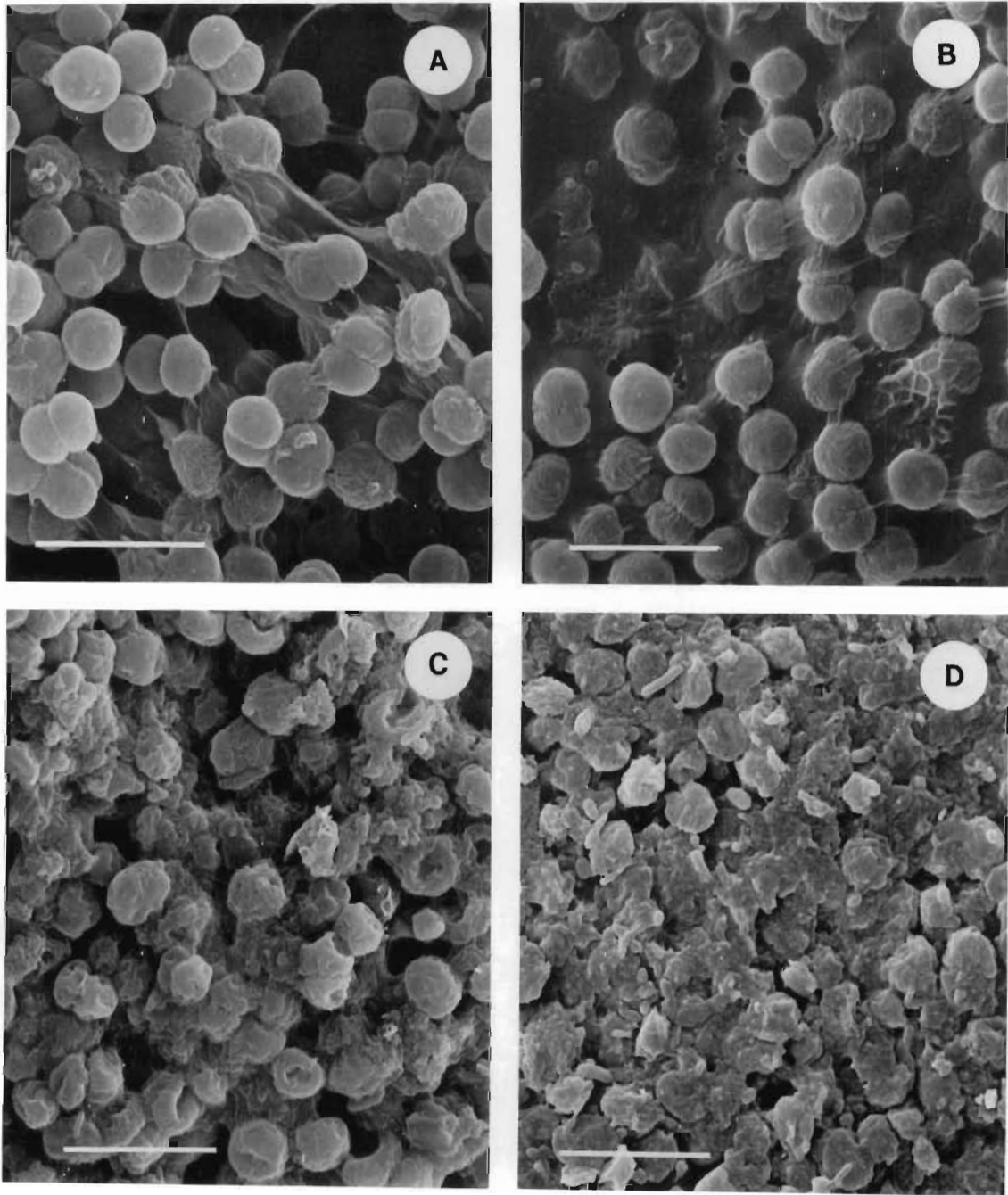


PLATE 6.2 Scanning electron micrographs of *M. aeruginosa* from Hartbeespoort Dam, 20 August 1986. (A) planktonic populations, main basin, 3 m depth; (B) hyperscum, 10 cm depth; (C) hyperscum, compact layer, 5 mm depth; (D) hyperscum, surface crust. Bars are 12.5 μm .

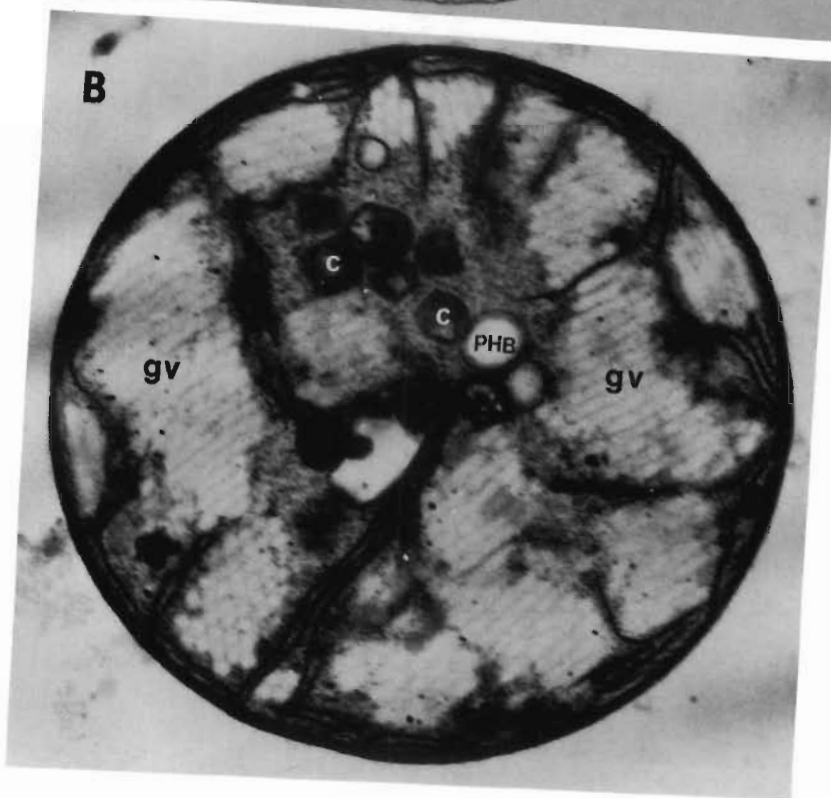
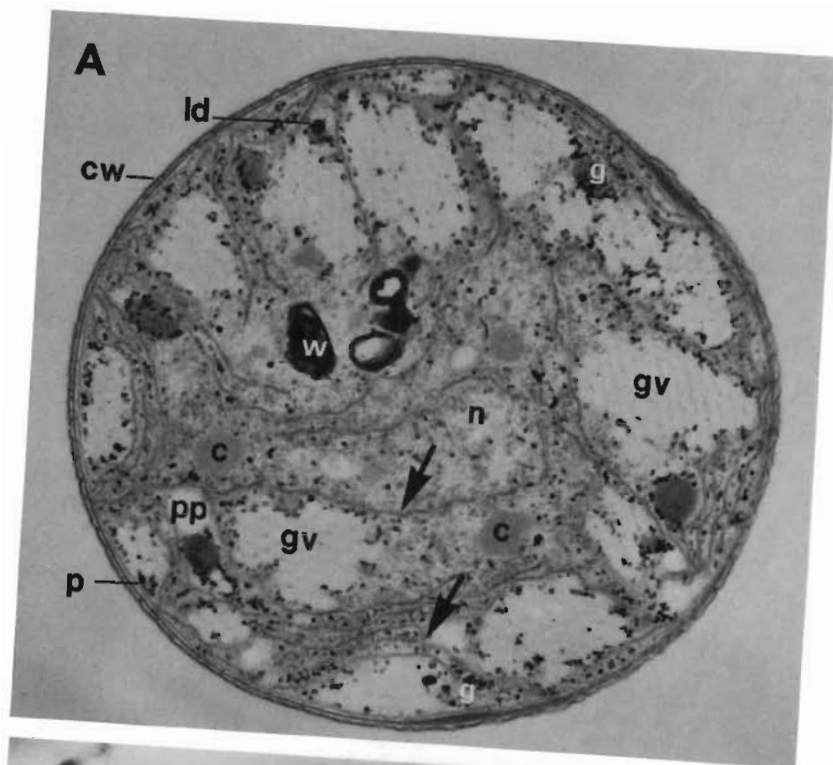


PLATE 6.3 Ultrastructure of *M. aeruginosa* from the main basin of Hartbeespoort Dam. (A) Planktonic cell, 3 m depth, July 1986, median section. Cell delimited by cell wall (cw) and plasmalemma (p). The nucleoplasm (n) contains various types of granules. Thylakoids (arrowed), solitary or in stacks, traverse the protoplasm. Gas vacuoles (gv) are concentrated around the cell periphery. Storage granules consist of glycogen granules (g), visible as small, dark granules dispersed in the vicinity of the thylakoids, polyphosphate bodies (pp), carboxysomes (c), lipid droplets (ld) and membraneous whorls (w). Magn. x 22 000 (B) Cell from a thick surface bloom, June 1986. PHB - poly- β -hydroxybutyrate granule. Magn. x 30 000.

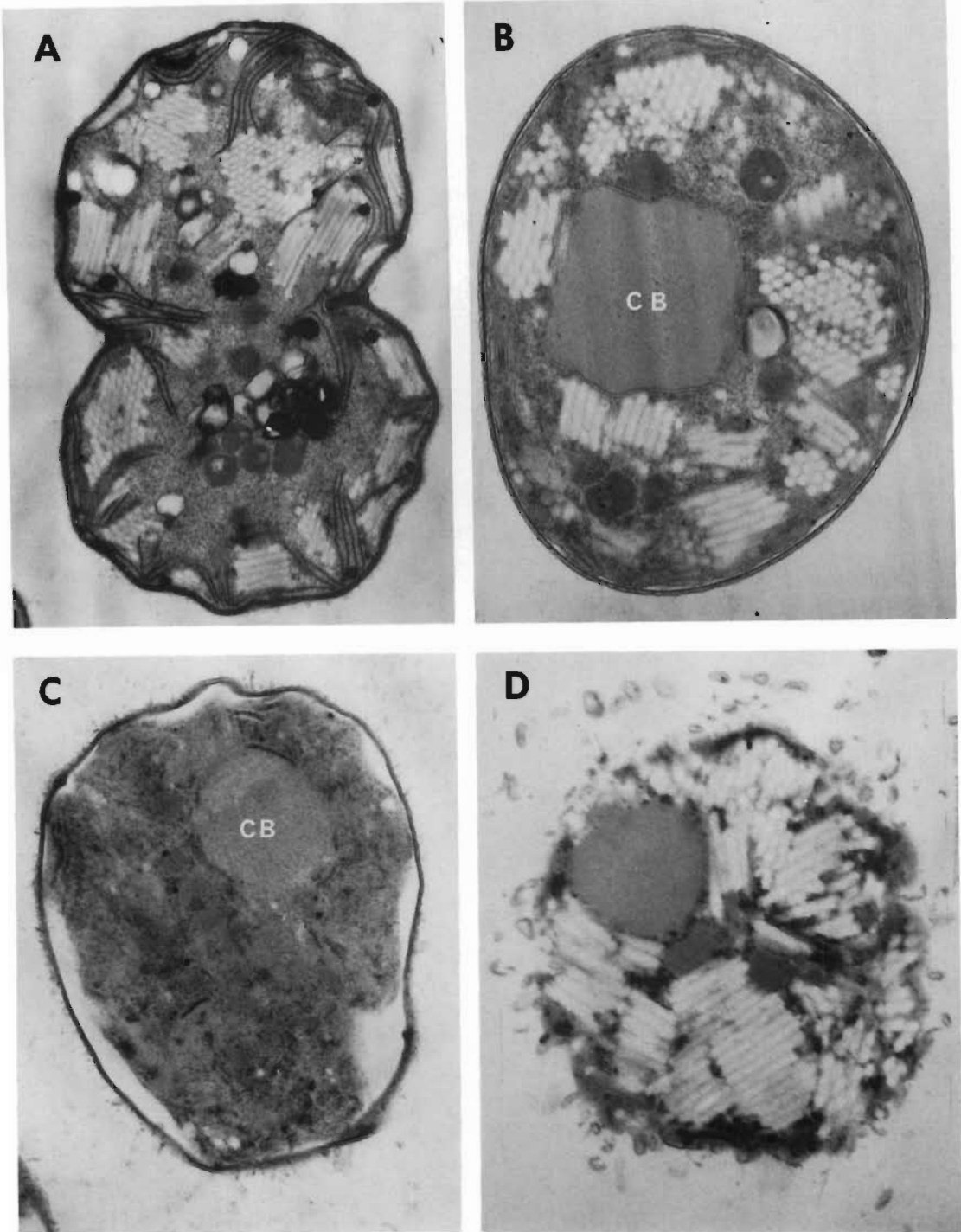


PLATE 6.5 Ultrastructure of *M. aeruginosa* from a hyperscum.
 (A) Compact layer, 3 June 1986. Cell partially dehydrated. Magn. x 18 000.
 (B) Compact layer, 29 July 1986. CB - crystalline body. Magn. x 25 000.
 (C) Crust, exposed side, 20 August 1986. Magn. x 18 000.
 (D) Crust, bottom side, lysed cell with contents leaching out, 29 July 1986. Magn. x 31 000.



PLATE 6.6 A hyperscum at the shelter of the dam wall of Hartbeespoort Dam, 11 August 1983, showing photobleaching of a zone of newly-accumulated *M. aeruginosa* (indicated by arrows) with exposure to a mean total radiation flux (300-2500 nm) of $3740 \mu\text{E m}^{-2}\text{s}^{-1}$ between 11:30 h (top) and 14:10 h (bottom). Water in the bottom photo appear greyish due to a surface bloom.

from the surface over the uppermost ca 10 mm, as was evident from light, fluorescent, and scanning electron microscopy (Plates 6.1, 6.2). With declining depth the cells lost their spherical shape and shrunk in size (mean diameter of 5 μm in the bulk layers; 4 μm in the compact layer and ca 2-3 μm in the crust; Table 6.1; Plate 6.2), in agreement with the increasing dehydration reported earlier (Table 5.3). In addition, the cells became increasingly colonized by bacteria (Plate 6.1, 6.2, Table 6.1) and gradually lost their DNA-fluorescence when stained with DAPI (4'-diamidino-2-phenyl-indole, a DNA-specific fluorescing stain; Plate 6.1).

(b) Ultrastructure

The ultrastructure of typical planktonic cells of *M. aeruginosa*, collected from 3 m depth to avoid surface scums, is shown in Plate 6.3a. As in all cyanobacteria, the protoplast was surrounded by a tripartite plasmalemma, outside which lay the four-layered cell wall (Plate 6.4c) numerically designated L1 to L4 by Jost (1965). The external sheath, composed of a complex mucopolysaccharide (Fogg *et al.*, 1973) was vaguely visible. The thylakoids, or a series of flattened membraneous sacs (Plates 6.3a, 6.4c) comprising the site of the lipophilic pigments (chlorophyll *a* and carotenoids) and of the photochemical reaction centers, were sparse. This was shown by Raps *et al* (1985) to be a characteristic of cells exposed to high light intensities. Gas vacuoles, evident in cross section as a bee-hive structure (Plate 6.3a), comprised on the average 30-40% of the section area.

Glycogen, the immediate product of photosynthesis and the main carbon and energy reserve, is stored in *M. aeruginosa* in small granules that are scattered amongst the thylakoids. In the planktonic cells glycogen granules were plentiful (Plate 6.3a). Other inclusion bodies were: lipid droplets around the cell periphery; polyphosphate granules, which occur in cyanobacteria grown with excess of phosphorus (Smith, 1982); and carboxysomes, which are membrane-bound, polyhedral-shaped organelles, containing the key enzyme for photosynthetic CO_2 fixation, ribulose-1,5 bisphosphate carboxylase (Codd and Marsden, 1984). Cyanophycin granules, containing the nitrogenous organic reserve, were not found. In addition to these regular cyanobacterial cell inclusions (Allen, 1984), membraneous whorls of unknown function were found in the central region of many cells (Plate 6.3a; cf. Jensen, 1985).

Cells collected from a thick (ca. 5 mm) surface bloom differed from the above in having more gas vacuoles (average of 50 - 70 % of the section area), little or no glycogen, and more thylakoids arranged in stacks (Plate 6.3b). Increase in gas vacuoles content has been previously associated with senescence (Reynolds, 1987 and references therein). The bloom cells contained most of the regular cyanobacterial inclusions, i.e. carboxysomes, polyphosphate bodies and lipid droplets, but no cyanophycin granules. Several irregular inclusions (Jensen, 1985) also appeared in most cells. One type was PHB granules containing the uniquely prokaryotic poly- β -hydroxybutyric acid (PHB), which have been found in *M. aeruginosa* by Reynolds *et al.* (1981). Occasionally a crystalline body was seen. These bodies were identified according to their precise striated substructure at high magnification (Plate 6.4f; cf. Reynolds *et al.*, 1981; Jensen and Baxter, 1981).

The general appearance of cells from within the bulk of the hyperscum at the beginning of the season (3 June 1986) was similar to that of bloom cells (Plates 6.4a, 6.3b). This could be expected since the hyperscum cells originated from the surface blooms. The ultrastructure of the cells did not change with depth between 1 cm and the bottom of the hyperscum. Cells were spherical and intact. Lysed or burst cells were not seen and the 4-layered cell wall and plasmalemma were intact (Plate 6.4c). Gas vacuoles comprised on the average 50% of the section area. Like the bloom cells, the hyperscum cells contained polyphosphate bodies, carboxysomes and lipid droplets, membraneous whorls and PHB granules. This meant that reserves of fat, phosphorus and of the main photosynthetic enzyme were stored in the cells and were available for utilization. Glycogen granules were scarce or absent, in agreement with the observation of Reynolds *et al.* (1981) that within 48 h in the dark *Microcystis aeruginosa* utilized all its glycogen reserves. The hyperscum cells differed from the bloom cells in having less (but distinct) thylakoids, and more and larger crystalline bodies.

Cells from the compact layer often appeared as if shrunk (Plate 6.5a), confirming previous observations that these cells were partially dehydrated. Gas vacuoles were plentiful and thylakoids were stacked in groups of 3-5 around the periphery and pointing towards the center. Cell inclusions in early June were similar to those in the bulk layers; i.e., carboxysomes, polyphosphate bodies, lipid droplets, PHB granules, membraneous whorls and large crystalline bodies.

The crust cells (Plate 6.5 c, d) were in the worst condition. Cells

were shrunk in size to 2.5 - 3 μm diameter, as could be expected in a dry environment where water content was only 14% (Table 5.3). The original spherical shape was distorted, and cell contents were often contracted and separated from the wall. Most of the ultrastructural detail of these cells was lost and replaced by uniform, grey, structureless contents (Plate 6.5c). Remains of thylakoid membranes or few gas vacuoles were occasionally visible. Crystalline bodies were surprisingly abundant and the last to maintain their intact structure, (Plate 6.5 c,d). Lysed cells with contents leaching out (Plate 6.5 d) occurred frequently in cells from deeper zones within the crust, that were protected from direct radiation.

(c) photosynthetic capacity

Konopka and Brock (1978b) considered photosynthetic capacity, or the maximum photosynthetic rate at light saturation, normalized per unit chlorophyll (P_{max}), to be a good measure of the physiological state of the algae. They reported high capacities before major population increases, reduced capacities before the populations diminished, and good correlations between P_{max} and growth rates. The potential for photosynthetic activity of the dark adapted *M. aeruginosa* from the bulk of the hyperscum was examined throughout the 1984 hyperscum season and compared with that of control main basin surface populations. Prior to each experiment the hyperscum and control cyanobacteria were acclimatized for 24 h to the main basin conditions, to avoid the preliminary response of dark-adapted photosynthetic organisms to a sudden exposure to light (details in section 2.5.4). Using the non parametric Mann-Whitney test for difference between means in non-normally distributed populations (Zar, 1974), P_{max} ($\text{mg C (mg chl)}^{-1}\text{h}^{-1}$) of the two populations were not significantly different (Table 6.2).

The two populations did not differ in other photosynthetic parameters: the light intensity at which photosynthesis became light-saturated, I_x ; the photosynthetic efficiency at low light levels, α ; and the cellular chlorophyll a content (Table 6.2). 'Shade algae', drawn from depth are characterized by a high cellular chlorophyll a content and high photosynthetic efficiencies at low light levels (Harris, 1978). The hyperscum cells, however, were drawn from beneath the crust where total darkness prevailed. No adaptation to low light levels could be detected, as demonstrated by the unaltered α and cellular chlorophyll content values.

TABLE 6.2 Means, ranges and results of Mann-Whitney non parametric tests for differences between means of several photosynthetic parameters for hyperscum (10 cm depth) and lake control populations of *M. aeruginosa* over the 1984 hyperscum season. See text for definition of parameters. NS - not significant ($p > 0.05$).

Parameter	h y p e r s c u m			l a k e			diff. between means
	mean	range	(n)	mean	range	(n)	
P_{max} , mg C (mg chl) ⁻¹ h ⁻¹	3.1	1.8 - 5.9	(12)	4.2	1.5 - 6.7	(12)	NS
I_{K} , $\mu E m^{-2} s^{-1}$	239	97 - 560	(12)	251	110 - 669	(12)	NS
α , mg C (mg chl) ⁻¹ E ⁻¹ m ²	.0155	.0040 - .0028	(11)	.0150	.0070 - .0194	(9)	NS
chl content, ng (10 ⁶ cells) ⁻¹	112	85 - 159	(13)	99	41 - 168	(12)	NS

6.2.2 Duration at the surface: the development of the crust

(a) field observations

Weekly field observations of the hyperscum surface layer revealed that its structure was continuously changing (Fig. 6.1). Exposure to direct insolation of a thick scum composed of green-looking *M. aeruginosa* colonies (step 0 in Fig. 6.1) led to bleaching of pigments at the top layer within a few hours (Step 1). For example, on 8 Aug 1983, *M. aeruginosa* colonies bleached with exposure to a mean total radiation flux (300 to 2500 nm) of 3740 $\mu E m^{-2} s^{-1}$ between 11:30 and 14:10 h (Plate 6.6). Within days the hyperscum surface was dyed purple-blue (Step 2), probably as a result of release of the water-soluble accessory pigments phycocyanin (blue) and phycoerythrin (red). These pigments are released when cyanobacteria die of photooxidation (Powles, 1984). Dehydration caused the crust to gradually dry up and crack into dark colored, irregular shaped segments of 5 -10 cm in length (3). Due to further water evaporation the segments shrank with time, thereby creating spaces into which buoyant colonies from beneath were forced. These newly exposed colonies were thus subjected to atmospheric oxygen and direct solar radiation (4). The same process repeated with the newly exposed surfaces (5, 6) and thus, a second and

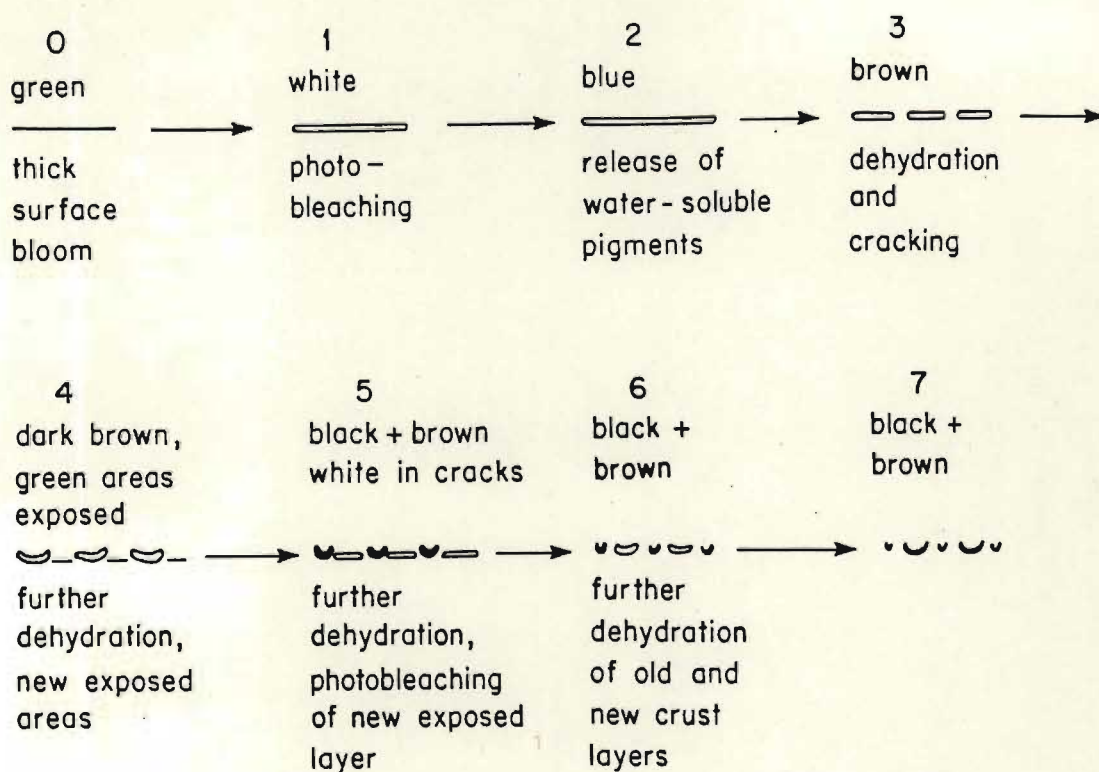


FIGURE 6.1 Schematic representation of the observed stages of development of the hyperscum crust, indicating the prevailing colors and processes.

consequent generations of crust developed (7). This process suggested continuous losses at the surface, at high rates, since cell concentrations in this layer were ten times higher than in deeper layers (Table 5.1).

(b) photosynthetic activity at the surface : a microelectrode study

During the initial stages of hyperscum build up, prior to prolonged dehydration and crust formation, colonies at the narrow illuminated zone at the surface, if alive, should have been photosynthetically active. Photosynthetic activity of *M. aeruginosa* at the surface of newly formed hyperscums (ca 2 - 5 days) was measured with microelectrodes. Figure 6.2 illustrates micro-depth profiles of oxygen concentrations and of photosynthetic activity over the uppermost 1-3 mm in freshly cored hyperscum samples with green bleached or purple-blue surfaces, corresponding to steps 0, 1 and 2 of Fig. 6.1, respectively.

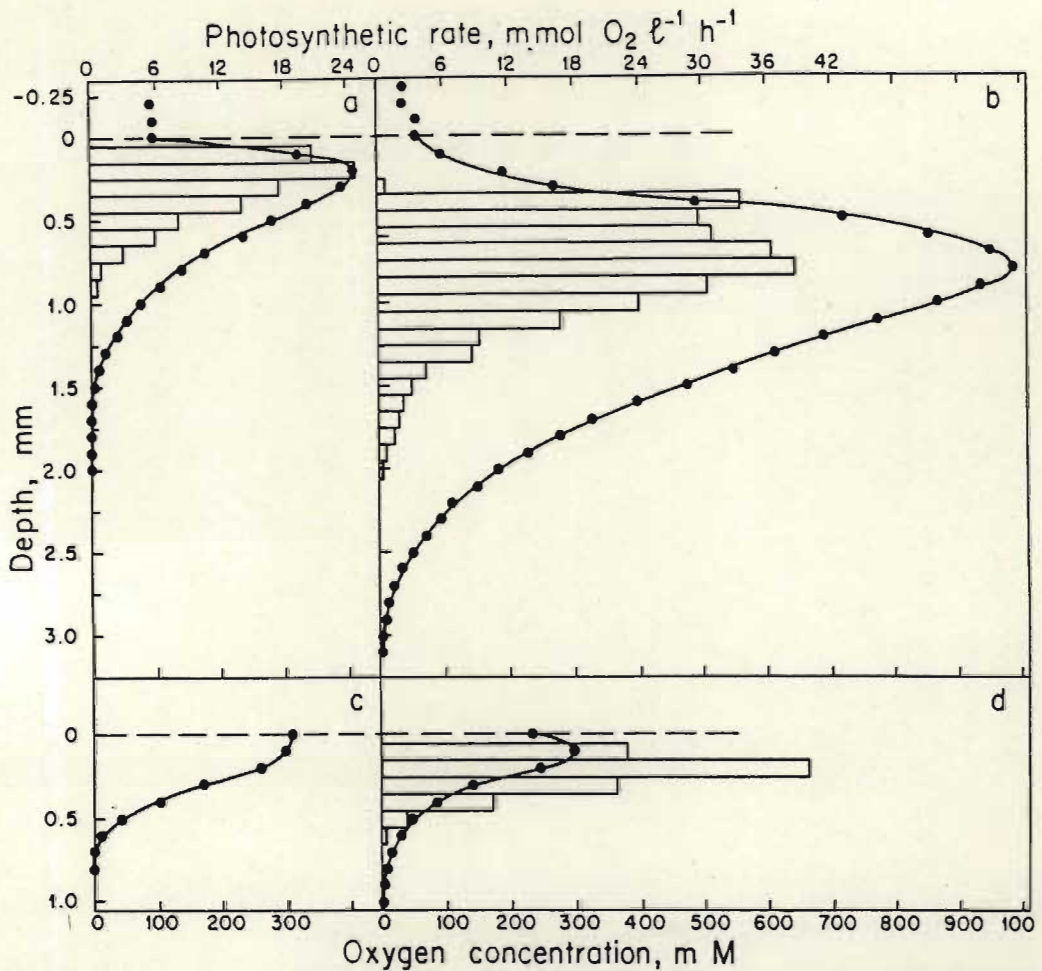


FIGURE 6.2 Depth profiles of oxygen concentration (circles) and photosynthesis (bars) over the upper 1 - 3 mm of newly formed hyperscums, at various stages of crust development. Prior to measurements core samples were kept in the dark and then illuminated for 10 min at $625 \mu\text{E m}^{-2} \text{s}^{-1}$, except (b) which was illuminated for 30 min at $1000 \mu\text{E m}^{-2} \text{s}^{-1}$. (a) green surface, (step 0 of Fig. 6.1); (b) newly exposed layer after uppermost 3 mm layer has been removed; (c) Purple-blue surface (step 2 of Fig. 6.1); (d) bleached surface (step 1 of Fig. 6.1).

In a green-surface hyperscum that was illuminated for 45 min at $625 \mu\text{E m}^{-2} \text{s}^{-1}$ photosynthesis was measurable to a depth of 0.9 mm (Fig. 6.2a). A maximum oxygen production rate of $25 \text{ mmol O}_2 \text{ l}^{-1} \text{ h}^{-1}$ was recorded at 0.2 mm depth. At 0.0 mm depth photosynthetic activity could not be detected, indicating total photoinhibition. The oxygen profile represents an instantaneous balance between O_2 production, uptake (respiration) and diffusion. At the depth of peak photosynthetic activity a concentration of $410 \mu\text{M O}_2$, or 167 % saturation at 19°C , was recorded. Complete anoxia was recorded from 1.6 mm and deeper.

Higher rates of photosynthetic activity were recorded when the upper 3 mm layer was removed, exposing to light and oxygen colonies that have been several days under dark anaerobic conditions (Fig. 6.2b). After 30 min in the light ($1000 \mu\text{E m}^{-2}\text{s}^{-1}$) peak photosynthetic activity of $38.8 \text{ mmol O}_2 \text{ l}^{-1} \text{ h}^{-1}$ at 0.8 mm depth led to oxygen concentration of $990 \mu\text{M}$, or 390% saturation. Photosynthetic activity was recorded down to 2 mm depth, indicating that this would be approximately the depth of the euphotic zone. Oxygen penetrated by diffusion to 3 mm depth; complete anoxia was recorded deeper. Surface inhibition of photosynthesis was also apparent.

In another experiment a time-series of oxygen depth profiles was recorded, following exposure to strong light ($1720 \mu\text{E m}^{-2}\text{s}^{-1}$) of a dark adapted layer after the top 3 mm layer was removed (Fig. 6.3). The initial oxygen profile, taken in the dark, demonstrated absolute anoxia. After 4 min in the light oxygen was recorded down to 1.3 mm depth, with a peak of $197 \mu\text{M}$ at 0.6 mm depth. Five minutes later oxygen was recorded to a depth of 2.3 mm and its peak, still at 0.6 mm depth, increased to $556 \mu\text{M}$ or 223 % saturation. With additional time in the light the oxygen peak shifted deeper and its value gradually declined. This indicated a gradually increasing substrate limitation of photosynthetic oxygen production in the shallower depths. Repeating the experiment with a pH microelectrode (Fig. 6.4) indicated that CO_2 was likely to be the limiting substrate: after 3.5 h in the dark the pH at the surface was 8.2 and declined with depth to 7.0. Following 30 min in the light ($1000 \mu\text{E m}^{-2}\text{s}^{-1}$) a dramatic change in the pH profile was noted, and a pH peak of 11.6 was recorded at the surface. After another 60 min in the light the pH at the surface declined somewhat to 11.3. Such high pH values were most probably a result of the high rates of photosynthetic activity (demonstrated in Fig. 6.2b) and utilization of the available CO_2 to a degree where its concentration became severely limiting.

Microprofiles of oxygen and photosynthetic activity in cores of bleached-surface samples (step 1 of Fig. 6.1) showed that despite relatively high subsurface rates of photosynthetic activity the oxygen concentration remained low (Fig. 6.2d), indicating that oxygen consumption rates were high.

In samples of phycocyanin-dyed surfaces (step 2 of Fig. 6.1) photosynthetic activity could not be detected (Fig. 6.2c). It was concluded that the photosynthetic apparatus of the cells within the euphotic

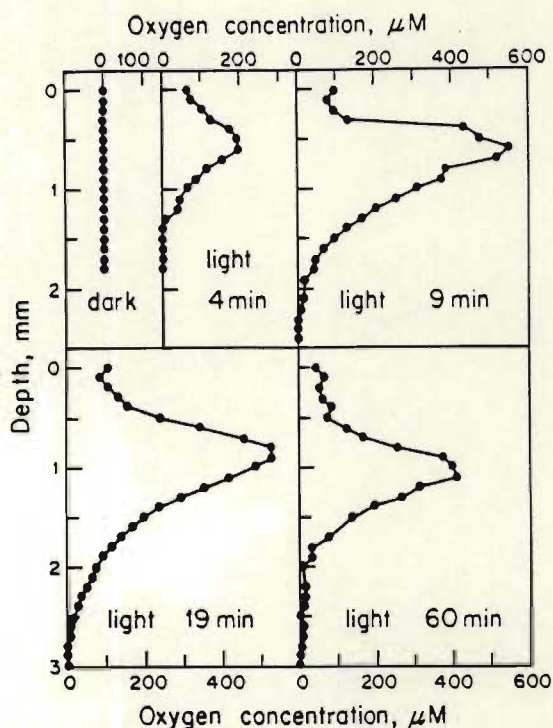


FIGURE 6.3 A time series of oxygen depth profiles from the initial exposure to light ($1720 \mu\text{E m}^{-2} \text{s}^{-1}$) of a dark adapted hyperscum layer, after the uppermost 3 mm layer has been removed.

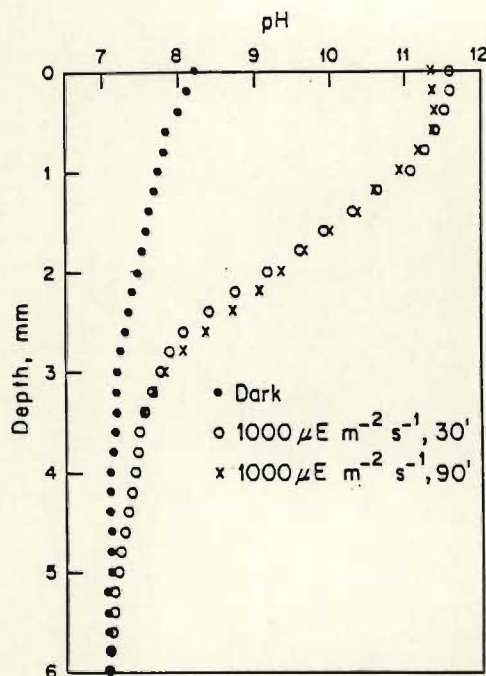


FIGURE 6.4 Light and dark depth profiles of pH in a newly exposed layer of a hyperscum.

zone was damaged. Indeed, as shown earlier, thylakoids and carboxysomes were not found in crust cells. The shape of the oxygen profile (maximum at 0.0 mm, no subsurface peak and anoxia already at 0.7 mm) also indicated that the only source of oxygen was diffusion of atmospheric gases. With time, as the upper crust dehydrated and hardened, it is likely that diffusion of atmospheric oxygen was reduced to a minimum, but this still needs confirmation.

Photosynthetic capacity (P_{max}) values calculated for the microelectrode-measured photosynthesis rates, using estimated chlorophyll a concentrations from Fig. 5.1 and equal molar ratios to convert C to O_2 , were lower (max: $1.5 \text{ mg C mg Chl h}^{-1}$) than the potential capacity values measured using the ^{14}C method (Table 6.2). This, however, could be expected because, as shown above, the rate of photosynthesis at the hyperscum surface was most of the time substrate limited.

(c) ultrastructure

From the above it is apparent that significant changes in cellular ultrastructure should have taken place over the first few days of hyperscum formation. Unfortunately, samples for TEM were not collected then. From 3 June onwards the description of crust cell ultrastructure given in section 6.2.1b did not change much with time (Plate 6.5).

(d) pigments

Despite the photobleaching of chlorophyll at the uppermost layer of the crust, mean chlorophyll a concentrations over the layer were extremely high (range: 1.2 to 4.6 g l⁻¹; Fig. 6.5). This indicated that light was absorbed so rapidly that photooxidation of the pigment was limited to a very narrow zone at the top, below which chlorophyll a was not destroyed. In the dark chlorophyll a is degraded, through chemical oxidation, into phaeopigments (Daley and Brown, 1973). The proportion of phaeopigments in the crust continuously increased with time, from 6 % on 3 June 1986 to 64 % by the end of August. The steep decline in chlorophyll a over August coincided with a steep increase in phaeopigments (Fig. 6.5).

6.2.3 Duration within the compact layer

(a) pigments

Chlorophyll a concentration in the compact layer declined from 1.3 g l⁻¹ on 3 June 1986 to 0.5 g l⁻¹ on 15 July, followed by an increase to a maximum of 1.6 g l⁻¹ on 11 August and again decline to 0.9 g l⁻¹ by 27 August (Fig. 6.5). During most of this period (until 20 August) the proportion of phaeopigments was maintained below 15 % (Fig. 6.5), suggesting that the temporal changes in chlorophyll a probably reflected the variability in colony compaction rather than growth or decomposition. On 20 August the proportion of phaeopigments suddenly increased to 43 % (Fig. 6.5). This coincided with a sharp decline in chlorophyll (Fig. 6.5), which implied chlorophyll degradation at that time.

(b) ultrastructure

By late July most of the cellular inclusions disappeared, with the exception of carboxysomes and crystalline bodies. Most cells had one or

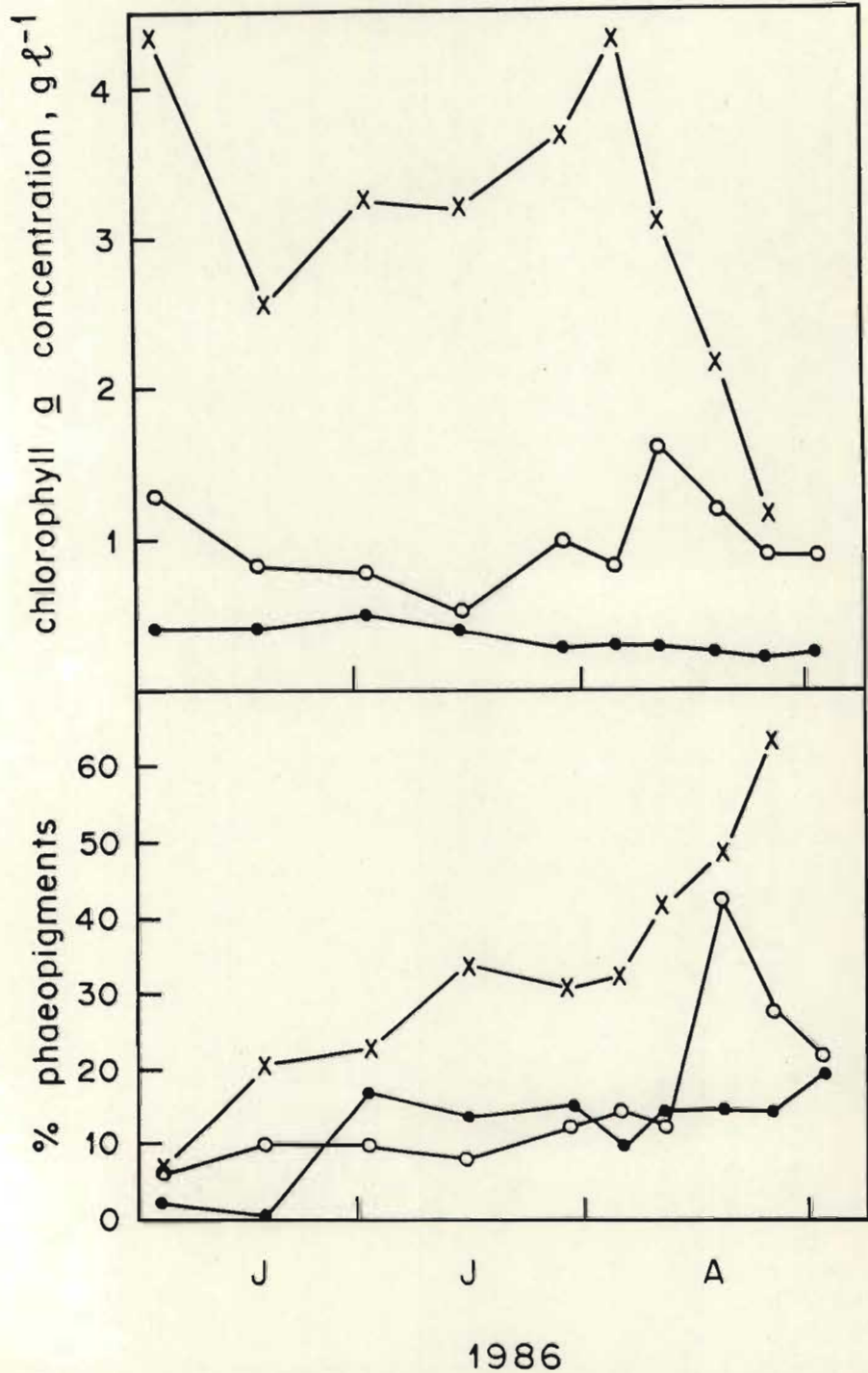


FIGURE 6.5 Changes with time in chlorophyll a concentration and in phaeopigments, expressed as % of the total chlorophyll-derived pigments, for the different hyperscum layers during winter 1986. (x) - crust; (o) - compact layer under crust; (●) - 10 cm depth.

two large crystalline bodies, which comprised up to 30 -40% of the section areas (Plate 6.5b). By 20 August it was evident that cells in this layer were decomposing (Plate 4.6e). Shapes ranged from normal round cells, through round cells with plasmalemma separated from the cell wall leaving empty space between the wall and the cell contents, to cells without cell wall that still maintained integrity of the contents (possibly an artifact of rehydration of dehydrated cells during the fixation procedure), to completely faded cells.

6.2.4 Duration within the bulk of the hyperscum

(a) cell numbers and pigments

In 1984 the changes with time in cell numbers and in chlorophyll a concentration (ranges: $1.4 - 2.5 \times 10^9$ cells ml^{-1} and 163 - 293 mg Chl l^{-1}) were small, although slow but significant declines in both parameters were obtained when linear regression lines were fitted to the data from mid-July 1984 onwards (Fig. 6.6). Based on these regression equations (given in the legend for Fig. 6.6) chlorophyll a declined by 24 % (from 226 to 173 mg l^{-1}) and cell numbers by 32 % (from 2.4 to 1.7×10^9 cells ml^{-1}).

Phaeopigments gradually increased with time, but the increases at 10 cm depth in both 1984 and 1986 were not very large: in 1984 phaeopigments increased from 6.6% of the total chlorophyll-derived pigments at the beginning of June to a maximum of 21 % by the end of August (Fig. 6.6). In 1986 a similar increase from 3.1 % to 20.0% occurred (Fig. 6.5). For comparison, the mean phaeopigment content of the top 0 - 4 m layer in the main basin during the major *Microcystis* growth season (November 1984 to January 1985) was $10.7 \% \pm 3.8$ SD (range: 5.4 - 18.6 %), but at 15 m depth in the anaerobic hypolimnion where decomposition prevails (Hutchinson, 1967), the proportion over the same period was $35.2 \% \pm 8.2$ SD (range: 27.25 - 53.70).

(b) ultrastructure

While changes with time, between June and August, in the ultrastructure of planktonic and bloom populations of *M. aeruginosa* were insignificant (not shown), cells within the bulk of the hyperscum underwent apparent changes. The electron microscope image of the cells after ca 2 months in the hyperscum was one of reduced density, resulting with consistently faded photographs (Plate 6.4b). In comparison with the cells from 3 June 1986 described earlier, cells on 20 August 1986 had less cellular inclusions (Plate 6.4a,b) : polyphosphate bodies were

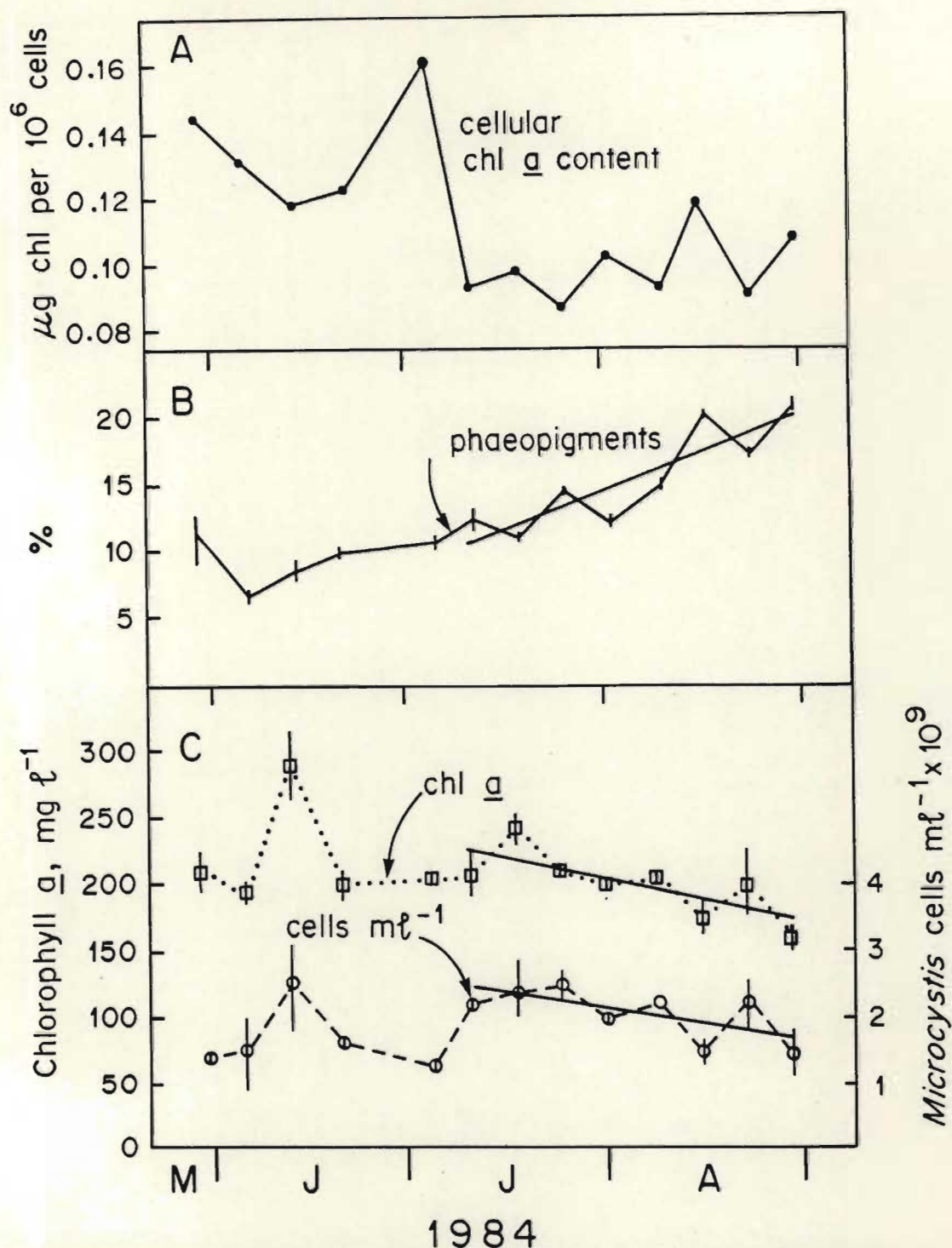


FIGURE 6.6 Changes over time within the bulk of the hyperscum (10 cm depth). Phaeopigments are expressed as percentage of the total chlorophyll-derived pigments. Equations for the linear regression lines fitted to the data from 10 July onwards were as follows:

$$\begin{aligned} \% \text{ phaeopigments} &= 10.69 + 0.18 X, \quad n=8, \quad r=0.86, \quad p=0.01 \\ \text{Chl a, mg l}^{-1} &= 227 - 1.07 X, \quad n=8, \quad r=0.78, \quad p=0.01 \\ 10^{-9} \text{ cells ml}^{-1} &= 2.46 - 0.02 X, \quad n=8, \quad r=0.69, \quad p=0.05 \end{aligned}$$

where X =time in days. Vertical bars in Fig. c indicate range of duplicate measurements.

scarcely seen, membrane whorls and PHB granules were absent. Possibly the reserve materials stored in these granules were used for cell maintenance. Thylakoids and several (ca. 4-6) carboxysomes were found in most cells, in accordance with the evidence that these cells maintained their photosynthetic capacity. Occasionally cells lost some of the cell wall layers (Plate 6.4c,d) but the plasmalemma remained intact and burst or lysed cells were not found.

(c) photosynthetic capacity

Changes with time in the photosynthetic capacity of *M. aeruginosa* from the hyperscum (10 cm depth) and from the main basin are shown in Fig. 6.7. The declines of P_{max} for both populations over May and early June 1984 can be ascribed to the decline in water temperature from 19.8 to 12.3°C (Fig. 6.7). While P_{max} of the two populations was not significantly different over the entire data set (Table 6.2), it is apparent from Fig. 6.7 that from mid-July onwards P_{max} values in the hyperscum tended to be lower than those of the main basin populations. When only these later data were considered, the difference was significant ($n_1 = n_2 = 6$, $p < 0.05$), indicating some deterioration with time of the physiological condition of *M. aeruginosa* in the bulk of the hyperscum. Yet, the fact that P_{max} was still measurable by the end of the hyperscum season proves that at least a proportion of the cells at 10 cm depth retained their viability.

(d) Sinking losses

Sedimentation rates of *Microcystis* under the hyperscum throughout the winter 1984 hyperscum season are shown in Fig. 6.8. Compared with the mean standing crop of *M. aeruginosa* in the hyperscum excluding the crust (extrapolated from cell numbers at 10 cm depth and hyperscum thickness for each sampling date) of 4.3×10^{10} cells cm^{-2} , sinking losses from the hyperscum were extremely low. In June, July and early August sinking losses ranged from 0.9×10^6 to 5.7×10^6 cells $cm^{-2} d^{-1}$. Over these $2\frac{1}{2}$ months only <1% of the standing stock was lost by sedimentation. Sinking losses increased significantly during the final stages of hyperscum breakdown (Figs 6.8, 5.4c) reaching a maximum of 2.54×10^7 cells $cm^{-2} d^{-1}$ between 16 and 22 August 1984. But even those increased rates accounted for an additional loss of only ca 1%. In total, only 1-2% of the hyperscum *Microcystis* was lost via sedimentation. It is concluded that sedimentation losses were insignificant, stressing the importance of the high positive buoyancy of the colonies in the hyperscum.

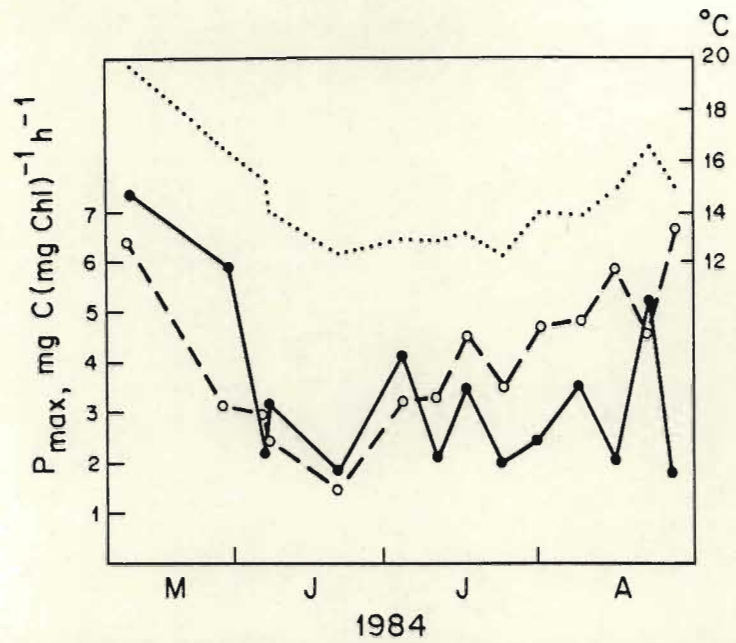


FIGURE 6.7 Changes with time in the potential photosynthetic capacity (P_{max}) of *M. aeruginosa* from the hyperscum (●) and from the main basin surface populations (○) throughout the hyperscum season. Dotted line marks water temperature at 1 m depth.

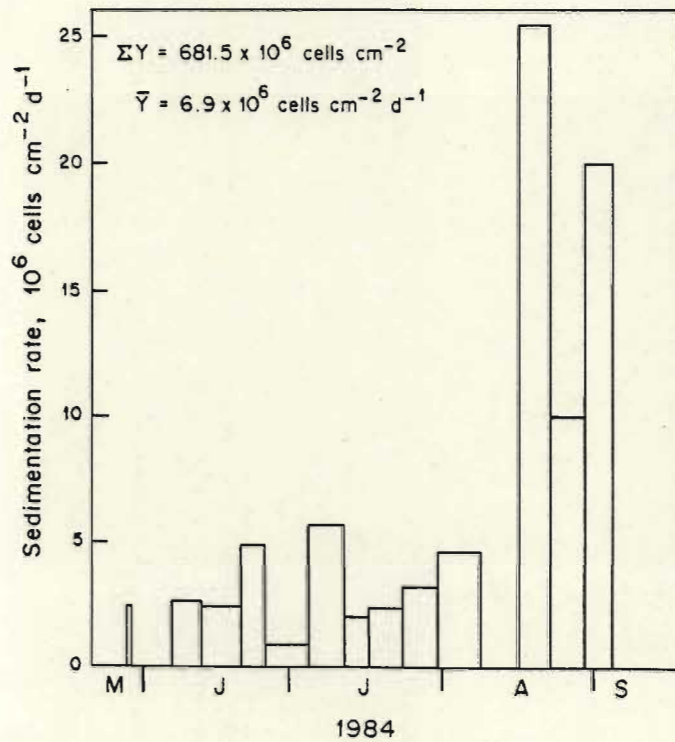


FIGURE 6.8 Changes with time in sediment trap catches under the hyperscum. Histogram widths are proportional to the duration of trap exposure and their heights to the sedimentation rate of *M. aeruginosa*.

6.3 DISCUSSION

The data presented in this and the previous chapters point to the existence of spatial separation within the hyperscum between a zone at the surface of lethal physical conditions, a zone beneath the surface where stressful and probably lethal chemical conditions developed, and a deeper zone of more moderate conditions, which nevertheless, deteriorated after 2 - 3 months. At the surface colonies were trapped in their position, because buoyant colonies from underneath forced them upwards while water movement was restricted to diffusion (section 5.2.3). These colonies were therefore continuously exposed to direct solar radiation. The microelectrode studies have demonstrated that photosynthetic activity of *M. aeruginosa* colonies at the surface became rapidly photoinhibited, substrate limited, and then ceased within hours of exposure to light intensities $> 625 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Figs 6.2, 6.3, 6.4). Photooxidative death, which follows severe photoinhibition over time (Powles, 1984), takes place when cyanobacteria are subject to high light intensities, oxygen saturation and CO_2 depletion (Abeliovich and Shilo, 1972; Eloff *et al.*, 1976). All these conditions existed at the hyperscum surface within minutes of exposure to midday solar radiation: the incident intensities of $> 1000 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 3.1c) were photoinhibiting, and photosynthetic activity rapidly depleted the CO_2 supplies while causing oxygen enrichment. The rapid bleaching of colonies at the surface (Plate 6.6) and the release of accessory pigments were also indicative of photooxidative death (Powles, 1984).

Colonies at the surface were subject to another potentially lethal condition - evaporative dehydration. This process operated over longer time scales (days) than photooxidation, so it was not the initial cause for cell death. Topachevskiy *et al.* (1969), however, claimed that a small proportion of the cells of beached, dry crusts of *M. aeruginosa* from the Dnieper reservoirs retained their viability and could grow after rehydration.

The high concentrations of chlorophyll a that were maintained in the crust till mid-August (Fig. 6.5) are indicative of the original biomass in the crust but are not necessarily indicative of a viable population. Fallon and Brock (1979; 1980) have indicated that following cell death morphological integrity disappears more rapidly than chlorophyll. At the uppermost surface of the crust chlorophyll a was subject to photooxidative destruction, a light- and oxygen-dependent

process through which the pigment is converted directly into a colorless residue (Daley, 1973; Daley and Brown, 1973) that cannot be identified by conventional chlorophyll methods (Moss, 1968). But just below the uppermost layer photooxidative conditions did not exist due to light attenuation and oxygen consumption. In the dark chlorophyll *a* is degraded into phaeophytins, a process which occurs through chemical oxidation and not through bacterial activity (Daley and Brown, 1973). The rate of chemical oxidation of the chlorophyll at the bottom of the crust was probably limited by the availability of oxygen. This may explain why phaeopigments in the crust increased relatively gradually during June and July (Fig. 6.5). During August, when the hyperscum was breaking and atmospheric oxygen may have entered through newly formed cracks, chlorophyll declined and concomitantly phaeophytins increased sharply (Fig. 6.5).

Evidence that *M. aeruginosa* cells in the crust were mostly dead ranges from the total loss of their photosynthetic capacity (Fig. 6.2c), an early sign of cell death (Fallon and Brock, 1979; 1980), to the destruction of their morphological and ultrastructural integrity (Plates 6.2d, 6.5c,d), and their infestation by bacteria (Plate 6.1d). The absence of thylakoids and carboxysomes in these cells (Plate 6.5d) is in agreement with their lack of photosynthetic activity. Their reduced diameter and distorted shapes (Table 6.1, Plate 6.2d) were most likely a result of dehydration.

The microelectrode studies have demonstrated that light and oxygen did not penetrate deeper than 3 mm of a new, non-crusted hyperscum (Fig. 6.2b). After cessation of photosynthetic activity at the surface due to photoinhibition and photooxidation the aerobic zone shrunk to < 1 mm (Fig. 6.2d). With the development of a dry, dark-pigmented crust, light and oxygen penetration were probably restricted to an even narrower zone.

The compact layer beneath the crust was protected from the damages of direct insolation. Other conditions, however, developed over time to render this dark anaerobic environment lethal to *M. aeruginosa*. The key factors were the proximity to the surface and the extremely high cell concentrations. Partial evaporative dehydration was evidenced by water content of only 77 % of the total (cells + interstitial water) weight (Table 5.3) and by the shrunk appearance of the cells under the SEM and TEM (Plates 6.2c, 6.5a). For comparison, water comprised 94 % (± 3 % SD) of the wet weight of pre-filtered, thick suspensions of *Microcystis* (Table 5.3).

Inter-cellular water comprised only 20 - 40 % of the total volume of a newly formed, non-crusted hyperscum (Fig. 5.1) and a considerably smaller proportion in a mature hyperscum. It was argued earlier (section 5.2.3) that water movement in the hyperscum was restricted to diffusion. The scarcity of interstitial water in the compact layer would have slowed down diffusion rates. In addition, with the exception of cracks, this layer was sealed from above by the crust.

The compact layer was overlain by a layer of photooxidized, dead cells, which comprised a substrate for bacteria-mediated anaerobic decomposition. This was evidenced by the presence of volatile fatty acids and gas bubbles containing N₂, methane and CO₂ (Tables 6.6, 6.7). Supporting evidence was the high numbers of attached bacteria (Plate 6.1, Table 6.1), although their activity was not measured. Microbial-mediated mineralization of dead cyanobacteria was shown to be rapid (Fallon and Brock, 1979; Rogers and de Pinto, 1983) and to occur at similar rates under aerobic and anaerobic conditions (Fallon and Brock, 1979; Cole *et al.*, 1984).

Due to the lack of water movement and the sealing from above by the crust, decomposition products could not be transported out of the compact layer, with the exception of release of some of the gases through cracks. Their dilution through diffusion downwards along concentration gradients was slowed by the small amounts of interstitial water. Consequently, concentrations of end-metabolites of anaerobic processes, such as ammonia, sulfide, methane and CO₂, increased with time to reach potentially toxic levels (Abeliovich and Azov, 1976; Azov and Goldman, 1982; Knobloch, 1969).

The proximity to the surface resulted also with extreme diel temperature variations, from close to freezing at night to > 20°C at midday (section 5.2.3), which may have increased the stress on cells. Temperatures above 20°C enhanced metabolic processes and therefore the utilization of stored reserves, as was also evidenced by the absence of most storage granules in thin sections of the cells (Plate 6.5). High temperatures during the day enhanced rates of other enzymatic processes such as cell wall lysis.

Light and electron microscopy indicated that a large proportion of the cells in this layer were decomposing (Table 6.1, Plates 6.2c, 6.4e). There is, however, evidence that lethal conditions in the compact layer developed with a lag of several days after those in the crust: when the uppermost 3 mm of a newly accumulated hyperscum were removed, photosynthetic activity in the light was high (Fig. 6.2b).

With increasing distance from the surface conditions were moderated: dehydration, which caused cells to shrink and colonies to compact, diminished. Consequently, cells retained their intact shape (Plates 6.2b, 6.4a,b) and the amount of interstitial water increased (Fig. 5.1). With distance from the surface and increasing proximity of the underlying lake water temperature fluctuations were moderated. The temperature at 10 cm depth was maintained during most of the hyperscum season below 12°C (Fig. 5.4). The low temperature reduced basal metabolism rates so that stored cellular reserves could last longer. Rates of bacteria-mediated decomposition were also slowed. In addition, due to the distance from the zones of death and decomposition at and near the surface, products of decomposition took time to diffuse and reach potential toxic concentrations.

For at least 2 months cells at 10 cm depth maintained their photosynthetic capacity at levels that were not significantly different from those of main basin populations (Fig. 6.7). The fine structure of cells from 10 cm depth was also similar to that of cells from surface blooms in the main basin (Plates 6.2a,b, 6.3b, 6.4a). Cell numbers remained practically unchanged and the proportion of phaeophytins remained low (Fig. 6.6). All these indicated that *M. aeruginosa* could survive at this position in the hyperscum.

With time, however, there is evidence that the condition of the cells gradually deteriorated. Gradual declines in cell numbers and chlorophyll concentrations, concomitant with increases in phaeophytins were recorded from mid July onwards (Fig. 6.6). This corresponded with declining photosynthetic capacity compared to that of lake populations (Fig. 6.7). However, even at the end of the hyperscum season photosynthetic activity of cells from 10 cm depth was still measurable (Fig. 6.7), indicating that at least a proportion of the cells was viable, or that all cells were stressed and performed badly, but were not dead. Transmission electron microscopy revealed cells that are mostly depleted of their storage granules, but with intact photosynthetic apparatus. Occasionally, cells with partially lysed cell wall were found, although completely lysed cells were not seen (plate 6.4d). The characteristic faded appearance of the cells after 2 - 3 months in the hyperscum (Plate 6.4b) was strikingly similar to the "pallid" appearance that Reynolds *et al.* (1981) described as characteristic of *M. aeruginosa* cells from benthic sediments of Blelham Tarn. In both cases the cells were retrieved after a prolonged period of dark, anaerobic conditions.

It is not clear what caused the deterioration of the condition of *M. aeruginosa*. The changes coincided with large increases in interstitial ammonia and SRP concentrations (Fig. 5.5), and with the period of the gradual breakdown of the hyperscum (Fig. 4.7c). A possible explanation is that decomposition products that continuously diffused downwards from above reached toxic levels at that time. It is also possible that the gradual breaking of the hyperscum and associated events of penetration of atmospheric oxygen triggered chemical and biochemical processes that harmed the cells.

In conclusion, a hypothetical dynamic model of the fate of a *M. aeruginosa* colony that enters a hyperscum is represented schematically in Fig. 6.9. A colony that arrived below a hyperscum and was not carried away by currents, became overbuoyant in the dark and floated into the bottom of the hyperscum. With time it migrated upwards, due to its own positive buoyancy as well as due to the buoyancy of colonies rising from underneath and the collapse of cells at the top. It survived in the dark, anaerobic environment by maintaining low levels of basal metabolism while utilizing stored reserves. The colony may or may not have reached the zone of decomposition near the surface, where it would die. With the aging of the hyperscum and the accumulation of decomposition products that could not escape, the zone of decomposition became wider. Photooxidation at the surface, it

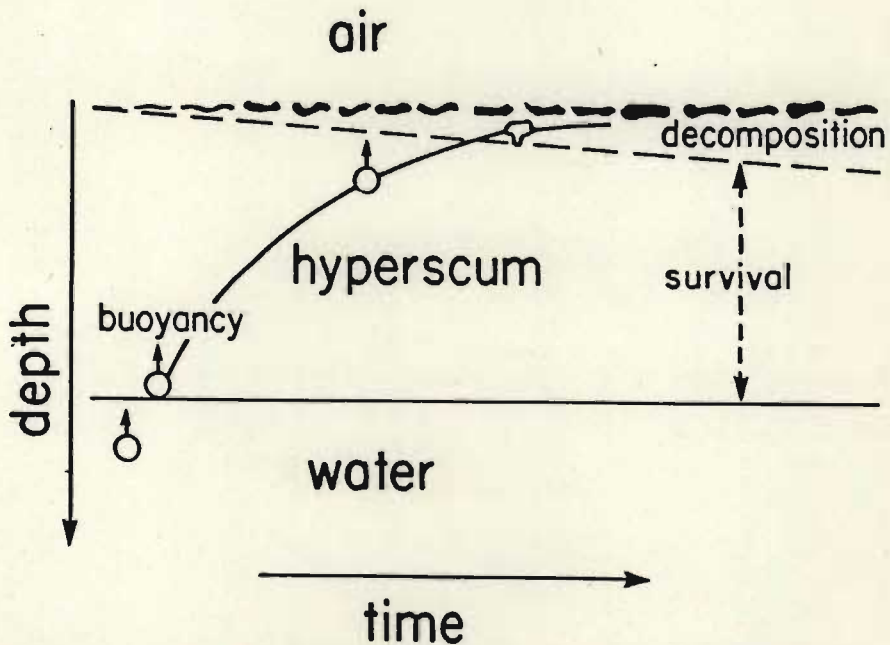


FIGURE 6.9 A conceptual model of the fate of a *Microcystis aeruginosa* colony entering a hyperscum.

seems, played an important role at the initial stages of hyperscum formation. Later, when decomposition prevailed within the underlying compact layer, cells arriving at the surface were already dead. Dehydration then played an important role in that it caused the compaction and shrinking of the crust and nearby layers, thereby creating space for more colonies from below.

According to this model, a hyperscum is essentially a site of a continuous cycle of death and dehydration at the surface and upward migration of colonies from below to replace those that died. However, not all colonies entering the hyperscum will necessarily die in it. It was the interplay between the age of the hyperscum at the time a colony entered it, the distance from the surface, the rate of upward migration of colonies and climatic events that determined whether an individual colony will reach the lethal zone.

CHAPTER 7

CONCLUDING DISCUSSION

A conceptual model summarizing the annual cycle of *M. aeruginosa* in Hartbeespoort Dam is presented in Fig. 7.1. The main growth phase begins after the onset of thermal stratification in spring, coinciding with increases in water temperature, insolation and stability (Figs 3.1, 3.5) and high grazing pressure on other algal species (Jarvis, 1986). In early summer, nutrients available in excess of growth requirements, warm temperatures, high insolation and increasing lake surface area due to seasonal rains, lead to a rapid growth of the population (Fig. 3.5), until self-shading limits light availability and further growth. The post-maximum summer populations maintain themselves throughout autumn and most of the winter, despite suboptimal temperatures that severely restrict their growth rate. Apparently, *Microcystis aeruginosa* succeeds in maintaining its population throughout winter and in persisting as the dominant species (Fig. 3.6) by remaining within the illuminated layers, while at the same time sustaining low losses.

At water temperatures below about 15°C the growth rate of *M. aeruginosa* is practically zero (Konopka and Brock, 1978a; Kruger and Eloff, 1978; Kappers, 1984; Reynolds, 1984), so that photosynthesis has to support only basal metabolism. Respiration rates of cyanobacteria have greater Q_{10} values than photosynthesis (Jewson, 1976; Robarts and Zohary, 1987). Therefore, respiration rates decline faster than production rates as temperatures decline, and at low temperatures a relatively larger proportion of gross production is available for cell metabolism.

Low wind speeds and solar heating over Hartbeespoort Dam cause the formation of diurnal thermoclines shallower than the euphotic zone even during periods of low stability of the entire water column (Figs 3.1, 3.10). Due to its buoyancy mechanism *Microcystis* can maintain itself within shallow diurnal mixed layers, and thus remain within the illuminated zone, while non-buoyant species sink (e.g. Fig. 3.11). The study in Hartbeespoort Dam has demonstrated the importance of distinguishing between the depth of the seasonal thermocline, z_m ,

and the depth of the diurnal thermocline, z_1 . It has shown the profound influence that the daily pattern of z_1 , as opposed to the seasonal pattern of z_m , can have on phytoplankton species composition.

The low cellular chlorophyll content and high $I_{0.5}$ values (section 3.3) of *M. aeruginosa* from Hartbeespoort Dam are indicative of its adaptation to survival under the high light intensities at the surface (Harris, 1978; Reynolds, 1984). By increasing colony size under calm conditions, the attenuation of light with depth is moderated. This deepening of the euphotic zone allows a larger proportion of the buoyant population access to light, while sinking species are shaded out. At the same time, individual cells within large colonies at the surface are exposed to a lower average light intensity because the colonies continuously roll and cells at the top shade those below. Possibly, photoinhibition is reduced in this manner.

Concurrent losses to the *M. aeruginosa* population in Hartbeespoort Dam are generally small. Colonies are typically too large to be grazed by zooplankton (Jarvis, 1986; Jarvis *et al.*, 1987). Sinking losses are relatively high throughout the winter (Fig. 3.7), but it is possible that during most of the winter sinking colonies are capable of upward migration, and that sinking cells are permanently lost only towards the end of winter (*cf.* Reynolds *et al.*, 1981). Other losses due to washout, parasitism, death and decomposition are probably small, with the exception of death and decomposition in hyperscums (see below). Sinking losses, together with decomposition in hyperscums, cause the eventual decline of the planktonic population in late-winter (Figs 3.5, 3.7, 7.1). It is important to note, however, that *M. aeruginosa* never disappears completely from the water column (lowest concentrations recorded: > 1000 cells ml^{-1}).

Despite the ability of *M. aeruginosa* to survive and remain dominant throughout winter (Figs 3.5, 3.6), by May-June the planktonic population is already 4-5 months old. An indication of senescence is the high gas vacuole content of cells participating in surface blooms (Plate 6.3b). Possibly, low growth rates under the low winter temperatures prevent the dilution of gas vacuoles through cell division. The excess gas vacuolation leads to overbuoyancy, and to the accumulation of colonies at the surface at high densities during calm weather. Under thick surface blooms $z_{0.5}$ may be reduced to only a few millimeters (section 6.2.1), below which colonies can not produce carbohydrate, and therefore cannot sink; to the contrary, in the dark the cells consume their

stored carbohydrate and become even more buoyant. Only turbulence can transport these colonies to greater depths in the water column.

Under the prevailing calm conditions in autumn and winter the blooms are carried by surface currents and accumulate into hyperscums. Hyperscums are therefore composed initially of post-maximal, probably senescent, overbuoyant populations. Once in a hyperscum, the probability of an overbuoyant colony to be released back into the water column is small: hyperscums form in protected bays, where turbulence is minimal; the bulk of the hyperscum is dark and positive buoyancy cannot be negated by producing carbohydrate; and overbuoyant colonies rising from beneath cause those within the hyperscum to move upwards and compact. Thus, the same buoyancy mechanism that provides *M. aeruginosa* with a range of potential advantages over non-buoyant species (access to atmospheric CO₂: Paerl and Ustach, 1982; Paerl, 1983; ability to overcome spatial separation between nutrients and light: Ganf and Oliver, 1982; van Rijn and Shilo, 1985; ability to float into the illuminated layers: Reynolds and Walsby, 1975; ability to maintain itself within illuminated shallow diurnal mixed layers: this study; shade non-buoyant species: all studies) causes it to become trapped for months on end in hyperscums. Thick surface blooms and ultimately hyperscums are therefore an inevitable consequence of the mechanism of buoyancy regulation in *M. aeruginosa*, under specific environmental conditions (hypertrophy, low wind speeds, wind protected embayments, high insolation).

Cells at the surface of new hyperscums die within hours of exposure to photooxidizing conditions. They later shrink in size through dehydration, thereby creating space at the surface for colonies from underneath. The underlying overbuoyant colonies are initially protected from photooxidation and dehydration, yet, they are destined to slowly migrate upwards, till they reach a zone where they die through photooxidation, dehydration or decomposition (Fig. 6.9). There is evidence that not all the cells entering the hyperscum die through one of these processes, and that the position and duration in a hyperscum play a major role in the fate of individual cells. The closer to the surface, the greater the stress on cells due to evaporative dehydration, accumulation of end-metabolites of anaerobic decomposition at potentially toxic concentrations, and extreme temperature fluctuations. With the aging of the hyperscum the zone of severe stress expands, as end-metabolites slowly diffuse downwards along concentration gradients.

The rate of colony death at the surface and the rate at which colonies migrate upwards were not measured. It is therefore impossible to say with certainty what proportion of the *M. aeruginosa* trapped in hyperscums is permanently lost. However, if the conceptual model in Fig. 6.9 is correct, then given a long enough period of time, every cell that enters a hyperscum is destined to die. Ultimately, climatic events determine how long a hyperscum would exist, and therefore whether a particular cell would reach the lethal zone or would be released to the water column.

When hyperscums broke due to increasing wind activity, field observations showed that colonies comprising it drifted away in wind-rows caused by Langmuir circulations. If the wind speed later declined, the colonies became dispersed over the main basin. A non-quantified, yet consistent, field observation was that on such occasions green colonies that remained at the surface photobleached within hours, so that the entire main basin became dotted with floating white colonies. These observations suggest that at least a proportion of the colonies released from the bulk of the hyperscum were photooxidized upon the sudden exposure to direct radiation and permanently lost in this manner.

Changes with time in the standing stocks of *M. aeruginosa* between May and November in years when a hyperscum formed (1983, 1984) and in 1985, when a hyperscum did not form, are shown in Fig. 7.2. While in 1985 the population-decline started earlier than in other years, the lowest standing crops were recorded in September in all years. The planktonic population started to increase in October each year, and this occurred irrespective of the presence or absence of hyperscums. During years with hyperscums the planktonic population was maintained several months longer than in 1985, when a hyperscum did not form. However, the late winter decline was not prevented by the occurrence of hyperscum. Furthermore, the spring increase of the population occurred at approximately the same time each year, irrespective of whether hyperscums formed. This suggests that hyperscums, although significant in the proportion of the population that they may encompass at any point of time, are not important to the long-term survival of the species. It is the relatively large residual winter planktonic standing crop, possibly supplemented by colonies emerging from the sediments, that comprise the inoculum for the spring growth and ensure the long-term survival of the species in Hartbeespoort Dam. Hyperscums are rather a product of hypertrophy

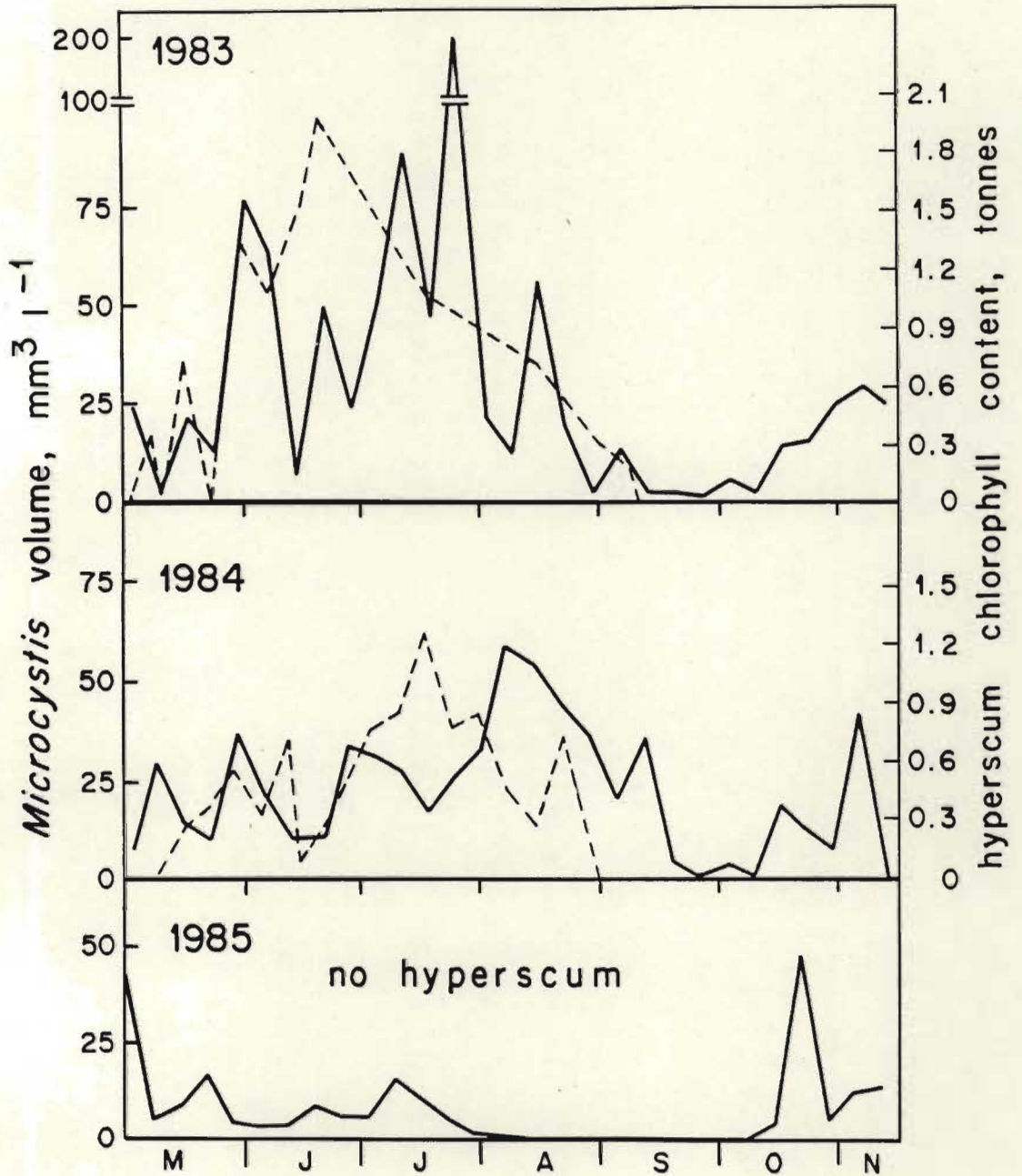


FIGURE 7.2 Changes with time in the abundance of planktonic *M. aeruginosa* (black line) and in the size of hyperscums, expressed as total chlorophyll a content (dashed line).

under certain climatic and topographic conditions, and a price that *M. aeruginosa* pays for the advantages incurred by its buoyancy regulation mechanism.

The annual cycle of *M. aeruginosa* in Hartbeespoort Dam differs from that in temperate lakes (cf. Reynolds *et al.*, 1981) in two major characteristics: (1) in Hartbeespoort Dam *M. aeruginosa* maintains its post-maximal planktonic population longer, till about mid-winter, and (2) the residual planktonic population at the end of winter is much larger than in temperate lakes. Thus, although a large proportion of the population sediments during winter, the renewed spring growth is not dependent on an inoculum originating from overwintering benthic colonies. In addition, a large proportion of the winter population in Hartbeespoort Dam may remain overbuoyant and become trapped in hyperscums.

These differences can be explained as resulting from differences in winter water temperatures between temperate and subtropical lakes. In temperate lakes water temperature declines in winter below 10°C, causing *M. aeruginosa* to lose its capacity to regain buoyancy in the dark (Thomas and Walsby, 1986) and consequently it sinks. In subtropical Hartbeespoort Dam water temperature in winter remained above 12 - 13°C so that the capacity to regain buoyancy was not completely lost and a planktonic population could be maintained throughout winter.

In another small South African lake (Jan Smuts Park Dam), situated about 80 km east of Hartbeespoort Dam and subject to similar topographic and climatic conditions, dense blooms of *M. aeruginosa* are common in summer, but Tow (1979) reported that the planktonic population disappeared in winter, when the cyanobacterium could be found only on the bottom sediments. The mean depth of this pan is only 1.2 m and in winter water temperature is lower than in Hartbeespoort Dam, 10-11°C. In Rhenosterkop Dam, some 170 km northeast of Hartbeespoort Dam, the winter surface temperature declined to a minimum of 13.5°C and a planktonic population of *M. aeruginosa* was maintained throughout the winters of 1986 and 1987 (Zohary, unpublished data). In subtropical Lake McIlwaine, Zimbabwe (18°S) winter temperatures declined to 15°C and planktonic populations of *M. aeruginosa* were maintained throughout the year (Robarts, 1979). These data support Thomas and Walsby's (1986) laboratory and field findings from temperate Abbots Pond, U.K., which show that the rate at which *M. aeruginosa* regained buoyancy reached a minimum at 11°C and was low below 14°C.

It is most likely that the mixing regime has an interacting effect on buoyancy, as was probably the case in Hartbeespoort Dam (see section 3.3).

The annual cycle of *M. aeruginosa* as presented by Reynolds *et al.* (1981) can now be extended to include subtropical and tropical lakes (Fig. 7.3). In temperate lakes (Fig. 7.3c), as in the model of Reynolds *et al.* (1981), planktonic populations increase in spring, bloom in summer and sediment out in autumn. In winter, *M. aeruginosa* is practically absent in the plankton, and the overwintering benthic stocks may comprise nearly 100 % of the previous summer's planktonic population (Reynolds and Wiseman, 1982). In spring, colonies emerging from the sediments provide the inoculum for renewed growth.

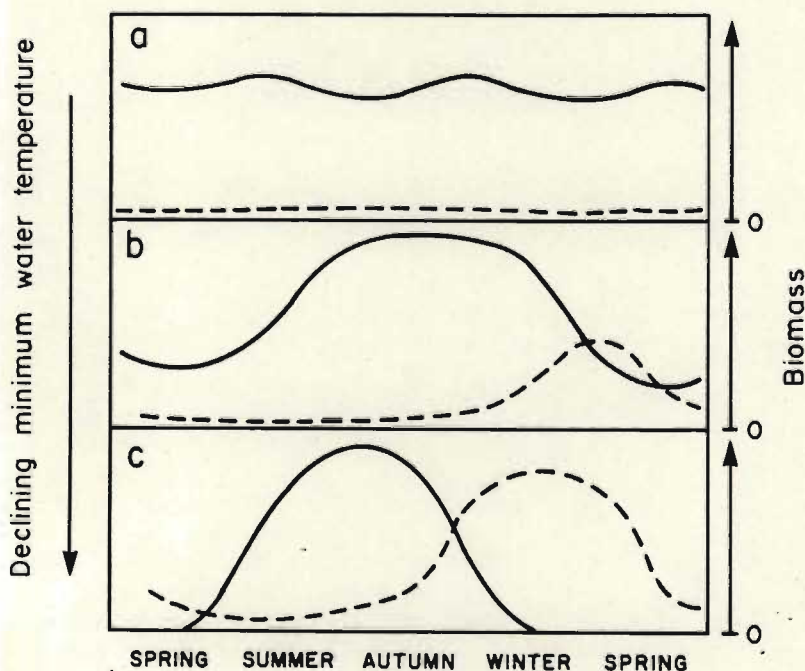


FIGURE 7.3 Schematic representation of the seasonal changes in the planktonic (solid line) and benthic (dashed line) standing stocks of *M. aeruginosa*, and how they change from tropical lakes with minimum water temperature $> 20^{\circ}\text{C}$ (a) to temperate lakes with winter temperature $< 10^{\circ}\text{C}$ (c). Subtropical lakes cover a range of intermediate situations, e.g. as shown in (b).

In tropical lakes (Fig. 7.3a) where water temperatures fluctuate around 20°C all year, diel cycles, nutrients and climatic events are more important than seasonal cycles in determining changes in the size of the planktonic standing crop of *M. aeruginosa*, and a planktonic population may persist throughout the year. An example is Lake George, Uganda, where large standing stocks of *M. aeruginosa* are maintained at a near steady-state all year, and the actual planktonic standing crop is determined by diurnal cycles of mixing and stratification (Ganf, 1974).

In subtropical climates the minimum winter temperature is often around the critical range of 11 - 14°C cited by Thomas and Walsby (1986). If the winter temperature is above the critical level for buoyancy loss, a planktonic population will be maintained throughout the annual cycle (provided that other factors, such as nutrients and mixing are permitting). As winter temperatures become colder, the planktonic population will begin to lose the ability to regulate buoyancy earlier in the annual cycle and an increasing proportion of the population will sediment out in winter. *M. aeruginosa* depends on benthic overwintering populations for its long-term survival only in lakes with winter water temperature below 10 - 12°C.

It is well established that with increasing enrichment of freshwaters from eutrophy to hypertrophy the cyanobacterial standing crop increases concomitantly with the extent and frequency of occurrence of surface blooms. Hyperscums are the ultimate of water blooms, which Reynolds and Walsby (1975) claimed to be an incidental event that serves no useful function in the biology of the cyanobacterium. Their view was later criticized by several workers who argued that scumming was an adaptive mechanism because it relieved carbon and nitrogen limitations (Paerl and Keller, 1979; Paerl and Ustach, 1982; Paerl, 1983; Lewis, 1983). While these advantages cannot be denied, the phenomenon of hyperscums serves to demonstrate that scums do form incidentally, even when the above advantages cannot be materialized, and that they have no vital function in the biology of the organism.

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