Seasonal variation of phytoplankton biomass in the Middle Vaal River, South Africa

Jan C Roos[1]* and AJH Pieterse[2]
[1] Department of Botany and Genetics, University of the Orange Free State, PO Box 339, Bloemfontein 9300, South Africa
[2] Department of Plant and Soil Sciences, Potchefstroom University for CHE, Private Bag X6001, Potchefstroom 2520, South Africa

Abstract

The chlorophyll-*a* concentration in the Vaal River (at Balkfontein; 1985 to 1989) was high (av. = 67 $\mu g \cdot \ell^{-1}$) and displayed great variation (8 to 360$\mu g \cdot \ell^{-1}$). An increasing concentration trend of 20 $\mu g \cdot \ell^{-1} a^{-1}$ was shown. The hydrology, particularly episodic floods through inputs from summer rain, plays an important role not only in the chemistry, but also in the biology of the Vaal River. The chl-*a* concentration was usually the lowest after the summer rain period. It stayed low for about two months and was then followed by a maximum concentration (bloom) in late winter to spring. The early bloom was dominated by diatoms, followed by a bloom usually dominated by green algae. The bloom was followed subsequently by a population crash. The enrichment of the river during floods by nitrogen (N) and phosphorus (P), usually leads to large phytoplankton blooms that occur approximately two to four months after floods. The average chl-*a* concentration in the Vaal River was statistically significant, correlated with the average total phosphorus (TP) concentration. Approximately 1 $mg \cdot \ell^{-1}$ increase in the average TP concentration will probably be associated by about 225$\mu g \cdot \ell^{-1}$ increase in the average chl-*a* concentration. This aspect could make it fairly simple to predict and possibly control the standing crop in the Vaal River.

Introduction

Rivers are complex physical, chemical, and biological systems (Petts, 1984). Qualitative and quantitative information of organisms growing in an ecosystem is of fundamental importance in understanding the functioning of ecosystems (Vollenweider et al., 1974). The dynamics of phytoplankton in rivers has not been investigated as much as it has in lakes and estuaries. Particularly, the relationship between phytoplankton and discharge, which is the main diagnostic feature of rivers when compared to lentic habitats, seems not yet to be fully understood.

The quality of many water sources in the Republic of South Africa (RSA) is declining. The decline is primarily a result of salinisation, eutrophication and pollution by trace metals that are micro-pollutants (DWA, 1986). This type of pollution applies especially to the Vaal River system (Braune and Rogers, 1987). Massive development of phytoplankton and macrophytes, especially water hyacinths (*Eichhornia crassipes*), occurs as a result of pollution and eutrophication (Pieterse, 1986; Roos, 1992). The Vaal River is the most important river in South Africa and can justifiably be called "the main artery of the South African heartland" (Braune and Rogers, 1987). However, only limited ecological studies on the river have been undertaken in the past.

Preliminary observations on spatial and temporal heterogeneity in phytoplankton and environmental variables as well as primary productivity in the Vaal River were made by Pieterse et al. (1986), Pieterse and Roos (1987; 1992), and Roos and Pieterse (1992). Physical and chemical aspects of the environment that influence phytoplankton were evaluated by Roos and Pieterse (1994; 1995b) and seasonal and related aspects of N and P were presented in Roos and Pieterse (1995a). They emphasised the important contribution of annual spates to TN and TP concentration, with suspended solids as an important transport agent in the Vaal River. However, seasonal variation of phytoplankton and quantitative evaluation of the relationship between various environmental variables have been investigated only for a brief period (Pieterse, 1986).

In the present study, phytoplankton biomass and environmental variables that influence their abundance are emphasised, and reference is made to specific algal species. In addition, the conditions that possibly cause the development of annual spring blooms of phytoplankton have been investigated, as well as which variable(s) possibly govern(s) the upper limit of phytoplankton biomass during blooms in the Vaal River.

Materials and methods

The present study was done in the lower region of the middle Vaal River system (South Africa) at the water intake (pumping station) of the Balkfontein purification plant (lat. 27° 23' 45"; long. 26° 30' 30") situated at a height of 1 240 m above mean sea level (see Roos and Pieterse, 1994; 1995a; b for map of the region). The width of the river at the sampling site is about 70 m, while the maximum depth is 6 m and the average depth is about 4 m.

In situ measurements in the Vaal River were done monthly over a period of four years (August 1985 to November 1989). Dissolved oxygen ($mg \cdot \ell^{-1}$) and temperature (°C) were recorded at noon (12:00 ± 1 h) at the surface and at each 0.5 m depth down to 3 m. A Yellow Springs YSI Model 54 A oxygen/temperature meter was used. It was calibrated with saturated (stirred) river water, taking the atmospheric pressure and temperature into account.

Surface pH was recorded with an Orion Research Model 231 digital pH meter that was calibrated (2-point method) with buffer solutions at pH 7 and pH 10. Turbidity was recorded with a Chemtrix Type 10 Turbidimeter and quantitatively expressed in terms of the scattering coefficient, i.e. in nephelometric turbidity units (NTU). A 100-$m\ell$ subsurface water sample was collected and preserved in 2% formalin (final concentration) for algal identification (Wetzel and Likens, 1991). The algal species with the greatest number of cells per unit volume of water was considered to be the dominant alga. However, co-dominance was frequently encountered

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* To whom all correspondence should be addressed.

☎ (051) 401-2265; Fax (051) 448-8772; E-mail pjcr@rs.uovs.ac.za

Received 24 February 1995; accepted in revised form 20 September 1995.

in which case both algae were recorded.

Chlorophyll-*a* (chl-*a*) concentration in the present study was determined spectrophotometrically according to the method given by Sartory (1982), with some modifications. Between 150 and 250 m*ℓ* Vaal River water was filtered through a glass fibre filter (GF/C, particle retention 0.7 µm), boiled (at 78°C) for 5 min in 10 m*ℓ* 95% ethanol, and then cooled in the dark. Absorbance of the extracted chl-*a* was read with a LKB (Biochrom) Ultrospec 4050 spectrophotometer at a wavelength of 665 nm. Three drops of 0.1N HCl were then added directly to the cuvette, which was inverted once to mix the extract, and the absorbance was read again after approximately 1 min. Background absorbance was read at 750 nm and subtracted from the readings obtained at 665 nm.

Chemical data at Balkfontein were obtained from the Department of Water Affairs and Forestry, Pretoria. They included silica silicon (SiO_2-Si), ammonium nitrogen (NH_4-N), nitrate nitrogen (NO_3-N), total phosphorus (TP), Kjeldahl nitrogen (KN; organic + NH_4-N) and river flow rate (discharge). Total nitrogen (TN) was calculated as KN plus NO_3-N. Dissolved inorganic nitrogen (DIN) was calculated as NH_4-N plus NO_3-N. All the automated and manual inorganic analytical procedures, routinely used in the Department of Water Affairs and Forestry water quality monitoring programmes, are described by Van Vliet et al. (1988).

Results

Phytoplankton biomass (chlorophyll-*a*)

During the present study period (August 1985 to November 1989) the phytoplankton biomass (chl-*a* concentration) in the Vaal River at Balkfontein ranged between 8 µg·ℓ^{-1} (November 1985) and an exceptionally high 360 µg·ℓ^{-1} (July 1989) with the average at 67 µg·ℓ^{-1} (Fig. 1). Frequency analysis showed that approximately 60 % of the samples (i.e. 25 out of 43) had chl-*a* concentrations of between 20 and 80 µg·ℓ^{-1} while 30 % of the samples (13 out of 43) exceeded 80 µg·ℓ^{-1} (Fig. 1).

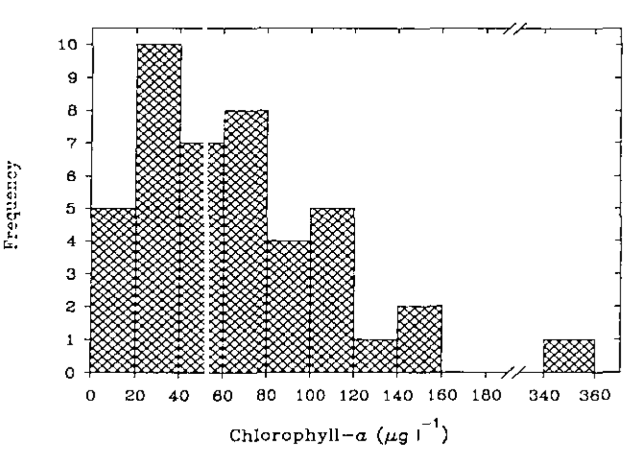

Figure 1
Frequency histogram of chlorophyll-a concentration in the Vaal River at Balkfontein during August 1985 to November 1989

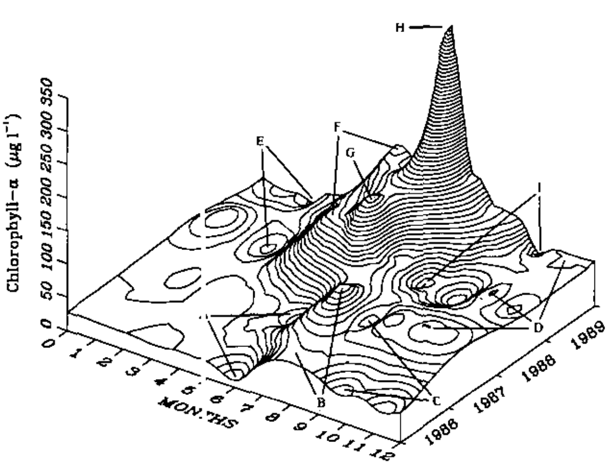

Figure 2
Three-dimensional surface plot of monthly chlorophyll-a concentration in the Vaal River at Balkfontein.

A = low autumn to winter concentrations (1986 and 1987)
B = spring diatom blooms during 1986 and 1987 respectively
C = low concentrations, i.e. biomass declines after blooms;
D = recovery to moderate summer concentrations
E = impact of 1988 and 1989 floods
F = winter diatom blooms during 1988 and 1989
G = winter green algal bloom during 1988
H = winter green algal bloom during 1989 following about six weeks after diatom bloom
I = low concentration, i.e. biomass declines after blooms

Annual variation of chl-*a* concentration in the Vaal River is presented in a three-dimensional surface plot that illustrates changes in chl-*a* concentration (Fig. 2). The chl-*a* concentration was usually relatively low during late summer to autumn (January to April; see A & E in Fig. 2), followed by a winter-spring algal bloom, coinciding with the dry season (see B, F, G & H in Fig. 2), with a relatively high residual population during early to mid-summer (October to December; see D in Fig. 2). Algal blooms usually occurred during the winter-spring period (June to September) when the total suspended solids concentration was relatively low (less than 30 mg·ℓ^{-1}), and high light availability therefore occurred (Roos and Pieterse, 1994).

The study period was characterised by a dry period (1985 to 1987), followed by summer floods in March 1988 and in February 1989 (Roos and Pieterse, 1994). Notable differences in the phytoplankton seasonality in the Vaal River occurred between the dry period (1985 to 1987) and the wet period (1988 to 1989), dominated by floods. The chl-*a* maxima during the wet period were much higher (av. 260 µg·ℓ^{-1}) than during the dry period (av. 88 µg·ℓ^{-1}; Fig. 2). The usual spring (August to September) bloom during the dry period was advanced to a winter (June to July) bloom during the wet period (Fig. 2).

Figure 2 illustrates the immediate impact of high discharge (floods) reducing the chl-*a* concentration (see E in Fig. 2), followed by algal blooms during the winter-spring period (see F, G & H in Fig. 2). The bloom collapsed (see I in Fig. 2), but the population biomass recovered to moderate concentrations during the summer period (see D in Fig. 2).

The maximum chl-*a* value during a specific annual cycle was related significantly to the average chl-*a* concentration of the same year as shown by the exponential equation (Fig. 3):

$$\text{Chl-}a\ (\text{max.}) = 24.6 * e^{[0.027*\text{Chl-}a\ (\text{av.})]} \qquad (1)$$

The importance of the relationship between the maximum and the average chl-*a* concentration lies in the fact that it might allow the prediction of extreme nuisance conditions that could be expected with increased average annual chl-*a* concentrations in the Vaal River.

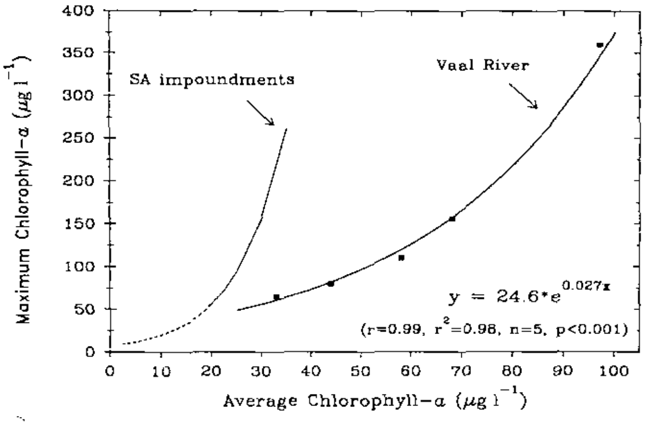

Figure 3
Exponential correlation between the maximum vs. average annual chlorophyll-a concentrations in the Vaal River at Balkfontein (1986 to 1990, solid line), and in 31 South African impoundments (dashed line; Walmsley, 1984)

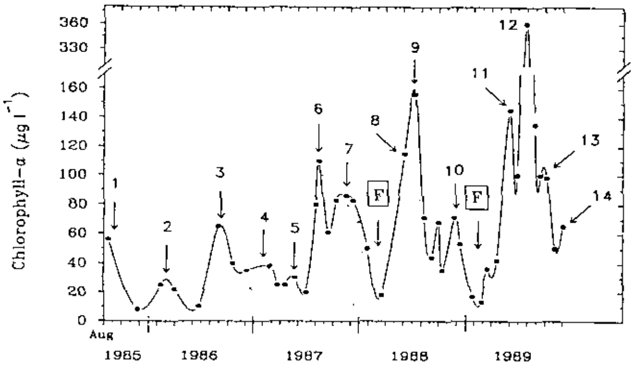

Figure 4
*Seasonality of phytoplankton biomass and dominant Vaal River species at Balkfontein. Note the spring (sometimes winter) diatom blooms which are followed by green algae and the increasing trend in chlorophyll-*a *concentration during the study period. Fs represent the impacts of 1988 and 1989 floods.*

1 = 1985-08-14 (spring): Pedinomonas rotunda *(green)* & Stephanodiscus hantzschii *fo.* tenuis *(diatom)*
2 = 1986-02-18 (summer): Cyclotella meneghiniana *(diatom)* & Scenedesmus lefèvrii *(green)*
3 = 1986-08-29 (spring): Cyclotella meneghiniana *(diatom)*
4 = 1987-02-26 (summer): Carteria fornicata *(green) &* Cyclotella meneghiniana *(diatom)*
5 = 1987-05-25 (autumn): Chlamydomonas bicocca *(green)* & Euglena hemichromata *(euglenoid)*
6 = 1987-08-17 (spring): Stephanodiscus hantzschii *fo.* tenuis *(diatom)*
7 = 1987-10-13 (summer): Carteria fornicata *(green)*
8 = 1988-06-02 (early winter): Stephanodiscus hantzschii *fo.* tenuis *(diatom) & some greens*
9 = 1988-07-08 (mid-winter): Micractinium pusillum *(green)*
10 = 1988-11-21 (summer): Carteria fornicata *(green)*
11 = 1989-06-01 (winter): Stephanodiscus hantzschii *fo.* tenuis *(diatom)*
12 = 1989-07-24 (winter): Chlamydomonas incerta *(green)*
13 = 1989-10-06 (summer): Sphaerodinium *sp. (dinoflagellate)*
14 = 1989-11-28 (summer): Carteria globosa *(green)*

Succession of dominant phytoplankton species

Representatives of four major algal taxa were found to be dominant during the study period, namely the Bacillariophyceae (diatoms), Chlorophyceae (green algae), Dinophyceae (dinoflagellates) and the Euglenophyceae (euglenophytes). The dominant algal species in the Vaal River during this study were *Stephanodiscus hantzschii* fo. *tenuis*, *Cyclotella meneghiniana* (diatoms), *Pedinomonas rotunda*, *Scenedesmus lefèvrii*, *Carteria fornicata*, *Chlamydomonas bicocca*, *Chlamydomonas incerta*, *Micractinium pusillum*, *Carteria globosa* (green algae), *Euglena hemichromata* (euglenophyte) and *Sphaerodinium* sp. (dinoflagellate) (Fig. 4).

The seasonality of biomass and of dominant phytoplankton species in the Vaal River usually showed maximum concentrations in winter to spring, dominated by diatoms (see No. 8 & 11 in Fig. 4) and followed by dominance of green algae (No. 9 & 12 in Fig. 4) in the summer and autumn. However, on several occasions a mixture of diatoms and green algae were present at relatively high concentrations (see 1, 2, 4 & 8 in Fig. 4).

The interspecific competition for nutrients determines the species composition and seasonal succession of phytoplankton in lakes (Tilman and Kilham, 1976). Therefore, the influence of TP, TN:TP ratios, silicon, discharge and temperature on phytoplankton in the Vaal River will be discussed in later paragraphs.

Phytoplankton and phosphorus

In the Vaal River, the total phosphorus (TP) concentration was high (av. = $202 \mu g \cdot \ell^{-1}$), but phosphate phosphorus (PO_4-P) concentration was low (av. = $16 \mu g \cdot \ell^{-1}$). A statistically significant correlation ($r^2 = 0.76$) was demonstrated between the annual average chl-*a* concentration and average TP concentration (Fig. 5), which is independent of the TN concentration (see Fig. 8). The relationship was best described by:

$$\text{Chl-}a = 0.55 * (\text{TP})^{0.88} \qquad (2)$$

Comparable relationships, based on a large number of lakes, were demonstrated by the OECD (1982) and Stockner and Shortreed (1985; Fig. 5). However, different chl-*a* concentrations were associated with the same TP concentration. In the Vaal River a significant correlation ($r^2 = 0.86$) was demonstrated between summer maximum TP at annual river high flow and the average spring chl-*a* concentration (Fig. 6), i.e.:

$$\text{Chl-}a = 0.15 * \text{TP} + 32 \qquad (3)$$

Therefore, the TP input during the annual flood periods (summer-autumn) and the magnitude of the winter-spring bloom are apparently related to one another. This relationship has a predictive capacity.

Several authors have also sought to relate average summer standing crops to the TP concentration in lakes obtained at the beginning of the growing season, i.e. at the winter overturn or during spring. For example Riley and Prepas (1985) showed a highly significant relationship between the spring TP concentration and summer chl-*a* concentration for both stratified (Fig. 6) and mixed lakes.

Phytoplankton and TN:TP ratios

The average total nitrogen (TN) to total phosphorus (TP) ratio (TN:TP) in the Vaal River was relatively low at 11 and usually

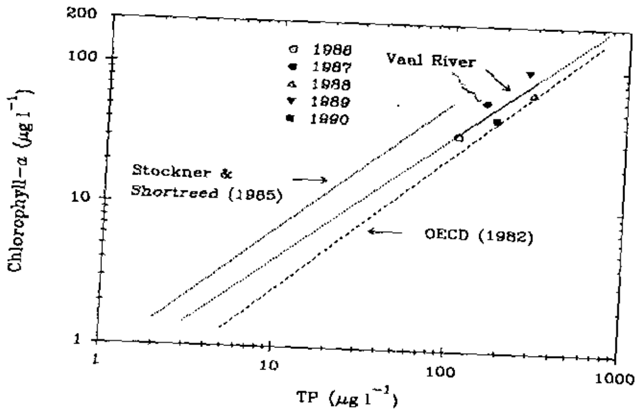

Figure 5
Relationship between the average annual chlorophyll-a and average total phosphorus (TP) concentration in the Vaal River at Balkfontein
(short solid line, Chl-a = $0.55\,(TP)^{0.88}$, $r = 0.87$, $r^2 = 0.76$, $n = 5$, $p < 0.05$). Dotted part of this line represents the extrapolation of the relationship. The lower dashed line is from OECD (1982) i.e. (Chl-a = $0.28\,(TP)^{0.96}$, $r = 0.88$, $r^2 = 0.77$, $n = 77$, $p < 0.001$) and the upper dashed-dot line is from Stockner and Shortreed (1985), i.e. (Chl-a = $0.92\,TP - 0.09$, $r = 0.76$, $r^2 = 0.58$, $n = 50$, $p < 0.001$).

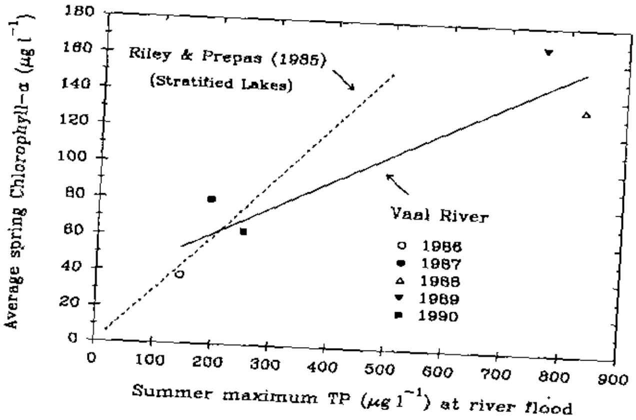

Figure 6
Relationship between average spring chlorophyll-a concentration and summer maximum total phosphorus (TP) concentration in the Vaal River.
($y = 0.15x + 32$, $r = 0.93$, $r^2 = 0.86$, $n = 5$, $p < 0.01$). The dashed line indicates the relationship between the average summer chlorophyll-a and TP concentration at spring overturn demonstrated by Riley and Prepas (1985), i.e. $y = 1.015TP - 0.555$, $r = 0.80$, $r^2 = 0.64$, $n = 31$, $p < 0.001$ for stratified lakes

the lowest during flood periods (Roos and Pieterse, 1995a). The chl-*a* concentration in the Vaal River was positively correlated with the TN:TP ratio ($r = 0.85$, $r^2 = 0.42$, $n = 42$, $p < 0.001$) which suggests that the TP concentration was, relative to TN, lower when the chl-*a* concentration was high, resulting in a high TN:TP ratio, and vice versa.

The lowest TN:TP ratio of 2.8 (on 1989-02-22) was encountered four months before the highest chl-*a* (360 μg·l^{-1}) was recorded on 1989-07-24. A statistically significant inverse correlation ($r^2 = 0.85$) between the summer minimum TN:TP during river flood and the maximum chl-*a* concentration was therefore observed (Fig. 7), i.e.:

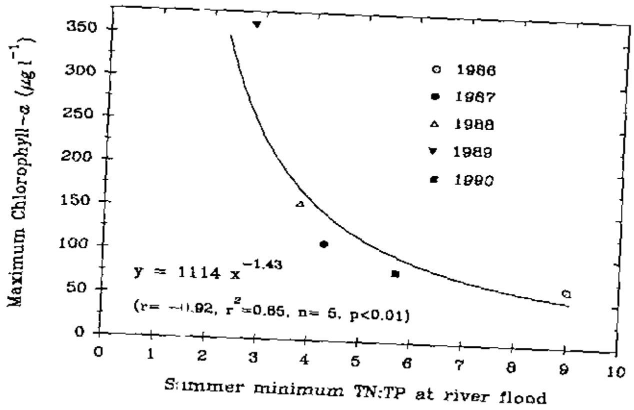

Figure 7
Relationship between maximum chlorophyll-a concentration and summer minimum TN:TP ratio during the annual high flow in the Vaal River at Balkfontein

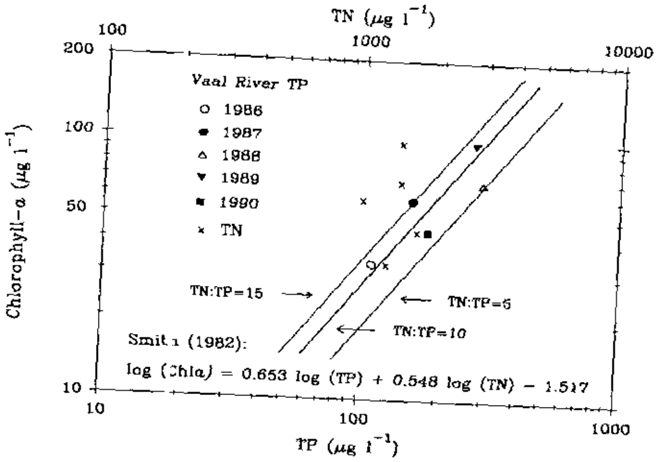

Figure 8
Relationship between the average annual chlorophyll-a concentration and TP as well as TN concentration in the Vaal River. The three lines were calculated (predictions) from a multiple regression analysis model, assuming a constant TN:TP ratio of 5, 10 and 15 (Smith, 1982)

$$\text{Chl-}a_{\max} = 1\,114\,(\text{TN:TP})_{\min}^{-1.43} \qquad (4)$$

However, Smith (1982) indicated by a multiple regression equation that the chlorophyll yield in 127 north latitude lakes was related to both TP and TN, i.e.:

$$\log(\text{Chl-}a) = 0.653\log(\text{TP}) + 0.548\log(\text{TN}) - 1.517 \qquad (5)$$

Application of Smith's (1982) equation on chlorophyll yield (assuming a constant TN:TP ratio of 10) fits the Vaal River data well, which suggests that N is a co-limiter (solid line, Fig. 8). The model predicts a family of parallel lines whose position is a function of the TN:TP ratio (Fig. 8). The average annual chl-*a* concentration produced is probably also dependent on TN:TP ratios, i.e. higher TN:TP ratio is associated with higher average annual chl-*a* concentration at a given TP concentration (Fig. 8).

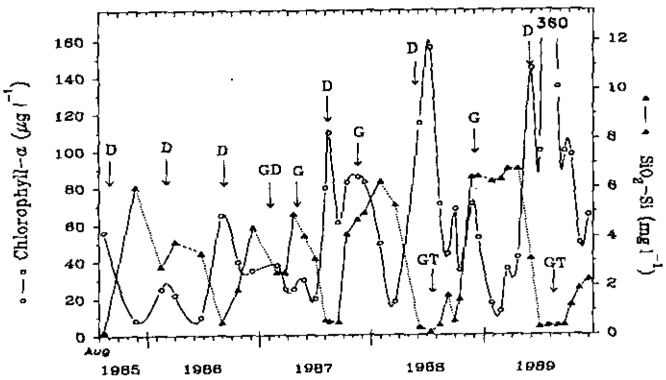

Figure 9

Seasonal variation in chlorophyll-a and silica silicon concentration (SiO_2-Si) in the Vaal River at Balkfontein. D = a diatom-dominated phytoplankton assemblage (note concurrent low Si concentration); GD = a period dominated by green algae where a fair proportion of diatoms were present; GT = phytoplankton dominated by green algae, but the low Si concentration is ascribed to exhaustion by a previous diatom population

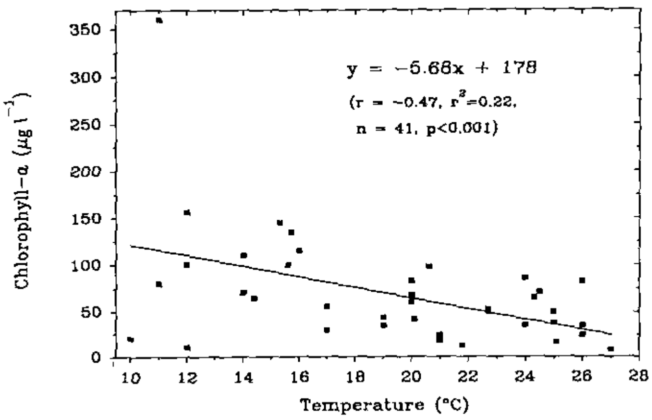

Figure 10

Relationship between water temperature and chlorophyll-a concentrations in the Vaal River at Balkfontein during the study period (August 1985 to November 1989)

Phytoplankton and silicon

The silica silicon (SiO_2-Si) concentration in the Vaal River displays seasonal variability with values ranging between 0.1 mg·ℓ^{-1} (during the winter) and 6.8 mg·ℓ^{-1} (during summer; Fig. 9), with an average concentration centred at approximately 3 mg·ℓ^{-1}. Low silicon concentrations in the Vaal River coincided with phytoplankton assemblages dominated by diatoms (see D's in Fig. 9), a process called biogenically induced desilification (Lund, 1964). Therefore, an inverse relationship between silicon and chl-*a* concentration was illustrated ($r = -0.62$; $r^2 = 0.38$, $p < 0.001$, $n = 43$). The time delay between summer maximum Si and winter maximum chl-*a* was approximately four months (Fig. 9). This four month time-lag is similar to the time-lag of approximately four months demonstrated between TP input during annual flood periods and the spring bloom.

Phytoplankton, discharge and temperature

The relatively low chl-*a* concentration in the Vaal River from January to April can be ascribed to increased flow due to summer rain with a resultant dilution and wash-out action, especially during flood periods (Figs. 2 & 4). Yet the inverse correlation between discharge and chl-*a* was at a low significant level ($r = -0.33$, $r^2 = 0.11$, $p < 0.05$, $n = 43$). The peak phytoplankton concentration in the Vaal River occurred at relatively high discharges of between 86 and 153 $m^3 \cdot s^{-1}$.

Water temperature in the Vaal River measured at midday (min. = 10°C, max. = 27°C) followed, with a slight lag, seasonal changes in average atmospheric temperatures (Roos and Pieterse, 1994). Algal blooms and high photosynthetic rates occurred during the winter-spring months (June to August) when the water temperature was 14 ± 2°C (Roos, 1992). This phenomenon resulted in an inverse relationship between chl-*a* concentration and water temperature (Fig. 10).

Discussion

Phytoplankton biomass (chlorophyll-a)

The result of eutrophication becomes apparent principally through the development of large blooms of algae as the increased potential productivity of the aquatic system responds to available energy from sunlight. The phytoplankton biomass (chl-*a* concentration) in the middle Vaal River has increased significantly over the last 20 years (DWA, 1986). In 1973, 92% of samples from the Vaal Barrage (upstream from Balkfontein) had chlorophyll concentration levels below 5 µg·ℓ^{-1}. By 1982, 87% of samples had chlorophyll concentration levels exceeding 15 µg·ℓ^{-1}, while 34% of samples exceeded 35 µg·ℓ^{-1} (DWA, 1986). During this present study (1985 to 1989), 90% of samples had chl-*a* concentration levels exceeding 20 µg·ℓ^{-1}, while 30% of samples exceeded 80 µg·ℓ^{-1} (Fig. 1). A trend analysis of the chl-*a* concentration revealed an annual increase of 20 µg·ℓ^{-1} for the period 1985 to 1989 (see Fig. 4).

In the Vaal River, the observed chl-*a* concentration range (8 to 360 µg·ℓ^{-1}) and the average annual chl-*a* concentration (33 to 98 µg·ℓ^{-1}), fall within the range of eutrophic systems (Vollenweider et al., 1974; Walmsley, 1984). The chl-*a* concentration in the Vaal River is high in comparison with other river systems of the world, e.g. River Thames (about 10 to 250 µg·ℓ^{-1}; Whitehead and Hornberger, 1984), River Meuse (0.2 to 120 µg·ℓ^{-1}; Descy et al., 1987), and the lower River Rhine (5 to 70 µg·ℓ^{-1}; Admiraal et al., 1992).

Walmsley (1984) demonstrated a highly significant exponential relationship between the maximum vs. average annual chl-*a* values for 31 South African impoundments (Fig. 3). The relationship for the lentic systems differs from the lotic conditions in the Vaal River (Fig. 3; Eq. (1)). The reason for the difference in the relationships is not clear at present. The relationship for the impoundments, however, implies relatively low average chl-*a* concentrations (possibly caused by turbid conditions), and that evidently high chl-*a* concentrations were reached only for short periods. This aspect needs to be investigated in more detail.

Succession of dominant phytoplankton species

Different types of waters have different algal floras. According to Round (1985) and Reynolds (1992), the diatoms (Bacillariophyceae) and coccoid Chlorophyta tend to be the common organisms in rivers and, of the diatoms, the small centric species of the genera *Stephanodiscus* and *Cyclotella* are undoubtedly the most common (e.g., in the River Thames; Lack, 1971, the upper Mississippi River; Baker and Baker, 1981 and in the River Murray; Walker, 1992).

The phytoplankton in the African rivers is generally dominated by Bacillariophyceae in the open water, while in associated backwaters, flood plains and reservoirs, the Volvocales and Dinophyceae are more important (Egborge, 1974). In the Vaal River, Pieterse and Roos (1987) showed that the diatoms and chlorophytes were the best represented algal groups in the Vaal River for the entire period during which the river was investigated (April 1985 to February 1986). During this present study the phytoplankton blooms in the Vaal River were dominated by the diatoms *Cyclotella meneghiniana* and *Stephanodiscus hantzschii* fo. *tenuis* and the chlorophytes by *Carteria fornicata, Pedinomonas rotunda, Chlamydomonas incerta* and *Micractinium pusillum* (Fig. 4).

The diatoms *Stephanodiscus hantzschii* fo. *tenuis* and *Cyclotella meneghiniana* usually dominated the spring bloom in the Vaal River (Fig. 4), followed by dominance of green algae in the summer. A similar sequence was observed in other river systems, for example, in the River Meuse (Descy et al., 1987), in the River Murray (Walker, 1992) and in the River Oshun, Nigeria, (Egborge, 1974). Thus, the Vaal River phytoplankton assemblage exhibits similarities with that of European and other African rivers.

Diatoms are characteristically abundant during winter in temperate lakes when low insolation and deep mixing require efficient photosynthesis (Harris, 1986). This adaptation to a wide range of photon flux densities may, in part, explain why diatoms are often associated with spring blooms. Another important feature that could promote *Stephanodiscus* sp. growth in the Vaal River is intensive vertical mixing and the relatively low TN:TP ratio that occurred during floods (Roos and Pieterse, 1995a). Harris (1986) suggested that during strong vertical mixing conditions and at TN:TP ratios smaller than 10, there is a 50% probability that *Stephanodiscus* sp. would occur. The diatoms *Stephanodiscus hantzschii* fo. *tenuis* and *Cyclotella meneghiniana* were apparently very successful competitors in the Vaal River under conditions of low temperatures (Fig. 10), high silica concentration (Fig. 9) and low TN:TP ratio.

Phytoplankton and phosphorus

Pieterse and Toerien (1978) demonstrated a significant positive correlation between average chl-*a* and phosphate (PO_4-P) concentrations in Roodeplaat Dam. However, it has been generally observed that blooms of planktonic algae appear in freshwater when phosphate and nitrate concentrations are at their lowest (Fogg, 1980). During this study, no significant correlation was apparent between chl-*a* concentration and PO_4-P, but an inverse tendency (although not statistically significant) was observed, probably because assimilable forms of N and P usually decrease simultaneously with biomass increase. The high phytoplankton biomass and low PO_4-P concentration in the Vaal River suggest a rapid turnover of PO_4-P and that much of the TP that enters the river eventually becomes available to the algae.

However, a direct measurement of phosphate in water rarely gives any accurate measure of P available to algae (Fogg, 1980; Reynolds, 1984). A measurement of the concentration of a nutrient (state variable) is not a sufficient indication of whether or not it is limiting. What needs to be known is the pool size and the rate of turnover (Harris, 1986). Thus, because inorganic P is utilised rapidly, can be stored in excess of immediate needs, and has a short turnover time, the total amount of P (TP) present may be a better index of the trophic status of water. This is an important statement in that many of the eutrophication parameters and models proposed in South Africa (e.g. Thornton and Walmsley, 1982) are primarily based on phosphate, which can be misleading if the larger TP pool and potential biologically available P are not taken into account.

The concern for eutrophication has promoted a great deal of scientific effort towards the formulation of descriptive and predictive models of phytoplankton responses to enrichment with particular nutrients. The essence of the quantification of the effect of eutrophication is to determine "how much phytoplankton" for "how much nutrients" (Reynolds, 1984).

A significant correlation was demonstrated between the average chl-*a* concentration and average TP concentration in the Vaal River (Fig. 5) and has been documented by a number of investigators in a variety of aquatic systems (e.g. Schindler et al., 1978; OECD, 1982; Stockner and Shortreed, 1985; McComb and Davis, 1993). The relationship for the Vaal River (Fig. 5, Eq. 2) could make it relatively simple to predict the average standing crop in the Vaal River. For example the relationship implies that a 1 $mg \cdot \ell^{-1}$ increase in the average TP concentration (e.g. 0.2 to 1.2 $mg \cdot \ell^{-1}$) will probably be associated with an almost 225 $\mu g \cdot \ell^{-1}$ increase in average chl-*a* concentration.

The lines in Fig. 5 represent different slopes and thus different chlorophyll concentrations per unit TP. For example, at a TP concentration of 500 $\mu g \cdot \ell^{-1}$ the associated chlorophyll concentration would be 109, 130 and 460 $\mu g \cdot \ell^{-1}$ for the OECD, Vaal River and Stockner and Shortreed relationships respectively. In this regard Schindler et al. (1978) indicated that more chlorophyll was produced per unit P in the Experimental Lakes Area (ELA) than in other lakes. This is probably because all the P added to the ELA lakes was PO_4-P, while in other lakes a high proportion of P inputs was almost certainly not biologically available.

The relationship between average annual chl-*a* concentration and average TP concentration could be of practical value for controlling eutrophication in the Vaal River. Reducing water fertility, preferably by controlling P, which appears to be the key element limiting primary productivity, is generally regarded to be the most desirable eutrophication control strategy (e.g. Schindler et al., 1978; Smith, 1982; Riley and Prepas, 1985; Lukatelich and McComb, 1986; Nicholls and Hopkins, 1993). Equation 2 suggests that eutrophication of the middle Vaal River may be alleviated or reversed by reducing the average TP concentration in the river, i.e. 0.23 μg chl-*a*$\cdot \ell^{-1}$ per μg TP$\cdot \ell^{-1}$. Nicholls and Hopkins (1993) showed that declines in phytoplankton biomass in Lake Erie's western basin averaging about 5% per year over the period 1970 to 1985 were related to decreased TP loading to the western basin of about the same magnitude.

Several investigations have shown that the summer chl-*a* concentration in lakes is closely correlated with the TP concentration at spring overturn (Sakamoto, 1966; Riley and Prepas, 1985; Stockner and Shortreed, 1985). Lukatelich and McComb (1986) showed, in the Peel-Harvey estuary system, that the magnitude of a *Nodularia* sp. bloom depended on the amount of P entering the system in winter, but the two events were separated in time by some 2 to 4 months.

Figure 6 (Eq. (3)) suggests that the magnitude of the winter-spring bloom in the Vaal River is possibly determined by the amount of nutrients (especially TP) entering the river during the preceding summer floods. The difference in slope between the predicted yield in the Vaal River and that for stratified lakes, indicates lower chl-*a* yield for high TP concentrations in the Vaal River (1988 and 1989) suggesting that a lower proportion of TP was biologically available or utilised. Hoyer and Jones (1983), among others, have shown, for a given concentration of TP, that the chl-*a* yield is reduced in comparison with non-turbid waters.

Phytoplankton and TN:TP ratios

The chl-*a* concentration in the Vaal River was positively correlated with the TN:TP ratio. Downing and McCauley (1992) have shown that algal biomass is nearly uncorrelated with TN:TP at low TP, but steeply and positively correlated with TN:TP at high TP.

Several investigators have used N to P ratios to indicate which of these essential nutrients potentially limits production. Sakamoto (1966) concluded that chlorophyll yield (in Japanese lakes) was possibly dependent only on TN when TN:TP was less than 10, and only on TP when the TN:TP ratio was greater than 17. However, Hoyer and Jones (1983) indicated that in Midwest reservoirs (Missouri) with TN:TP less than 10, nitrogen accounted for the same amount of variance in chl-*a* as did P.

The average TN:TP ratio of 11 in the Vaal River corresponded to typical eutrophic conditions (see Downing and McCauley, 1992). At this TN:TP ratio chlorophyll yield was possibly dependent on both TN and TP. The average DIN:DIP ratio of 57 suggests phosphate limitation in the Vaal River. High TN:TP ratios (> 18) were usually associated with higher chl-*a* concentrations (> 100 $\mu g \cdot \ell^{-1}$). This observation suggests that P may limit algal growth during high phytoplankton concentrations in the Vaal River. Lower TN:TP ratios during river floods i.e., higher concentrations of TP relative to TN were accompanied by a higher maximum chl-*a* concentration (Fig. 7; Eq. 4), stressing the importance of TP in affecting the upper limit of phytoplankton biomass during blooms.

Eutrophication of water bodies is often followed by significant shifts in phytoplankton composition towards blue-green algae (Steinberg and Hartmann, 1988; Downing and McCauley, 1992). In the Vaal River blue-green algal species occurred occasionally (Pieterse, 1986), but they did not reach high concentrations during the study period. Because the Vaal River is eutrophied and subjected to high loading of N and P (Roos and Pieterse, 1995a), the question arises why blue-green algal blooms have not occurred in the Vaal River during the present period of study. Several conditions in the Vaal River can be considered favourable to blue-green algal growth. For example, the high salinity in the Vaal River (av. = 512 $mg \cdot \ell^{-1}$; Roos and Pieterse, 1995b) could probably favour blue-green algal growth (Fogg et al., 1973). The relatively high pH of the Vaal River at Balkfontein (av. = 8.1; Roos and Pieterse, 1995a) could also be beneficial to blue-green algae which have various capabilities that enable them to thrive and outcompete eucaryotic algae at high pH and/or low carbon dioxide concentration (Shapiro, 1990).

The following information possibly shows that the key factor that determines blue-green algal dominance is the N:P ratio. It is generally accepted that the TN:TP ratio is an important determinant of the species composition of natural populations in lakes (see Takamura et al., 1992 for references). Studies showed shifts from green algae and diatoms to blue-green algae as the TN:TP ratio in the lakes decreased (Schindler, 1977), and vice versa (Smith, 1982). Recently, in Hartbeespoort Dam (South Africa), the absence of the *Microcystis aeruginosa* during 1988/89 was ascribed to the low epilimnetic phosphate concentration and the increasing N:P ratios, i.e. from about 4 to 10 (Chutter, 1989).

It is clear from the above discussion that low TN:TP or inorganic N:P ratios are most probably associated with the stimulation of blue-green algal growth. The average inorganic N:P ratio in the Vaal River was 57 (Roos and Pieterse, 1995a), a value that is apparently too high to favour a blue-green algal bloom. However, the average TN:TP ratio was 11, which possibly indicates more favourable conditions for blue-green algal growth, but the probability that blue-greens will occur at this ratio is evidently less than 50% (Harris, 1986). Downing and McCauley (1992) showed that TN:TP is high in oligotrophic lakes and very low in eutrophic lakes, declining in a curvilinear fashion with increased TP. Therefore, increased TP concentration in the Vaal River (with a resultant decrease in TN:TP to less than five), will most probably cause a shift in the algal assemblages from diatom and greens to one dominated by blue-green algae. Under the low TN:TP conditions N limitation would probably occur because low TN:TP only exists at high TP in aquatic systems, which in itself suggests that N limitation is greatest at high TP (Downing and McCauley, 1992). Recently, cyanobacteria became important in the Vaal River. The frequency of blooms of *Oscillatoria simplicissima* (a cyanobacterium), which is associated with low N:P ratios (unpublished data), is increasing in the Vaal Barrage.

Phytoplankton and silicon

According to Cushing and Dickson (1976), aquatic plants and plants in general are integrators of environmental variables and they respond to changes in environmental factors with a certain lag period occurring between the environmental stimulation and its response. Descy et al. (1987) showed that in the River Meuse, the phytoplankton growth phase began in spring and maxima were reached during the summer period, i.e. approximately three months later. An example of this kind of time-lag in the Vaal River can be seen in the illustrated inverse relationship between silica and chl-*a* concentration (Fig. 9). High silica concentrations were usually followed, after several weeks, by an increase in phytoplankton biomass. This observation corresponds with those in other investigations that showed sharp decreases in silicon concentrations during diatom blooms (Lund, 1964; Lack et al., 1978; Lukatelich and McComb, 1986; Descy et al., 1987).

Harris (1986) indicated that the spring diatom bloom in freshwater may be terminated in several ways, but a combination of grazing, Si depletion, thermal stratification and sedimentation usually ended the bloom. The classical work of Lund (1964) in Lake Windermere, England, also showed spring diatom blooms, while the subsequent decline of the diatom populations was attributed to the exhaustion of dissolved silica. In the Vaal River Si depletion is most likely terminating diatom blooms because Si concentrations during spring diatom blooms in the Vaal River reached levels likely to limit growth, i.e. concentrations usually declined to below 0.5 $mg \cdot \ell^{-1}$ during the diatom bloom period (Fig. 9). The development of certain diatom populations is limited, at least partially, by concentrations from 0.5 to 0.8 mg $SiO_2 \cdot \ell^{-1}$ (Reid and Wood, 1976). Silicon, decreasing from 3 to 0.5 $mg \cdot \ell^{-1}$, was believed to have played a major role in limiting the *Asterionella formosa* bloom in Lake Windermere (Lund, 1964).

Phytoplankton and discharge

Egborge (1974) concluded that seasonal variation in abundance of phytoplankton of the River Oshun, like many West African rivers, was primarily influenced by changes in the physico-chemical properties of the water which themselves were determined by the abundance and distribution of rainfall. The apparent insensitivity of phytoplankton biomass to discharges at Balkfontein, suggested by the low inverse correlation coefficient (r = -0.33), could possibly be ascribed to the numerous weirs in the middle Vaal River that in essence decrease the flow velocity and increase the residence time, which counteracts the dilution of phytoplankton and permits the building up of high phytoplankton concentrations (cf. Lack, 1971; Reid and Wood, 1976; Petts, 1984; Ertl, 1985). The weak correlation could also be ascribed to regulated releases (discharges) from the Barrage of water with relatively high chl-*a* concentrations.

However, the major impact of flood waters on Vaal River phytoplankton was clearly illustrated in this study (especially the floods during March 1988 and February 1989), which can be summarised as follows: The floods almost completely removed phytoplankton populations (chl-*a* concentrations were reduced to less than 18 $\mu g \cdot \ell^{-1}$; Figs. 2 and 4) which resulted, in turn, in higher total suspended solids (Roos and Pieterse, 1994). The increased silt-load reduced light penetration and thus the underwater light climate, so that low areal photosynthetic rates prevailed (Roos, 1992). Total phosphorus (TP) and nitrogen (TN) were increased to peak concentrations during the flood which were approximately 6 times (for TP) and 3.5 times (for TN) higher than the average for the previous two years (Roos and Pieterse, 1995a), and which resulted in a very low TN:TP ratio (see Fig. 7). These high TP and TN concentrations evidently served as an important source (and reserve pool) of nutrients that stimulated subsequent algal growth. Silica concentration also increased because of the high silt load as well as the high water temperatures (Roos and Pieterse, 1995a). Thus, as far as the nutrients are concerned, potentially favourable conditions for algal growth were created during the floods. Although nutrients were present in high concentrations in the Vaal River during and after the floods, the phytoplankton could not attain maximum productivity because light penetration was restricted by the turbidity of the water (Roos and Pieterse, 1994). The weeks following the flood were typified by low discharge, an increase in salinity and decreased turbidity (increase in water transparency) via settling of particulate matter and flocculation caused by high salinity (Roos and Pieterse, 1995b). Suspended silt was gradually depleted in the river, thereby lifting the light limitation and permitting a vigorous bloom of phytoplankton initially dominated by diatoms. Thus, within approximately four to eight weeks after the floods a winter diatom bloom developed, which was followed by a bloom of green algae (Fig. 4). The diatom blooms appeared to collapse once silicon was exhausted and the green algal bloom collapsed once P, and possibly nitrogen, were exhausted.

Depending upon the intensity of the spring diatom bloom and the concurrent removal of nutrients during the development of the bloom, fewer nutrients are available for a subsequent green algal pulse. After periods of intensive flooding (in 1988 and 1989), the available nutrient levels following on the diatom bloom, were sufficient to allow the development of intensive green algal blooms (Figs. 2 and 4). It is clear that, while physical factors may limit growth rates under particular conditions, the addition of nutrients to the Vaal River is all that has been required to lead to an increase in phytoplankton biomass.

The phytoplankton concentration in the Vaal River between 1985 and 1987 (years of low discharge and reduced nutrient input), was significantly lower than the concentrations following the 1988 and 1989 floods (Fig. 2). The higher chlorophyll maxima during the wet period (1988 to 1989, Figs. 2 and 4) supported Goldman's (1988) conclusion that years of heavy precipitation and runoff corresponded with years of elevated primary productivity in Lake Tahoe. Lukatelich and McComb (1986) also reported that *Nodularia spumigena* blooms (blue-green) in the Peel-Harvey estuary system (Australia) were particularly intensive during years when there had been relatively large river flows. The increased chlorophyll concentrations and the advancement of the spring bloom in the Vaal River during the wet period can probably be ascribed to a nutrient stimulus (especially by N and P inputs) caused by flood discharge (Roos and Pieterse, 1995a). Billen et al. (1994) also showed that the time of the onset of spring algal blooms in rivers is mainly controlled by hydrology.

Phytoplankton and temperature

The behaviour and properties of natural populations usually depend on dynamic equilibrium between several processes which are affected to differing extents by temperature changes. The complexity of interactions usually makes it difficult to predict from observations under controlled conditions on individual components what the effect of variation in temperature will be on the composition and properties of the assemblages. However, temperature is a significant factor influencing the growth rates of various types of algae (Raymont, 1980). Little data are available to verify the supposition that algae grow faster at higher temperatures in rivers (Reynolds, 1992).

The inverse relationship demonstrated in the Vaal River between temperature and chl-*a* is in contrast to most South African impoundments where the maximum chl-*a* concentration coincides with high water temperature (Walmsley, 1984). The highest frequency of maxima was in January. The stimulation of algal growth by increased temperature in the Vaal River was probably obscured by the impact of high nutrient levels after the floods and subsequent improved light availability, as well as the ability of diatoms to maintain high growth rates at low temperatures. Dominance by diatoms during blooms is often restricted to periods when the temperature is low (less than 15°C), i.e. during the winter-spring period (Løvstad and Bjørndalen, 1990).

The seasonality of phytoplankton biomass in South African impoundments is different from that of the Vaal River because, normally, some degree of stratification of the water is necessary to reduce the passage of algal cells from the relatively shallow photosynthetic zone to the aphotic zone (Grobbelaar, 1985). In many lakes and estuaries phytoplankton productivity and biomass increased during summer stratification when the mixed surface layer was shallow, and exposure of the phytoplankton to irradiance increased (Cloern, 1987). Even in a clear but deep lake like Lake Constance, Sommer (1985) indicated that mass growth of algae cannot start before thermal stratification begins, because only a warmer surface layer can keep cells in the photic zone.

Seasonal development of assemblages which can be predicted on a basis of dynamic changes in environmental variables occurs. However, much more data are needed before a PEG-model (Plankton Ecology Group; see Sommer et al., 1986) can be compiled for the Vaal River. The PEG-model consists of detailed sequential statements which describe detailed seasonal events that occur in the plankton of fresh water. Results from the present study support the view of Harris (1986) who stated that phytoplankton are integrating machines that trace environmental fluctuations and are adapted to growth in fluctuating environments.

Acknowledgements

The authors are grateful to the Water Research Commission and the University of the Orange Free State for financial support for a research programme on the ecology of the Vaal River. The Department of Water Affairs and Forestry provided chemical data, and Mrs AR Schmid assisted during observations in the field as well as with laboratory analyses.

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