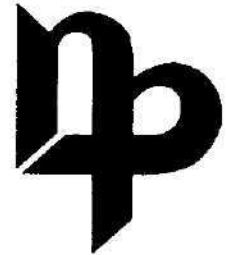


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Limnology of Lake Midmar

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C.M. Breen

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PREFACE

South Africa does not have abundant water resources and provision of water for urban and industrial growth has required not only the construction of numerous impoundments, but also the transfer of water from one catchment to another. All major rivers will soon be regulated to the extent that little, if any, of the natural flow will reach the sea. With such dependence on stored water, and with ever increasing return of effluent to river systems, there is a growing need for the development of guidelines for the management of man-made lakes.

The Committee for Inland Water Ecosystems of the National Programme for Environmental Sciences recognised that management should be based on an understanding of the fundamental aspects of the functioning of man-made lakes. Funds made available by the Department of Environment Affairs, the Water Research Commission and the CSIR made possible the development of a research programme directed at the variety of conditions encountered in South African impoundments: relatively clear and unproductive (Midmar), highly productive with excessive algal growths (Hartbeespoort) and two turbid silty systems (Wuras and Le Roux). This report presents a synthesis of the research findings of Lake Midmar.

Lake Midmar is a shallow turbulent lake subject to periodic draw-down. These conditions create considerable instability in the water column and greatly influence the structure and functioning of the system. Analysis of how the lake may be expected to respond to altered nutrient loading illustrates both the inherent limitations of currently available empirical predictive models, and the site specific nature of response. Thus the way in which nutrient load is estimated may alter the prediction from acceptable to unacceptable water quality, yet the lake is not highly productive. Application of general models is constrained by both the specific characteristics of the lake which appear to buffer response against changing nutrient load, and the relative insensitivity of the models. We are now at the stage where we know the limitations of currently available models and have a good idea as to why they exist, but have little alternative to offer. Exciting prospects exist for synthesis and critical analysis of the research on the four lakes (Hartbeespoort, Le Roux, Midmar and Wuras) but if we are to benefit fully, the synthesis must address specific goals. Those which seem important to us are:

the identification of the limnological responses affecting water quality which are of universal application. Some such as phosphorus load are well known whereas others may still require to be identified and quantified;

analysis of the importance of site specific factors in both the catchment and lake as modifiers of limnological response;

development of predictive models incorporating the interactions between the responses and site factors alluded to above;

assessment of how catchment processes, lake processes and water quality interact to influence optimization of multipurpose use of water resources.

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ABBREVIATIONS USED IN THE TEXT

Ad	Water abstracted from the lake
ALK	Alkalinity
AMAX	Light saturated rate of photosynthesis
AP	Ultimate available phosphorous
BAPP	Cumulative available phosphorus
B	Mean chlorophyll a within the euphotic zone
Chi a _l	Chlorophyll a
Colloidal - P	Phosphorus attached to colloids
COND	Conductivity
Dd	Discharged compensation water
DON	Dissolved organic nitrogen
EA	The integral hourly rate of photosynthesis per unit area
EEA	The integral daily rate of photosynthesis per unit area
Ed	Evaporation loss
Ec	Extinction of irradiance by dissolved matter
Ep	Extinction of irradiance by particulate matter
Et	Total irradiance extinction
Ew	Extinction of irradiance by water
kPAR	The attenuation coefficient of photosynthetically active radiation
F.S.L.	Full supply level
g	Acceleration due to gravity
I	Irradiance
I _o	Surface irradiance
I _z	Irradiance at depth z
k	Algal rate constant
KNF	Kjeldahl nitrogen on filtered water
KNU	Kjeldahl nitrogen on unfiltered water
L _d	Seepage water loss
In	Natural logarithm
Ml	Megalitre..
n	Number of samples
NH ₃ -N	Ammonia nitrogen
NO ₂ -N	Nitrite
NO ₃ -N	Nitrate nitrogen
p	Density of water
PAAP	Provisional algal assay medium
PAAP-N	Provisional algal assay medium without nitrogen
PAAP-P	Provisional algal assay medium without phosphorus
Pd	Direct precipitation loading
PO ₄ -P	Orthophosphate phosphorus
³² P	Radioactive phosphorus
³² PO ₄	Radioactive phosphorus as orthophosphate
r	Correlation coefficient
r ²	Coefficient of determination
Re	Total surface inflow from rivers
Ri	Richardson's number
s	Time in seconds
S	Stability of the water column

SBAP	Soluble biologically available phosphorus
Sd	Perimetral seepage inflow
SRP	Soluble reactive phosphorus
SS	Suspended solids
TDN	Total dissolved nitrogen
TDP	Total dissolved phosphorus
TDS	Total dissolved solids
TPU	Total phosphorus in unfiltered water
Total-P	Total phosphorus
t	Time elapsed
u	Velocity of water
ug/l	Microgram per litre
x	Mean
Z	Depth
Zeu	Depth of the euphotic zone
Zm	Depth of mixing

THE LIMNOLOGY OF LAKE MIDMAR

1. SUMMARY

Enrichment of aquatic systems with plant nutrients (eutrophication) is causally related to human activities and is therefore a world wide problem. The effects and symptoms of eutrophication in South Africa are well documented (Toerien, et al. 1975; Bruwer, 1979) and this has led to promulgation of legislation to control soluble reactive phosphorus concentration in sewage and other point source effluents discharged into major water supply rivers (Government Gazette, 1980; Kroger, 1981). The standard set is that the concentration of soluble reactive phosphorus (SRP) should not exceed 1 mg/l . The implications of this standard are however not fully understood, and the Committee for Inland Water Ecosystems (CIWE) of the Council for Scientific and Industrial Research (CSIR) initiated a study of four South African impoundments (Midmar, Wuras, Hartbeespoort and Le Roux) to provide the understanding required for planning and management. These impoundments reflect the variety of South African man-made lakes ranging from oligotrophic (Midmar) to hypertrophic (Hartbeespoort) and from relatively clear (Midmar) to very turbid (Wuras and Le Roux). The study of Lake Midmar therefore provides a useful basis for comparison with both turbid and eutrophic systems.

Water quality in the Mgeni river and its tributaries has recently been characterised by Kroger (1981). With the exception of the lower reaches where new impoundments (e.g. Inanda) may be expected to be eutrophic, the water quality is of a high standard. Kroger (1981) concluded, however, that current legislation (the 1 mg/l phosphorus standard) alone is 'unlikely to be effective in preventing eutrophication¹ and that additional solutions will have to be sought if acceptable water quality is to be maintained. This observation emphasises that whilst understanding the limnology of South African aquatic ecosystems will help in the search for solutions to water quality problems and will facilitate management, it is not a solution in itself because this can be achieved only by a holistic approach to watershed management.

Lake Midmar is a shallow (mean depth 11,1 m) well mixed water body receiving most of its water from agricultural catchments. It is used extensively, for recreation and as a supply of potable water for the Durban/Pietermaritzburg area. It is the highest-lying of the three dams on the Mgeni river (Midmar, Albert Falls and Nagle) and therefore has the greatest potential for management as a source of good quality water.

Water quality is largely determined by the relationship between nutrient load and hydrology of the lake and therefore each system is unique. Simple models have, however, been developed and their applicability to predicting the response of Lake Midmar to various management options is assessed in this report. The investigation has demonstrated clearly that current models are sensitive to error in the estimation of nutrient load. These errors which arise from inadequate data in both short-interval and long-interval sampling may prejudice prediction to the extent that, under prevailing conditions, the lake could be predicted to vary between oligotrophic and eutrophic, a situation which does not occur. Effort must therefore be directed at the development of sampling strategies for accurate load estimation in all South African systems, if we are to be able to confidently predict the consequences of various

management options. Although this study provides guidelines for obtaining a good estimate of the load, it was derived during unusually dry conditions and may not therefore be generally applicable. Load could be adequately estimated by daily sampling during summer and weekly sampling during winter.

The predictive models show that increasing demand for water which reduces the stored volume relative to the nutrient load will adversely affect water quality in Lake Midmar. This will be easily aggravated if point sources of nutrient loading, such as would arise with urban development in the catchment, are allowed to develop. These adverse effects on water quality will, however, be offset by the proposed introduction of good quality water from the Mooi river. More data are required before this effect can be accurately quantified.

The results show that raising the wall height to increase storage capacity, will not significantly affect the trophic status and water quality under present loading conditions. If, however, the nutrient load is allowed to double, which would still not represent a high load, serious water quality problems could arise. These are likely to be considerably more severe in a deeper lake with a more stable water level, than in the present shallow well mixed system which experiences considerable drawdown in most years. The best options for provision of additional stored water are the introduction of good quality water from the Mooi river or constructing another shallow impoundment. The consequences of introducing water from the Umkomaas river need to be examined.

The prevailing physical conditions in Lake Midmar facilitate management for good quality water because they create conditions which favour adsorption of phosphorus, the production rate limiting nutrient, thereby reducing its concentration in the water. Altering the physical conditions by raising the dam wall, will favour periodic development of an anoxic deep-water layer (hypolimnion) in which phosphorus release will be favoured. When the lake mixes, blooms of algae will develop and create water quality problems.

Lake Midmar is regarded as slightly turbid when compared with other South African man-made lakes. The turbidity is generated principally by shore-line erosion and resuspension within the lake and not by inflow of turbid water. Turbidity in Lake Midmar will therefore not be significantly reduced by impoundment construction upstream. Unlike the situation in the very turbid lakes (e. g. Wuras), turbidity in Lake Midmar can not be expected to significantly attenuate production by light limitation. In addition, since the sediment load in the water column is resuspended silt and not new silt entering the lake, it cannot be expected to have a long-term role in buffering the system against phosphorus enrichment by adsorption.

Good quality water with low algal production is compatible with high fish production only when the water levels are sufficiently stable to permit development of a littoral community of higher plants and large algae. The typically fluctuating water levels of Lake Midmar restrict this development and thus Lake Midmar does not, under current nutrient loading, support large fish populations.

This study has shown that Lake Midmar is naturally suited for management directed at the supply of good quality water. This objective provides

not only for the provision of potable water to a large part of the population of Natal, but also for recreation which has become such an important component of the multipurpose use of the upper Mgeni system.

Recommendations

This study has emphasised the value of good quality water in the upper Mgeni catchment and has demonstrated that natural processes in Lake Midmar favour management for good quality water. It is therefore recommended that:

- (i) Every effort should be made to protect the quality of the water in the upper Mgeni system.
This task would be facilitated by the appointment of a co-ordinating committee (River Authority) to ensure development is compatible with water quality objectives;
- (ii) More attention should be given to the development and application of predictive models;
- (iii) A comprehensive strategy should be developed for the estimation of phosphorus loads in rivers so that the data are available when predictions are required;
- (iv) Impact assessments should be prepared for all proposed developments. These should be initiated as soon as practicable;
- (v) A workshop be held to synthesise research and development information for the Mgeni river. The objectives should be to set goals and identify research needs.

2. INTRODUCTION

The Mgeni river system has particular significance in the Province of Natal because it is strategically positioned as the water supply for the Pietermaritzburg-Durban complex. Some 45 per cent of the population of the Province are dependent upon it for their water supply and it supports 20 per cent of the industrial output of the whole country (Town and Regional Planning Commission 1973). The number of people dependent upon the river is expected to reach 4 million persons by 1990 and the water supply of 1000 Ml/d from the three existing dams, Midmar, Alberts Falls and Nagle is expected to be fully utilized by 1984. Current critically low water levels which have developed gradually over a period of three years, emphasise the importance of both promoting more economical use of water and of increasing the amount of stored water.

The catchments of the Midmar and Albert Falls dams demand particular attention when planning for the provision of water to the Durban-Pietermaritzburg area because they produce three quarters of the run-off entering the Mgeni river. The high run-off from relatively small rural catchments yields water of good quality. Thus in the Upper Mgeni water quality is currently determined largely by input of nutrients from diffuse sources (Kroger 1981). The potential significance of the Howick and Mpopopheni urban developments as point sources of enrichment is controversial since it depends on projected growth rates, efficiency of effluent treatment, and the capacity of the river to 'recover'¹ after introduction of effluent. In this report therefore we are able only to examine the response of Lake Midmar to hypothetical situations such as may arise under conditions of altered hydrology and loading.

Four principal options for increasing the supply of stored water in the Mgeni river have been proposed:

- construction of a low level dam at Inanda;
- raising the wall of Midmar dam;
- introduction of water by pipeline from the Mooi river;
- introduction of water by pipeline from the Umkomaas river.

The last three of these options have direct implications for water stored in Lake Midmar and while raising the wall and diversion of the Umkomaas are still in the planning stage, the Mooi river pipeline is scheduled to become operational early in 1984.

It was originally proposed to conduct a comparative study of Midmar and Albert Falls lakes, two very similar impoundments (Figure 1, Table 1) receiving slightly different loadings. Such a study would have been valuable because predictions made on the basis of the Midmar study could have been validated by reference to the slightly enriched Albert Falls Lake. For various reasons and on the recommendation of the Evaluation Panel the comparative study did not materialise and thus the study reported here was confined to Lake Midmar.

The objective of the study was to gain an understanding of the Limnology of Lake Midmar with view to:

- developing a conceptual model reflecting loading, mixing, sediment-water interactions, light availability and the main energy pathways;

- developing an efficient sampling strategy for estimation of nutrient loading;
- validation of current eutrophication models with the Midmar data,
- provision of guidelines for assessment of the impact of development and management options.

Table 1 Selected limnological characteristics of Midmar and Albert Falls lakes.

MIDMAR		ALBERT FALLS	
1044 m	Altitude	656 m	
909 km ²	Catchment area	1,650 km ²	
177,2 x 10 ⁶ m ³	Volume at FSL	292,7 x 10 ⁶ m ³	
1560 ha	Surface area at FSL	2,484 ha	
23 m	Maximum depth at FSL	24 m	
11,4m	Mean depth at FSL	11,8m	
Shallow slope/clay	Shoreline type	Shallow slope/clay	
Low	Suspended solids	Low	
200 mg/JZ	Total dissolved solids	200 mg/SL	
Potable/angling/ boating	Utilization	Potable/angling boating	

3. DESCRIPTION OF THE UPPER MGENI CATCHMENT

The Mgeni and its tributaries the Lions, Karkloof and Umzinduzi provide the major water resource for the Durban-Pietermaritzburg complex (Figure 1). Midmar dam impounds water in the Mgeni and Lions river and outflow passes to the Albert Falls dam which also receives water from the Karkloof river. Discharge passes downstream to Nagle dam which is provided with a sedimentation weir and diversion canal which reduces sediment accumulation and nutrient loading (Kroger 1981). The Umzinduzi river is dammed above Pietermaritzburg (Henley dam) and joins the Mgeni below Nagle dam. The site of the proposed low-level Inanda dam is on this stretch of the river near Durban.

3.1 Physiography

The catchment lies within the Karroo System, the highlands comprising the shales, mudstones and sandstones of the Beaufort Series whilst the rest of the catchment, the mistbelt and uplands between 915 m and 1372 m consist of erodible soft sandstones and shales of the Ecca Beds (Figure 2). Typical of the Karroo System, the strata contain hard doleritic intrusions which have had a most beneficial effect in determining the bed slope of the river and account for the wide valleys above Midmar and Albert Falls, but have consequently also resulted in the impoundments being fairly shallow. The gradient between these two impoundments is steep (mean slope of approximately 11 metres per kilometre) resulting in an altitude differential of nearly 400 m over the 35 kilometres separating them.

Altitudinal variation over the upper Mgeni catchment has considerable implication in determination of the climate of the area. Rainfall varies between 750 mm and 1300 mm annually (Figure 3) being highest in the highlands where it has resulted in the formation of highly-leached yellow-brown soils which have low fertility, low erosion hazard and high phosphorus-retention potential. The uplands are moderately leached and more suitable for agriculture. As in most parts of South Africa, the rainfall is markedly seasonal with wet summers and dry winters. A consequence of this is that the impoundments on the Mgeni may, during dry periods, experience considerable draw-down (Figure 4). The high rainfall results in the Mgeni, together with its tributaries the Lions and Karkloof rivers, having one of the best run-off systems in the country.

Bioclimate

The highlands' biotic potential is essentially thickets with Montane *PODOCARPUS* forest. Much of the highlands is still covered by indigenous vegetation with only twenty per cent being arable. The mistbelt has a *PODOCARPUS* forest climax, but most is either cleared or degraded. The uplands contain the most suitable soils with a second-third class potential for intensive agriculture.

Urban development is a major consideration in the utilisation of these impoundments. By 1975 the total outlay of public funds on water

impoundment, extraction and purification at Midmar, Albert Falls and Nagle Dams amounted to 50 million rand and is expected to exceed R100 million towards the end of the century.

Current development of the Mpophomeni Township, will provide housing for 40 000 people immediately above Lake Midmar. The Albert Falls dam being at a lower altitude lies in a hotter area than Midmar and is downstream of both Mpophomeni and the Merrivale-Howick complex. It is estimated that Howick will gradually increase its discharge of sewage effluent to 1,36 Ml/d, in spite of the proposal to orientate development towards recreation instead of industry. With the development of recreation sewage effluent may be expected to increase markedly. This is illustrated by the numbers of people visiting Midmar dam: 34 000 in 1971 and 459 000 in the 1982/83 financial year. A report by the NIWR showed that even in 1967 there was a marked deterioration of water quality in the Mgeni river below Howick.

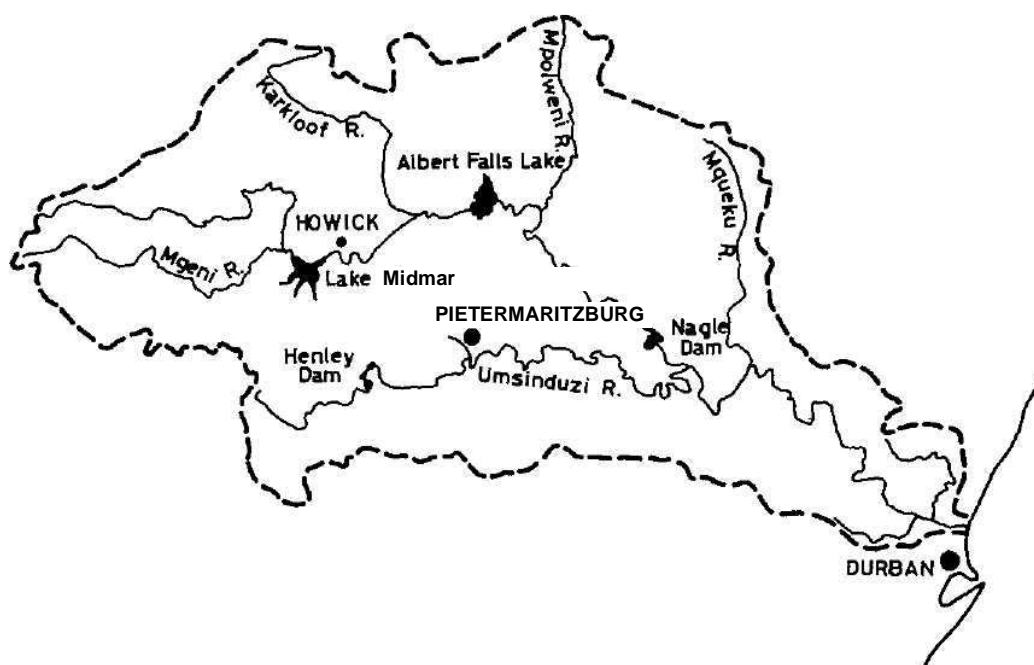


Figure 1 The Mgeni river catchment

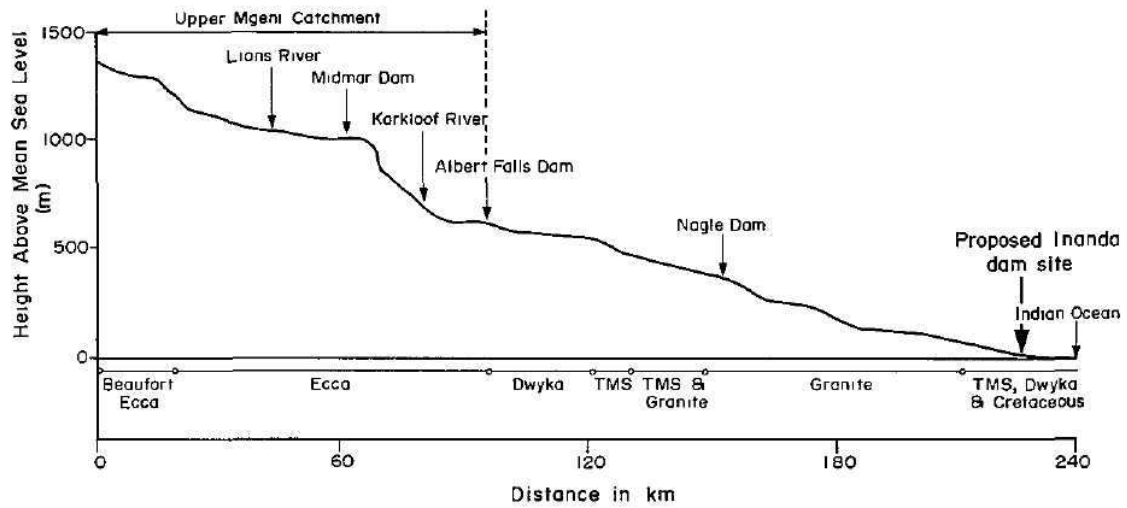


Figure 2 Profile of the Mgeni river showing the upper Mgeni catchment and the geological strata

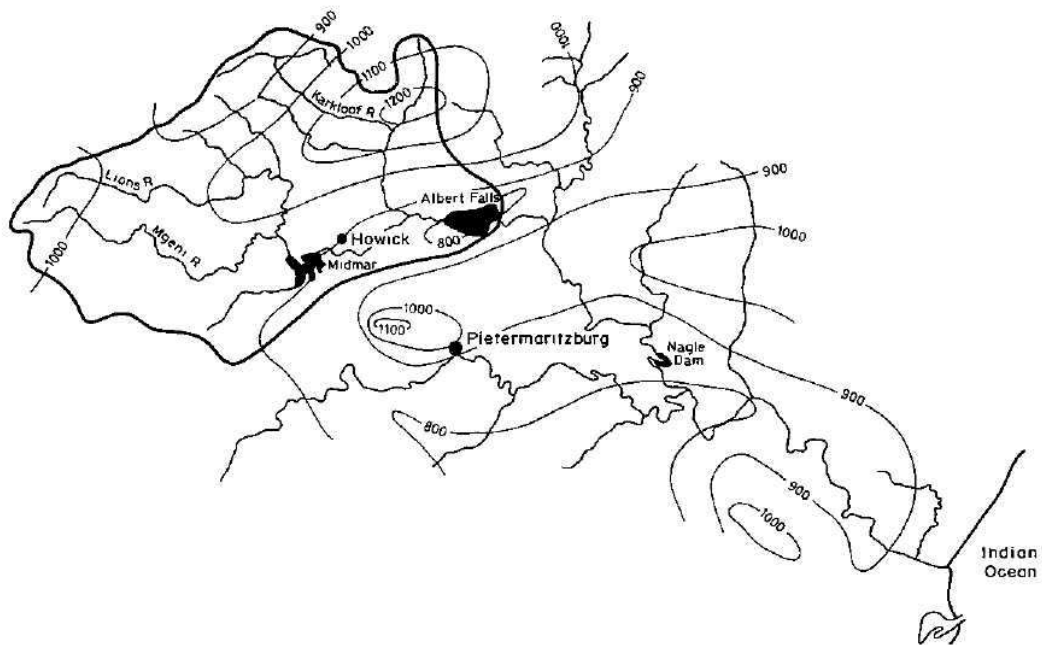


Figure 3 Rainfall in the Mgeni catchment

3.3 Recreation

Midmar dam was built between 1962 and 1965 at a cost of 4,5 million rand. The impoundment rapidly became a popular recreation centre and about 500 000 people - days are spent there each year. The Natal Parks Board have spent R1,5 million on capital expenditure associated with recreation during the past seven years and revenue has totalled R2,5 million during the same period (excluding costs of travel to and from the resort). The availability of Lake Midmar as a recreation centre has also contributed to the establishment of associated enterprises (e.g. Outdoor equipment retailers). This considerable investment in recreation should be safeguarded by protecting the water quality of the Upper Mgeni catchment.

3.4 Hydrology

It is well established that nutrient load is not directly proportional to flow and that in consequence, accurate estimation of load requires data on how concentration varies with flow. Since most predictive models are based on load, it is obviously desirable that it should be accurately estimated. The infrequency of gauging weirs and limitations in their design contribute to the difficulties of estimating load in the Mgeni, but within these constraints the importance of sampling frequency in load estimation could be investigated.

The response of the lake to nutrient loading is influenced by the hydrology of the lake, particularly the residence time. As residence time changes temporarily, according to long-term variations in rainfall and to changing demands on the stored water, the same load may elicit different responses at different times.

Within lake processes also modify the response of the lake to changes in nutrient loading and therefore provide opportunities for eutrophication management. In most in-lake management procedures the chemical conditions are modified through the indirect manipulation of the physical conditions e.g. destratification and hypolimnetic discharge. The relationships between hydrology, physical, chemical and biological conditions in the lake must be understood if lake management is to be effective.

4. PHYSICAL AND CHEMICAL LIMNOLOGY

4.1 THE PHYSICAL AND CHEMICAL ENVIRONMENT J.

Heeg

Introduction

The biological processes within a lake are ultimately expressions of the chemical and physical environment which the lake provides. The chemical environment is at least in part a reflection of conditions in the catchment, and is the final determinant of water quality in terms of plant nutrient availability, concentrations of undesirable substances and organic and inorganic pollution. Physical processes, imposed on the lake in the long term by climate and in the short term by weather fluctuations, have a marked effect on the biota, both directly through determining the hydroclimate and indirectly by governing the availability of nutrients, oxygen, etc. This study on the physical and chemical limnology of Lake Midmar was undertaken to define the physical and chemical environment and to establish its links with the fauna and flora and with meteorological conditions obtaining in the area.

The data presented here derive from continuous monitoring of meteorological parameters, weekly determinations of the hydroclimate and monthly chemical analyses of the dissolved solids in the water of the lake. The investigation covered the period October 1980 to December 1982, and data were collected from all five stations in the lake shown in Figure 4. Conclusions drawn from the data are based on all stations. Station 1, located in the main basin of the lake has been used as an illustrative example in all instances where generalizations are made, while supportive or comparative information from the other stations is included where pertinent. Where long term comparisons are of interest, data from Walmsley (1976) are included.

Temperature

The greatest biological activity in Lake Midmar, judged by primary production rates and zooplankton distributions, takes place in the top two metres of the water column. Temperatures here will, therefore, have the greatest impact on the biota. Figure 5 shows the fluctuations in mean temperature and temperature at one metre below the lake surface for the main basin over the period October 1980 to December 1982. Maximum temperatures are attained in November/December, and minima in July. The surface temperature range of 12°C lies between that for a 20 metre deep station on Hartbeespoort (12°C to 26°C) (Seaman 1977) and for Lake le Roux (11 °C to 23°C).

Stability of the lake

Temperature, together with the action of the wind, determines stratification and therefore stability of the lake, a major factor in the vertical distribution of substances in solution, suspensoids and non-motile organisms. Stability of the water column at any given point can be expressed in terms of the density gradient at that point which is, in turn, a function of the temperature gradient.

In this context:

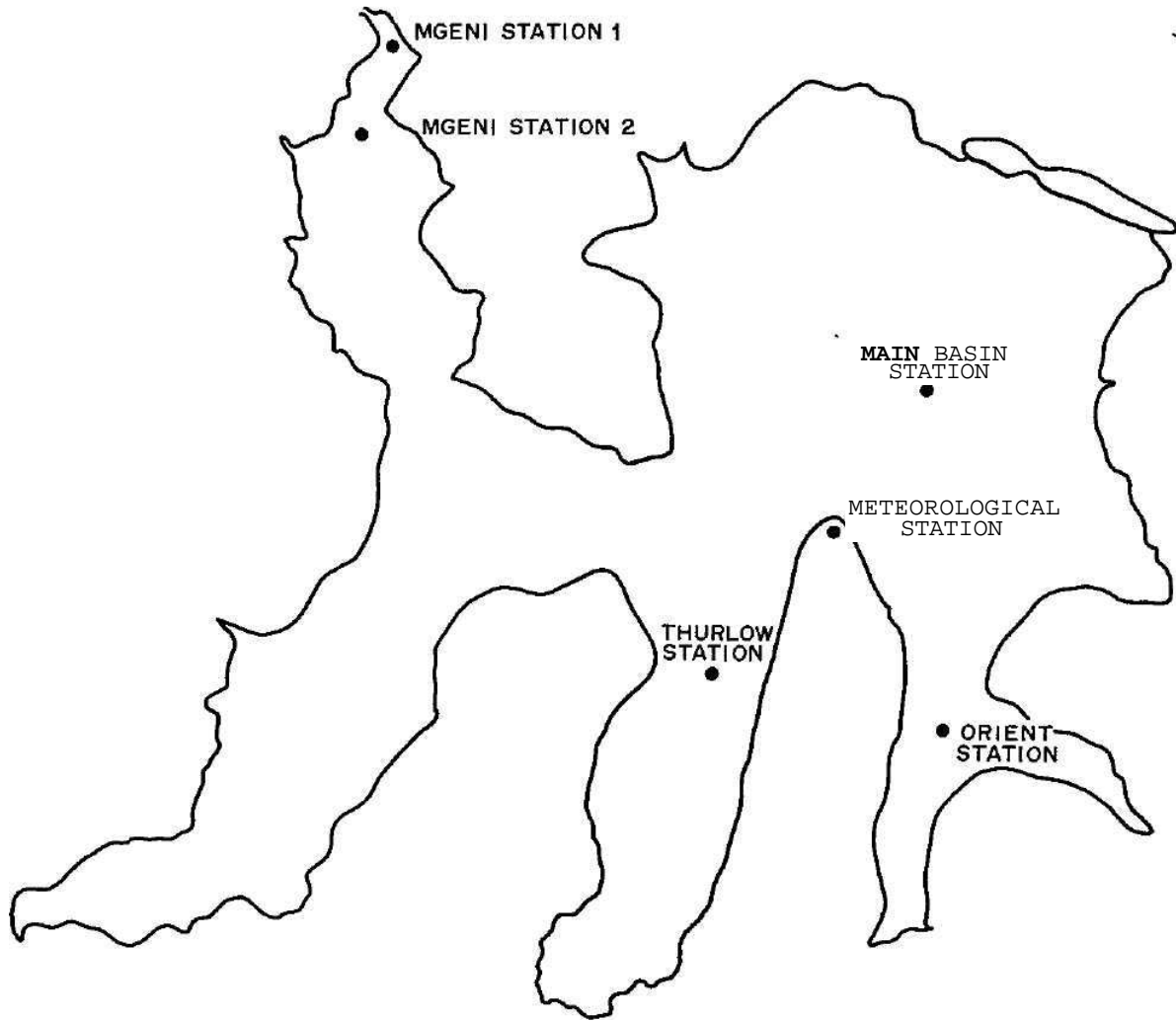


Figure 4 The location of sampling stations in Lake Midmar

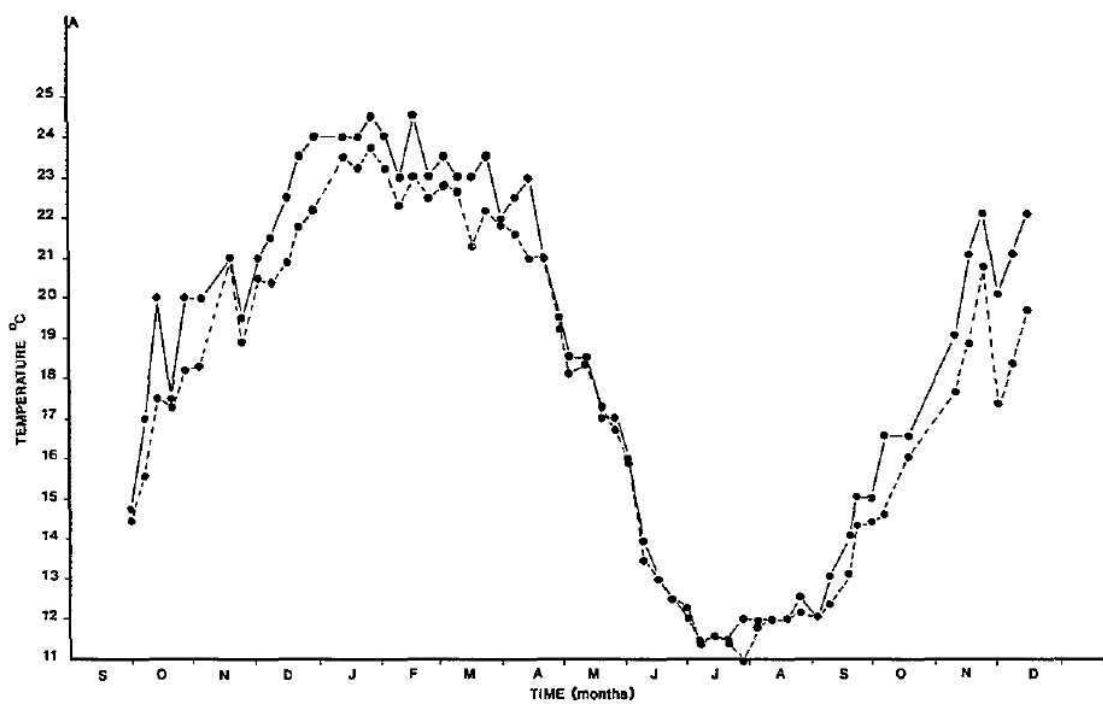
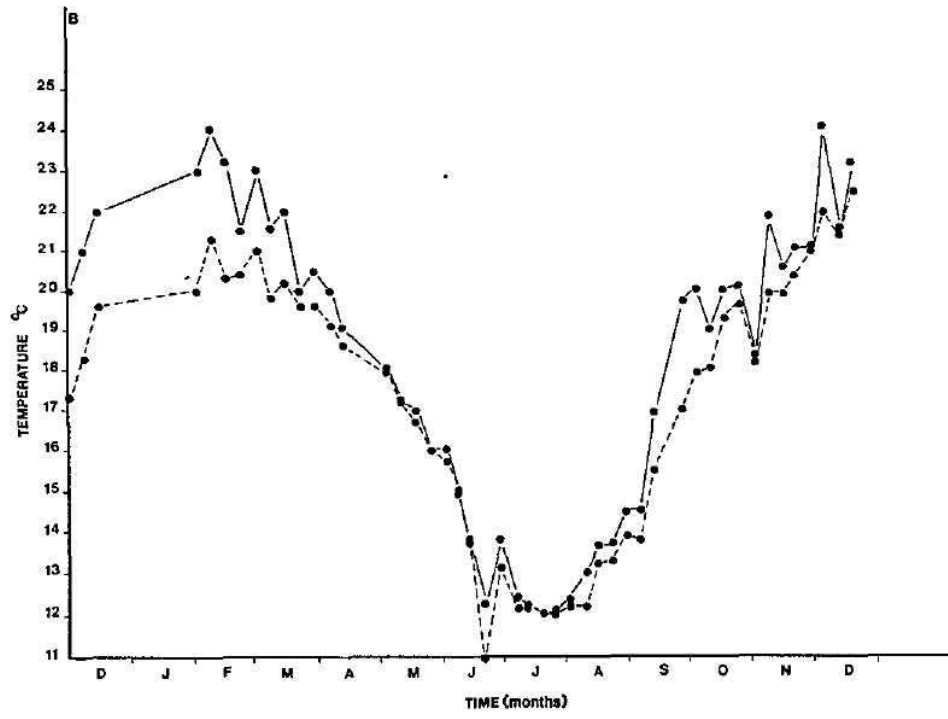


Figure 5A and B Fluctuation in mean temperature and temperature one metre below the surface

Stability of water column = $S = Cg/p - dp/dz$)

where g = acceleration due to gravity = 9.81 m/s^2
 p = density of the water in kg/m^3 , which is temperature dependent, and, z = depth of the water column in metres.

Negative stability may occur when the surface water is at a lower temperature than the bottom water, thus giving rise to convection currents.

Figure 6 shows the variations in stability of the water column at Main Basin Station during the period October 1980 to December 1982. Marked fluctuations in the stability of the lake occurred during the summer months when water temperatures were high and heat loss through reradiation and conduction were low, conditions which favoured the formation of density gradients through surface heating, and thus stratification. The stability fluctuations during these periods could only be attributed to the action of the wind setting up currents within the lake and thus leading to a breakdown of density gradients. During the winter months there was a considerable heat loss from the lake, due principally to low night temperatures and clear skies. Water temperatures were therefore low, and the density difference per degree difference in water temperature considerably reduced. These conditions lead to minimal stratification, stability and change in response to wind action. Frequent total mixing of the water column resulted during these periods, further enhanced by convection currents as the surface water of the lake cooled.

Meteorological events and stability

The stability parameter used to describe conditions in the lake is an integral part of Richardson's Number, a non-dimensional number which expresses the ratio between turbulence suppression and turbulence stimulation.

Richardson's Number = $Ri = \frac{tg/p - dp/dz}{(du/dz)^2} = \frac{S}{\text{Vertical velocity gradient}^2}$.

where u = velocity of the water in the shear plane.

The shearing stress in the water column results from the action of the wind on the surface. From the above it is clear that as Richardson's Number decreases, so the turbulence stimulation, and hence vertical water movement and mixing, becomes more prevalent. When Richardson's Number falls below 0.25 large rolling vortices and local "explosive" increases in vertical mixing result (Mortimer, pers. comm.) In the main basin of Lake Midmar, where the stability maximum was of the order of 0.001/s during the present investigation, this critical value would have been

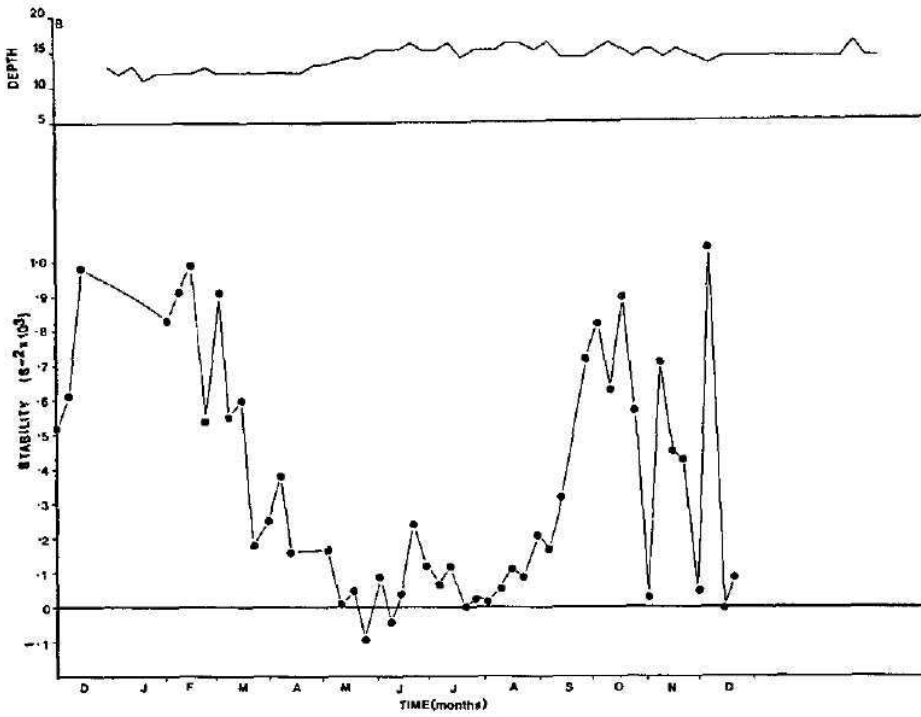
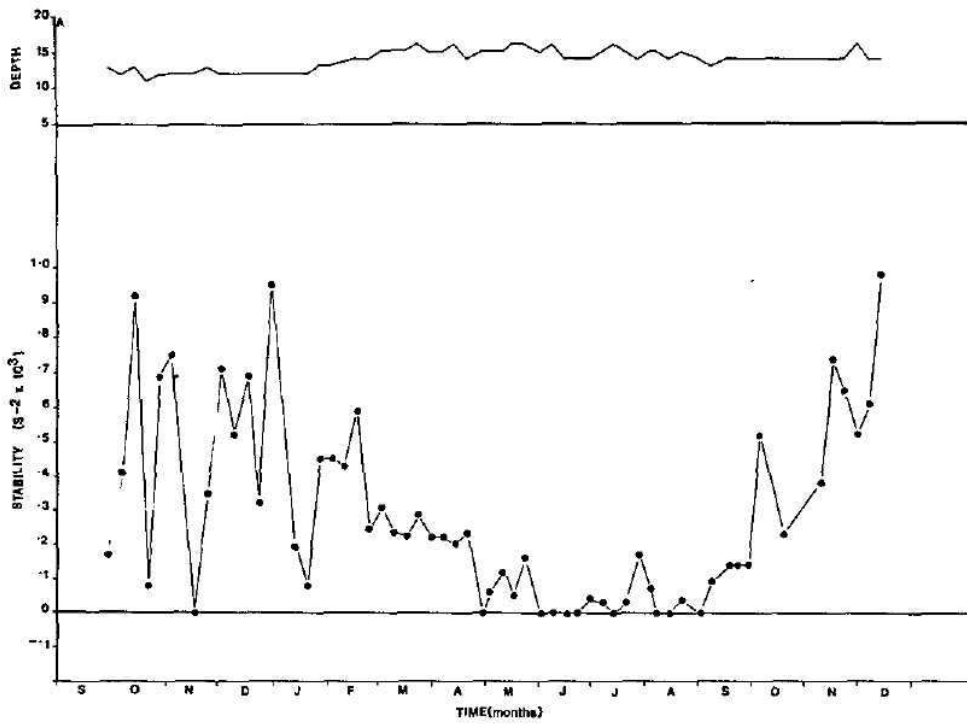


Figure 6A and B Variation in stability of the Main Basin Station

achieved by a velocity gradient of $-0,063/s$ over a 15 m water column. For stabilities around $0,0005/s^2$ the required velocity gradient falls to $-0,045/s^2$, while for the maximum of $0,0027/s^2$ recorded in Orient arm, a steeper gradient of $-0,104/s$ is needed.

A full analysis of the interaction between meteorological events and vertical transport requires the determination of current velocity profiles at various localities in the lake if it is to be founded on the theoretical basis considered above. Apparatus for such current measurements was not available during this investigation, therefore only empirical relationships could be established from the data collected. An extension of the applicability of these values is currently still under investigation.

The stabilities shown in Figure 6 were determined at weekly intervals, and each value therefore represents the product of the total weather conditions obtaining during the previous week. Changes in stability must consequently be seen as having been caused not only by wind velocity but also by the duration of wind action, since overcoming the inertia of the whole water column would not be instantaneous. Furthermore, successive days of moderate, sustained wind speeds over a period of several days may have the same effect as a single day of high wind velocity. Daily wind runs, rather than wind speed maxima, are therefore considered more appropriate for determining empirical relationships between the wind regime and vertical mixing. Analysis to date shows that a mean wind run of 185 km/d over a period of one week was sufficient to counter a change in stability. Mean weekly wind runs exceeding this value tended to reduce stability and therefore to break down any incipient stratification, whereas lower wind runs allowed stability to increase. In addition a wind run exceeding 250 km/d for any one day during a week reduced the stability by the end of that week, and when this value exceeded 300 km/d the whole water column was mixed.

The effect of water depth on water column stability can be seen by comparing Figure 7, the stability regime in Orient Arm, with Main Basin (Figure 6). The coefficients for the regression between change in the stability in Orient Arm and that in the Main Basin are 0,45 and 0,39 for positive and negative change respectively. The difference in depth between the two stations was 6 metres. An increase in depth of this magnitude therefore, reduced the effect of temperature increase by a factor of 0,45 giving rise to lower stability, but this was more than offset by a reduction in the effectiveness of the wind in breaking down the stability of the water column. The validity of extrapolation from these results to other depth changes is currently still under investigation, but there can be no doubt that any increase in storage will lead to greater and more stable summer stratification.

At the levels obtaining during the course of this investigation Lake Midmar had no permanent summer thermocline, wind action having been sufficient to counter stratification. Temperature, and therefore density, gradients existed, but these were never steep, and while bottom waters frequently showed a reduction in dissolved oxygen, anoxic conditions were never encountered.

The dissolved solids

Table 2 sets out the results of chemical analyses of Lake Midmar for the period October 1980 to December 1981, when, owing to the extremely

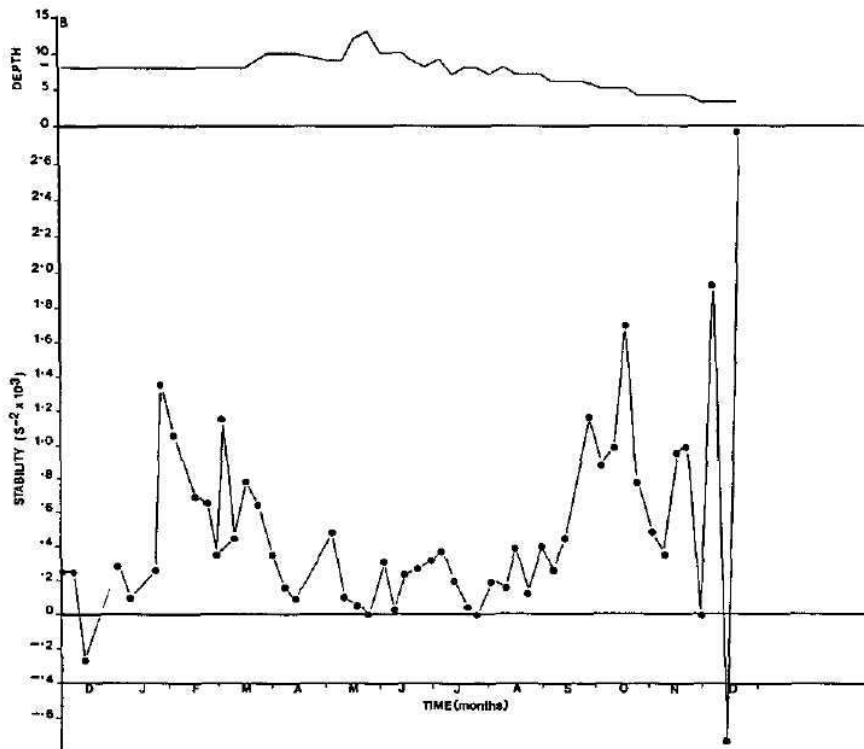
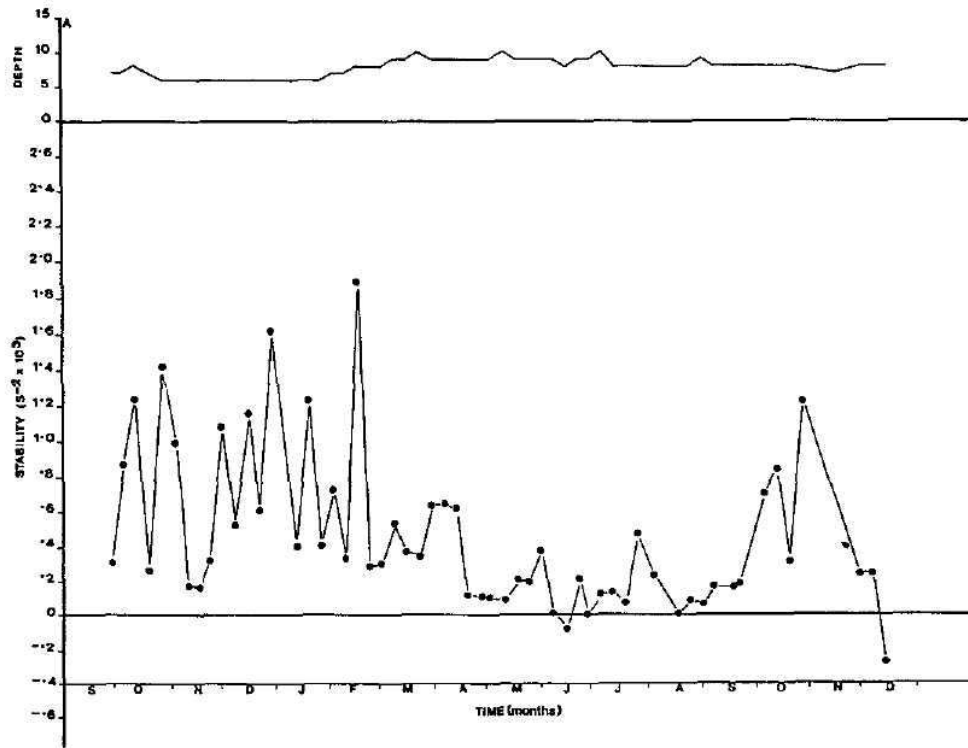


Figure 7A and B Variation in stability at the Orient Station

conservative nature of the dissolved solids composition, analyses were discontinued. Although variation coefficients are high for some components, it should be appreciated that, because of the very low concentrations, they reflect very small variations in absolute terms.

Table 2 Chemical composition of water from two depths of the Main Basin Station

Parameter	Position in water column					
	Top			Bottom		
	Mean	Standard error	Variation coefficient %	Mean	Standard error	Variation coefficient %
Calcium (mg/l)	3,68	0,10	22	3,77	0,10	22
Magnesium (")	3,86	0,11	23	3,83	0,13	29
Sodium (")	4,09	0,12	25	4,13	0,13	25
Potassium (")	1,23	0,03	23	1,28	0,03	22
Sulphate (")	0,63	0,07	26	0,68	0,10	32
Chloride (")	3,75	0,09	19	3,72	0,08	19
Bicarbonate (")	29,03	0,33	10	29,19	0,37	11
Silica as SiO ₂ (mg/l)	4,78	0,33	59	4,97	0,33	57
Nitrate ug/l	144	9,8	59	133	8,9	55
Phosphorus (total) ug/l	28	1,5	44	37	2,3	54
Phosphorus (SRP) ug/l	12	1,2	78	12	1,3	83
Total dissolved solids from conductivity (mg/l)	60	0,9	12	63	1,1	14

Changes in the chemical composition of Midmar water over the period 1973 to 1981 have been so slight as to be insignificant. Figure 8 compares the molar percentages of the dissolved solids as determined by Waimsley in 1973 with those for the present investigation.

The differences, when the very low concentrations of these ions are taken into account, are very small in absolute terms, and were largely attributable to the carbonate component and the divalent cations, calcium and magnesium, which are commonly associated with it. This component was the only one which showed major fluctuations with considerable increases following high inflows of river water. These increases were transient in nature, of short duration, and involved carbon dioxide/carbonic acid without materially affecting the bicarbonate concentration. The most likely source of carbon dioxide which would have coincided with high inflow rates was organic material carried in by the floods and decomposed in the lake. 1973/74 was a period of considerably greater inflow than that experienced during the present investigation and this could account for the differences in the carbonate complex.

Associated with the foregoing was the hydrogen ion concentration (pH). During the period under discussion the pH fluctuated within the range 7,5

to 8,2 with rapid drops to as low as 6,2 coinciding with the periods of carbon dioxide production. The normal range was one in which almost all carbon occurred as bicarbonate, and in which the buffer intensity was minimal, hence the dramatic drop in pH coincident with CO₂ production. Rayner (1982) reports surface pH values of 7,5 or lower for most of 1978. This may well reflect a more constant input of allochthonous organic material. Walmsley's (1976) figures for 1973/74 are in keeping with those of Rayner, but show consistently high carbon dioxide/carbonic acid values and consequently lower pH values for bottom waters. These results would be in keeping with more frequent and prolonged inflows during both 1973/74 and 1978/79 seasons. The general distribution of carbon in the lake during the period of the present investigation suggests that autochthonous carbon in the lake was normally in a state of dynamic equilibrium between the organic and inorganic state, as only periodic inputs of allochthonous carbon had a significant, though transient, effect on concentrations.

The extremely low values for both phosphorus and nitrate nitrogen are in keeping with Walmsley's figures for 1973/74. They represent 3% of the soluble reactive phosphorus and 8% of the nitrate nitrogen levels found in Hartbeespoort. The mean molecular ratio of nitrogen to phosphorus (SRP) is 5.5, compared with 17 in algal protoplasm, possibly indicating some nitrogen demand. The concentrations of these plant nutrients and their role in determining productivity will be discussed in greater detail elsewhere.

From this description of the physico-chemical limnology it is clear that water quality is of a high standard. The importance of physical and chemical processes as determinants of response of the lake, in general and of water quality in particular is discussed in subsequent sections of the report.

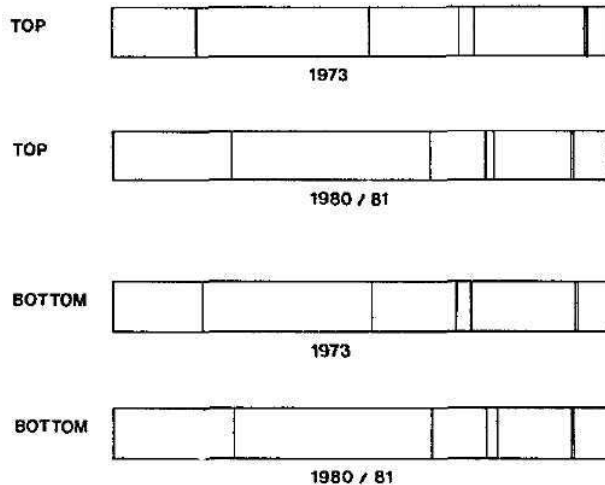


Figure 8 Molar percentages of the major cations and anions present in Lake Midmar during 1973 and 1980/81, illustrating the constancy in the composition of the dissolved solids. Blocks from left to right represent the molar percentages of Ca(OH)₂ , Mg(OH)₂ , NaOH, KOH, F⁻ CO₃²⁻ , H₂ SO₄²⁻ and HCl.

4.2 THE UNDERWATER LIGHT CLIMATE

E.G.J. Akhurst

Introduction

The metabolism and functioning of a lake ecosystem is dependent on solar radiation utilized during photosynthesis either directly in the lake, or indirectly in the catchment and exported as organic matter to the lake. In Lake Midmar fluctuating water levels have restricted the development of a littoral hydrophyte community so that the phytoplankton are the principal primary producers. The main factors influencing the rates of production by phytoplankton include temperature, the availability of nutrients, in particular nitrogen and phosphorus, and the 'underwater light climate'¹ which includes incident solar irradiance, underwater light attenuation and the relative proportions of illuminated and dark water within a mixed water column (Bindloss, 1976).

Solar irradiance incident on a lake surface is influenced by latitude, altitude, time of year and surface losses as a result of reflection. Within the water column the incident irradiance is reduced (attenuated) with depth as a result of both scattering and absorption. Thus the irradiance, I_z , at depth z is a function of the surface intensity (I_0) to the log base of the negative extinction coefficient (E) at the depth z , in metres (Wetzel, 1976): $I_z = I_0 e^{-Ez}$. Within a lake the natural total extinction coefficient (E_t) is influenced by the water itself (E_w), absorption by suspended particles (E_p) and dissolved compounds (E_c) in such a way that: $E_t = E_w + E_p + E_c$.

For a particular lake E_w is likely to remain a constant while E_p and E_c will be determined by processes within the catchment and lake itself. The influence of catchment processes will be seasonal since they are dependent on river flow which exports dissolved organic compounds and suspended material to the lake. Further, this influence is likely to show considerable variation between lakes with respect to the quantities and their subsequent role in determining the underwater light climate. Within the lake both the phytoplankton and inorganic particulate suspensoids, maintained in suspension by wind induced wave action, have the potential to influence E_t . The particulate suspensoids may originate directly from the resuspension of sediment material or from material generated by shore line erosion. The relative amounts of material resuspended from these sources will be dependent on the prevailing winds and features of the morphometry of a particular lake basin.

In systems where the attenuation of light with depth is rapid the euphotic zone, where the underwater light climate is suitable for phytoplankton growth, will be shallow. While some algae are able to regulate their position within the water column, for most their physical movement into and out of the euphotic zone is dependent on wind induced water movements. Where the euphotic zone is shallow both the rate of water movement and the ratio of the euphotic zone depth (Z_{eu}) to depth of mixing (Z_m) are critical in determining the time spent under favourable light conditions and hence in regulating algal periodicity and productivity (Tailing, 1971).

In this chapter the relative importance of suspended particles and

dissolved compounds in determining the pattern of light attenuation measured in Lake Midmar and light as a factor regulating phytoplankton productivity will be discussed. In addition, the implications of changes in the underwater light climate for lake functioning will be assessed.

The underwater light climate

When primary productivity was measured, the attenuation of photosynthetically active radiation (PAR) was determined as kPAR, and during 1982 filters were used to measure the attenuation of blue, green and red light. The seasonal variation in the vertical attenuation coefficients and the mean vertical attenuation coefficients of the three filters used are presented in Figure 9 and Table 3 respectively.

Table 3 Mean vertical extinction coefficients for blue, green and red light during 1982

Wavelength at mid-point of filter nm	Mean vertical extinction coefficient ln units/m (Standard error)
443 Blue	2,71 (+ 0,11)
550 Green	1,63 (+ 0,07)
670 Red	1,33 (+ 0,05)

The rapid attenuation of blue light and lower attenuation coefficient for red light is characteristic of turbid waters (Ganf, 1974; Tailing, 1965), and in Table 4 it can be seen that, on the basis of secchi depth, a measure of water transparency, Lake Midmar occupies an intermediate position between the clear waters of Roodeplaat and the turbid water of Bridle Drift lakes.

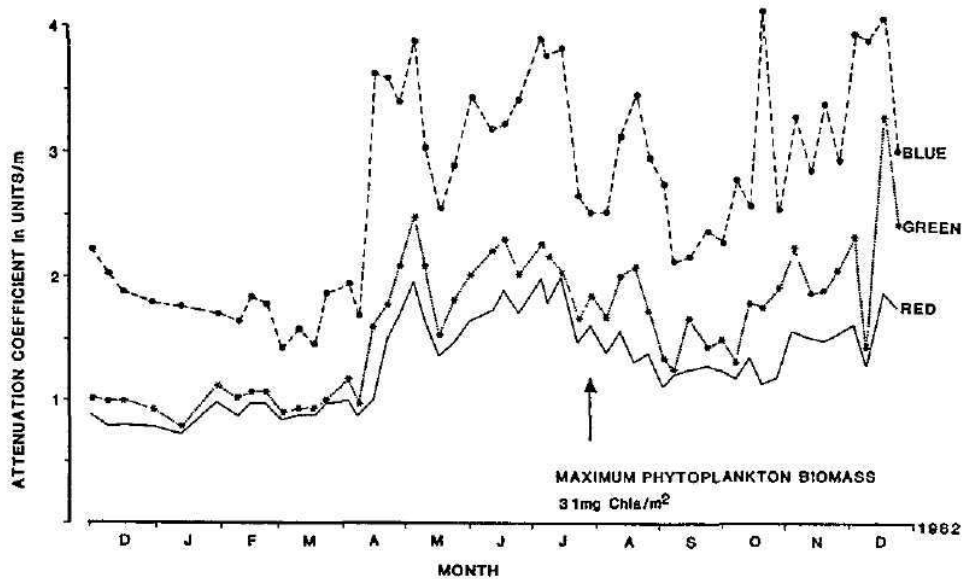


Figure 9 Seasonal variation in attenuation coefficients of red green and blue light

Table 4 Secchi depths for a range of South African impoundments
(from Walmsley and Butty, 1980 and Stegmann, 1982)

Impoundment	Secchi Depth (m)		
	Mean	Max	Min
Bridle Drift	0,1	0,15	0,07
Laing	0,17	0,45	0,04
Wuras	0,25	0,56	0,07
Nahoon	0,37	0,78	0,05
Bloemhof	0,66	1,05	0,32
Bospoort	0,75	2,0	0,2
Midmar	1,31	2,0	0,59
Buffelspoort	1,4	3,2	0,8
Rust der Winter	1,4	3,0	0,6
Nagle	2,5	4,37	0,9
Albert Falls	2,51	4,37	1,5
Rietvlei	2,92	4,85	1,1
Rodeplaat	3,49	8,8	1,0

In Figure 10 the absorption of light over the spectral range of PAR (400-700 nm) by dissolved organic compounds (filtered lake water) and suspended particles (unfiltered lake water) are compared. These results confirm the rapid attenuation of blue light shown earlier, and when the absorbance due to dissolved organic compounds and suspended particles is expressed as a percentage of the total absorbance it is clear that, while dissolved organic compounds contribute to the attenuation of light (30,2%), suspended particles (69,8%), inorganic and organic, dominate the attenuation of light in Lake Midmar. However, these results were obtained during 1983 when, as a consequence of the drought and lower water levels, Lake Midmar was more turbid (mean secchi depth 0,4 m) than during 1981 - 198'2 (mean secchi depth 1,0 m). Under less turbid conditions it would be expected that the absorbance due to dissolved organic compounds would be similar to that in Figure 10 (filtered lake water) whereas the absorbance due to suspended particles would decrease (unfiltered lake water, Figure 10). Therefore in partitioning the total absorbance into the absorbance due to dissolved organic compounds and suspended particles, it is clear that under less turbid conditions the differences between the absorbance due to dissolved organic compounds and

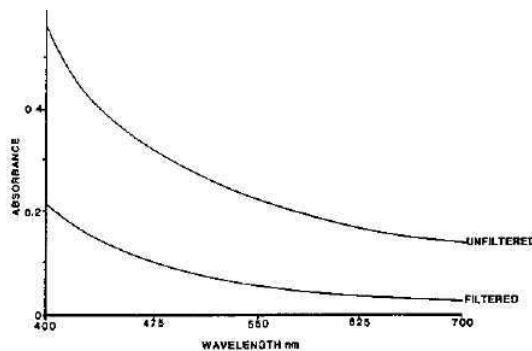


Figure 10 Absorption of light over the PAR range of wavelengths, 400 700 nm for filtered and unfiltered lake water, after correction for the absorption by distilled water.

suspended particles would not be as pronounced as that shown in Figure 10.

The suspended particles responsible for the rapid attenuation of light in Lake Midmar may be organic, as phytoplankton, or inorganic, as silt or resuspended sediment material. The role of phytoplankton in influencing light attenuation is secondary, since, even when the peak biomass (31 mg Chi a/m³ in the euphotic zone) was measured, the vertical attenuation coefficient for red light was lower than that of green light (Figure 9). In addition the relationship between kPAR and chlorophyll a. (mg Chi &/m³ in the euphotic zone) while significant is negative ($r = -0,62$, $F = 10$, $P > 0,01$ $n = 34$) which suggests that, while the phytoplankton do not contribute significantly to the attenuation of light, the size of the phytoplankton standing crop is influenced by the availability of light since standing crops are highest when lake is less turbid i.e. the attenuation of light is less rapid and kPAR low.

The relationship between the vertical attenuation coefficient (kPAR) and inorganic suspensoids (measured as turbidity in NTU) is linear ($r = 0,65$, $F = 11,7$ $P > 0,01$, $n = 34$) but the relationship is not as strong as that reported by Stegmann (1982) for the turbid waters of Wuras ($r = 0,94$, $n = 78$, also Table 4). In contrast in both Lake Me H.waine and Hartbeespoort Dam (Robarts, 1979 & 1982 respectively) phytoplankton are the major component accounting for the attenuation of light and green light had the lowest vertical attenuation coefficient. In the case of Hartbeespoort the relationship between the minimum attenuation coefficient and mean chlorophyll a[^] concentration in the euphotic zone while significant ($r = 0,72$, $n = 54$) was not particularly strong (Robarts, 1982).

Source of the inorganic suspended material

Since the observed turbidity in Lake Midmar is due to inorganic particulate suspended material it is necessary to determine the relative contributions of river borne suspended material and resuspended material generated within the lake. In Figure 11 it can be seen that the pattern of loading of total suspended solids entering Lake Midmar was markedly seasonal and highest during the summer months. Although detailed analysis of this material has not been made, there is evidence that a considerable proportion may be organic in nature (Chapter 3.1). If river borne suspended material was the dominant component then it would be anticipated that turbidity would increase and reach maximum values at times of high river flow during the summer period, November to March. Archibald, Warwick, Fowles, Muller & Butler (1980) have shown that this was not the case in Lake Midmar with turbidity being highest during the winter months. This has been confirmed by the present study where it can be shown that river inputs of suspended material do not have a significant influence on the light climate at the Main Basin Station (Figure 12) since the correlation between secchi depth and total suspended solids entering the lake was not significant ($r = 0,19$, $n = 95$).

These results support the view that suspended material generated within the lake through sediment resuspension and shore-line erosion is the primary cause of the turbidity within Lake Midmar. The contribution of shore-line erosion to inorganic particulate material has not been quantified. To investigate the movement of suspended particulate material within the lake sediment traps were placed at different depths

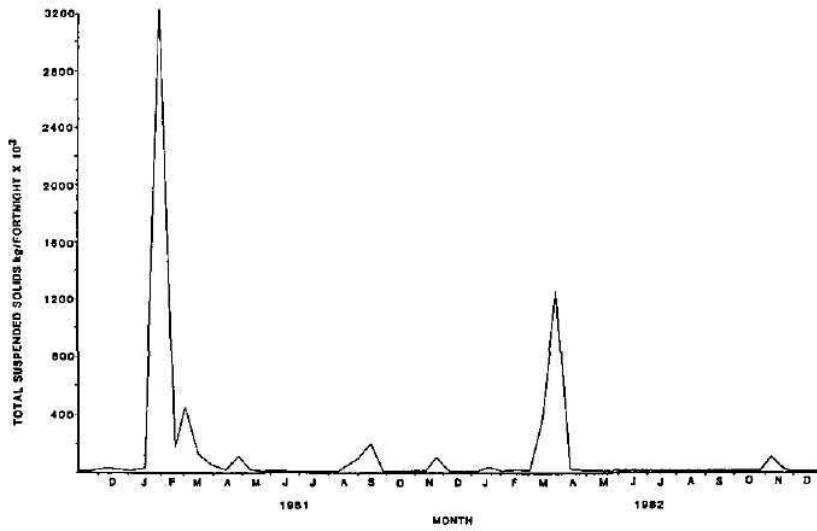


Figure 11 Seasonal variations in river loads of total suspended solids

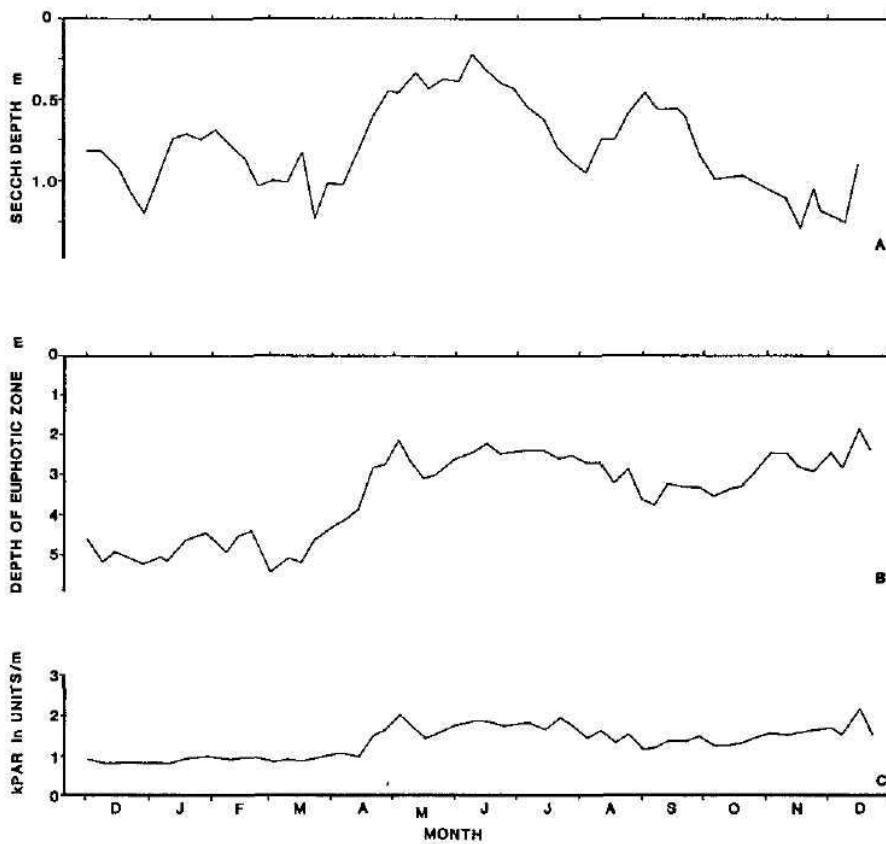


Figure 12 Seasonal variation in underwater light climate during 1982 at Main Basin

- 12A Secchi disc depth
- 12B Depth of Euphotic zone and
- 12C kPAR, extinction coefficient for photosynthetic active radiation

and stations in the lake during the period May 1980 - February 1981 (Data from I. Johnson). The results of this study are presented in Figures 13 and 14 where it can be seen that:

- i) there is a gradient in the amount of material maintained in suspension by wind induced wave action from the lake surface to the sediment surface (Figure 13) with the largest amounts of material being trapped near the sediment surface;
- ii) There are marked seasonal differences in the amounts of material collected.

In summer when the mean weekly wind velocities were generally higher most of the material was trapped just above the sediment surface (1 m), and the amount of material maintained in suspension in the water column was low, as can be seen in the catches from the other sediment traps (3 - 12 m above the sediment surface). In contrast in winter, when the mean weekly wind velocities were generally lower and more variable, the catches from all the sediment traps were higher. Thus the isothermal conditions that prevail in winter allow the water column to be more effectively mixed which increases turbidity. This accounts for the greater attenuation of light during the winter months.

- iii) On most occasions less material was trapped in the Mgeni inlet than at other sites in the lake (Figure 14) and it can be concluded that river borne material makes a relatively small contribution to the suspended material within the lake.
- iv) The spatial variation is not unexpected because the dendritic morphology of Lake Midmar increases compartmentalization within the lake so that the parts with extensive shallow regions below the water surface and with greatest fetch are most turbid.

It is concluded that the turbidity of Lake Midmar is largely attributable to inorganic particulate material derived from shoreline erosion and resuspension in the shallow zones.

The regulation of phytoplankton productivity by light

The euphotic zone in Lake Midmar, is shallow (mean depth Z_{eu} 3m, range 1,4 - 5,4 m) relative to the mean depth of the lake (11,1 m) and this has important implications for where the phytoplankton can photosynthesise, and the form of the productivity - depth profile. The profile, which does not take account of turbulent mixing, since it was measured with static incubation flasks, has both a horizontal and vertical component (Figure 15). The horizontal component relates to changes in rate of production with depth and is defined by the maximum rate of production (A_{max}) whereas the vertical component relates to the depth over which photosynthesis can occur and is defined by Z_{eu} . In this Chapter the influence of light attenuation with respect to the vertical component will be discussed and the relationship between light and the horizontal component will be considered in Chapter 4.3

The main effect of the rapid attenuation of light in Lake Midmar is to cause the productivity - depth profile to be compressed vertically with the result that only a fraction of the total lake volume is available as a favourable environment for algal growth. The full impact of turbidity

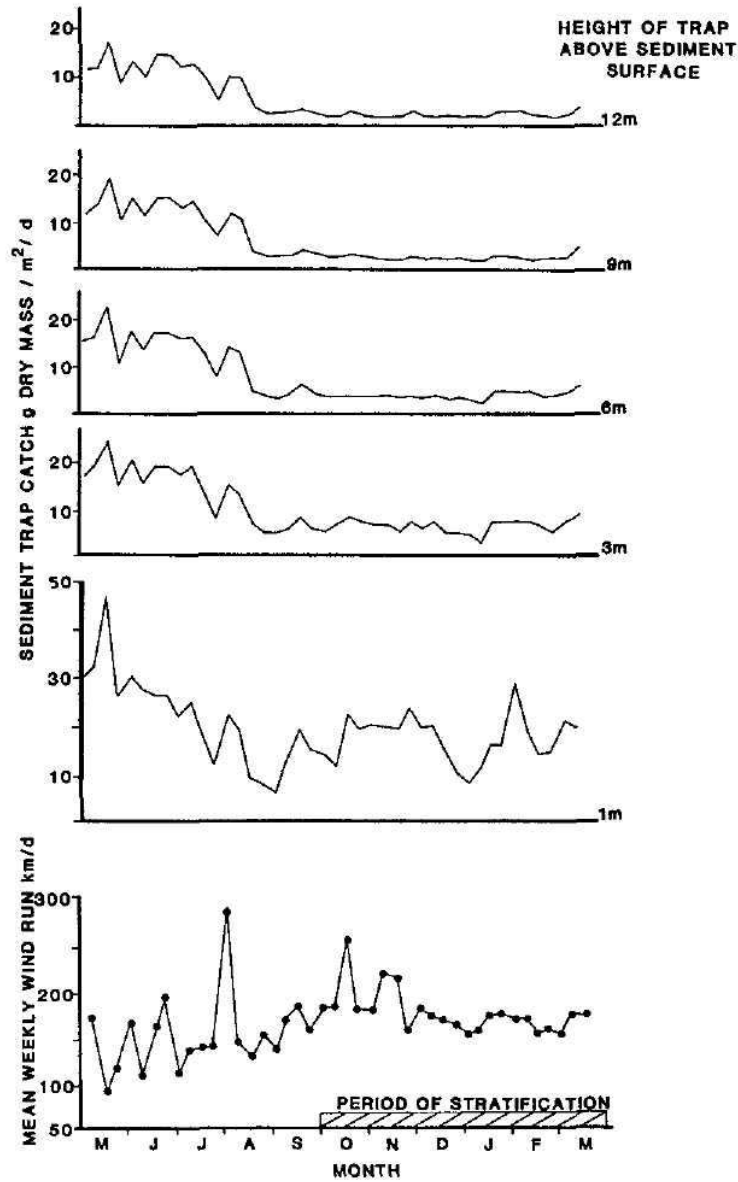


Figure 13 Variation in sediment trap catches with depth at Main Basin for the period May 1980 - March 1981

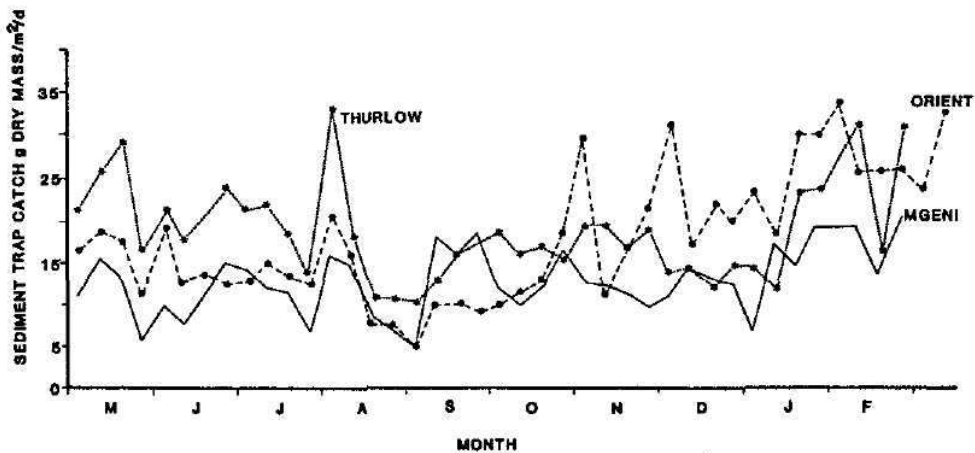


Figure 14 Sediment trap catches in different stations of Lake Midmar at ca 12m for the period May 1980 - February 1981

on the vertical component of the profile can, however, only be assessed once the effect of turbulent mixing within the water column has been considered. In Lake Midmar the prevailing winds exert a considerable influence on the physical properties of the lake (Chapter 3.1) as evidenced by the low stability values (mean 0,03 range - 0,09 to 1,04) and high values of Z_m , the mixing depth. If the approach of Reynolds, Wiseman, Godfrey and Butterwick (1983) is used, Z_m ranged between 0 m and 16,5 m, mean 11,8 m for the period 1981 - 1982 indicating that mixing is likely to be an important component of the physical environment, particularly when the mean depths of the euphotic zone (3m) and lake (11,1 m) are considered.

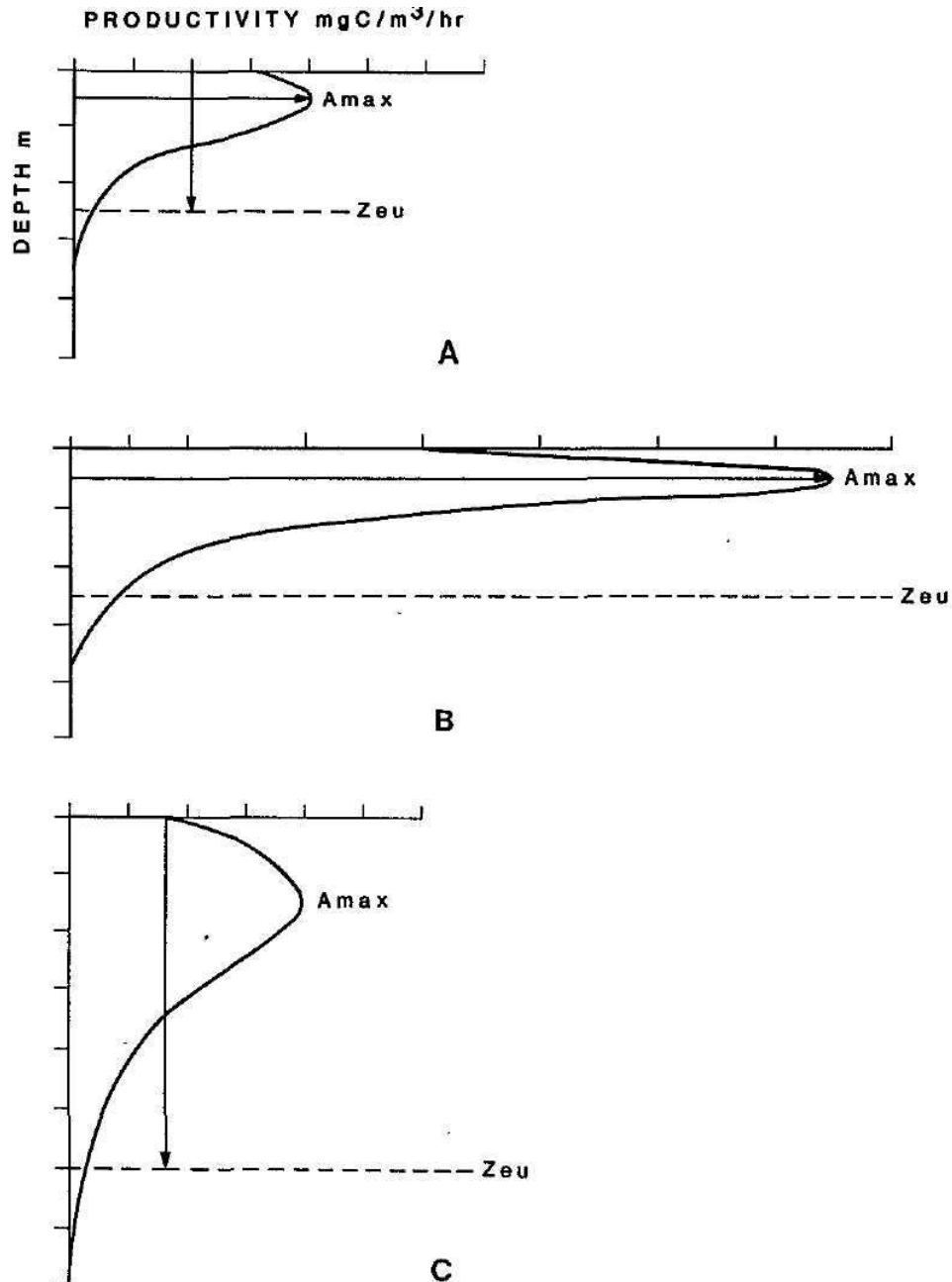


Figure 15A Generalized productivity depth profile
 15B Effect of changing A_{max} through nutrient enrichment
 15C Effect of changing Z_{eu} through reduction of suspended material.

The relationship Z_e/Z_m has been shown to be an important determinant of phytoplankton species composition and primary productivity in lakes (Talling, 1971 and Harris, Haffner and Piccinin, 1980). According to Reynolds and Walsby (1975) growth of bloom-forming species, such as MICROCYSTIS, is restricted to those lakes where the average values of Z_e/Z_m fall within the range 0,5-3,5. In Lake Midmar the value of Z_e/Z_m ranged between 0 and 4,6 (mean 0,33) during 1981 - 1982 and although the mean value is below that reported as favouring bloom-forming species, this was not always the case because it varied seasonally. Winter conditions, March - August were less favourable (mean 0,17; range 0-0,36) than during the summer months, September - February, (mean 0,43, range 0 - 4,6). The seasonal variation in Z_e/Z_m can be partly attributed to the changes in Z_e resulting from increased turbidity in winter, but it is also influenced by the pattern of mixing. The isothermal conditions prevailing in winter, facilitate mixing over the whole water column and values of Z_m are high (mean 14,1 m) whereas in summer mixing is less effective and values of Z_m are lower (mean 9,6 m). If the rate of circulation through Z_m is slow, i.e. one cycle per daylight period then, using the mean value of Z_e/Z_m (0,33), the algae will spend only 33% of their time under conditions where the light climate is favourable for photosynthesis. The pattern of mixing is therefore an important concept when considering the extent to which light climate limits primary productivity, and it is discussed in Chapter 4.3

Response to changes in the underwater light climate

From a management point of view Lake Midmar is an important source of high quality water and it will play an increasingly important role because of the urban development that is adversely affecting water quality in the lower Mgeni. The current drought has highlighted the need to increase the storage capacity of Lake Midmar in an effort to buffer the effects of future droughts and to meet the increased demand for high quality water that is expected in the near future. In addition, inter-basin transfer of water is presently planned to supplement the flow of the Mgeni to meet present and future demands. Algae increase the costs of producing high quality water and it is therefore necessary to assess the extent to which the proposed developments outlined above will affect the underwater light climate and, indirectly, the response of the phytoplankton and the costs of water purification.

It has been shown earlier that the euphotic zone in Lake Midmar is shallow and influenced primarily by inorganic particulate suspended material generated within the lake. Further at present the ratio Z_e/Z_m is sufficiently low for conditions to be generally unfavourable for the development of algal blooms. It is therefore important that the present turbid conditions, should be maintained. Increasing the storage capacity of Lake Midmar by raising the level of the dam wall has implications for both Z_m and Z_e because the increase in the size of the lake would increase the fetch and wind-induced turbulence would increase Z_m . The associated increase in lake volume would, however, increase the stability of thermal stratification. If the summer stratification becomes more stable the resultant resistance to mixing would increase and the effects of increasing wind fetch on Z_m would be cancelled out. Thus, during summer the value of Z_m would be less than present values which would create conditions more favourable for bloom-forming algae. Because the shallow areas inundated at the heads of the different arms are

sources of resuspended material any change in their area relative to the rest of the impoundment will affect turbidity and hence Zeu. A more stable water column during the summer stratified period would counter this because more material would settle out below the thermocline from where it would not be resuspended into the euphotic zone.

Thus, the consequences of raising the dam wall would result primarily from changes in the pattern of summer stratification. The stronger and more persistent stratification would create an underwater light climate more favourable for algal blooms and reduce water quality. However, this effect will be ameliorated by the incorporation of new shores, still bearing a mantle of easily eroded material which will provide new sediment, for some years after raising the wall, in much the same way as has been the case up to the present time. Thus it is considered that raising the wall of Midmar dam will have little impact on the present underwater light climate.

An alternative approach to increase the storage capacity would be the construction of an upstream pre-impoundment the main impact of which would be to reduce the amounts of river borne suspended material entering Lake Midmar. This option has the advantage that present values of Zeu/Zm would be maintained as river borne suspended material is not the primary factor determining the turbidity.

The proposed inter-basin transfer of water from the Mooi to the Mgeni to augment present low river flows does not appear to pose any threat to the water quality of Lake Midmar. The catchment of the Mooi river is located in geological formations very similar to those found in the catchment of the Mgeni and thus there is little danger of flocculation of the suspended material within the lake as a result of changes in water chemistry.

Table 5 The effects of raising the wall of Midmar dam on the under-water light climate (Zeu) and mixing of the water column (Zm)

Impact of raising the dam wall	Influence relative to present mean values of Zm (11.8 m) Zeu (3.04 m) and ratio Zeu/Zm (0.25)			Conditions for bloom forming algae	Influence on water treatment costs
	Zm	Zeu	Zeu/Zm		
1. More stable summer stratification	Less mixing	Less turbid	Increase	More favourable	Increased
2. Increase wind run/fetch	Greater mixing	More turbid	Decrease	Less favourable	No increase
3. Increase shallow areas at heads of arms	No change in mixing	More turbid	Increase	Less favourable	No increase

Opinions differ as to whether the Mpophomeni township provides a significant potential threat for water quality through nutrient enrichment by sewage effluent. The results of this study, discussed in

Chapter 4.3, show that with the present underwater light climate the rates of phytoplankton production are nutrient, and not light limited so that an increase in the present nutrient loads would increase phytoplankton productivity even if there was no change in the light climate. However, it is doubtful whether the light climate would remain unchanged following nutrient enrichment. Walmsley (1980) reported that in a turbid impoundment (Lindleyspoort) the water transparency increased i.e. Z_{eu} increased, following artificial enrichment. He attributed this to the influence of phytoplankton on the flocculation and sedimentation of inorganic suspended material and the effects of an increase in mineral content on the stability of suspended colloidal particles. The resultant increase in Z_{eu} , assuming no change in Z_m , would increase the value of the ratio Z_{eu}/Z_m and create conditions more favourable for algal blooms and increase the costs of producing high quality water.

Key question and answer

- i.) What is the relationship between light and photosynthesis and how is this influenced by silt and resuspended material?

Lake Midmar is a turbid lake with a shallow euphotic zone where conditions are favourable for photosynthesis. From the form of the productivity-depth profiles, measured using a static series of flasks and therefore not accounting for mixing, it is clear that near the lake surface there is an excess of light available for photosynthesis since, with the exception of two overcast days, the profile showed light inhibition at the surface. However, the rapid attenuation of light as a result of the turbidity leads to a vertical compression of the productivity - depth profile.

The turbidity in Lake Midmar is due to inorganic particulate material maintained in suspension by wind induced turbulence. While considerable amounts of silt are introduced into the lake at times of river flow, particularly at the end of summer, February - March, this does not have a significant effect on the underwater light climate. The pattern of light attenuation observed in Lake Midmar is primarily determined by within lake processes, with shore line erosion and the resuspension of sediments acting as sources of the inorganic particulate material. Productivity is however principally controlled by the rate of nutrient supply.

4.3 EXTERNAL NUTRIENT LOADING C.G.M, Archibald.

Introduction

Eutrophication results from an increase in the nutrient load reaching a water body, and predictive models thus require estimates of nutrient loading. It has been suggested that the broad confidence limits attached to most predictive models results partly from the accuracy of the estimate of external nutrient loading. The sensitivity of predictive models to errors in load estimation can be assessed only after the load has been intensively sampled, permitting calculation of the Best Possible Estimate of the load. Estimates based on less frequent sampling can then be compared with the Best Possible Estimate to evaluate the loss of accuracy and to permit development of a rational sampling strategy for load estimation.

In this section attention is directed at the development of an efficient sampling procedure for accurate estimation of nutrient load. Sensitivity of predictive models to accuracy of load estimation is dicussed later (Chapter 7).

Description of the subcatchment

There are four subcatchments above Lake Midmar:

The Mgeni subcatchment is the largest and provides the major discharge into the Lake, exceeding 70% of the total run-off for any given period of the year. Land use is predominantly agricultural combined with open grasslands and as there is no urban or industrial development, load derives from diffuse sources;

The remaining three subcatchments, Kwaggishi, Nguku and Umthinzima together represent only 11,7% of the total watershed area, most of which is agricultural. The only possible point source of nutrient discharge is the Mpophomeni township (Figure 1) which, at the present time, has a negligible influence on the nutrient load entering Lake Midmar.

Sampling strategy and computation of load

A distinctive feature of the Mgeni river and probably of most other large South African rivers, is the high variability of the flow and therefore the frequency of measurement will determine the reliability of export estimates from the catchment. The variation of a load estimate will be due to a combination of slow, long-term changes (not easily distinguishable within an annual cycle of events), seasonal changes, short-term regular changes (diurnal pattern) and changes of irregular occurrence and magnitude with no recognisable pattern. The sampling strategy used in the estimation of surface run-off was designed in relation to the expected discharge from each catchment.

Daily loads from the Mgeni river were computed from the product of mean concentration and daily average flow data. A less intensive monitoring programme (fortnightly spot flow and concentration) had to be used for an estimate of the export from each minor sub-catchment. The frequency of sampling and methods of computation of the loads are summarised in Table

6. An estimate of the total annual external load is therefore derived from the summation of daily estimates of the major surface inflow to the lake, fortnightly estimates of the three minor surface inflows and an estimate of bulk precipitation (atmospheric) of total phosphorus and nitrogen.

The Best Possible Estimate of the load

The daily sampling interval used in the estimate of the nutrient load from the Mgeni river has permitted a theoretical evaluation of different sampling frequencies within that data set in terms of their deviation from the Best Possible Estimate. A descriptive analysis of the two successive twelve month periods indicates the variability of the concentration of variates such as suspended solids (C.V.% 319;196) soluble reactive phosphorus (C.V.% 100; 90), total phosphorus (C.V.% 124; 105) nitrate-nitrogen (C.V.% 90; 144), all of which are directly associated with eutrophication of a system (Table 7). Flow data also showed a positive skewness in distribution despite the drought conditions and therefore infrequent sampling intervals would be likely to introduce bias towards low flow concentration relationships. Smith and Stewart (1977) reported that bias towards low flow conditions over-emphasised nutrient concentrations and resulted in over estimates of annual loads if mean values were used. Cullen and Smalls (1981) experienced similar difficulties and stressed the importance of covering the changes in nutrient concentration under different flow regimes with a sampling frequency proportional to discharge. Unfortunately a flow interval sampling schedule was not practically possible in this investigation and therefore the Best Possible Estimate of the annual load was given by the daily sampling strategy at the gauged Mgeni catchment.

The effect of increasing or decreasing the sampling frequency on the accuracy of an estimated annual load is demonstrated by data in Table 8a. Increasing the sampling interval from one day to 30 day intervals dramatically increases the range of possible divergence from the Best Possible Estimate for any given variate. Using a fortnightly interval (a strategy adopted in small ungauged catchments) as an example, variates such as suspended solids, total phosphorus and Kjeldahl nitrogen (unfiltered) show a great range in divergence from the Best Possible Estimate. These variates are closely associated with the high variability in flow during transport via overland run-off, erosion and flushing of accumulated river sediment. The divergence from the Best Possible Estimate for total phosphorus (unfiltered) ranged from over-estimation by 128% to under estimation of 45% in 1980/181 for example (Table 8b).

For both years the average divergence resulted in an under-estimate of the load of between 16 and 21%. With the exception of the soluble reactive phosphorus constituent of the load during 1980/81, the majority of soluble components of the load e.g. nitrate and silica show a smaller range in divergence and on average an underestimate of the Best Possible Estimate of the annual load.

A reduced sampling frequency of once a day during summer and once a week during low winter flows showed no significant improvement on a 7 day interval schedule throughout the year. Once a month sampling (i.e. 30 day interval) is of little value in determining accurate estimates because of the large discrepancies which can occur from using mean values of flow and concentration (Table 8a). Much of this data set was obtained

Table 6 Summary of methods used to calculate nutrient loads for Midmar Dam (1979-1983)

System	Sampling Station	Frequency of Sampling	Period of Sampling	Method of Computing Nutrient Loads
<u>AGRICULTURAL/URBAN RUN-OFF</u>				
<u>Gauged Catchments</u>	"MMRI" - Confluence below Petrusstroom and Lions river weirs (U2M13 and U1M07)	Daily spot flows/daily average flows Daily concentrations	April 1980 - March 1983 (ongoing)	The product of daily average flows (summed for 2 weirs x catchment factor) and mean daily concentration to produce a daily load
	"MMRO" outflow from Midmar dam (U2W01)	Daily average flows/ fortnightly spot flows fortnightly spot concentrations	October 1979-March 1983 (ongoing)	The product of daily average flows (summed over 14 days) and spot concentration to give a fortnightly load
<u>Ungauged Catchments</u>	"MMR2" Kwaggishi stream "MMR3W" Nguku stream "MMR4" Umthunzima stream	Fortnightly spot flows and concentrations	October 1979-March 1983 (ongoing)	The product of spot concentration and spot flows x 14 to give a fortnightly load
<u>Precipitation</u>	"MMD6" in situ raft site near dam wall	Bulk precipitation on monthly basis or irregular periods based on rain events	October 1979-March 1983 (ongoing)	The product of the nutrient deposition coefficient and the surface area of dam per unit of time

Table 7 Condescriptive analysis of physico-chemical characteristics of the Mgeni river inflow into Lake Midmar

APRIL 1980 - MARCH 1981					
VARIABLE	MEAN	MINIMUM	MAXIMUM	C.V. %	NO. CASES
FLOW m ³ /s	2,52	0,27	21,14	164	365
pH	7,41	6,51	8,00	3	348
SS mg/l	15,00	1,00	658,00	319	365
COND mS/m	6,6	2,5	10,9	22	365
TDS mg/l	44	17,0	73	22	365
ALK mgCa-					
Co ₃ /l	28	4,0	47	28	348
CO ₂ mg/l	2,4	0,7	8,0	42	348
SRP µgP/l	2	0	33	100	365
TSP µgP/l	9	3	53	51	365
TPU µgP/l	28	7	598	124	365
NH ₃ µgN/l	14	2	114	76	365
KNF µgN/l	202	96	1440	42	365
DON µgN/l	187	86	1326	42	365
KNU µgN/l	332	115	3700	74	365
NO ₃ µgN/l	113	2	663	90	365
NO ₂ µgN/l	1	0	8	122	365
Si mgSi/l	4,4	3,5	5,2	7	365
APRIL 1981 - MARCH 1982					
VARIABLE	MEAN	MINIMUM	MAXIMUM	C.V. POT	NO. CASES
FLOW	2,29	0,32	26,65	135	365
pH	7,41	6,73	7,94	3	365
SS	12,00	0,7	221	196	365
COND	6,0	3,8	16,1	15	365
TDS	40	25	107	15	365
ALK	24	9	38	17	365
CO ₂	2,2	0,5	8,3	56	365
SRP	4	0	33	90	365
TSP	11	3	56	58	365
TPU	29	7	226	105	365
NH ₃	17	2	456	204	365
KNF	219	95	1274	65	365
DON	201	78	1089	59	365
KNU	334	150	2066	74	365
NO ₃	226	32	3905	144	365
NO ₂	2	0	61	199	365
Si	4,2	2,6	7,9	14	365
Fe mg/l	14	4	59	61	365
C.l mg/l	2,9	1,6	18,3	55	365
SO ₄ mg/l	1,789	0,6	11,7	71	328

Table 8a Divergence (%) of nutrient load estimates obtained from different sampling intervals (days) from the Best Possible Estimate of the load (BPE) derived from daily sampling (a) April 1980 - March 1981 : (b) April 1981 to March 1982

VARIABLE		3		7		14		30		*		BPE (DAILY)	
		(a) 1980/81	(b) 1981/82	(a) 1980/81	(b) 1981/82	(a) 1980/81	(b) 1981/82	(a) 1980/81	(b) 1981/82	(a) 1980/81	(b) 1981/82	(a) 1980/81	(b) 1981/82
Suspended Solids	Max	32,8	-18,1	75,7	-28,8	190,6	-44,7	409,8	100,4	75,6	-26,9	kgx10 ³	kgx10 ³
	Min	16,1	2,8	10,6	-0,1	-7,4	2,1	12,7	1,2	10,5	-1,0	3300	1690
	Mean	-4,4	-8,8	-16,1	-17,2	-21,5	-24,3	-32,0	-31,4	-16,3	-15,7		
Total dissolved solids	Max	1,9	-2,1	3,8	-8,9	5,9	-9,6	16,8	9,3	3,9	-8,8	kgx10 ³	kgx10 ³
	Min	0,2	0,3	-0,2	-1,1	-0,2	0,2	0,8	-0,1	-0,1	-0,5	2490	2890
	Mean	0,5	-1,0	1,4	-1,2	2,4	-1,7	6,8	-1,8	1,7	-0,7		
Soluble reactive P	Max	30,5	-9,5	65,3	-23,6	129,5	-43,8	249,2	-60,8	65,9	-18,7	kg	kg
	Min	-6,7	7,1	-18,3	4,1	7,9	-5,1	0,6	6,2	-2,5	-0,8	262	455
	Mean	0,1	-3,7	-2,6	-9,0	4,6	-18,9	-6,4	-28,8	21,3	-7,9		
Total phosphorus	Max	-17,6	-12,6	51,4	-21,7	128,4	-38,5	272,7	-61,4	51,4	-20,0	kg	kg
	Min	-10,4	-1,3	-3,8	2,8	-0,1	8,2	-12,5	0,2	-3,8	-1,0	4377	3560
	Mean	-3,6		-11,6		-16,1		-21,1		-11,8	-11,3		
Nitrate nitrogen	Max	5,7	-8,3	10,5	-22,5	-14,9	-43,5	-25,5	-51,6	10,9	-21,1	kg	kg
	Min	-1,2	-2,4	-3,3	-1,6	1,2	-1,6	-1,1	-0,2	-1,8	-0,2	13860	25067
	Mean	-0,3	-4,6	-2,3	-12,4	-4,4	-20,8	-6,7	-28,9	-3,5	-11,7		
Kjeldahl N (unfiltered)	Max	-12,5	-7,7	34,9	-15,5	84,8	-24,9	183,7	-46,4	35,1	-14,7	kg	kg
	Min	-5,6	-2,0	-2,8	1,0	-2,8	-1,6	4,5	2,4	2,8	0,1	39535	33984
	Mean	-2,4	-4,9	-7,7	-9,3	-11,1	-15,5	-13,4	-21,2	-7,8	-8,7		
Silicon	Max	-0,6	-1,7	-1,2	-5,1	-4,9	-6,3	-6,9	-12,3	-0,9	-5,0	kgx10 ³	kgx10 ³
	Min	-0,03	0,2	-0,03	-0,8	-0,3	-0,1	0,1	-0,7	0,08	0,8	340	325
	Mean	-0,03	-0,6	0,04	-0,6	-0,6	-2,2	-1,1	-4,0	0,2	0,1		

*Sampling frequency: Once a week in winter and once a day in summer
 -Underestimation

Table 8b A comparison of the divergence (%) of nutrient load estimates of the Mgeni inflow (MMR1) to Midmar Dam on a fortnightly basis with the Best Possible Estimate (BPE) derived from daily sampling (1980-1981)

Variable	SS kgx10 ⁶	TDS kgx10 ⁶	SRP kg	TSP kg	TPU kg	NH ₃ kg	KNF kg	DON kg	KNU kg	NO ₃ kg	NO ₂ kg	SI kgx10 ³
Best possible estimate (BPE)	3,30	2,49	262	879	4 377	1 019	17 449	16 428	39 535	13 860	49	340
Sampling run	NUTRIENT LOAD ESTIMATES FROM 14 SAMPLING RUNS											
1	3,06	2,49	138	706	3 288	870	16 029	15 159	33 384	11 964	139	332
2	4,45	2,63	162	674	4 511	837	16 753	15 922	38 415	13 188	168	336
3	3,93	2,45	183	749	4 383	1 018	16 663	15 652	37 638	12 283	140	335
4	1,30	2,55	231	870	2 638	1 098	17 183	16 085	29 778	14 342	128	345
5	1,29	2,61	374	1 085	2 622	1 281	18 035	16 745	29 934	13 501	129	343
6	1,07	2,54	282	915	2 454	929	17 603	16 674	29 884	11 955	112	339
7	1,04	2,61	209	916	2 391	947	16 893	15 935	27 203	12 878	133	346
8	1,45	2,62	170	801	2 761	1 020	16 721	15 701	29 004	14 028	117	342
9	2,23	2,64	189	872	2 517	1 002	17 756	16 753	30 415	13 648	119	341
10	1,30	2,56	220	864	3 537	1 275	17 748	16 472	35 711	13 380	111	344
11	9,59	2,48	600	1 121	9 997	1 228	16 859	15 631	73 064	15 339	145	324
12	1,58	2,58	410	998	3 211	604	17 304	16 700	31 643	14 345	163	335
13	1,43	2,59	160	722	3 068	668	17 437	16 817	30 873	12 702	122	335
14	2,54	2,38	172	698	4 044	935	16 509	15 570	35 159	11 795	103	331
Mean	2,59	2,55	250	857	3 673	979	17 110	16 130	35 150	13 247	134	338
Mean divergence from BPE %	-21,5	2,4	4,6	-2,5	-16,1	-3,9	-1,9	-1,8	-11,1	-4,4	-10,1	-0,6
Maximan divergence %	190,6	5,9	129,5	27,5	128,4	-40,7	-8,1	-7,7	84,8	-14,9	31,3	-4,9
Minimum divergence %	-7,4	-0,2	7,9	-0,8	0,1	0,1	0,2	0,3	-2,8	1,2	-5,9	-0,3

- underestimation

during drought intensive conditions and very few short term irregular events were monitored e.g. catchment thunderstorms. It is very likely that when these conditions prevail the divergence from the Best Possible Estimate for sampling intervals greater than one day will be even larger.

The main components of the load

Phosphorus has been reported as the probable limiting factor of productivity in most water bodies, particularly those classified as oligotrophic, but other components of the load have also been monitored because there is no good reason to believe that all the constituents behave in the same way in relation to different flow regimes. This is exemplified by phosphorus where sorption by particulate material plays a vital role in the reduction of soluble components of the load and subsequent settling in the receiving waters reduces the available phosphorus for algal growth.

The largest surface source of external phosphorus to Lake Midmar is derived from particulate matter contained in the run-off and this exceeded 75% of the total phosphorus load during summer each year. It was never less than 50% of the winter load despite the reduced flows. Much of the total phosphorus reaching the lake from surface run-off is therefore in a form which is not readily available for algal growth.

The readily utilisable soluble reactive phosphorus fraction however, was never more than 10% of the total phosphorus load during summer or 20% during winter although the latter was in fact a smaller amount (Table 9).

The inorganic nitrogen component varied between 30 and 45% of the total nitrogen load during summer and winter each year, whereas particulate nitrogen ranged from 14 -40% of the total nitrogen load. The dissolved organic fraction constituted approximately 30-40% of the load each year. The algal available N/P ratios of the external load were high, clearly indicating that phosphorus was the limiting nutrient particularly since the external input was predominantly in an unavailable particulate form.

Soluble silica loads were an order of magnitude greater than nitrogen and two orders of magnitude greater than phosphorus and the constant input relative to nitrogen and phosphorus indicates that it is unlikely to be the growth rate limiting nutrient for algae.

The sources of the external load

The relative amounts of nitrogen and phosphorus derived from surface run-off are presented in Table 10. The Mgeni inflow produced by far the greatest amount of nitrogen (88%) and phosphorus (80%) on average for the period of investigation. An additional but small amount was produced from a combination of the remaining small catchments, and the balance was determined as bulk precipitation.

The mean deposition rate for the bulk precipitation was obtained from 21 observations at roughly monthly intervals and was determined as 0,374 kg P/ha/yr and 7,88 kg N/ha/yr. Direct input to the lake was calculated seasonally to produce the annual contribution which varied from 9-14% of the total external phosphorus input and from 13-16% of the total external nitrogen load.

During three successive years the phosphorus load from run-off fluctuated from 1471 kg to 5661 kg and 4826 kg while the nitrogen load followed a

Table 9 SEASONAL TRENDS IN TOTAL SURFACE RUN-OFF TO LAKES MIDMAR

(a) 1979-1980 (b) 1980-1981 (c) 1981-1982

	FLOW $m^3 \times 10^6$			SOLUBLE REACTIVE PHOSPHORUS (kg)			TOTAL PHOSPHORUS (kg)			SOLUBLE SILICA ($kg \times 10^3$)			TOTAL INORGANIC NITROGEN (kg)			DISS. ORGANIC NITROGEN (kg)			TOTAL NITROGEN (kg)		
	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)
OCTOBER	3,43	2,73	2,64	5	12	7	69	78	40	18	13	10	914	745	396	467	615	426	1818	1641	978
NOVEMBER	3,03	1,80	2,95	8	5	17	77	42	285	14	9	14	554	151	2600	547	377	1335	1272	710	4995
DECEMBER	4,46	8,32	7,34	8	34	42	89	477	395	24	39	36	895	2019	5574	1050	1774	2471	2024	5998	9314
JANUARY	3,44	7,09	9,38	7	24	28	82	283	358	18	32	41	595	1350	2254	787	1520	2063	1680	4422	6019
FEBRUARY	9,32	28,93	5,81	10	84	39	809	1960	232	53	172	27	4506	6146	1582	6831	9009	1306	12885	22648	3788
MARCH	4,49	29,34	23,15	11	143	240	141	2218	2222	32	106	121	1834	6536	12068	1147	3831	8703	3326	24464	28548
SUMMER SUBTOTAL	28,23	78,21	51,27	49	302	373	1267	5058	3532	159	371	249	9298	16947	24474	10839	17126	16304	23005	59883	53642
APRIL	2,21	5,67	15,35	5	14	169	66	114	1044	11	29	84	351	990	5992	479	921	4384	1071	2454	13791
MAY	1,39	3,78	4,35	6	15	22	31	83	60	7	18	23	135	516	888	197	528	647	433	1416	1675
JUNE	1,32	3,34	3,83	6	11	10	37	71	67	8	16	21	204	523	915	172	530	591	489	1275	1573
JULY	0,70	2,12	2,04	1	12	5	11	46	27	4	8	9	54	414	348	101	365	275	216	814	704
AUGUST	0,88	3,22	2,06	2	13	17	21	86	43	5	13	8	30	711	229	149	507	295	237	1475	654
SEPTEMBER	1,48	6,77	1,42	4	47	6	38	203	33	8	27	5	86	2273	557	343	1387	1410	671	4980	2203
WINTER SUBTOTAL	7,97	24,90	29,05	24	112	229	204	603	1294	43	111	150	860	5427	8929	1441	4238	7602	3017	12414	20600
ANNUAL TOTAL	36,19	103,18	80,32	73	414	602	1471	5661	4826	202	482	399	10158	22374	33403	12280	21364	23906	26022	72297	74242
SUMMER INPUT AS % OF TOTAL	77,9	75,9	63,8	67,1	72,9	62,0	86,1	89,3	73,2	78,7	77,0	62,4	91,5	75,7	73,3	88,3	80,2	68,0	88,4	82,8	72,3

Table 10 Estimates of annual external nutrient load input to Lake Midmar (1979-1982)

Oct. 1979 to Sept. 1980	FLOW m ³ x10 ⁶	SRP kg	TSP kg	TPU kg	NH ₃ kg	NO ₃ kg	TIN kg	DON kg	TOT N kg	SI kgx10	SS kgx10 ³
MMR1 (Mgeni inflow)	31,89	57	279	1 240	630	8 150	8 820	11 406	22 613	167	1 063
MMR2-4 (Other surface inflows)	4,31	16	50	231	159	1 228	1 357	874	3 409	35	160
Total surface input	36,20	73	329	1 471	789	9 378	10 177	12 280	26 022	202	1 223
Precipitation input	9,77			243					4 236		
Total input	45,97			1 714					30 258		
Oct. 1980 to Sept. 1981											
MMR1 (Mgeni inflow)	95,68	349	1 084	5 055	1 301	18 202	19 715	19 670	65 430	429	3 620
MMR2-4 (Other surface inflows)	7,50	65	150	606	284	2 587	2 842	1 794	6 867	53	582
Total surface inflow	103,18	414	1 234	5 661	1 585	20 789	22 557	21 464	72 297	482	4 202
Precipitation	10,69			583					14 767		
Total input	113,84			6 244					87 064		
Oct. 1981 to Sept. 1982											
MMRI (Mgeni inflow)	70,88	520	1 176	4 045	1 801	25 353	27 544	21 948	63 655	334	416
MMR2-4 (Other surface inflows)	9,43	82	168	781	146	6 103	6 780	1 958	10 587	65	817
Total surface inflow	80,31	602	1 344	4 826	1 947	31 456	34 324	23 906	74 242	399	1 233
Precipitation	11,03			600					11 273		
Total input	91,34			5 426					85 515		

similar trend by increasing from 26022 kg to 72297 kg and 74242 kg. Nutrient export coefficients have been determined from mean values for each subcatchment but because of a clustering of "dry" years together, no "wet" year characteristics are available.

During this dry period the Mgeni subcatchment has been less productive than each of the smaller subcatchments in respect of phosphorus loss per unit area per year except that of the Nguku (Table 11)

Table 11 Mean annual export coefficients of phosphorus and nitrogen from the four subcatchments of Lake Midmar

Subcatchment	Area (hectares)	Mean Annual Export Coefficients		
		(Kg/ha/yr)		
		Total phosphorus	Total nitrogen	N/P
Mgeni	80 300	0,04	0,62	15,5
Kwagqishi	6 100 2	0,05	0,61	12,2
N.guku Um thin zima	900 1 900	0,03 0,07	0,53 0,78	17,6 11,1

The increased export rate from the Umthinzima catchment stresses the potential importance of urban development in respect of both the total load and of its proportional contribution under changing hydrological conditions. Although current projections for development of the Mpophomeni Township indicate that water quality in Lake Midmar will not be adversely affected to a significant degree (Bruwer and Kroger pers. comm.), they are based on 'controlled development' with adequate effluent treatment. It should be borne in mind however, that the water supply authorities will probably have little or no jurisdiction over the operation of the sewage treatment works and of effluent standards. In this event alternative options such as pre-impoundment may have to be implemented.

Seasonality of Loading

Since the mean annual run-off to lake volume ratio is near unity (0.90) it can be expected that the water quality of the lake and the hydrological regime of the system will be greatly influenced by the chemical characteristics of the run-off and the pattern of inflow from the Mgeni. The hydrological regime was markedly seasonal with low winter flows and erratic, short lived summer spates of varying amplitude, superimposed on the increased summer base flow conditions. For each and every variate the summer input (October - March) exceeded 60% of the total annual input to the system (Table 9). In some cases e.g. suspended solids, the summer load represented over 90% of the total annual input from surface run-off. This seasonal cycle was distinctly repetitive, although during the dry conditions which prevailed there was no marked double summer peak in monthly sediment loads described by Roberts (1973) for other large Natal rivers. The first peak in monthly loads usually occurred at the onset of seasonal run-off, but a second and more substantial peak occurred during late summer (February through April) during periods of maximum discharge, when load becomes a function of the rate of production of material in the catchment.

A clearer picture of the pattern of summer loading is obtained by analysis of the flow "events", here defined as that volume of water equal to or greater than 1% of the full supply capacity of the dam, discharged from the catchment per week.

During the summer of 1979/80 only four such events occurred, all in February, when just over 30% of the summer flow produced 65% of the total phosphorus load and 50% of the nitrogen load. In the summer of 1980/81 there were 13 events of which 11 were substantial inputs between the end of January and March. During this period 75% of the summer inflow occurred producing 82% of the phosphorus and 75% of the nitrogen for the summer season. Only 8 events were recorded during summer of 1981/82, two of which occurred in early summer but did not represent significant amounts in the load. Two late summer events (March - April) represented 45% of the summer inflow and produced 63% of the phosphorus and 50% of the nitrogen for that season.

Key questions and answers

1. What is the best sampling strategy to obtain the Best Possible Estimate of the surface load?
The Best Possible Estimate of the external surface load entering Lake Midmar was derived from daily monitoring of the large gauged catchment of the Mgeni, and fortnightly monitoring of the ungauged smaller subcatchments. Sampling intervals of greater than one day lead to an increase in the possible range in divergence from the best estimate. Soluble components of the load behave differently from particulate fractions and since the latter are associated closely with run-off, daily sampling is recommended if possible.
2. What are the main components of the load?
Much of the phosphorus load introduced to the lake was in particulate form (75% of summer input) which is not readily available for algal growth, while 50-60% of the nitrogen was in soluble easily utilised form, and substantial quantities of soluble silica were constantly present in the load. The N/P ratios in most cases indicated a potential phosphorus limitation of algal growth rate in the system.
3. What are the main sources of the load?
The major input of nutrients was derived from diffuse agricultural sources which can best be controlled by more efficient use of fertilizers and soil conservation improvements. However, the highest export of nutrients per unit area per unit of time occurred in the small Umthinzima catchment in which the nutrient source was derived from urban run-off and dairy waste. Future management should take account of methods to control enrichment from point sources.
4. How does the load vary seasonally?
The patterns of nutrient loading and rainfall were related and load was markedly seasonal. The most significant finding was that the period of maximum external loading occurred at the end of summer each year when longer hydraulic residence times prevail in the lake, and when winter isothermal conditions increase circulation of the water column within the lake.

5. How important is frequent sampling of spate flows in the estimation of load?

This question has remained unanswered because the drought conditions have not presented the opportunity to monitor short-term storm events. A flow interval strategy would be the best approach in assessing the nutrient input from such events but it was impractical for this study.

External nutrient loads can be provided also by the periodic resubmergence of the drawdown zone. Analysis of nutrient loading is therefore incomplete without an assessment of the contribution from this source under varying hydrological conditions,

4.4 EXTERNAL NUTRIENT LOAD - THE DRAWDOWN ZONE E.G.J. Akhurst

INTRODUCTION

The nutrients present in a lake ecosystem at a particular time are derived from two sources: autochthonous or internal nutrient load, derived from processes occurring within the lake and external (allochthonous) nutrient load from sources outside the confines of the lake ecosystem. The allochthonous nutrient load enters the lake either as river flow from drainage of the catchment or as rainfall incident on the lake surface. In addition, in South African impoundments, the drawdown zone may also contribute to the allochthonous load particularly when conditions favour the colonisation of the drawdown zone by terrestrial vegetation. This chapter examines the importance of the drawdown zone in relation to the other allochthonous inputs to Lake Midmar and whether this source of nutrients should be considered in the management of Lake Midmar.

Origin and size of the drawdown zone

The presence of a clearly defined drawdown zone reflects the marked seasonality of the river flow entering the system with the result that, on an annual basis, the inputs are less than the losses, by evaporation and discharge from the lake. The size of the drawdown zone will be determined by both the magnitude of the difference between the inputs and losses and the morphometry of the lake basin. The period of exposure and extent of the drawdown zone is also influenced by the pattern of river flow. Under normal conditions during the summer months the drawdown zone will be much reduced, if present at all, since the lake will be at or near to full supply level, while during winter and early spring it will reach its maximum size. Any factor influencing either the input or losses from the system will therefore influence the annual pattern of inundation and exposure outlined above.

Significance of the drawdown zone

There is some evidence that the seasonal exposure and inundation may influence the cycling of nutrients, in particular phosphorus. The work of Willett (1979) has shown that in soils that were flooded and subsequently exposed, the capacity for phosphorus adsorption was significantly enhanced. The increase in both the maximum P-adsorption and the bonding energy for P resulted from a decrease in the crystallinity of the free iron oxides. While this aspect has not been investigated in South Africa it would be expected that the importance of this phenomenon would depend on the soil type and extent of a particular drawdown zone.

Another way in which the drawdown zone may contribute to the allochthonous nutrient load would be following inundation of this zone and the subsequent decomposition and release of nutrients from terrestrial vegetation that had colonized the drawdown zone during the period of exposure. However, under normal conditions the period of exposure is during winter, a time that is unfavourable for plant growth and establishment and hence the contribution to the total nutrient load by terrestrial vegetation would be small.

The importance of the drawdown zone to lake functioning under normal

conditions therefore lies in its contribution to the turbidity of the system by acting as a source of suspended material through shore-line erosion. This aspect is discussed in Chapter 4.2.

Under normal conditions it would appear that Lake Midmar has a clearly defined but narrow drawdown zone since at no time during the period 1976-1979 was the lake less than 90% full (Figure 16). Little colonization of the drawdown zone by terrestrial vegetation occurred so that under these conditions the drawdown zone acted primarily as a source of suspended material. However, for the period 1980-1982 as a consequence of the drought and reduced river inputs, the size of the drawdown zone was increased (Figure 16). At the end of 1981 the drawdown zone occupied ca 25% of the total lake area, i.e., 3,9 square kilometres, while by the end of 1982 the area had increased to ca 41%, i.e., 6,4 square kilometres. In addition to the increase in area the pattern of exposure and inundation of the drawdown zone had changed. Thus the period for which the lake was at full supply level had been contracted to only 2 weeks in April 1982.

During the summer period, 1981-1982, colonization of the exposed area by terrestrial vegetation, grass and herbaceous weed species, had taken place by the end of summer. Immediately prior to inundation the terrestrial vegetation occupied ca 62% of the available area i.e. 2.4 square kilometres. During 1982-1983 the area of the drawdown zone increased further. Contrary to expectations the area colonized by terrestrial vegetation was lower than at the end of the previous season, i.e., only ca 28% (1,8 square kilometres) of the available area was colonized. The drought played a significant role in restricting the development of the terrestrial vegetation community through preventing the successful establishment of seedlings in the drier, steeper sites and the greatest development of this vegetation occurred at the heads of more shallow arms.

Contribution to the nutrient load

The potential contribution to the allochthonous nutrient load by the terrestrial vegetation colonizing the drawdown zone can only be realized following inundation and the subsequent decomposition of the plant material. While this condition was met for a short period in April 1982 when the lake was at full supply level, during 1983 the lake never reached full supply level.

Estimates of the standing crop of the terrestrial vegetation were made at the end of February 1982 and 1983, i.e., they represent an estimate close to the maximum standing crop at the time of inundation. The results of these analyses are presented in Table 12.

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The differences in standing crop and hence nutrient content between 1982 and 1983 were not unexpected. The period 1981-1982 saw the initial colonization of this zone and represents one season's growth from seed to mature plants. The period of inundation in 1982 was short as the lake was at full supply level for only 2 weeks. This period of inundation was probably too short to kill the below ground portion of the grasses which had been established prior to inundation and would have produced the next" season's standing crop.

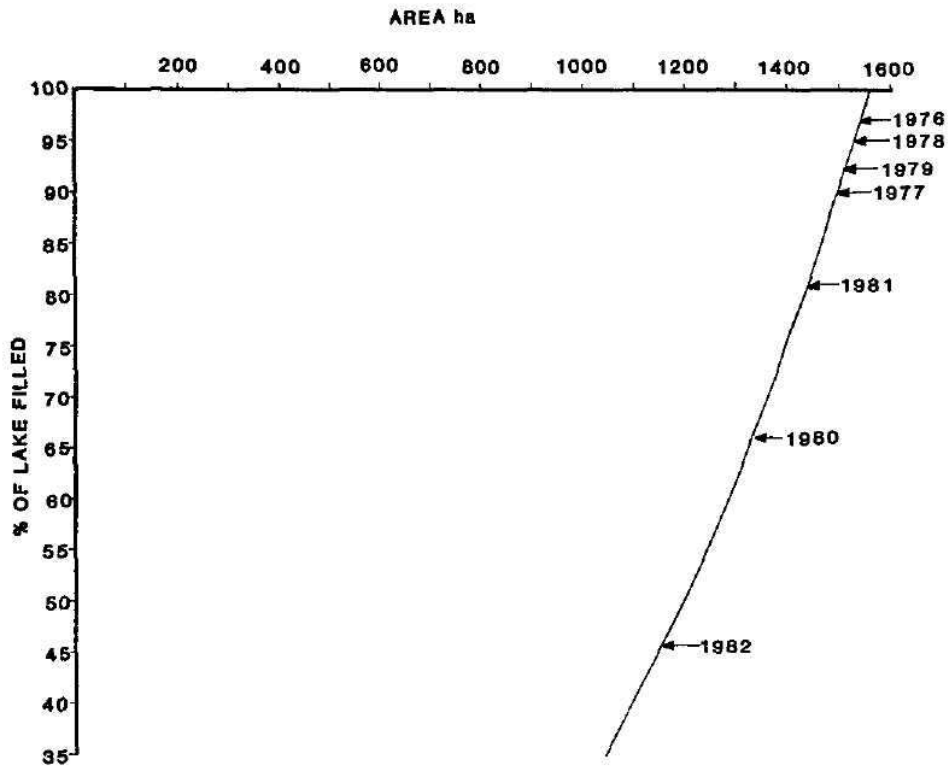


Figure 16 Area of Lake Midmar in relation to amount of water present as a percentage of capacity at full supply level for each year at end of winter, September 1976 - 1982, indicated by arrows

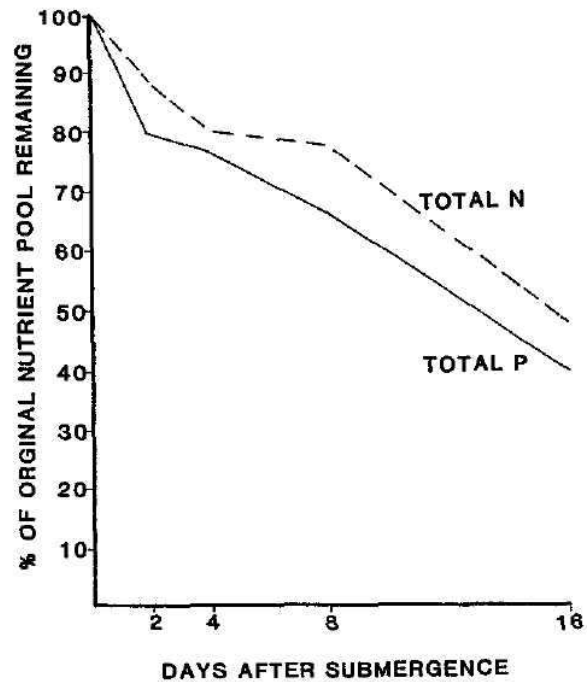


Figure 17 Pattern of release of total N and total P from decomposing terrestrial vegetation as % of original nutrient pool still remaining.

Decomposition of this terrestrial vegetation was biphasic (Figure 17) which is consistent with results obtained for other emergent and floating leaved macrophytes (Howard-Williams and Howard-Williams, 1978) and for CYNODON DACTYLON which occupies a similar position in the Pongolo floodplain (Furness and Breen, 1980). Unfortunately decomposition was measured over a period of 16 days only but on the basis of these results an estimate of the decomposition rate, as the time taken for the initial mass to be reduced to 50% (T/2) has been made. The value of T/2, ca 28 days, suggests that the decomposition rates are more rapid than those reported for other emergent macrophytes, but is similar to that of C. DACTYLON on the Pongolo. This rapid decomposition rate is supported by the observation that on exposure of this zone only the more resistant stem bases remained.

Table 12 Standing crop and amounts of total nitrogen and total phosphorus bound in the terrestrial vegetation of the drawdown zone for 1982 and 1983

Year	Area km ²	Mean standing crop g/m ² (standard error)	Total nitrogen g/m ²	Total phosphorus mg/m ²	Total nutrient content of drawdown zone (kg)	
					nitrogen	phosphorus
1982	2,4	119,3(+13,7)	1,65	168,2	3952	404
1983	1,8	355,8(+37,7)	5,64	496,0	8250	900

In assessing the relative importance of this source of nutrients to the total nutrient pool of a system such as Lake Midraar it is necessary to compare this source with other inputs (Table 13).

Table 13 Relative contribution of all sources of external nutrients to Lake Midmar for the 1981-1982 season

Total River Input		Bulk Precipitation (Rainfall and dry fallout)		Terrestrial vegetation	
Total N kg	Total P kg	Total N kg	Total P kg	Total N kg	Total P kg
62 900	5 262	12 017	640	3 953	404

The rivers draining the catchment are the major source of nutrients entering Lake Midmar as the external load (Table 13). It has been shown earlier that the present study was conducted during a drought so that under normal conditions the contribution of both the river and bulk precipitation inputs would be even greater. The internal nutrient load played the dominant role in the cycling of nutrients in Lake Midmar when the changes in the amounts of total phosphorus entering the lake are considered in relation to the amounts present within the lake during the 1981-82 season (Figure 18). This aspect is discussed in more detail in Chapter 4.5.

Implications for management

Colonization of the drawdown zone by terrestrial vegetation may become a feature of many South African impoundments as a result of future increased demands for water. Under such conditions the present pattern of exposure during the winter months and inundation of the drawdown zone, with the lake at full supply level, for most of summer and autumn will change. Thus impoundments such as Lake Midmar will be at full supply level for a shorter period at the end of summer and early autumn. The drawdown zone would therefore be present for most of the year and available for colonization at a time, spring to early summer, more favourable for plant growth than is the case under present conditions. To quantify the nutrient input from terrestrial vegetation following colonization during spring and summer the actual and maximum, all the available area colonized, nutrient inputs from this source have been calculated for 1982 and 1983 (Table 14). In addition the expected change in phosphorus concentration in the lake, at full supply level following inundation, has been calculated based on the assumption that all the phosphorus will be released, during decomposition of the terrestrial vegetation, as soluble reactive phosphorus (SRP).

Table 14 Actual and maximum nutrient inputs from drowned terrestrial vegetation and predicted change in lake concentration of SRP during 1982 and 1983

Year	Area colonized	Area Available	Total phosphorus in vegetation	Total phosphorus content of draw-down zone kg.		Change in SRP concentration (jig/fi) in lake when at fully supply	
				Actual	Maximum	Actual	Maximum
	km ²	km ²	mg/m ²				
1982	2,4	3,9	168,2	404	656	2,3	3,7
1983	1,8	6,4	496,0	900	3174	5,1	18,0

The changes in SRP concentrations in the lake represent theoretical maxima by virtue of the assumptions made in their calculation, and it is clear that the input of nutrients from drowned terrestrial vegetation will have a significant impact on lake functioning only if very large areas are colonized (6,4 square kilometres, maximum for 1983).

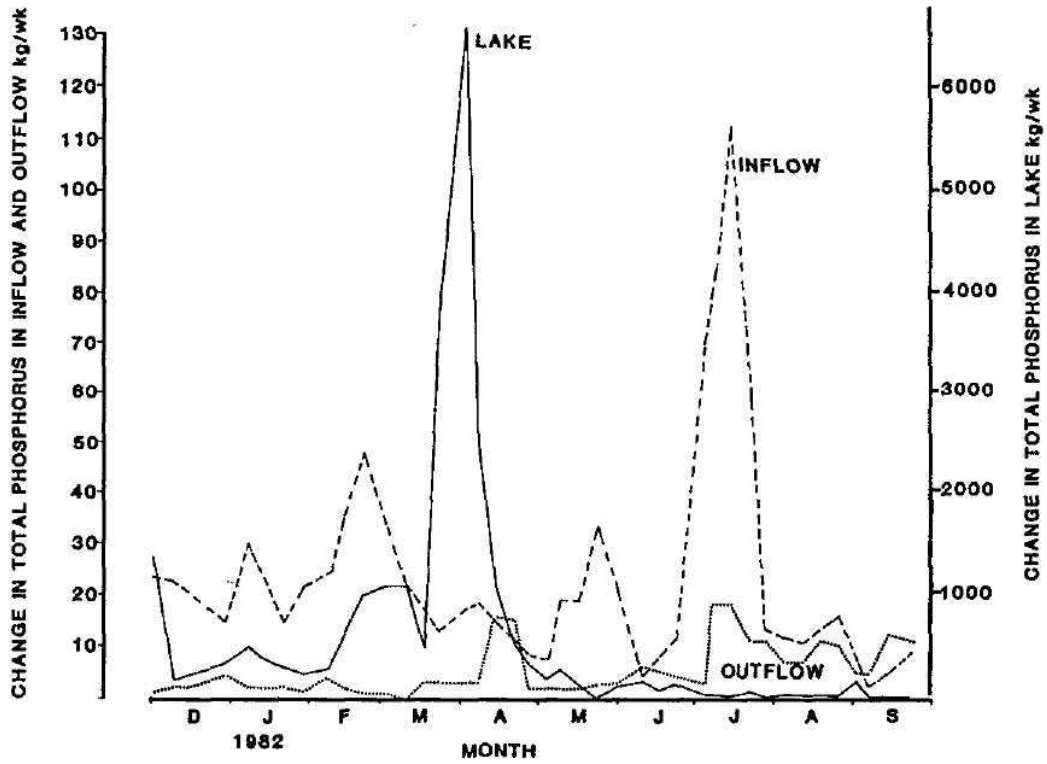


Figure 18 Changes in the amounts of total phosphorus within the lake, the inflow and the outflow on a weekly basis.

Key question and answer

What is the role of the drawdown zone in lake functioning?

The seasonality of rainfall and hence river flow from the catchments of most South African impoundments results in fluctuating water levels within the impoundment. As a consequence a drawdown zone, which is seasonally exposed and inundated, replaces the littoral zone of lakes where the water level is stable. The presence of a drawdown zone is important because:

- littoral macrophytes are generally poorly represented with the result that the phytoplankton of the open waters are the principal primary producers;
- the lack of macrophytes influences the species composition of organisms in other trophic levels;
- the drawdown zone acts as a source of inorganic particulate material through shore-line erosion and hence contributes to the turbidity of a lake;
- the seasonal exposure and inundation of soils in the drawdown zone may influence the cycling of nutrients in particular phosphorus.

During this study the pattern of exposure and inundation was modified by the drought and as a consequence the drawdown zone was colonised by terrestrial vegetation. This terrestrial vegetation acts as an external source of nutrients only if the drawdown zone is inundated and decomposition of the vegetation takes place. The results of this study have shown that the nutrient input from this vegetation occurs as a pulse at the end of summer. However, it is unlikely that this nutrient pulse poses a threat to water quality for two reasons:

- the timing of the input, since at the end of summer temperature is likely to limit the response to this supply of nutrients;
- relative to other sources of nutrients in Lake Midmar the terrestrial vegetation represented the smallest input.

It is concluded that nutrient dynamics in Lake Midmar are therefore determined principally by the external nutrient load entering via rivers and the extent to which this is modified by internal lake processes.

4.5 INTERNAL NUTRIENT LOADING AND NUTRIENT CYCLING
 CM. Breen and A.J. Twinch

Introduction

Conflicting views on the importance of internal phosphorus loading in impoundments are still frequently expressed by researchers, and they cause confusion in the minds of those charged with management of impoundments. The widely divergent opinions are symptomatic of an incomplete understanding of the exchanges which take place, the factors which influence these exchanges within a particular system, and how both vary from system to system.

In this chapter we discuss the exchange of phosphorus between four major compartments of Lake Midmar: water, bottom sediment, suspended inorganic sediment and phytoplankton, and attention is then directed at the implications of the findings in the management of Lake Midmar and other systems.

Sediment water exchange

There are few exceptions to the general rule that sediments can function as both a source and a sink for phosphorus. Net gain (by sorption and precipitation) occurs when water phosphorus concentrations exceed the equilibrium concentration and net loss (by desorption and solubilisation) results when concentrations in the water decrease below the equilibrium.

Steady state conditions

Radiotracer experiments show that steady state is characterised by a dynamic equilibrium where sorption and desorption occur at equal rates (Figure 19). The equilibrium concentration of soluble reactive phosphorus (Table 15) is on the order of 7 - 9 ug/l in Lake Midmar and since concentration of the growth rate limiting nutrient shows a first-order zero-order relationship with growth rate the low concentrations, under steady state conditions, will constrain growth rates of species requiring high concentrations for rapid growth, and will favour other species which can effectively use phosphorus at low concentrations.

Table 15 Data describing the release of ³²P by sediments following enrichment with PO⁴. Data from Twinch (1980).

PO ₄ added ug/S-	SRP at equilibrium	Rapid phase release constant k/min	Slow phase release constant k/min
0	7	1,75	0,09
50	9	2,01	0,03
100	7	2,46	0,05
200	9	3,27	0,02
X	8	2,37	0,05

Since the direction of sediment water phosphate flux is dependent on the dynamic equilibrium (i.e. on diffusion gradients between sediment pore water and overlying water) the sediments have the potential to serve as phosphate sinks or sources depending on conditions in the overlying

water. Generally in Lake Midmar SRP concentrations in the inflows (x 4,4, min 1,3, max 19,5 ug/l Figure 20) are lower than those in the lake (x 7,9, min 1,2, max 35 ug/l Figure 20) and lower than the experimentally determined equilibrium concentration in water overlying sediments (ca 7 ug/l). Thus, whilst SRP loading rate (flow x concn.) is at times fairly high, the concentration of the inflow is usually equal to or less than the equilibrium concentration, which suggests that the inflow would tend to favour release of phosphate from bottom sediments in the lake at most times. Furthermore, SRP concentrations in the lake water and in the outflows (Figure 20) may be elevated well above the theoretical equilibrium levels at times, indicating that concentrations in the lake are not exclusively dependent on sediment water phosphate equilibria. Another factor, which is discussed later, is the nature of the SRP, and whether it is a good index of phosphate capable of exchange with sediments.

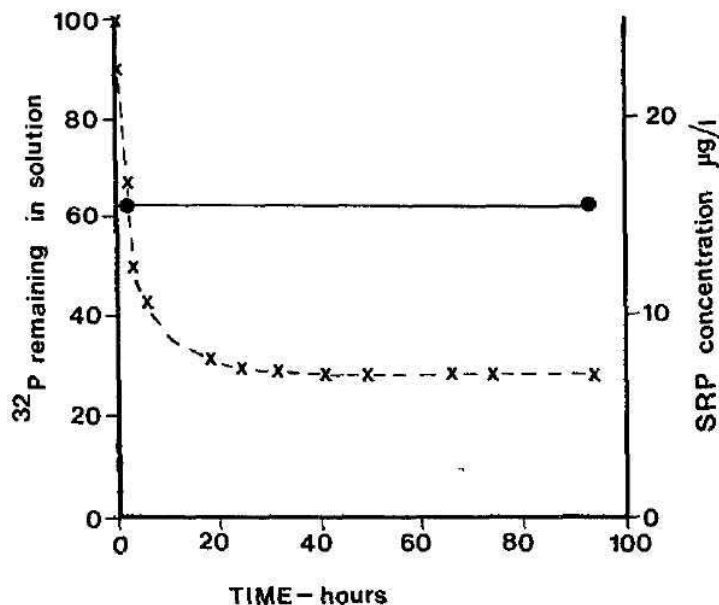


Figure 19 ³²P uptake by sediments in intact sediment: water systems.

Enrichment with phosphorus

Enrichment of water overlying sediments with phosphate permits analysis of the sorption process. Sorption by sediments is biphasic, with the initial phase being particularly fast (Table 16) indicating that sediments in a well mixed system such as Lake Midmar, can provide for a rapid net flux of phosphate into the sediment. The capacity of sediments to continue to adsorb phosphate depends on their structure and the extent to which adsorption sites are saturated. The moderately leached soils of the Natal midlands yield sediments with high phosphate fixing capacity, and increasing the concentration of P_0 , in the water resulted in increased rates of fixation (Figure 21) and equilibrium concentrations remained fairly constant (Table 16). Provided phosphate loading is not excessive enrichment is not expected to increase the rate at which phosphorus could be desorbed from the sediments.

Table 16 Data describing exponential curve fits to the fast and slow phases of sediment $^{32}PO^4$ uptake (Twinch and Breen, 1982).

	Fast phase		Slow phase	
mean	k/h	n	k/h	n
	16,0	2	0,10	5
	17,4	2	0,12	6
	16,8		0,11	

The nature of the sediments changes with time due to the incorporation of organic material. In Lake Midmar the 'new' sediments which overlie the drowned soil exhibit a 20% lower phosphorus adsorption maximum (i.e. less can be adsorbed) and a 60% lower bonding energy constant, suggesting that the phosphorus is more easily desorbed (Twinch and Breen, 1982). The net effect of these changes is a more mobile phosphorus pool in the surface sediments which may facilitate more rapid release of sediment phosphorus in response to reductions in equilibrium concentrations due to the diluting effect of inflowing water or to algal demand in the water. It must be stressed however that in Lake Midmar the capacity to adsorb phosphorus remained very high despite the current change in the sediment. This reflects both the low levels of organic production and high rates of mineralisation in the system.

Enrichment with nitrogen

Since nitrogen follows phosphorus closely as the growth rate limiting nutrient in Lake Midmar, enrichment with nitrogen ensures that phosphorus is growth rate limiting. This in turn, should favour desorption from the sediments as phosphorus in the water is utilised by algae. When isolated columns of water (with sediment) were enriched with nitrogen, two important observations were made; during the period of declining temperatures enrichment did not result in a net flux of phosphorus from the sediments, whereas in summer considerably elevated levels of phosphorus were detectable (Figure 22). These data provide good evidence that the sediment can release phosphorus in an algal-available form even under aerobic conditions in the water column (Twinch and Breen, 1980). This hypothesis is substantiated by the periodic within lake increases in

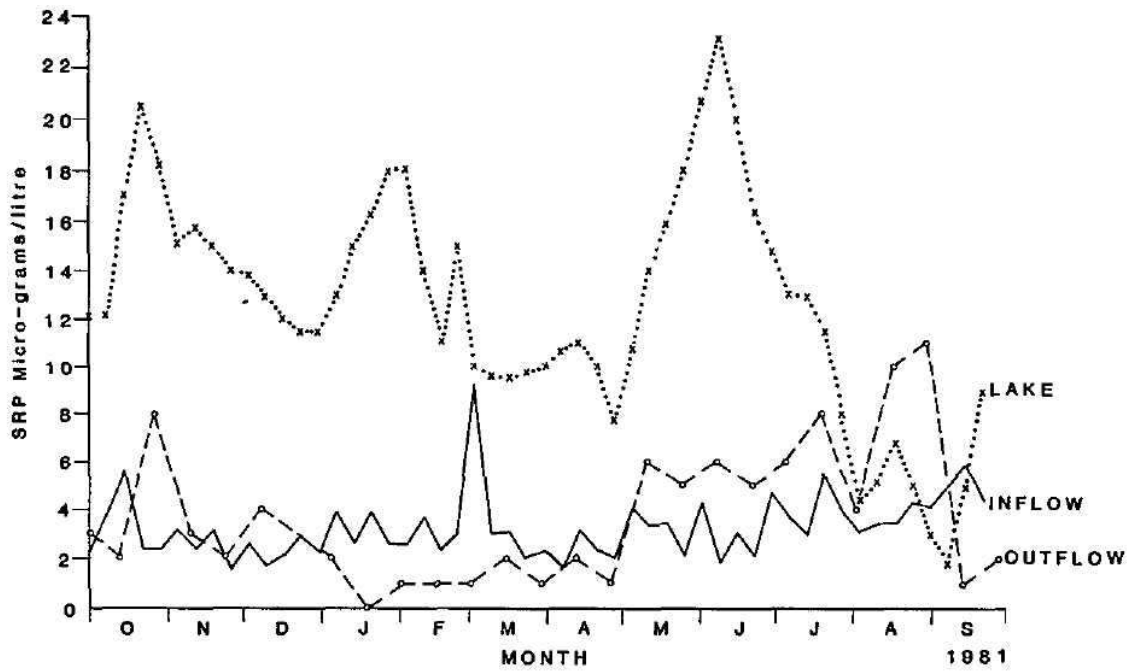


Figure 20 The concentrations of SRP in the inflowing water, the lake and overflow.

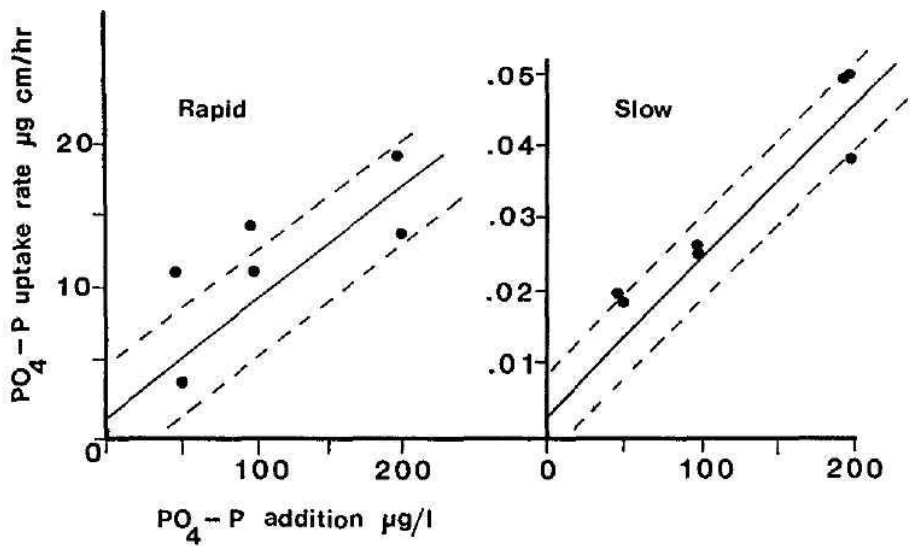


Figure 21 The influence of increasing PO₄-P enrichment sediment/water systems on the PO₄-P uptake rates (solid line obtained by linear regression analysis, broken lines indicate 95% confidence limits).

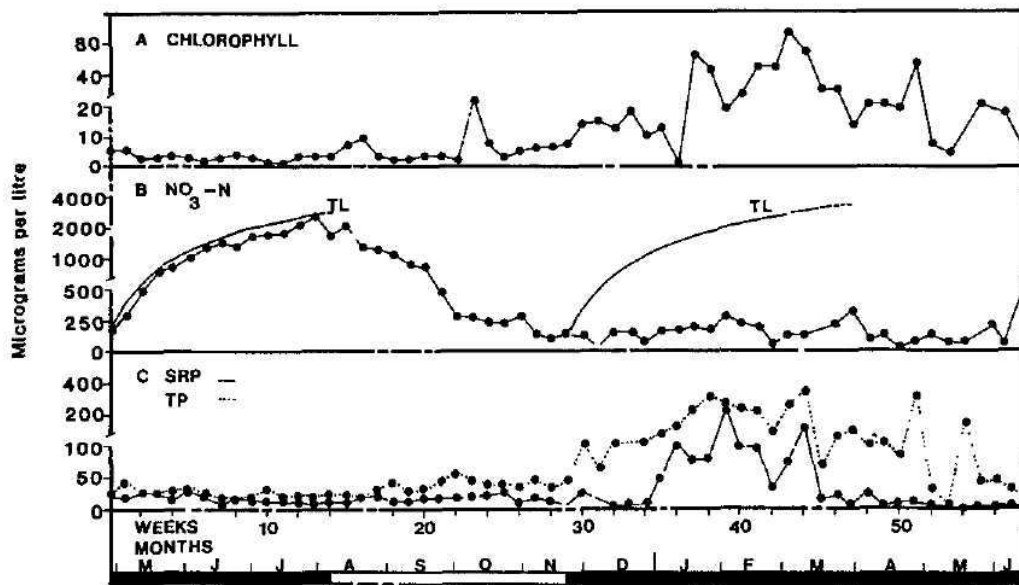


Figure 22 Changes in chlorophyll (A), $\text{NO}_3\text{-N}$ (B), SRP and total P(C) concentrations in the column + N. Total load applied (TL) during the winter period of enrichment and during the first eighteen weeks of the summer period indicated. Shaded areas represent periods of enrichment. A break in the vertical axis represents a change from a linear to a doubling scale.

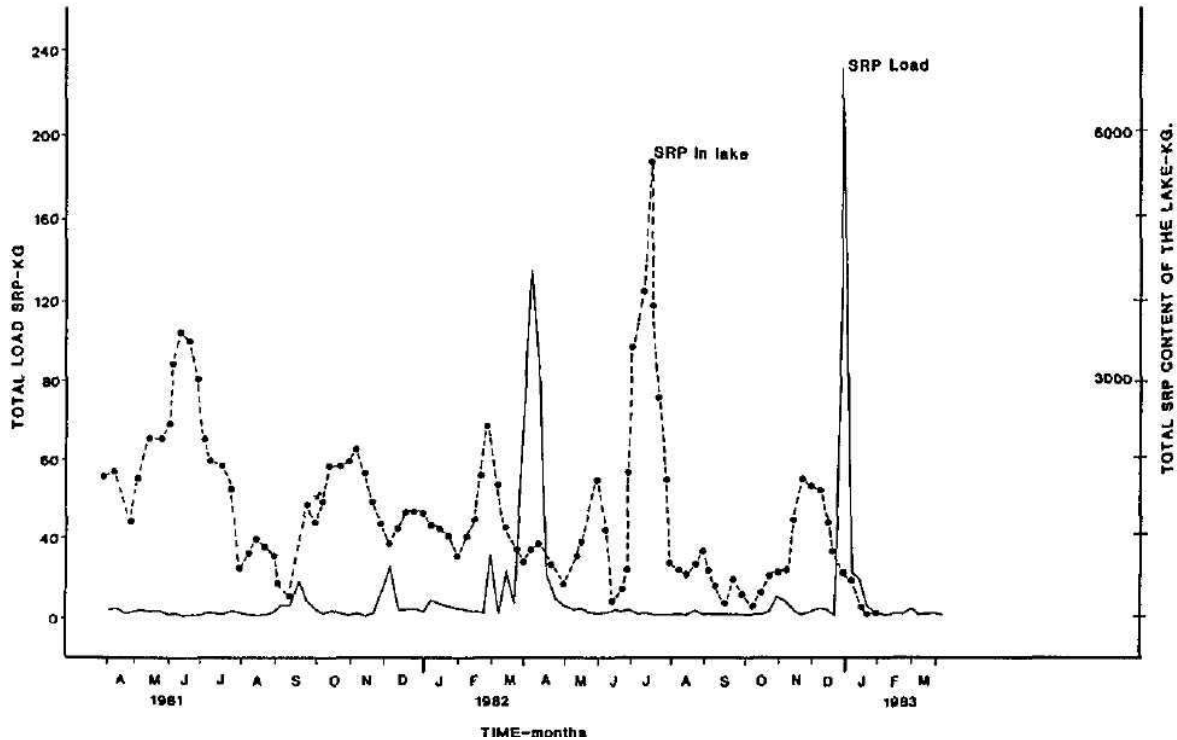


Figure 23 Total SRP load entering Lake Midmar compared with total amount of SRP in the lake. SRP could increase by up to 5000 Kg over a period of 5 weeks when total allochthonous load was ca 10 Kg.

soluble reactive phosphorus which cannot be accounted for by external loading (Figure 23). The data also indirectly support the hypothesis that net desorption is consequent upon algal uptake causing phosphorus concentration to decline below the equilibrium.

This is however not the only process which favours algal uptake of sediment phosphorus. There is considerable evidence in the literature to show that reducing conditions in the sediment result in high concentrations of phosphorus in the interstitial water which, by diffusion or mixing, can elevate the concentration in overlying hypolimnetic water.

However, the extent to which hypolimnetic phosphate contributes to phosphate availability in the epilimnion is not clear since diffusion through the metalimnion is slow. Being a shallow dendritic lake, exhibiting weak stratification and poor hypolimnion development, Lake Midmar is probably dominated by aerobic sediment/water exchange processes.

The extent to which 'internal'¹ or 'autochthonous' loading occurs in the turbulent Lake Midmar may be gauged from the data in Figure 23. These data show that the total amount of SRP held within the water of Lake Midmar may increase by 5000 kg even when little or no allochthonous loading was detectable and provides convincing evidence of the potential for internal loading to influence algal production.

Another striking facet of the data in Figure 20 is the considerable elevation of SRP concentration above the equilibrium concentration. At least two plausible explanations may be offered:

Reducing conditions prior to entrainment of sediments into the water column enhanced desorption and solubility so that the interstitial water contained high concentrations which raised levels in the overlying water when mixing occurred. Three observations make this improbable; the sediments contain too little (ca. 3%) organic carbon to permit reducing conditions to develop to a significant degree; the surficial sediments are resuspended too frequently, and the dilution effect resulting from mixing of interstitial water with the overlying water would be so great as to yield only small increases in SRP.

The second explanation is based on the observations that SRP may include phosphorus fractions which, unlike PO_4^{3-} , do not exchange freely with the sediment. When labelled soluble-P was fractionated on a Sephadex column and the fractions were placed over sediment cores, only the PO_4^{3-} fraction exchanged directly with the sediment (Figure 24). The origin of these large molecular mass colloidal phosphorus fractions which do not exchange with the sediments, and which may therefore explain the apparent anomaly of SRP concentration in excess of the equilibrium, is discussed later.

Exchange with inorganic suspensoids

This aspect has not been addressed to any degree in the present study but, because of its potential significance, a brief assessment of current views on phosphorus exchange with suspended sediments is given.

An essential difference in concept between exchange with sediments and with suspended sediments is that in the former algae may have closer contact with the sediments, whereas in the latter both are in motion, and direct prolonged contact is not established. Although there is evidence that sediments contain considerable amounts of potentially available phosphorus (e.g. Grobler and Davies 1979, Howard-Williams and Allanson 1980, Furness and Breen 1978), surprisingly few attempts have been made to assess availability while the sediment is in suspension. Chass and Styles (1980) measured release from sediments suspended in 0,01 M nitrilotriacetic acid and concluded that available particulate phosphorus may be as much as 15 times greater than the SRP. De Pinto et al. (1981) used a more 'natural' approach in which suspended algae were separated from suspended sediment by a 0,45u pore size membrane. Their studies demonstrated conclusively that the release of available phosphorus from the suspended sediments could be described by a first order saturation function of the biologically available phosphorus:

$$BAPP(t) = AP I - EXP(-0,171t)^2$$

where BAPP (t) = cumulative available phosphorus released from sediments (ug P/100 mg dry sediment).

AP = ultimate available phosphorus in a new sample (ug P/100 mg dry sediment).

0,171 = rate of release of available phosphorus from sediments (per day).

t = incubation time of sediments in lake water column (days).

In an assessment of the possibility of phosphorus release from river-borne sediments when they enter Lake Erie, De Pinto et al. (1981) concluded that there was a strong probability that sediments would be transported a considerable distance before all the potentially available phosphorus had been released. Release is, however, dependent on a dynamic sediment/water phosphate equilibrium (as already discussed in relation to bottom sediments) and in some instances, i.e. under polluted conditions, river borne sediments may reduce soluble phosphate concentrations in the water via adsorption, whilst in others steady state equilibrium conditions can be maintained.

These data implicate sediment associated P as a potentially important contributor to phosphorus loading in the lake and support the observations made at Lake Midmar which show periods of very significant internal phosphorus loading.

Algae water exchange

Algae take up most, if not all, of their phosphorus as PO_4 and the biological availability of phosphorus in fresh water is dependent on the dynamic exchange with suspended inorganic sediments has already been considered and attention here is directed at the soluble forms of phosphorus.

Soluble fractions and phosphorus availability

Where PO_A was used as a tracer to generate labelled phosphorus fractions in Midmar lake water, fractionation of the soluble components showed the progressive incorporation of $^{32}PO_4$ into a colloidal fraction with a molecular weight 5000 (Figure 25). Thus at least two soluble

fractions are involved in dynamic exchange, and their availability for algae was assessed using algal bioassays in which observed yield could be compared with the yield predicted from the concentration of SRP (Twinch and Breen, 1982). This permitted comparison of the chemically measured SRP and the amount of phosphorus actually used by the algae in the bioassay. The relationship between SRP and SBAP (soluble biologically available phosphorus) shows that the ratio of SRP:SBAP decreased with increasing SRP concentration (Figure 26). These data indicate that when SRP concentrations were low the algae were able to use additional sources of phosphorus, such as the colloidal fraction. At low concentrations the conventional SRP analysis may therefore underestimate the amount of phosphorus available to the algae.

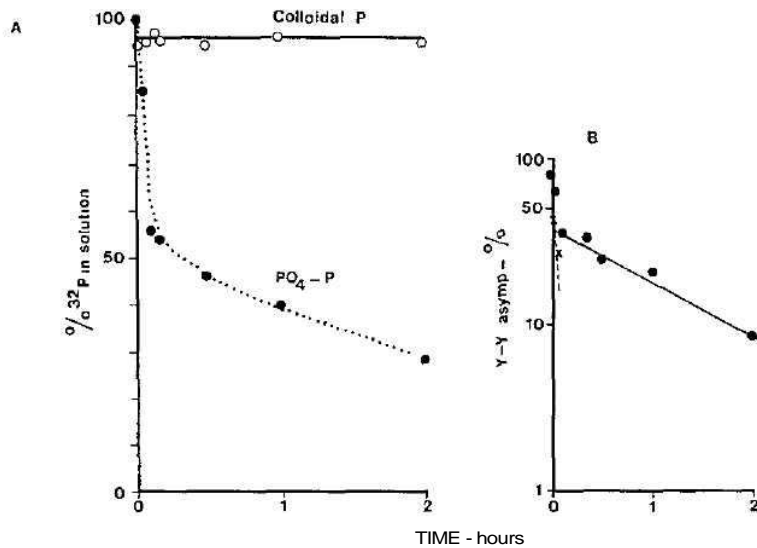
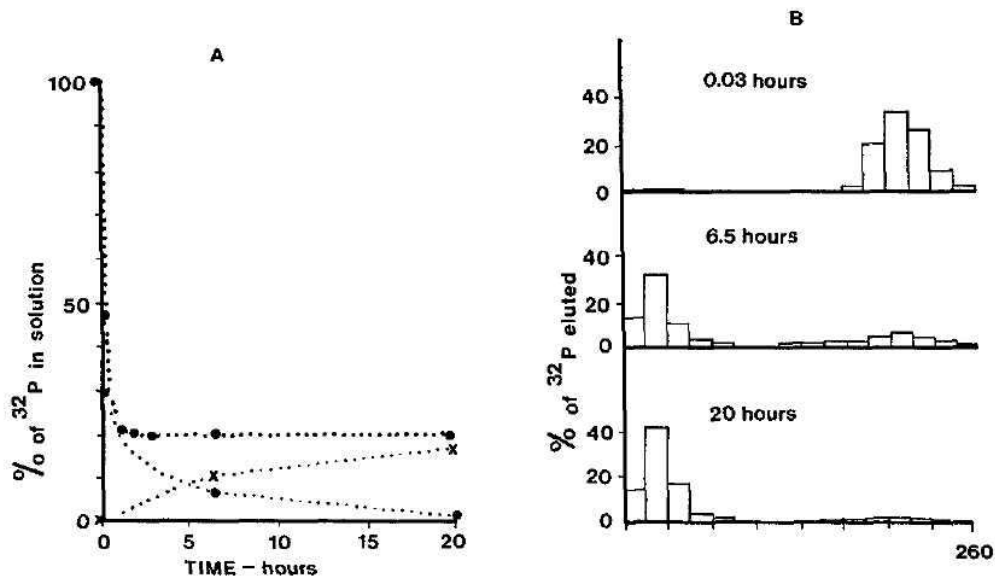


Figure 24A Uptake of labelled PO_4-P and colloidal-P from filtered lake water by intact sediment cores

24B Semilog plots of the difference between percent ^{32}P in solution and that at equilibrium



100 140 160 220
Elution volume - ml

Figure 25A Proportions of total ^{32}P , ^{32}P $\text{PO}_4\text{-P}$ and colloidal -P in solution during an uptake experiment.

25B Distribution of the soluble-P fractions at different times during the experiment.

Exchange Kinetics

The tracer uptake kinetics in Midmar water were, with four exceptions adequately described by a single exponential function indicating that exchange was monophasic (Table 17). This need not imply that there are only two compartments involved in the exchange, and although living organisms are generally predominant in the exchange (Tarapchak et al. 1981), a role for fine colloidal inorganic material passing through the 0.04 μ pore size filter could not be discounted. Exchange was apparently slower than with the sediments (Table 16) indicating that the biota would not compete well with sediment for PC⁺ when it enters the lake, particularly if the lake is turbulent and PO⁴ is rapidly brought into contact with the sediment.

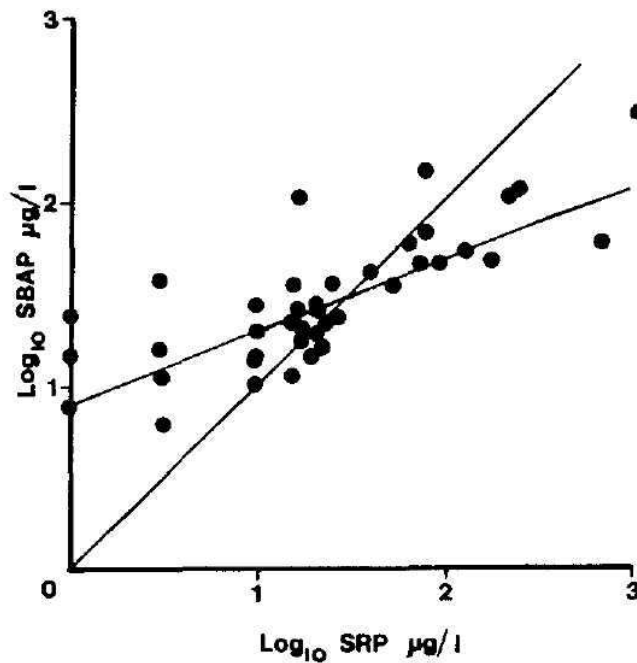


Figure 26 Log plots of SRP versus SBAP. The line was fitted by linear regression and the 1:1 ratio between parameters is shown. Regression equation : $\text{Log}_{x0} \text{ SBAP} = 0.9 + 0.41 \text{ Log}_{x0} \text{ SRP}$.

Table 17 Data describing the exponential transfer curves obtained when $^{32}\text{PO}_4$ was added to Lake water during 1978. The coefficient of determination (r^2) indicates good fit and the uptake is therefore monophasic. Data from Twinch (1980).

Date	r^2	Rate constant k/min
12/2	0,95	0,001
27/2	0,99	0,052
13/3	0,98	0,084
28/3	1,00	0,037
11/4	0,98	0,291
24/4	0,99	0,035
28/5	0,98	0,004
\bar{x}	0,98	0,030

The evidence indicates that PO_4 is transferred fairly rapidly, by biotic processes, to large molecular weight organic compounds which are released into the water (Lean 1973). Since some of these are measurable as SRP because of acid hydrolysis during the analytical procedure (Stainton 1980) they would be included in the estimate of SRP in the lake even though they may not exchange directly with the sediments. The data in Figure 24 show that colloidal phosphorus did not exchange directly with the sediments and, although colloidal P was not shown to contribute directly to SRP in Lake Midmar water, it has been shown using analogous fractions from other lakes (Stainton, 1981). The observed high SRP concentrations in the lake need not therefore reflect PO_4 concentrations in excess of the equilibrium; they may reflect the build up of colloidal phosphorus by biotic action. Periodic increases in SRP above the equilibrium concentration do not therefore detract from the hypothesis that net uptake or net release from the sediments reflects disturbance of the equilibrium. The ultimate fate of organically bound phosphorus is release as FO_4 whence it re-enters the dynamic PO_4 pool and may exchange with algae, inorganic sediments or lake-bottom sediments.

The capacity of the biota to take up PO_4 and release it in a form which cannot be sorbed directly onto the sediments, serves to temporarily isolate PO_4 probably derived from sediment desorption, since inflow SRP concentrations are usually lower than in lake concentrations from the sediment, and prolong its availability in the water column.

Implications for lake management

Under conditions of low nutrient loading the lake acts as a net sink for total phosphorus largely because of the deposition of silt. It can however act as a net source of SRP when various in-lake processes (desorption and algal uptake) elevate lake concentrations above those in the inflowing water. In practical management terms however, whether it is a source is of little consequence. More important is its behaviour under increased loading.

Under conditions of increased loading sorption is expected to predominate for four reasons; (i) sediment sorption rates are very rapid when the equilibrium concentration is exceeded; (ii) the high degree of turbulence ensures favourable conditions for sorption of phosphorus by

the sediments; (iii) the equilibrium concentration is low relative to the phosphorus concentration in the inflowing water; (iv) perhaps the most important is that nitrogen closely follows phosphorus as the growth rate limiting nutrient so that unless increased phosphorus loading is accompanied by increased nitrogen loading the algae cannot take advantage of available phosphorus.

These factors combine to buffer the lake against the consequences of increased phosphorus loading in the inflow, and make the lake responsive to management for eutrophication control provided nitrogen loading is controlled. This aspect is discussed in more detail in Chapter 7.

Key questions and answers

1. How rapidly can PC₂ be released from the substratum?
The maximum measured release rates were 32 mg/m²/d. This potential release greatly exceeds allochthonous loading, but it is never realised under natural conditions.
2. What is the extent of the pool of available P in the sediment?
At a conservative estimate ca 2ug/mg of sediment phosphorus is available to algae. Since the first two centimeters of sediment are involved in exchange, there is considerable algal-available phosphorus.
3. How does the character of the substratum change with enrichment?
Phosphorus becomes less tightly sorbed onto the sediment and hence more freely available. The potential is for increased internal loading and reduced response' to management.
4. How does the biotic component induce phosphorus accumulation above the equilibrium concentration?
The biota take up P(\ and release it in an organic form which does not exchange directly with the sediments.
5. Can eutrophication be induced by addition of nitrogen alone?
Yes, but the response is slow. This situation was used to derive phosphorus release rates and is not likely to occur under natural conditions since sewage effluent contains both nutrients.

The preceding Chapters show that productivity of Lake Midmar is dependent on external nutrient supply and on within lake processes which affect both the availability of nutrients and the physical environment. The next Chapter therefore considers the interaction of these factors in productivity.

5. PRIMARY PRODUCTION

5.1 THE PHYTOPLANKTON

R. N. Pienaar

Introduction

The algae growing suspended in the water column (phytoplankton) are the principal organisms involved in the biotic response to enrichment with nutrients, and are therefore used as an index of water quality. Oligotrophic systems, such as Lake Midmar, are usually characterised by a diverse phytoplankton composition and this decreases with eutrophication until the algal community is overwhelmingly dominated by a few species.

Few detailed studies have been made of the phytoplankton in South African lakes and consequently the changes that have taken place during eutrophication are poorly documented. This study was initiated principally to provide a record of the existing phytoplankton community structure against which future changes could be measured. Additional objectives were to identify the major determinants of spatial and temporal variation.

Phytoplankton identification

The identification of phytoplankton is notoriously difficult because of their often similar small size and shape. In addition, certain cells are adversely affected by the fixation process, so much so that they are either totally destroyed or changed to such an extent that they are not recognizable during the counting process. This in effect means that counts do not necessarily depict the dominant taxa but possibly those that have resistant cell walls, pellicles and/or thecae, which enable them to retain their characteristic shape thereby allowing them to be more easily identified during the counting procedure.

Representatives of the following classes of algae recorded in Lake Midmar exhibit this phenomenon:

- i) Class Euglenophyceae - particularly the more delicate colourless euglenophytes;
- ii) Class Dinophyceae - many of the small unarmoured dinoflagellates which occur in freshly collected samples from Lake Midmar disintegrate when fixed and are not observed during the counting procedure;
- iii) Class Chrysophyceae - although quite common in the freshly collected samples they were almost absent when fixed material was counted - e.g. PARAPHYSOMONAS was a common flagellate but never observed in the fixed material.
- iv) Class Cyanophyceae (Cyanobacteria) - a very important group in Lake Midmar. The small unicells were particularly difficult to identify with any certainty. One major concern that should be mentioned is the rare occurrence of MICROCYSTIS in the counted material. MICROCYSTIS was frequently observed in large numbers in plankton-net hauls and in the living phytoplankton samples. It

was, however, rarely observed in the colonial form in the counts. This could mean that either the colonies never sank during the settling period or that the colonies disassociated and that some of the very tiny prokaryote cells counted could have been single cells from disassociated MICROCYSTIS colonies.

Phytoplankton diversity

In this report attention is focussed on the major classes and the number of genera in each class (Table 18).

A total of 135 taxa belonging to 102 genera were identified. Some of these identifications should, at this stage, be regarded as tentative.

Table 18 Summary of representatives of the various algal classes found at Main Basin Station, Lake Midmar from 7/10/80 - 27/10/81

ALGAL CLASS	Genera	Taxa
Cyanophyceae (Cyanobacteria)	8	9
Bacillariophyceae	17	22
Chrysophyceae	8	10
Cryptophyceae	3	3
Euglenophyceae	5	9
Dinophyceae	2	3
Xanthophyceae	4	4
Chlorophyceae	53	70
Prasinophyceae	2	2
Incertae Sedis		3
Total	102	135

The most important algal classes were the Bacillariophyceae, Cyanophyceae, chlorophyceae and the Cryptophyceae and representatives of these four algal classes made up the major component of the phytoplankton population in Lake Midmar.

Taxa belonging to the other five algal classes were never found to make up a significant percentage of the total phytoplankton population.

Seasonal variation Class

Bacillariophyceae

During October 1980 the diatom MELOSIRA GRANULATA was very common in all the samples, making up to 94% of the total population. Numbers dropped towards the end of October and there were two small increases in diatom numbers during mid-November and December. Thereafter the numbers of diatoms remained low throughout late summer to the end of May with a small increase having been detected during mid-February,

During June 1981 there was an increase in MELOSIRA GRANULATA followed by a steady decline during August 1981 which levelled out in September/October.

In most of the samples that were analysed the majority of the MELOSIRA GRANULATA cells tended to accumulate in the deeper waters. It would

appear that this could be attributed to the presence of the dense siliceous frustule found in diatoms.

Class Cyanophyceae

It is interesting that the Class Cyanophyceae showed an almost opposite response when compared with the Bacillariophyceae. When MELOSIRA was blooming in October 1980 the Cyanophyceae made up only 14-20% of the population in surface waters and 1-12% in the deeper waters.

As the summer months proceeded the number of Cyanophyceae algal cells increased dramatically and were usually detected in high numbers in the surface to 6 metres of the water column. The maximum number of blue-green algal cells was found in mid-summer (December) to late summer/early autumn (mid-April). During the early summer months blue-green algae formed 70-90% of the phytoplankton population in the upper seven meters. During mid-March they were evenly distributed throughout the 13 metres of the water column. This trend continued from mid-March through to the end of May. A slight increase in blue-green algae was detected during the winter months but was four times smaller than the maximum numbers in the late summer samples.

Numbers again increased during early spring (September/October 1981) when they made up to 70-90% of the phytoplankton populations. They were much more prevalent than the MELOSIRA GRANULATA when compared with their numbers a year earlier (October 1980).

The important blue-green algae on a numerical basis were:

- a) MERISMOPEDIA - common during the blue-green algal peak.
- b) the "Pamella" - which is a name having no taxonomic status, could be cells that may be related to ruptured MERISMOPEDIA colonies
- c) MICROCYSTIS - was found to be present in some samples. To place the counts in perspective it should be noted that a single colony of MICROCYSTIS may be made up of many hundreds of very small cells and as each cell was counted individually the numbers of MICROCYSTIS cells could increase rapidly even though there were few colonies. MICROCYSTIS was found in large number only during the summer months in 1980 (December) and in spring (October 1981).

Class Chlorophyceae

The green algae did not exhibit any clear patterns as did the Cyanophyceae and Bacillariophyceae.

The major development of the green algal population occurred during October and November 1980 with CRUCIGENIA being the dominant during February-March 1981 (mid-summer) and BOTRYOCOCCUS BRAUNII was found to be the dominant species during the late summer months (March-April 1981).

The dominant members of the Chlorophyceae during the period October 1980 October 1981 were: CRUCIGENIA SP., BOTRYOCOCCUS BRAUNII, ANKISTRODESMUS SP., EUTETRAMORUS SP., COELASTRUM SP., AND SCENEDESMUS SP.

The Chlorophyceae tended to accumulate in the surface samples, however there were occasions where large numbers of green algae occurred at certain depths. A striking example was on 14 October 1980 where the numbers of green algal cells increased, at a depth of 5 metres, to the extent that they made a major contribution to the total population.

The maximum concentration of green algal cells (63% of the total population) was found at a depth of 6 metres during spring 1980 (21-10-1980).

Class Cryptophyceae

The distribution of cryptomonad flagellates was very erratic with respect to season. They were however found at greater concentrations in the first 5 metres of the water column except during December 1980, late January and September 1981, where they occurred more frequently at depths of 6-9 metres.

There were two common cryptomonad genera CHROOMONAS and CRYPTOMGNAS and they made up to 38% of the total phytoplankton population.

Class Chrysophyceae

Representatives of this class formed a small percentage (never more than 7%) of the total phytoplankton population and did not show any very marked seasonal fluctuations, with marginally more cells being found in December 1980 and again in February and October 1981. The two commonly recorded chrysophytes were DINOBYRON AND MALLOMONAS. The pattern of distribution did not appear to be related to depth.

Class Euglenophyceae

This class was not numerically important, as it never comprised more than 2% of the total population during the study period. The most commonly counted genus was TRACHELOMONAS which was found between October 1980 and December 1981. TRACHELOMONAS did not show much variation in its numbers with respect to depth although it occurred less frequently between 11 and 13 metres.

Class Dinophyceae

During the study period dinoflagellates were rarely counted in fixed material, probably due to the fact that unarmoured dinoflagellates were not preserved. They never comprised more than 0,25 % of the total population.

The depth/distribution relationship

There were several occasions when the distribution of different algal classes was related to depth at the Main Basin sampling site. The most striking examples were detected in the Class Bacillariophyceae and Cyanophyceae which showed almost opposite patterns of distribution down the water column. The diatoms at the start of the programme were very common at all depths in the water column but reached their highest numbers in the deeper water. Maximum numbers were always found between 9 and 13 metres. This could be attributed to the dense siliceous frustules which they possess causing them to sink but other explanations are possible. It has been conclusively shown that certain diatoms, including the centric diatoms, are able to regulate their position in the water column at a depth favouring maximum growth rate. This has not, as far as I am aware, been conclusively demonstrated for MELOSIRA GRANULATA despite it being a centric diatom.

The situation on 4 November 1980 may be taken as an example. Diatoms made up only 3% of the total population at the surface whereas at a depth of 12 metres they comprised 85%,

A contrasting situation was observed in the blue-green algae, where the majority of cells were found in the first 5 metres and low numbers occurred in the deeper waters. Their contribution to the total phytoplankton population varied between 90% at the surface and 0% at a depth of 12 metres.

The Chrysophyceae exhibited a similar distribution with respect to depth as the diatoms, with the maximum numbers occurring at the lower depths. In contrast, the Chlorophyceae did not exhibit a clear-cut trend in distribution with respect to depth, and high numbers occurred irregularly down the depth profile.

In occasional samples the green algae were found as large populations at a particular depth. On 14/10/80 for example, they contributed the highest percentage of total population (37%) at 5 metres and a similar trend was observed on 21/10/83 when they comprised 63% of total population.

Succession and seasonality

Physico-chemical and biological factors interact to cause seasonal and short-term fluctuations in phytoplankton standing crop and species composition. These interactions are discussed in Chapters 5.3 and 5.4.

5.2 SEASONALITY IN THE RATE OF PRIMARY PRODUCTION

E. G. J. Akhurst

Introduction

In spite of the differences that exist between lakes with respect to the phytoplankton of the pelagic waters a number of consistent features can be identified (Wetzel, 1976). These include the constancy of seasonal changes in phytoplankton biomass and numbers from year to year, on a short term basis, in the absence of perturbations by outside influences. Further, these changes in phytoplankton populations are often out of phase with the seasonal periodicity of primary productivity which in temperate oligotrophic lakes is clearly associated with the seasonal pattern of solar insolation. A similar periodicity might be expected in South African impoundments, however, by virtue of their geographical location the seasonal variation on an annual basis is not as pronounced. Thus, with respect to the pattern of stratification, South African impoundments can be generally classified as warm monomictic whereas the northern temperate lakes are cold dimictic systems.

This has important implications particularly during the spring period which in dimictic systems is a transitional phase between the breakdown of winter stratified conditions and the establishment of summer stratified conditions. Consequently during spring nutrient rich hypolimnetic waters are mixed throughout the water column at a time when water temperatures and solar irradiance are increasing. In contrast in a monomictic system, like Lake Midmar, mixing occurs throughout winter so that during spring when water temperatures and solar irradiance are increasing this is not accompanied by nutrient enrichment as it would be in dimictic systems. However, because of the seasonality of rainfall and river flow in the Lake Midmar catchment, the pattern of external (allochthonous) nutrient loading is markedly seasonal with a summer maximum.

This chapter considers the relationship between changes in the physical and chemical environment, the phytoplankton, and their productivity in Lake Midmar. It aims to establish:

- i) the extent of seasonal changes in the physical and chemical environment;
- ii) to what extent these changes influence the phytoplankton and primary productivity;
- iii) the implications of these findings for predicting the response of the lake to changing conditions.

The physical and chemical environment

The physico-chemical limnology and factors influencing the attenuation of light within the water column, i.e. the underwater light climate, have been described in Chapters 4.1 and 4.2. In this Chapter the seasonal changes in only those components likely to influence the phytoplankton and their productivity viz., water temperature, incident solar irradiance (I_0), river flow and external nutrient loading in relation to in-lake nutrient concentrations, are considered. There was marked seasonal periodicity in the mean monthly water temperatures of the surface waters

(0 - 5m) and hence of the euphotic zone (Figure 27a). The differences in the range of mean monthly water temperatures between 1981 (11,6 - 24,2° C) and 1982 (12,3 - 22,8°C) were small and probably not significant. The pattern of mean monthly irradiance incident at the lake surface (Figure 27b) while also seasonal was not as distinct as that for water temperature. The differences in mean monthly irradiance between 1981 and 1982 were more pronounced particularly during the summer period (October to March). These differences can be explained by postulating a greater incidence of cloud cover during the day in 1982 which, while reducing the effects of solar insolation, exerted a greater influence on the incident irradiance rather than on water temperature.

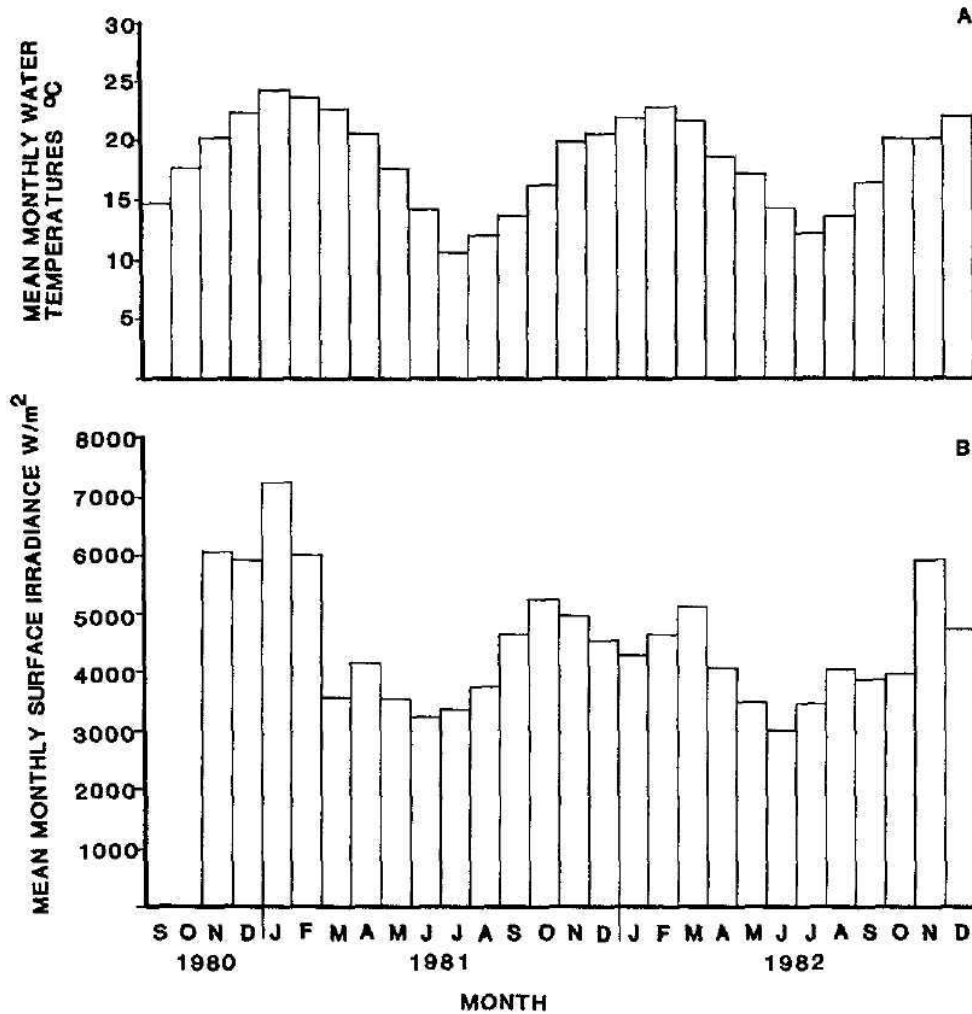


Figure 27 Seasonal changes in mean water temperature (0 - 5m) in euphotic zone (A) and incident irradiance in (B) at Main Basin Station,

The underwater climate was determined primarily by in-lake processes (Chapter 4.2) and was thus not directly influenced by variation in the surface irradiance, I_0 . Nevertheless, changes in I_0 for a particular light climate did influence aspects of the productivity depth profile (Figure 28). This influence was evident as changes in the depth at which the light saturated rate of productivity, A_{max} , was measured and the proportion of the profile that was light inhibited, and is discussed later (Chapter 5.3). It is clear that I_0 by itself was not limiting productivity since on only two overcast days was the maximum value of productivity measured at the surface, on all other occasions, maximum productivity was measured below the surface of the water column. The depth ranged between 0,25 and 2 m with a mean of 0,7 m.

Riverflow being determined by events within the catchment is influenced by both the pattern of rainfall and properties of the soils present in the catchment. For the Mgeni river, which accounts for more than 70 % of the total river input to Lake Midmar, it can be seen that pattern of river flow and hence external nutrient loading is markedly seasonal (Figure 29) with river flow increasing in October through March and reaching a maximum in late summer/autumn (February - April). This pattern was evident in both years despite the drought which reduced the river inputs to Lake Midmar significantly.

The concentrations of soluble reactive phosphorus (SRP) and nitrate nitrogen within the lake did not show a seasonal pattern (Figure 30). This lack of periodicity was expected since the changes in nutrient concentrations within the lake reflect the balance between external and internal processes (Chapter 4.5). The extent to which changes in river flow have an effect is determined by the concentration difference between the incoming river and the lake, and relative volumes of inflowing and stored water. However, because nutrients (particularly phosphorus) may enter in a form (soluble) different from that predominant in the lake (particulate), river inputs may, while not causing a change in the concentration in the lake, provide a source of nutrients more readily available to the phytoplankton than those already present within the lake. This aspect requires further study because it has important implications which will be discussed later.

Changes in primary productivity

The form of the productivity - depth profile (Figure 28) in Lake Midmar was found to be similar to that reported in other freshwater and marine studies. With the exception of two overcast days, the profile had both a light inhibited and light limited component. The lower limit of the profile, defined by the euphotic zone, showed a strong seasonal variation (mean depth of euphotic zone 3 m range 1,4 - 5,4 m) and was greatest in the summer months. The factors influencing this pattern have been described in Chapter 4.2. The depth at which the light saturated rate of production, A_{max} , was measured varied between 0,25 - 2 m with a mean value of 0,7 m and although influenced by changes in the surface irradiance I_0 , it was determined primarily by light attenuation within the water column.

The area enclosed by the productivity - depth profile is termed EA, the hourly rate of production per unit area as $\text{mg C/m}^2/\text{hr}$ and is used in the calculation of EEA, the daily rate of production per unit area as $\text{mg C/m}^2/\text{d}$, and the annual estimate of phytoplankton primary productivity.

The changes in the values of EA and EEA measured during this study are presented in Figures 31 and 32 together with mean values and ranges for 1981 and 1982.

From these results it can be seen that:

Estimates of the rates of primary production and estimates of annual primary productivity were significantly different (Figures 31 and 32). The increase measured during 1982, at a time when river inputs had been reduced as a consequence of the drought, is of particular interest and possible causes are discussed later;

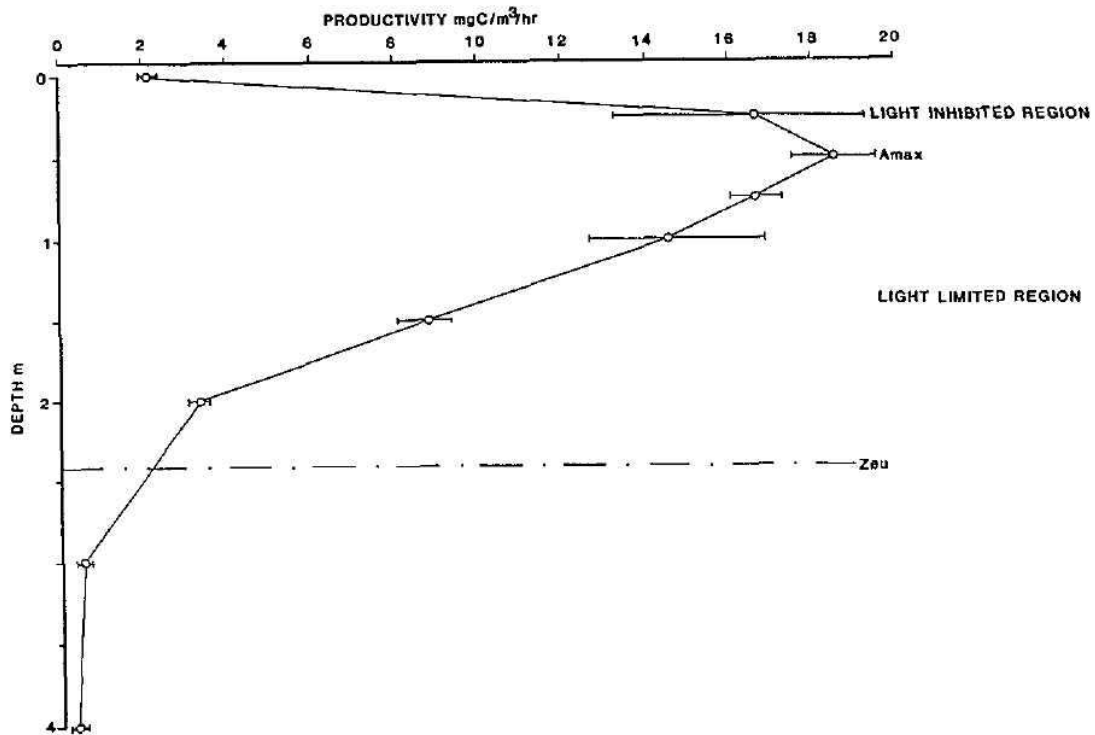


Figure 28 Form of the productivity depth profile.

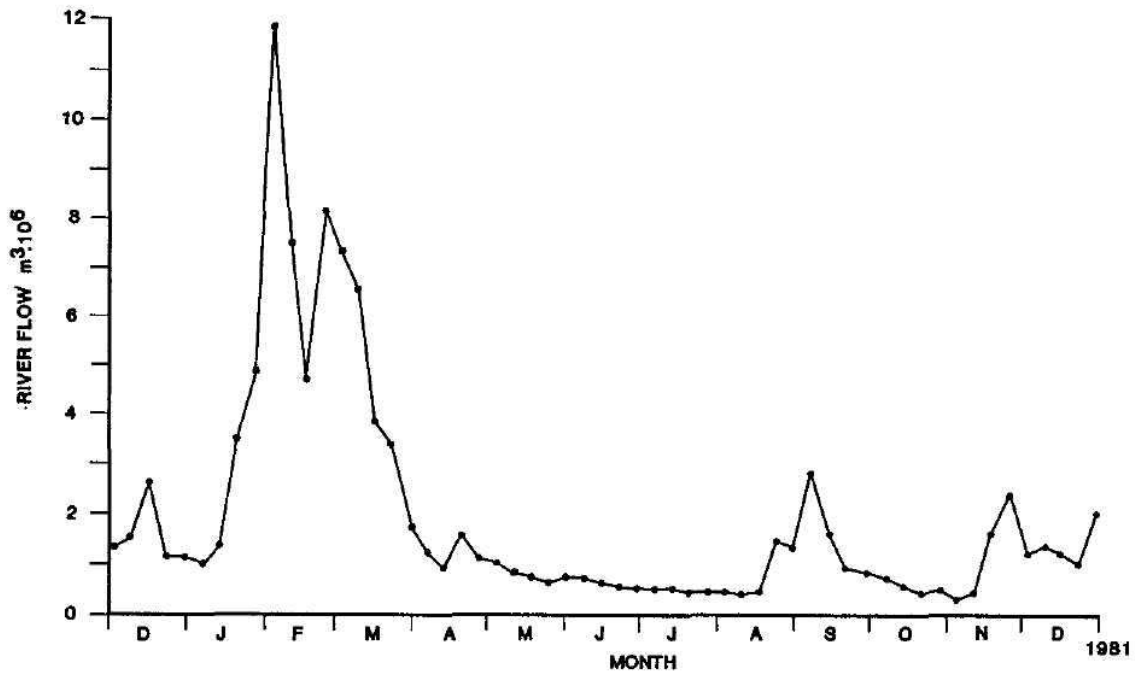


Figure 29 Seasonal variation in inflow of the Mgeni River.

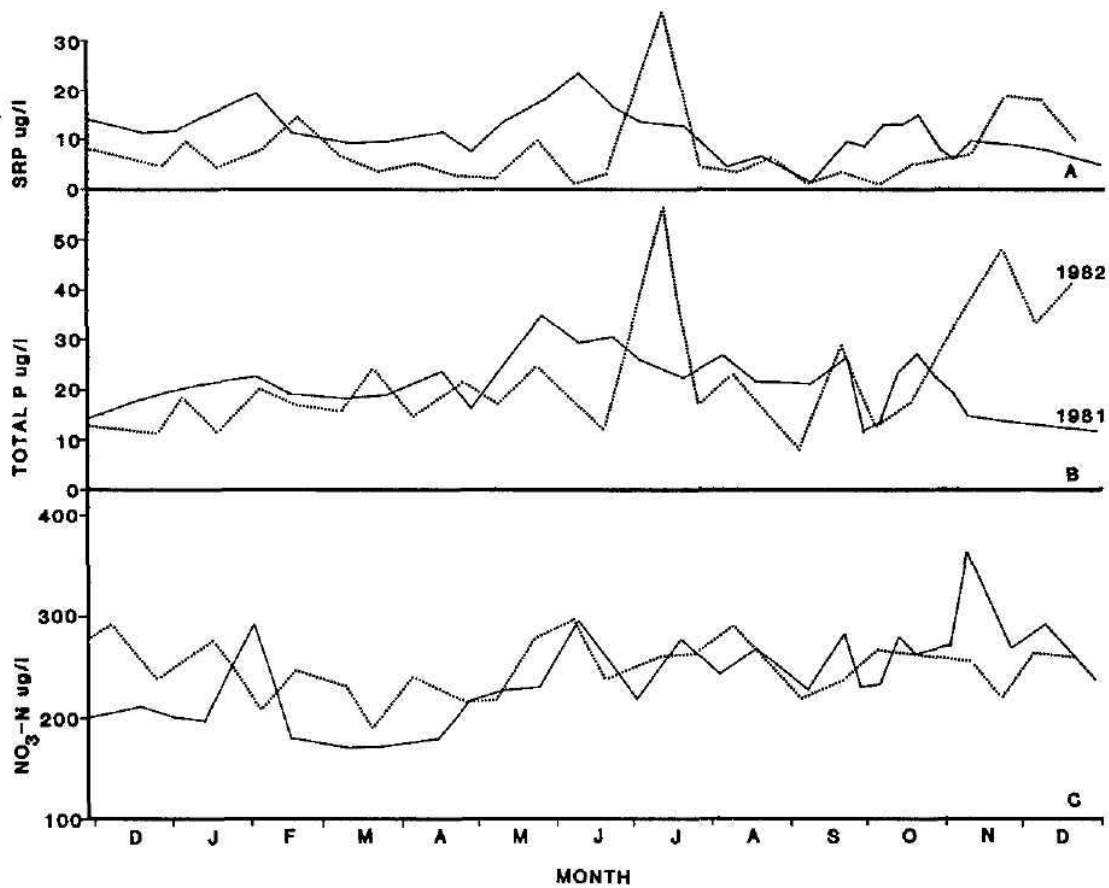


Figure 30 Seasonal variation in concentration of SRP, total-P and NO₃-N at the Main Basin Station.

Despite increasing temperatures and incident radiation during spring there was no evidence of a significant increase in the rate of production (Figure 31). These results indicate that nutrients were the rate limiting factor and that the water column was fully mixed during the winter, as would be expected in a warm monomictic lake.

There was no evidence of seasonal periodicity in productivity (Figure 31). This suggests that changes in water temperature, I_0 and external nutrient loading, which earlier were shown to be markedly seasonal, play a minor role in regulating the peaks of phytoplankton productivity in Lake Midmar. Further when the two years were compared, the differences between water temperature, I_0 and external nutrient loading, were not reflected in the estimates of productivity. It is therefore postulated that in Lake Midmar internal processes, which are not markedly seasonal in their variation, are the major determinants of the variation in productivity. This is not surprising since the internal processes play an important role in nutrient cycling, particularly of phosphorus (Chapter 4.5).

- When the values of primary productivity obtained during this study are compared with those measured in other South African lakes and impoundments (Table 19) it can be seen that they are very similar to those reported for Swartvlei which are the lowest recorded for African lakes (Robarts, 1976). When compared on a worldwide basis (Wetzel, 1976), Lake Midmar can be classified in the ultra-oligotrophic to oligotrophic range.

Table 19 Comparison of rates of primary production of phytoplankton in South African lakes and impoundments of different trophic status

Lake/Impoundment	ΣA mgC/m ² /hr		$\Sigma \Sigma A$ mgC/m ² /d		Source
	Mean	Range	Mean	Range	
Midmar	11,5	4,4-25,9	86,8	17,4-243,2	1981 This study
	24,5	0,9-53,4	162,2	11,5-422,7	1982
Swartvlei	22	13,1-36,9	-	-	Robarts, 1976
Sibaya	-	-	807,6	227 -1847	Allanson & Hart, 1975
Wuras	89,6	19 -192	726,9	129,2-1689,6	1979 Stegmann, 1982
	90,4	28,5-162	723,8	205,2-1425,6	1980
McIlwaine	451,2	248,1-652	3908,9	1640-6030	Robarts, 1979
Hartbeespoort	-	46,3-2292	-	380-17500	1982 Robarts and Zohary (in press)

Species composition of the phytoplankton

Lake Midmar supports a high phytoplankton species diversity representing several algal classes (Chapter 5.1). When species composition by algal class was expressed as a percentage of the total numbers present, four classes were of particular significance viz. Bacillariophyceae (diatoms) Chlorophyceae (green), Cryptophyceae and Cyanophyceae (blue-green). Changes in total numbers of phytoplankton (Figure 33) and the contribution by the four classes (Figure 34) showed that:

- there was marked seasonal variation in phytoplankton numbers with the highest numbers being counted in the summer, October - March (Figure 33);

The Cyanophyceae were dominant during the summer months when the phytoplankton numbers were highest. However, in winter, when phytoplankton numbers are lowest, representatives of other algal classes, in particular the diatoms and green algae, made a greater contribution to the total species composition (Figure 34).

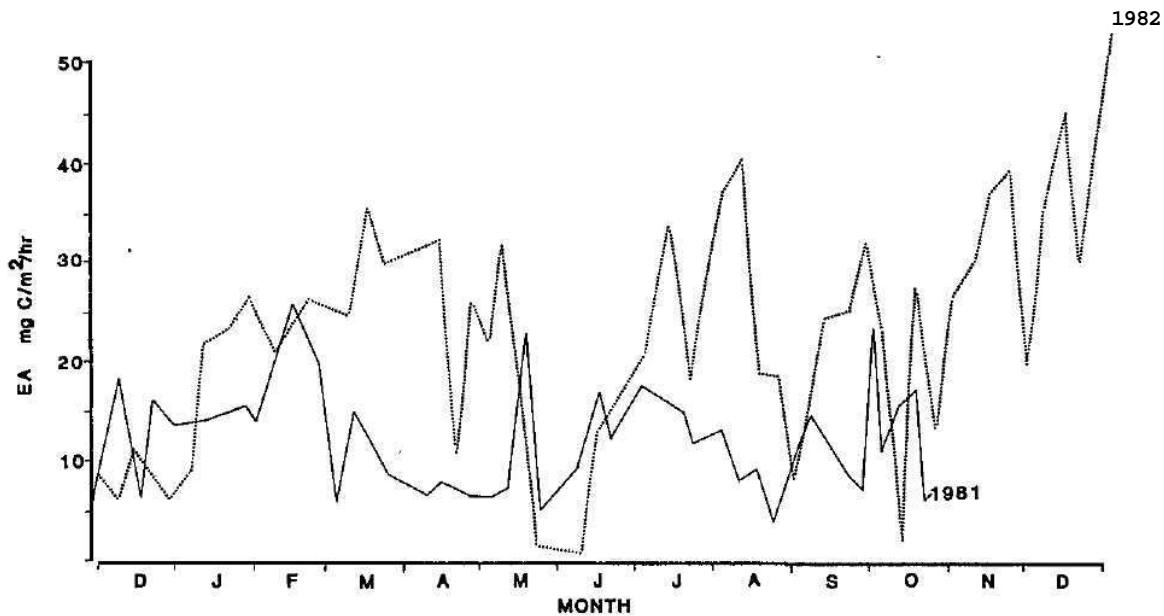


Figure 31 Seasonal variation in EA, mg/C/M²/hr measured at Main Basin Station.

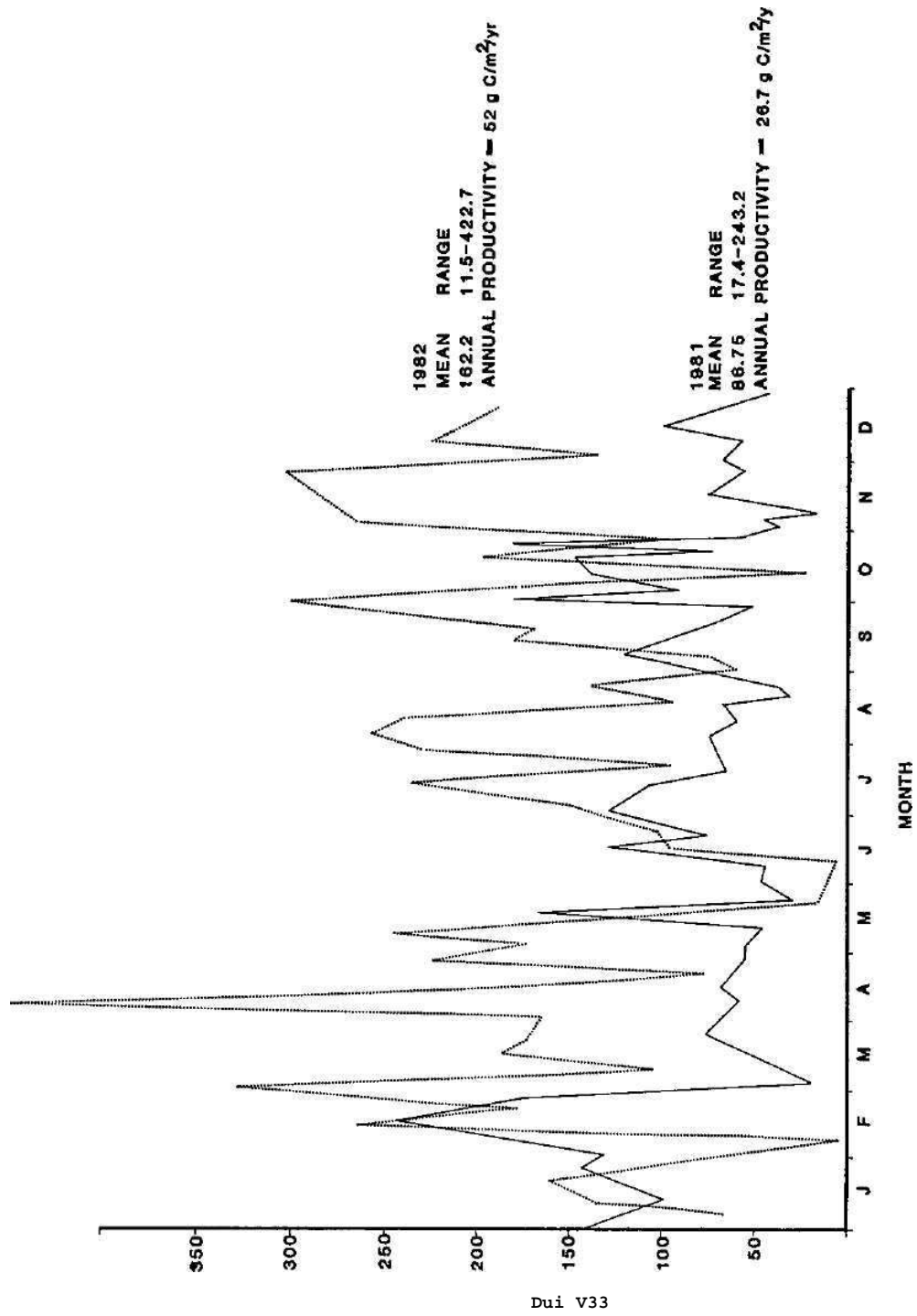


Figure 32 Seasonal variation in EEA or Main Basin Station,

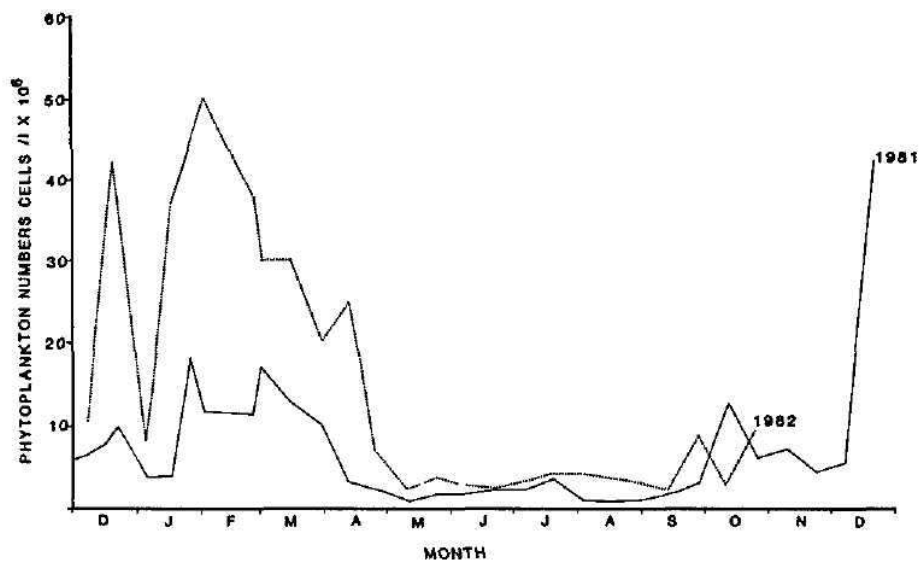


Figure 33 Seasonal variation in phytoplankton numbers.

The periodicity of the major algal classes in 1981 and 1982 appeared to contradict the lack of seasonal pattern in primary productivity. However, this anomaly can be explained by postulating that different classes viz. Bacillariophyceae, Chlorophyceae, Cryptophyceae and Cyanophyceae, differ with respect to their efficiency of production under oligotrophic nutrient conditions. This can be seen if productivity when the numbers of blue green algae were highest, 54 million cells/l EA 26,7 mg C/m²/hr, is compared with that when the diatoms were most numerous, 3 million cells/l EA 37,3 mg C/m²/hr. As a result it would be expected that specific productivity (Amax/B) would also vary according to which algal class was dominant, i.e. contributing more than 50% of the total phytoplankton species composition, at a particular time. The differences between those occasions when blue green algae (mean 3,9, range 0,5 - 9,1 mg C/m⁻² Chi a/hr) and when other algal groups, in particular the diatoms, (mean 4,8, range 0,3 - 12,5 mg C/mgChla/hr) were dominant were not as great as would be expected. However, in comparing specific productivity in this way, it is important to bear in mind the very small size of one of the dominant blue-green algae, 'Palmella' (0,09 - 1,83 mm) relative to the pore size of the filters used for the chlorophyll analyses (Whatman GP/C mean pore size ca 1,5 urn) and productivity estimates (0,45 urn membrane filter). Thus determinations of phytoplankton standing crop (B) made at times when blue green algae were dominant are an underestimate and as a consequence specific productivity (Amax/B) has been overestimated on those occasions. Thus the actual differences in specific productivity between the different algal classes are probably greater than the estimates given earlier.

The differences in efficiency of production shown by members of different algal classes although not accounting for the pattern of variation, would explain the discrepancy between the seasonal variation in numbers and the similarity between productivity estimates measured at different times of the year. This raises the question as to why the diatoms, which are more efficient than the blue green algae in Lake Midmar, did not dominate the phytoplankton throughout the year. Two important controlling factors, the effects of turbulence and selective grazing by zooplankton on the diatom populations, are discussed in Chapters 5.3 and 5.4.

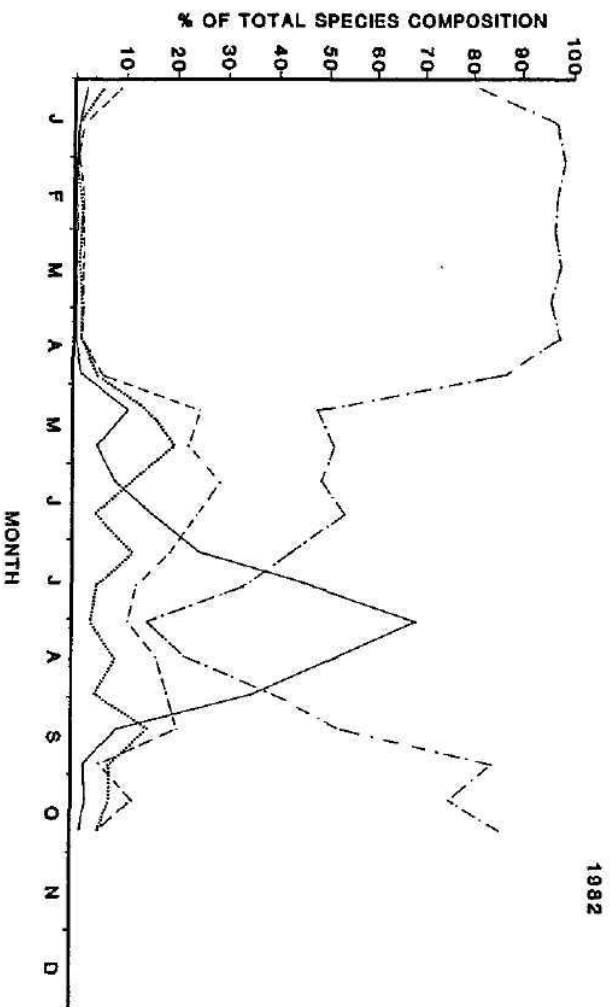
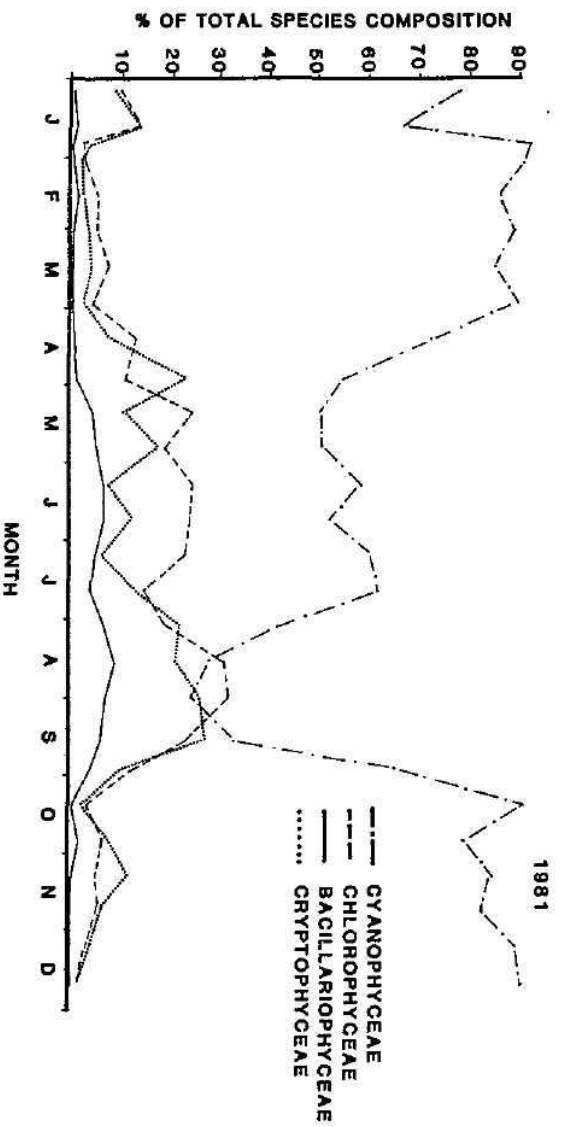


Figure 34A Seasonal changes in contribution to phytoplankton species composition as % of total for the four major algal classes.

34B Changes in the contribution to total phytoplankton species composition as % of total during 1982, for the four major algal classes.

Comparison of the change in phytoplankton numbers (Figure 33) with those in productivity, as EA, (Figure 31) showed that the highest values of EA were measured after the numbers of phytoplankton cells had increased and during the decline phase rather than at times when the numbers were highest. This would be expected in an oligotrophic system where nutrient limitation was the principal factor regulating productivity. Thus at times when the numbers were highest, competition for the available nutrients would be greatest thereby preventing the maintenance of high rates of specific production. However, during the decline phase, when numbers are decreasing, the competition for nutrients would be reduced and this together with mineralization of dead algal cells would lead to an increase in the pool of available nutrients. Similarly the differences in phytoplankton numbers and productivity between 1981 and 1982 (Figures 31 and 33) can be explained by postulating a greater turnover of nutrients through internal processes during 1982. Thus while the concentrations of SRP measured during 1981 and 1982 were not significantly different (Figure 30) the rates of exchange, between the different components of phosphorus cycle, must have increased thereby making more nutrients available for phytoplankton growth. It is considered that the decreased lake volume, resulting from high export relative to import during the drought period, created conditions that favoured wind induced mixing of the water column and increased the rates of internal fluxes within the lake. These are particularly important in the dynamics of phosphorus which tends to be the growth rate limiting nutrient (Chapter 4.5).

Implications for management

Variation in water temperature, incident irradiance and external nutrient loading in Lake Midmar were markedly seasonal. However, changes in the concentrations of the -potential growth rate limiting nutrients, nitrogen and phosphorus, are influenced more by in-lake processes in which water column instability plays a major role. Consequently, although phytoplankton numbers show seasonal periodicity this is not evident in their rates of production. The unpredictable changes in the productivity reflect the frequently changing lake environment, particularly in respect of nutrient availability. Because within-lake processes are controlled by the prevailing environmental conditions, particularly wind, there are limited options for manipulation by management. Any change that leads to greater stability of the water column would be detrimental to the maintenance of the present low phytoplankton productivity, particularly if such a change resulted in an increase in the availability of the growth rate limiting nutrient, phosphorus.

Key questions and answers

- i) What is the impact of short term changes in factors such as wind, turbulence and rainfall on primary production?

The rate of phytoplankton primary production was not markedly influenced by seasonal changes in the lake environment. Consequently, short term climatic changes were important regulators of primary production through their potential to change the underwater light climate, the pattern of internal nutrient loading and the rate of mixing within the water column.

- ii) How is the rate of primary production influenced by the interactions between external and internal loads and season?

River flow into Lake Midmar was markedly seasonal, as were changes in the pattern of external nutrient loading. However, the internal nutrient loading was more related to internal processes such as wind induced mixing and turbulence. Whilst there was also marked seasonality of incident irradiance and water temperature this was not reflected in the pattern of primary production. Changes in the internal nutrient loading were the major determinants of primary productivity.

- iii) To what extent is the spring bloom related to changes in nutrient concentrations or changes in water temperature?

The results have shown that the rate of primary production during the spring period was not significantly different from any other period during the year. This is to be expected in a monomictic lake where there is no spring overturn associated with the increasing water temperatures. The numbers of phytoplankton increased in response to the increasing water temperatures during spring. At this time there was also a major change in the species composition with a change from dominance by the green algae and diatoms to dominance by blue green algae. It is suggested that this reflects selective grazing by zooplankton, with the increase in water temperatures stimulating an increase in the grazing of green algae and diatoms but not of the blue green algae. The lack of increase in productivity despite the significant increase in numbers of blue green algae, was thought to be due to the blue green algae being less efficient as primary producers. This view was supported by the observation that the specific productivity when blue -greens were dominant (mean 3,9, range 0,5 - 9,1 mg C/mg Chi a/hr) was lower than when diatoms were dominant (mean 4,8, range~*0,3 - 12,5 mg C/mg Chi a/hr).

- iv) To what extent does temperature limit productivity in winter ?

The interaction between temperature and productivity is complex and while there is an almost universal relationship between temperature and productivity, this was not evident in Lake Midmar where the interaction between temperature and productivity was overshadowed by the response to nutrients and nutrient availability. The probable cause of the lack of a temperature-productivity response was the seasonal change in species composition. In summer the phytoplankton were almost exclusively blue-green algae whereas in winter members of the green algae, diatoms and members of the Cryptophyceae made up a greater proportion of the phytoplankton population. This difference was also apparent in the numbers of phytoplankton, the highest numbers being counted in summer. The fact that the productivity did not differ significantly between winter and summer could be explained if the different algae varied in their efficiency of production. This appeared to be the case in Lake Midmar since the specific productivity values were lowest when blue-green algae were dominant (mean 3,9, range 0,5 - 9,1) and highest when the diatoms were the dominant algae (mean 4,8, range 0,3 - 12,5 mg C/mgChl a/hr).

5.3 INTERACTIONS BETWEEN PRIMARY PRODUCTIVITY, LIGHT, TEMPERATURE AND NUTRIENT LIMITATION

E. G. J. Akhurst

Introduction

The process of photosynthesis is dependent on the availability of light energy, carbon dioxide and water. In addition, to sustain the growth of photosynthetic organisms, a supply of mineral nutrients is also required. In lakes the attenuation of light with increasing depth effectively restricts photosynthesis to the euphotic zone (zone above the depth at which the surface irradiance of photosynthetically active radiation, PAR, is attenuated to 1%) and the factors influencing attenuation in Lake Midmar have been described in Chapter 4.2. Realization of the potential for photosynthesis is further influenced by the amounts of those nutrients required to sustain growth. In this respect the productivity, or rate of photosynthesis, will be limited by the nutrient supplied in the least amount relative to the requirements of the photosynthetic organism at a particular time - the law of minimum (Ruttner, 1963). While there is considerable variation between lakes in relation to the amounts of nutrients present, reflected in their trophic status, productivity is generally limited by either the availability of nitrogen or phosphorus. Thus in a relatively turbid, oligotrophic lake, such as Lake Midmar, both the availability of light energy and nutrients have the potential to regulate phytoplankton productivity.

In Chapter 5.2 it was shown that the values of EA, the hourly rate of production per unit area as $\text{mg C/m}^2/\text{hr}$, measured during this study (1981 mean 11,5, range 4,4 - 25,9, 1982 mean 24,5, range 0,5 - 53,5) were similar to those measured for Swartvlei which are the lowest recorded for an African lake (Robarts, 1976). This chapter will examine the role of temperature, light and nutrients and their relative importance in regulating phytoplankton productivity and their implications for management.

Regulation of the productivity - depth profile

Phytoplankton productivity was measured using a static series of lake water samples incubated over a range of depths (0-5m). The form of the productivity - depth profile (Figure 35) was similar to that found in other primary productivity studies and can be broken down into two components - a horizontal component, defined by A_{max} the light saturated rate of production, and a vertical component, defined by Z_{eu} the lower limit of the euphotic zone. The value of A_{max} measured at a particular time is a function of two variables, the size of the phytoplankton standing crop at that time (B) and the efficiency of that standing crop in producing new organic matter, the specific productivity, A_{max}/B (mg C/mg Chi a/hr). In contrast, the value of Z_{eu} is dependent on the pattern of light attenuation which, as was shown in Chapter 4.2, can be summarized by the attenuation coefficient for photosynthetically active radiation k_{PAR} . The value of k_{PAR} being highest when the penetration of light within the water column is lowest i.e. light is rapidly attenuated. Thus changes in either A_{max} or Z_{eu} have the capacity to influence the area enclosed by the productivity - depth profile or EA, the rate of production per unit area. To establish the relative importance of light and nutrients in regulating primary productivity it is necessary to determine the extent to which EA is dependent on A_{max} or k_{PAR} .

Relative importance of Amax and kPAR in determining EA

In Chapter 4.2 it was shown that EA had both a vertical and horizontal component defined by kPAR or Zeu and Amax respectively. The significant linear relationship between EA and Amax/kPAR (Figure 36a) confirmed the importance of these two parameters in determining EA. The relationship between EA and Amax (Figure 36b) was also linear but there was a greater scatter of the individual values than for the relationship between EA and Amax/kPAR. However, the relationship between EA and kPAR (Figure 36c) was not significant ($F=3,09$, $n=99$) and was most variable on those occasions when $kPAR > 2$, i.e. when the light attenuation was less rapid and the depth of Zeu > 2 m. Thus on most occasions Amax was the major determinant of EA and only when the attenuation of light within the water column was not rapid did kPAR influence EA. This was expected since kPAR (mean 1,6, range 0,8 - 4,3 In units /m) and Zeu (mean 3, range 1,4 - 5,4 m) were less variable than Amax (mean 11,6, range 0,7 - 38,4 mg C/m²/hr) during this study.

On the basis of these results it can be concluded that although Lake Midmar is a turbid system, the attenuation of light was less important than nutrients in regulating phytoplankton productivity since Amax, by definition, is the light saturated rate of production. In addition, on most occasions the incident irradiance was not important in limiting productivity since on two overcast days only, was Amax measured at the surface. On all the other occasions Amax was measured at some depth below the surface (mean value 0,7 m). Thus on most days there was sufficient light penetrating the water column to saturate the rate of photosynthesis, and there was an excess of light energy at the lake surface which caused light inhibition of the rate of photosynthesis.

Regulation of Amax

The measured value of Amax at a particular time is a function of two variables, the size of the phytoplankton standing crop (measured as B, the mean standing crop, mg Chi [^]/m², in the euphotic zone) and the efficiency of that standing crop in producing new organic material (the specific productivity: Amax/B mg C/mg Chi a./hr). In attempting to assess which factors influence these parameters (Amax, B and Amax/B) the correlation coefficients, r, have been calculated for 1981 and 1982 (Table 20).

Table 20 Correlations between Amax, B or Amax/B and temperature, SRP, total P and nitrate nitrogen for 1981 and 1982 (n = 48)

	Temperature	SRP	Total P	NO ₃ -N	\bar{B}
Amax 1981	-0,1	0,44**	0,26	-0,15	0,25
1982	0,04	0,25	0,51	-0,06	0,46**
\bar{B} 1981	0,29	0,33*	-0,001	0,25	-
1982	-0,45**	0,18	0,12	0,34*	-
Amax/ 1981	-0,35*	0,2	0,3*	-0,33*	0,28
B 1982	0,27	0,04	0,12	-0,46**	-0,27
Significant at 0,05* and 0,005** probability levels					

Although a number of the correlations are significant none are particularly strong and the most striking feature of these data was the differences between the two years in respect of the correlations between A_{max} , B or A_{max}/B , and physico-chemical parameters. The only exception to this lack of a consistent pattern, which in some instances involved a change from a positive to negative relationship or vice versa, was the relationship between A_{max}/B and nitrate nitrogen which was negative in both years. The differences between the two years are consistent with the changes in both the numbers and the species composition of the phytoplankton which has been described in Chapter 5.2

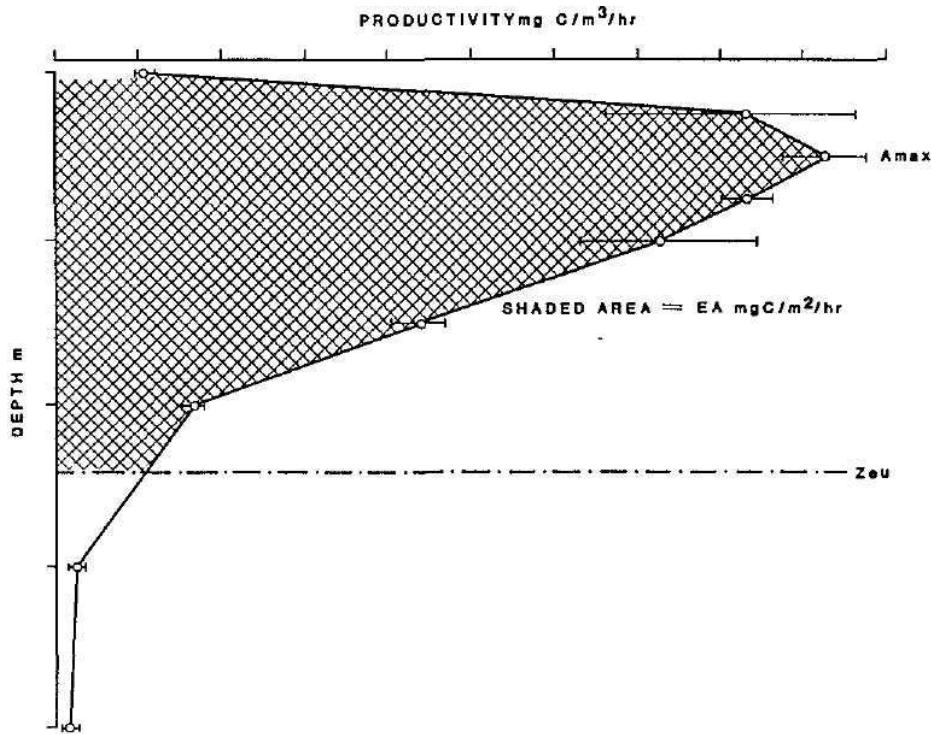


Figure 35 Form of productivity - depth profile during the study period. Productivity values as mean, horizontal bar range.

Temperature

The general lack of correlation between temperature and A_{max} , B or A_{max}/B and the fact that when significant the relationship was negative suggests that temperature was not the primary factor limiting either the size of the standing crop or phytoplankton productivity. This view is supported by the pattern of seasonal change described in Chapter 4.2, where it was shown that the changes in water temperatures were markedly seasonal, although this was not reflected in the productivity data.

Nutrients

In attempting to establish the relative importance of nitrogen and phosphorus as regulators of phytoplankton productivity in Lake Midmar during 1981 - 1982, monthly nutrient enrichment studies were conducted. These experiments were designed to establish which nutrient was the production rate limiting nutrient, and the extent to which the availability of these nutrients influenced the size of the standing crop and the specific productivity of the phytoplankton. The experiments

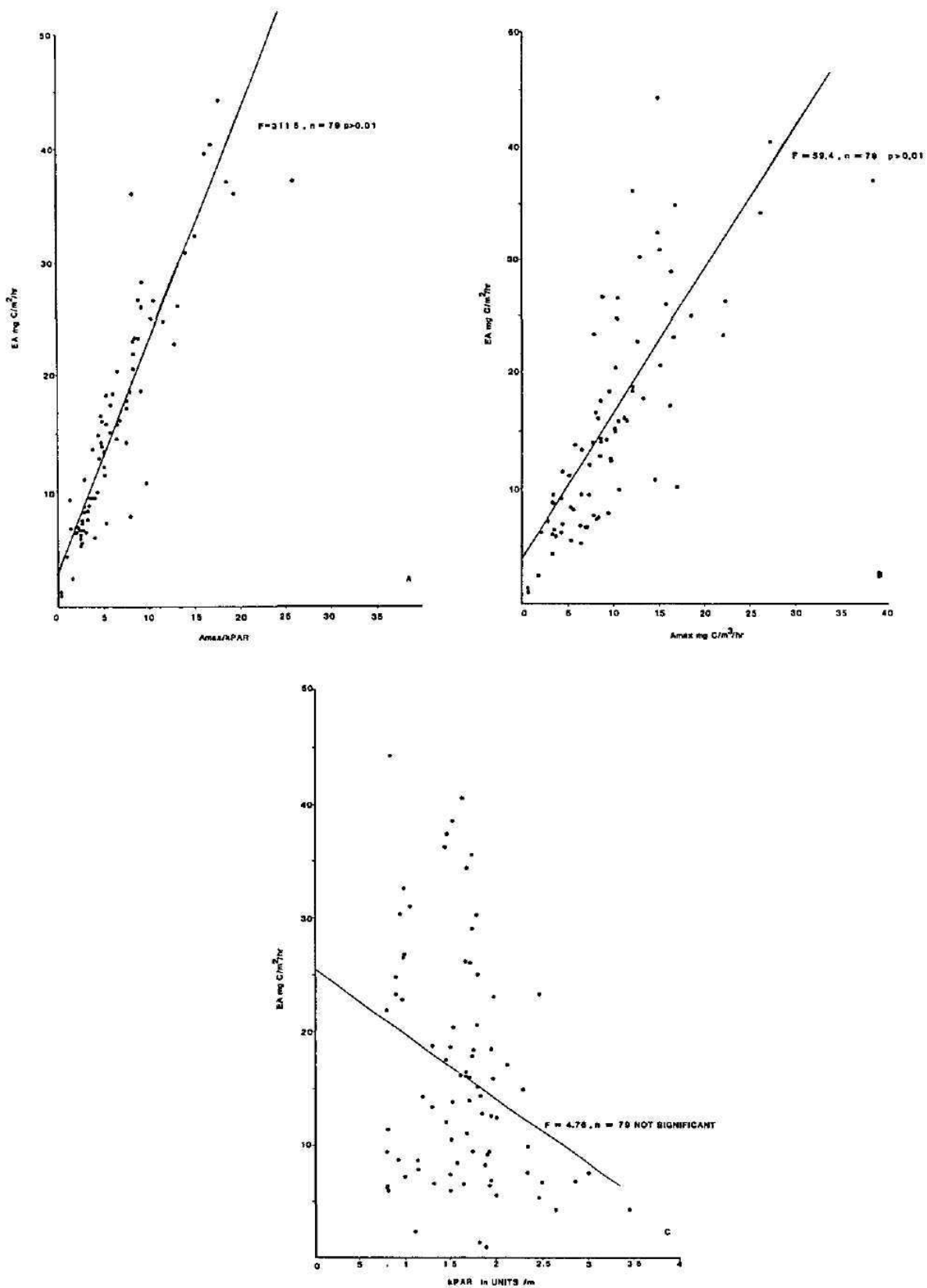


Figure 36A The relationship between EA and Amax/kPAR.
 36B The relationship between EA and Amax.
 36C The relationship between EA and kPAR.

involved the isolation of a small volume (ca. 60l) of lake water to which various enrichments of the nutrient medium, PAAP, were added. Treatments used were a Control to which no nutrients were added; PAAP without N and P, PAAP without P; without N and complete PAAP medium. Water was not in contact with the sediments and stirring was effected by wave action transmitted through a paddle.

Although these experiments were conducted over a range of lake water temperatures, the response of the different treatments followed a consistent pattern. In those treatments receiving phosphorus (PAAP-N and PAAP), as orthophosphate, there was an initial rapid uptake of the added phosphorus (Figure 37a). The changes in nitrate-N were less consistent, on some occasions there was a marked, but slower uptake in only the PAAP treatment (Figure 37b), while on other occasion this pattern was recorded in both the PAAP and PAAP-N treatments (Figure 37c).

The response of the phytoplankton was through changes in Amax/B (Figure 38a) and the size of their standing crop (Figure 38b). The response of Amax/B was more rapid and was followed by an increase in the standing crop at a time when Amax/B was decreasing. These changes were generally restricted to those treatments receiving phosphorus (PAAP and PAAP-N)

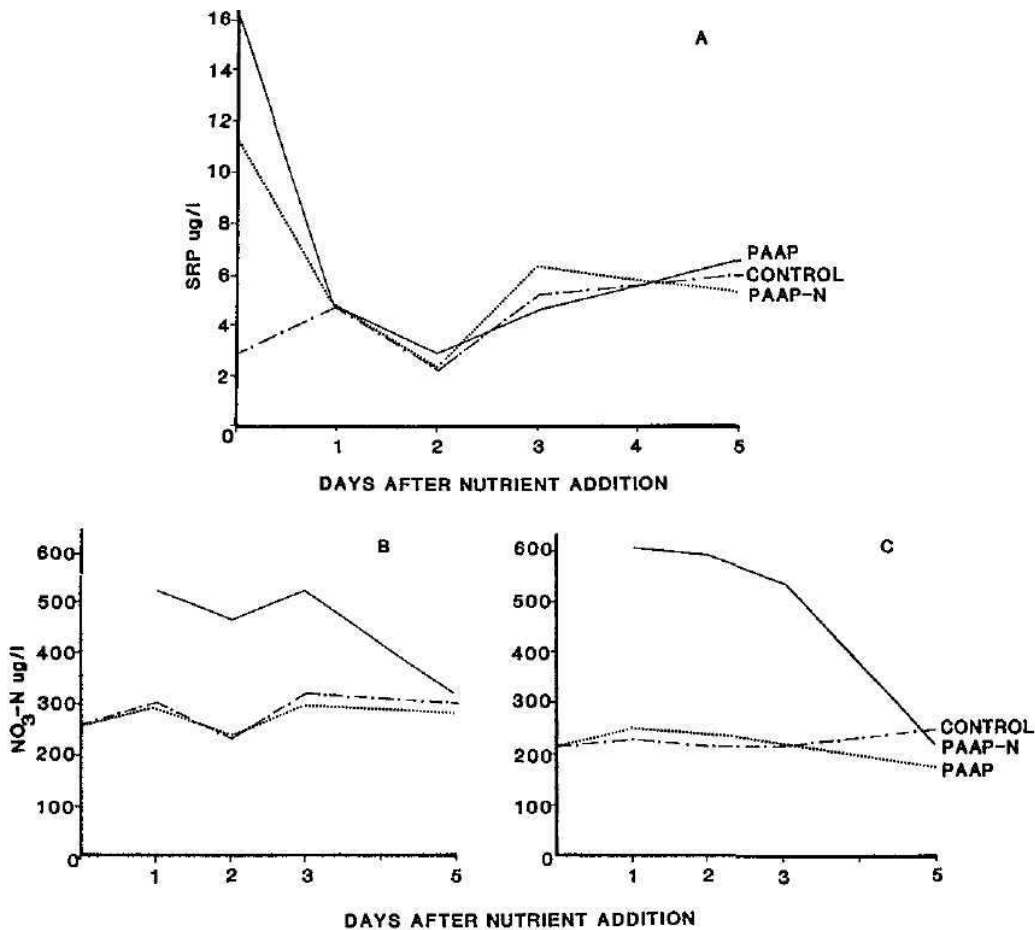


Figure 37A Changes in SRP concentrations in Control, PAAP-N and PAAP treatments.

37B Changes in NO₃-N concentrations in Control PAAP-N and PAAP treatments.

37C Changes in NO₃-N concentration in Control PAAP-N and PAAP treatments.

with no significant Response being measured in those treatments receiving only nitrogen (PAAP-P). However, it must be borne in mind that while some algae have the capacity to fix nitrogen, notably members of the Cyanophyceae, this is not true for phosphorus and that in these experiments the water and phytoplankton were isolated from the sediments, an important source of nutrients, particularly, phosphorus.

The interesting feature of the changes in A_{max}/B measured in these experiments was that although the values increased they did not exceed the maximum value measured in the open water during the study i.e. 12,5 mg C/mg Chi a/hr. Thus the capacity for an increase in A_{max}/B in response to nutrient enrichment was limited. This was not surprising since the specific productivity reflects the physiological state of the phytoplankton and is influenced by other factors such as: the stage in the life cycle of a particular algal cell; the species composition of the phytoplankton; and the availability of other nutrients e.g. silica in the case of diatoms.

Comparison of the productivity - depth profiles for the control and PAAP treatments (Figure 39a) shows that the form of the productivity - depth profile remained the same but the rates of productivity were significantly increased in the PAAP treatment and phosphorus was thus the production rate limiting nutrient. However, when the rates of production were expressed as productivity per unit chlorophyll (Figure 39b) there was no significant difference between the two treatments. This suggests that in Lake Midmar the low phytoplankton productivity was due more to phosphorus limitation of the size of the phytoplankton standing crop than to limitation of the specific productivity.

Role of mixing

From the preceding discussion it is apparent that nutrients, in particular phosphorus, played the major role in limiting the productivity of the phytoplankton in Lake Midmar by restricting the size of the standing crop which reduces the value of A_{max} . The influence of the underwater light climate and incident irradiance appears to be secondary and was restricted to a reduction in the vertical component of the productivity - depth profile. Only on those occasions when the euphotic zone was particularly shallow and the attenuation of PAR very rapid (values of k_{PAR} in excess of 2 In units/m) did the light climate significantly influence the value of EA. Thus while Lake Midmar may be classified as a turbid lake the turbidity is not sufficient by itself to effect a significant reduction in EA.

In Chapter 4.2 it was shown that Lake Midmar was both turbid and turbulent with very low water column stability. Because turbulence influences the amount of time spent by the phytoplankton in the euphotic zone it could influence the interpretation of production data obtained by incubating samples at fixed depths in the water column. To assess the importance of mixing in a system like Lake Midmar the response of the phytoplankton to changing light conditions during incubation was investigated. Samples collected at 3 m or 5 m were incubated on several occasions at a depth of 0,5 m (depth at which A_{max} was measured) for different periods of time. In all cases the responses of the phytoplankton were similar and followed the pattern shown in Figure 40. These results show that the phytoplankton were well adapted to the turbulent conditions that prevailed within the lake and were able to respond rapidly to a change in the light climate. In addition, they

indicate that the horizontal component of the productivity - depth profile, A_{max} , was a function of the time spent under favourable light conditions. Consequently, if the mixing pattern within the lake resulted in the phytoplankton spending less than 4 hours at a depth where the light conditions were most favourable for growth, i.e. the depth at which A_{max} was measured, then the present estimate of A_{max} would be an overestimate. How significant this source of error is in the estimation of lake productivity cannot be determined until the rate of mixing is known. At present while it was possible to measure wind run and direction it was not possible to transform this into a rate of mixing within the water column. However, on the basis of the present ratio of Z_{eu}/Z_m and assuming that the mixed water column was completely circulated once during the daylight period the phytoplankton would spend only 33% of this time within the euphotic zone, ca. 4.3 hrs, and considerably less under the optimum light conditions, the depth at which A_{max} was measured.

On one occasion a series of bottles were incubated at 0.5 m intervals over 4 m and moved through the water column in an attempt to quantify the response of the phytoplankton to mixing. The rate of mixing was such that by the end of the 4 hr incubation period the surface sample was at 4 m and the sample initially at 4m has moved up to the surface. The results of this experiment when compared with a normal profile of static bottles incubated at the same time, are shown in Figure 41. It is evident that reduction of the horizontal component of the productivity - depth profile was compensated for by an increase in the vertical component, with the result that EA for the mixed profile was greater than the value obtained using static bottles (86% of the EA for mixed profile). Mixing therefore influenced both the vertical and horizontal components of the productivity - depth profile with the result that the use of static samples to measure productivity can lead to an underestimation of EA. This stresses the importance of both quantifying the mixing pattern within turbulent systems and taking it into account in the estimation of EA.

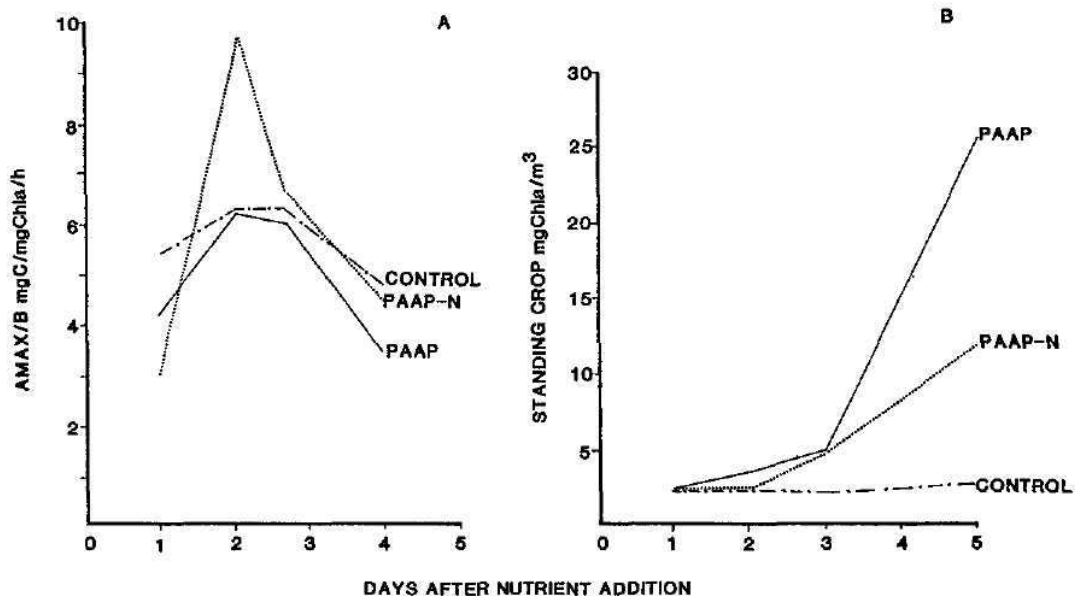


Figure 38A Changes in A_{max}/B in Control, PAAP-N and PAAP treatments.

38B Changes in standing crop in Control, PAAP-N and PAAP treatments.

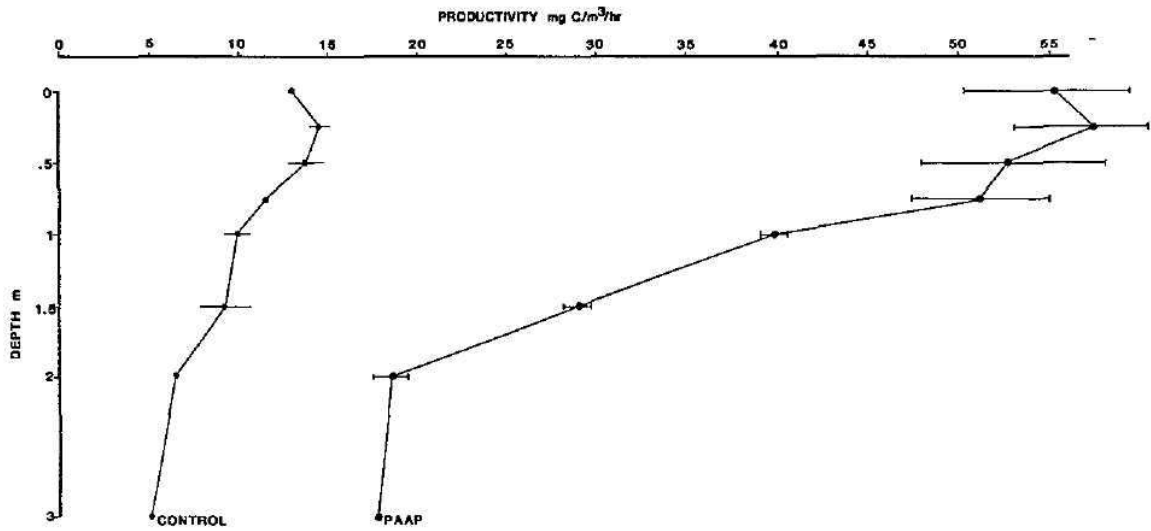
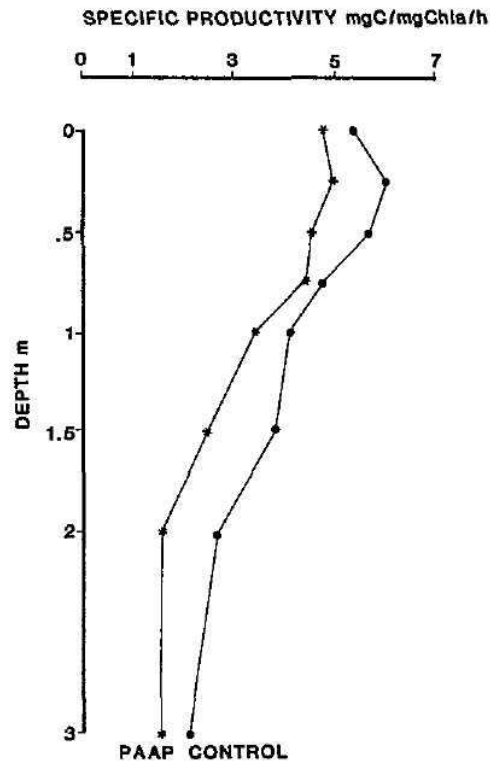


Figure 39A Form of the productivity - depth profile 5 days following enrichment with phosphorus.



39B Variation in specific productivity with depth 5 days following enrichment with phosphorus.

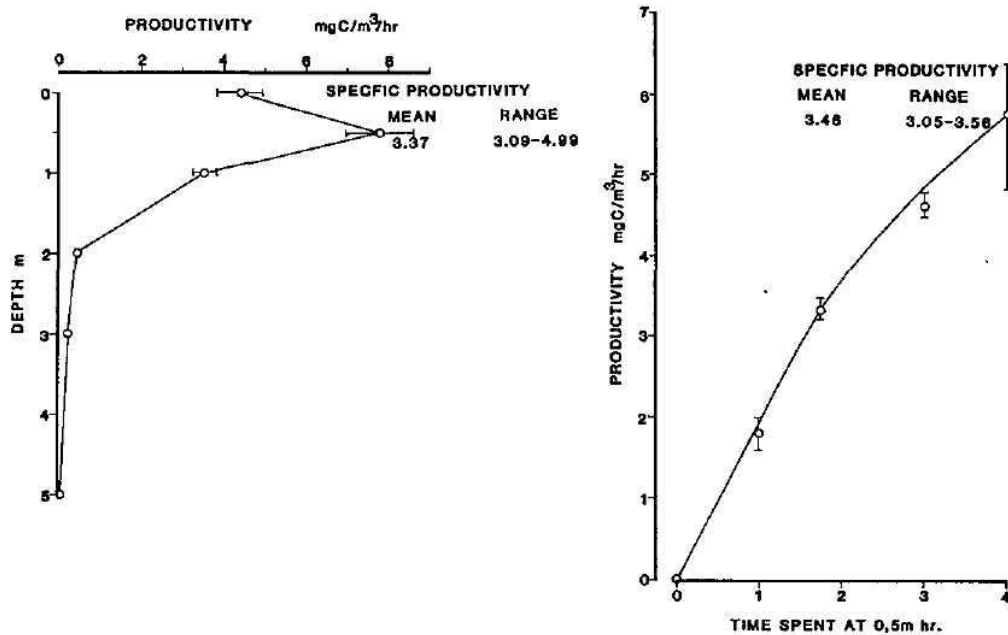


Figure 40 Normal productivity - depth profile (A) and productivity values obtained when samples collected at 5m incubated at 0.5m for different periods of time during a 4 hr incubation (B). Rest of incubation period spent at 5 m.

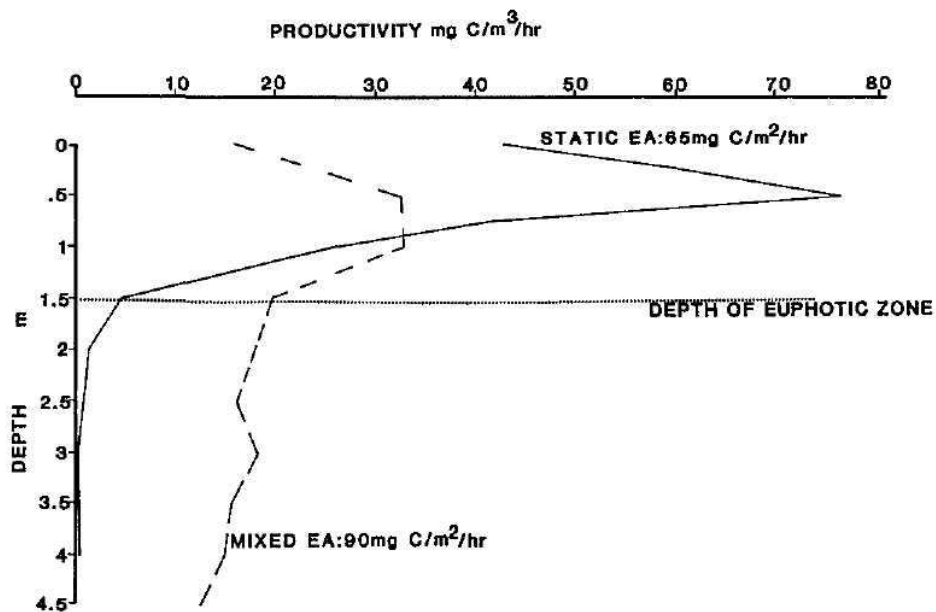


Figure 41 Productivity - depth profile using the static bottles and mixed profile bottles, moved from surface to 4 m over four moves.

Implications for management

This study of phytoplankton productivity made during the period September 1980 - December 1982 has shown that the availability of nutrients, in particular phosphorus, is the primary factor limiting the rate of production. Consequently any increase in the present pattern of nutrient loading and availability will lead to an increase in the phytoplankton standing crop and their productivity. The relationship is not simple because a number of factors, particularly adsorption of phosphorus, depress the response to increased loading (Chapter 4.3)

Although the turbid conditions in Lake Midmar lead to a vertical compression of the productivity - depth profile it is insufficient to significantly reduce the rate of production per unit lake area (EA). Present estimates, however, do not take account of mixing, and may therefore have underestimated the importance of the light profile in the water column.

Temperature does not appear to significantly regulate primary productivity. However zooplankton, which does show marked periodicity (Chapter 5.4) may mask this effect by grazing the phytoplankton more heavily during the summer, thereby restraining primary productivity.

Key questions and answers

1. How does the specific productivity i.e. A_{max} per unit chlorophyll EL , vary during the spring period?

From this study it is clear that the phytoplankton in Lake Midmar were able to respond rapidly, through changes in their specific productivity, to changes within the lake. Specific productivity reflects the physiological state of the phytoplankton and would be expected to fluctuate depending on the amounts of nutrients bound within an algal cell relative to the cell's requirements and the availability of nutrients within the water column. In a system like Lake Midmar, where phosphorus is the growth rate limiting nutrient it is not surprising that enrichment of the water with phosphorus, as orthophosphate, resulted in a rapid change in the specific productivity.

The pattern of change in specific productivity measured during this study showed a series of unpredictable pulses throughout the year in which increases in A_{max}/B preceded an increase in the phytoplankton standing crop which often reached a peak at a time when A_{max}/B was decreasing. The spring period was no exception with the changes of A_{max}/B being similar to those measured at other times of year. This unpredictable variation in A_{max}/B over time would be expected in an oligotrophic system where the growth rate limiting nutrient was in short supply. It reflects alternating periods of nutrient uptake during growth and the release through mineralisation.

2. Is the decrease in standing crop in November, following the spring bloom, associated with a decrease in specific productivity?

This study has shown that there was no distinct spring bloom and that throughout the year the standing crop fluctuated in an unpredictable manner. The results of both the field and enrichment studies showed that the initial response of the phytoplankton to a change in nutrient availability was through changes in their specific productivity followed by a change in the standing crop. On most

occasions the increase in standing crop was associated with a decline in specific productivity. Thus while a decrease in standing crop and specific productivity may occur in response to nutrient limitation these two indices of phytoplankton response were separated temporally.

Grazing by zooplankton appeared to be a selective process having greatest impact on the green algae and diatoms and thereby influencing the species composition of the phytoplankton leading to dominance by blue - green algae during the summer months. Although grazing occurs throughout the year there were two periods when the pressure of grazing was reduced: in mid-winter when low water temperatures inhibited the development of large zooplankton populations, and between October and November when the dominant species of the phytoplankton changed from green algae and diatoms to blue-green algae. Apparently the lack of a suitable prey species reduced the impact of grazing at this time.

For the rest of the year there appeared to be subtle interaction between nutrients, phytoplankton and zooplankton. These are summarized in Figure 42.

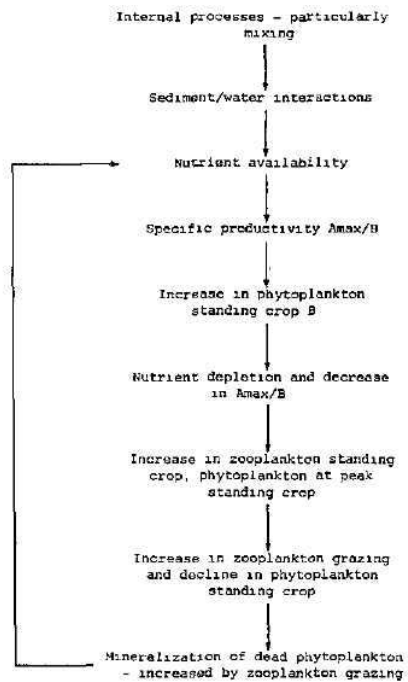


Figure 42 Flow diagram to show the major interactions between nutrients, phytoplankton and zooplankton.

3. How is the declining phase in standing crop influenced by nutrient enrichment?

Nutrient enrichment studies were conducted at monthly intervals during 1981 - 1982, and despite differences in the phytoplankton present at the time of enrichment, the pattern observed was similar to that in the open lake. Nutrient enrichment resulted in an increase in specific productivity followed later, when the specific productivity was decreasing, by an increase in phytoplankton standing

crop. While no attempt was made to exclude zooplankton from these, studies the associated increase in zooplankton was not sufficient to prevent the increase in phytoplankton standing crop. This response was restricted to those treatments receiving phosphorus suggesting that it was the primary growth rate limiting nutrient. In these studies the water was isolated from the sediments, a major potential source of phosphorus, which could account for the lack of response to enrichment with nitrogen alone, however, the greatest response to enrichment was measured when water was enriched with both nitrogen and phosphorus.

4. How does temperature influence the response to nutrient enrichment?

The results from the enrichment studies have shown that on all occasions there was a response in those treatments receiving phosphorus or a combination of nitrogen and phosphorus. However, although the response during winter was generally not as pronounced as that measured during the summer months this was not always the case. It is considered that the size of the standing crop at the start of the enrichment (the inoculum), the species composition of the phytoplankton and their physiological state were more significant than temperature in determining the response to enrichment. This supports the view that short term changes dominate over seasonal changes in determining the pattern of phytoplankton productivity.

5. What proportion of the productivity profile is light limited and which is nutrient limited?

The form of the productivity - depth profile, measured using stationary bottles, has a vertical component, Z_{eu} or EPAR, regulated by the attenuation of light, and a horizontal component, A_{max} , regulated by the availability of the growth rate limiting nutrient. Most of the variation in EA (area under the productivity - depth profile) is accounted for by A_{max}/k_{PAR} , with A_{max} accounting for most of the variation. Under the present turbid conditions in Lake Midmar the main influence of light is to cause a vertical compression of the profile. The main influence of changes in nutrient availability is to cause an increase in both the phytoplankton standing crop and their specific productivity which will increase A_{max} . The potential to increase the specific productivity is, however, limited and influenced by species composition, no such constraint applies for changes in standing crop. Thus the low phytoplankton standing crops present in Lake Midmar are nutrient - rather than light limited.

6. How important is turbulence in increasing productivity?

The shallow depth of the euphotic zone relative to the depth of mixing suggests that mixing may be an important factor regulating the form of the productivity - depth profile through changes in both the horizontal and vertical components of the profile. This has important implications for the estimation of productivity and in understanding the relative importance of light and nutrients in the regulation of productivity, however, unless the rates of mixing within the water column can be determined, it is not possible to quantify the relationship between turbulence and productivity. Mixing may exert an indirect effect on productivity by influencing the phytoplankton species composition and act as a constraint on the potential for large standing crops of bloom - forming algal species to develop should there be an increase in nutrient loading in the future.

5.4 RESPONSE TO ZOOPLANKTON GRAZING E.
G. J. Akhurst

Introduction

In systems, like Lake Midmar where pelagial processes are more important than littoral processes two principal food resources are available for grazing animals such as zooplankton. The microbial flora, of which bacteria would be the principal component, and the phytoplankton. Although no estimates of bacterial populations have been made, the oligotrophic nature of the system and the low organic content of the lake sediments, suggest that their numbers would be low and limited by the availability of suitable organic substrates. However, their contribution may be markedly seasonal, as there is evidence (Chapter 3.1) that significant amounts of organic material are imported from the catchment.

A number of the dominant zooplankton species namely DAPHNIA PULEX and METADIAPTOMUS TRANSVAALENSIS, and some of the other important species, DAPHNIA LONGISPINA, D. LAEVIS and DIAPHANOSOMA EXCISUM, utilize phytoplankton as a food source. Hence for these species both the physical environment, notably water temperature, and availability of food could limit their numbers, growth rate and breeding potential.

For the phytoplankton productivity, two determinants of the amounts of carbon fixed during photosynthesis and of the hourly rate of production per unit area as $\text{mg C/m}^2/\text{hr}$ (EA), are the size of the phytoplankton standing crop and its efficiency in producing new organic material, the specific productivity (expressed as mg C/mg Chi a/hr). Thus, if the zooplankton graze the phytoplankton they could significantly influence the size of the phytoplankton standing crop. The difficulty lies in determining when the potential influence is realized since estimates of the phytoplankton standing crop over a period of time reflect the balance between increases as a result of growth, and losses due to grazing, sedimentation and death of the algal cells.

The impact of zooplankton grazing on the phytoplankton has been assessed by comparing the numbers of zooplankton with phytoplankton specific productivity (mg C/mg Chi a./hr). Specific productivity was chosen as the index of phytoplankton performance is independent of grazing and is influenced by the species composition of the phytoplankton and their physiological state in relation to the physico-chemical environment. It was predicted that at times when the decline in phytoplankton standing crop was due to zooplankton grazing the specific productivity would remain constant or increase, as the competition for resources between the algal species decreased. However, should the specific productivity decline at the same time as the phytoplankton standing crop then some component of the physico-chemical environment would be responsible.

In this chapter the role of zooplankton grazing in influencing both the size and species composition of the phytoplankton standing crop is examined, and the implications of these findings for management are assessed.

Seasonal pattern of zooplankton grazing

The changes in zooplankton numbers at the Main Basin Station during this study are presented in Figure 43. Two features are of particular

importance:

there was a significant difference between the numbers of zooplankton counted in the two years;

the numbers, particularly during 1982, were very variable and while generally lower in mid-winter, June - July, there was no marked seasonality in the variation. This pattern indicated that food availability rather than temperature was the determinant of the size of the zooplankton population.

When the changes in mean phytoplankton standing crop in the euphotic zone and specific productivity are compared (Figure 44) two observations can be made:

- with the exception of the period July - August 1982 the phytoplankton standing crops were low;

the pattern of zooplankton grazing (Figure 44) suggests that, while not consistent throughout the year, the zooplankton were an important factor regulating the size of the phytoplankton standing crop.

To account for the differences between the zooplankton numbers in 1981 and 1982 and the fact that grazing was not a constant factor it is necessary to consider the phytoplankton in more detail. The changes in phytoplankton numbers (Figure 33) during the study showed that in 1982, numbers were much higher than those during the previous year. The differences in numbers of phytoplankton were, however, not of the same order of magnitude as those shown by the zooplankton (Figure 43). In addition consideration of phytoplankton numbers alone does not take account of the fact that grazing by zooplankton is likely to be a selective process since Arnold (1971) has shown that some zooplankton, notably DAPHNIA spp., are not able to digest many members of the Cyanophyceae.

Further, a study of the feeding appendages of the two main groups of herbivorous zooplankton, in Lake Midmar, has shown that the calanoid copepods are able to process much larger particles than the cladocerans which feed on very small particles ($< 1,2 \mu\text{m}$). The cladocerans would therefore feed principally on bacteria and possibly one of the principal blue-green algal species ("Palmella" size range $0,09 - 1,83 \mu\text{m}$) while the calanoids have been observed feeding on the diatom MELOSIRA GRANULATA (Rayner, unpublished data).

Comparison of the changes in contribution of the four major algal classes viz. Bacillariophyceae (diatoms), Chlorophyceae (green algae), Cryptophyceae and Cyanophyceae (blue-green algae) for 1981 and 1982 (Figure 34) shows a similar pattern during summer when members of the Cyanophyceae were dominant. However, in winter the two years were quite different, in 1981 members of the Chlorophyceae and Cryptophyceae made a greater contribution to the species composition while in 1982 members of the Bacillariophyceae were the dominant algae. An interesting feature of both years was the rapid establishment of members of the Cyanophyceae as the dominant algae during the spring period (September - October). This can in part be attributed to grazing, particularly during 1981 when the reduction in diatoms during October was associated with a sixty-fold increase in the density of calanoids. This peak of calanoids was short-lived and by the end of October, when blue-green algae were

dominant, the density of calanoids was only 30 % of the peak density. Coincident with this change in species composition was a three-fold increase in cladocerans in November 1981. The relationship between calanoids - diatoms and cladocerans - blue-green algae can be seen again in April 1982. During this period there was a rise in the numbers of diatoms and calanoids and a decrease in the numbers of blue-greens and cladocerans. However, the bloom of diatoms in July - August 1982 appears to have been largely unutilized by zooplankton and the lower water temperatures are thought to have been responsible for the low calanoid numbers at this time. The termination of the diatom bloom in September 1982 cannot be explained at present since there was no associated increase in calanoid numbers during this decline phase and no information on silica concentrations in the lake is available. The lack of a distinct diatom bloom in winter 1981 is thought to be due to differences in physical conditions in the lake (turbulence and turbidity) that existed between 1981 and 1982 as a result of the differences in water depths brought about by the drought and reduced river inflow in summer.

The pattern of change in the blue-green algae and cladocerans during 1982 was not unexpected bearing in mind that the generation time of ca. 30-40 days for these animals would lead to a lag in the response to an increase in food availability whereas mortality would cause a rapid decrease in numbers. During early winter, May - June 1982, the blue-green algae contributed ca. 50% of the phytoplankton population and this decreased to 15% by the end of July followed by a re-establishment of dominance during spring, September - October 1982 (Figure 34). The cladoceran numbers were initially high, during this period and the number of eggs per brood pouch indicated that there was sufficient food present. The population reached peak numbers in August and declined during September - October. Thereafter the numbers increased following the re-establishment of the blue-greens as the dominant algae.

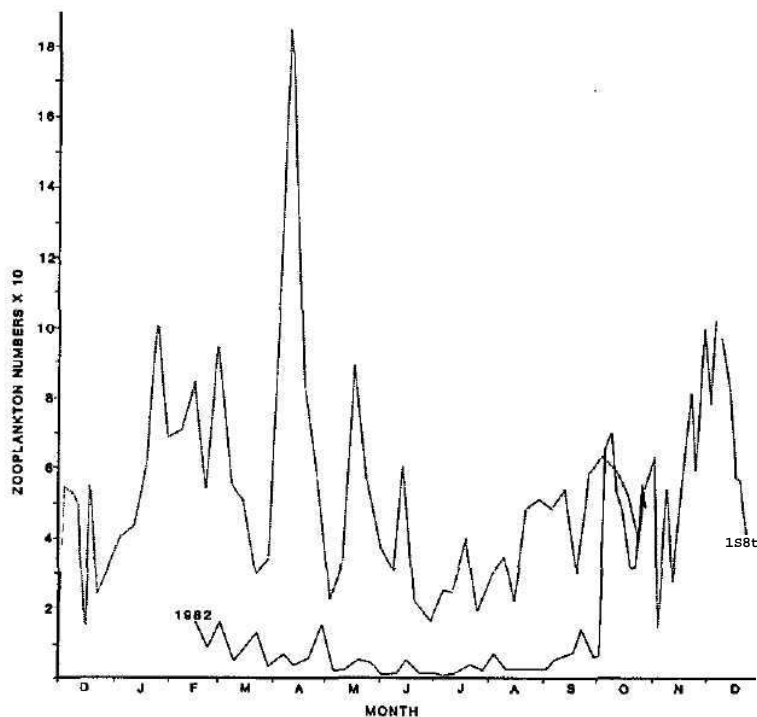


Figure 43 Seasonal variation in zooplankton numbers at Main Basin Station.

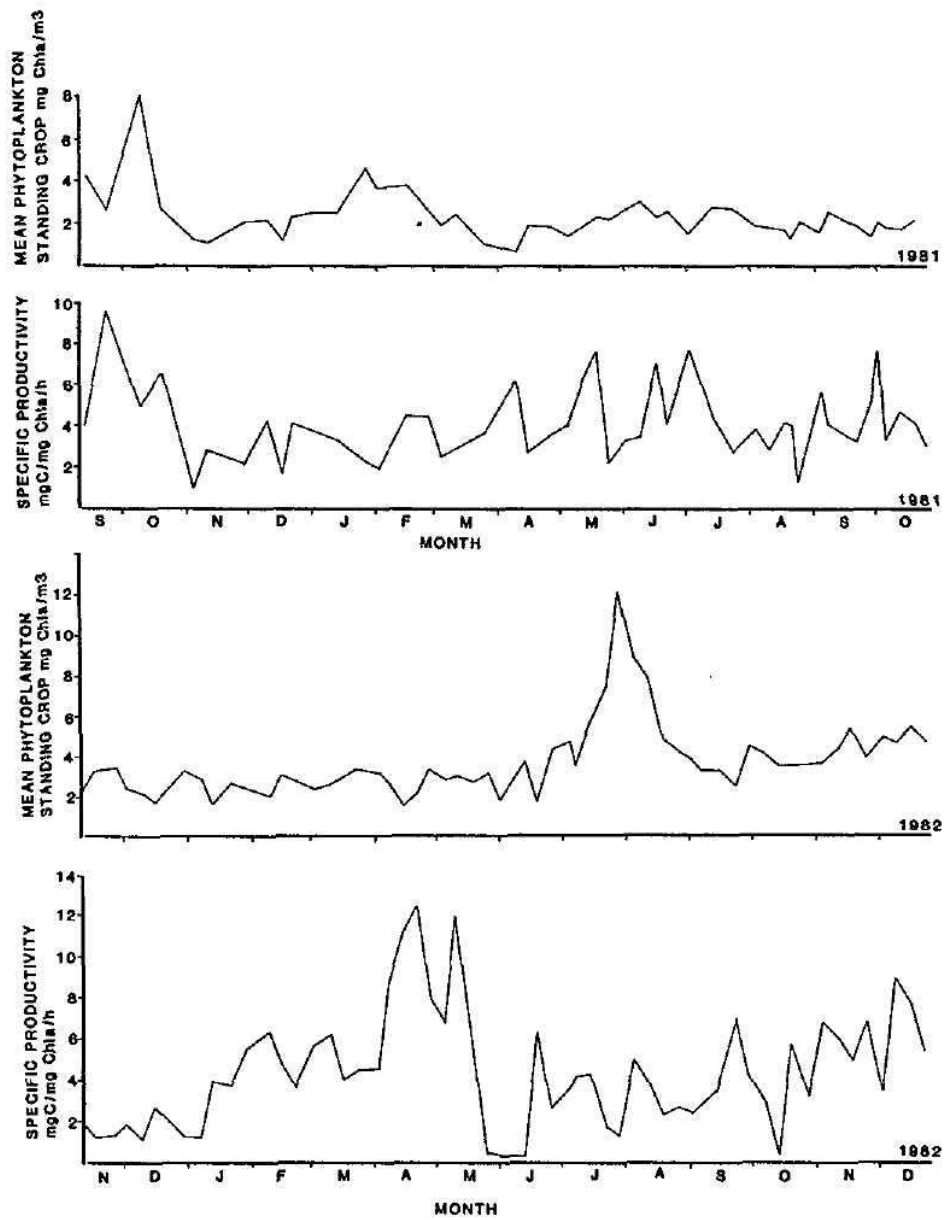


Figure 44 Changes in B, mean standing crop of phytoplankton and specific productivity at Main Basin Station.

These results support the view that grazing by zooplankton is a selective process and has important implications for the phytoplankton species composition at different times of the year.

The view that phytoplankton are an important food source for the zooplankton is reinforced by results from a study of the response of phytoplankton to nutrient enrichment. At the conclusion of these experiments, after seven days, the water that remained in each drum was filtered through a zooplankton net and the numbers of zooplankton, both as a total and as individual species, were determined (Table 21) by the counting procedure used in the open lake studies.

Table 21 The response of zooplankton, as total numbers of all species to nutrient enrichment of lake water, with PAAP nutrient medium and different combinations of Nitrogen and Phosphorus, during the 1981-1982 season

Date and Mean Water Temperature during enrichment period	Treatment				
	Control Lake water	-N & P	+N	+P	+N & P
22.12.81 20.7°C	36 000	41 433	78 200	133 167	101 778
26. 1.82 22.5°C	71 667	96 133	92 033	156 567	140 089
8. 4.82 20°C	49 800	56 667	73 000	165 267	129 822
1. 6.82 16°C	45 733	156 000	169 733	241 022	253 067
10. 8.82 12.6°C	15 867	9 167	12 056	9 667	13 833
6. 9.82 14.5°C	4 444	10 678	13 533	6 222	10 978
4.10.82 19.6°C	373 778	333 511	271 600	490 456	483 344
16.11.82 20°C	61 222	104 078	85 067	73 467	105 156
29.11.82 21.5°C	153 533	103 411	64 033	138 722	93 600

The results showed that:

the greatest changes in zooplankton numbers were recorded in the treatments which had the greatest effect on the phytoplankton i.e. where phosphorus or a combination of phosphorus and nitrogen were added;

- under favourable temperature conditions there was a rapid response to increased availability of food e.g. in June 1982 where the N + P treatment contained ca. 6 x as many zooplankton as the control.

sometimes zooplankton response was curtailed by either low water temperatures (August 1982, 12,6° C) or the availability of suitable phytoplankton in late November 1982 when members of the Cyanophyceae were the dominant algae.

- for some species, notably DAPHNIA PULEX and DIAPHANOSOMA EXCISUM, there was an associated increase in their reproductive capacity. Rayner (1982) in a study of the zooplankton of Lake Midmar, during the period March 1977 - June 1979, recorded an average clutch size for DAPHNIA PULEX of 1,5-3,8 eggs per brood pouch. In the phosphorus enriched treatments DAPHNIA PULEX with clutches of 5 - 8 eggs per brood pouch were recorded on a number of occasions when temperature conditions were favourable. A maximum of 20 were recorded in November 1981.

To test the validity of the assumption that specific productivity was not directly influenced by zooplankton grazing the lake water used to fill the drum was, on one occasion filtered through a zooplankton net. The response of the phosphorus enriched sample, from which zooplankton had been excluded was compared with that of lake water enriched with phosphorus. The pattern of response in both treatments was almost identical particularly in respect of the changes in specific productivity (Figure 45). Specific productivity declined between days 3 and 4 in both treatments indicating that it was not brought about by zooplankton grazing.

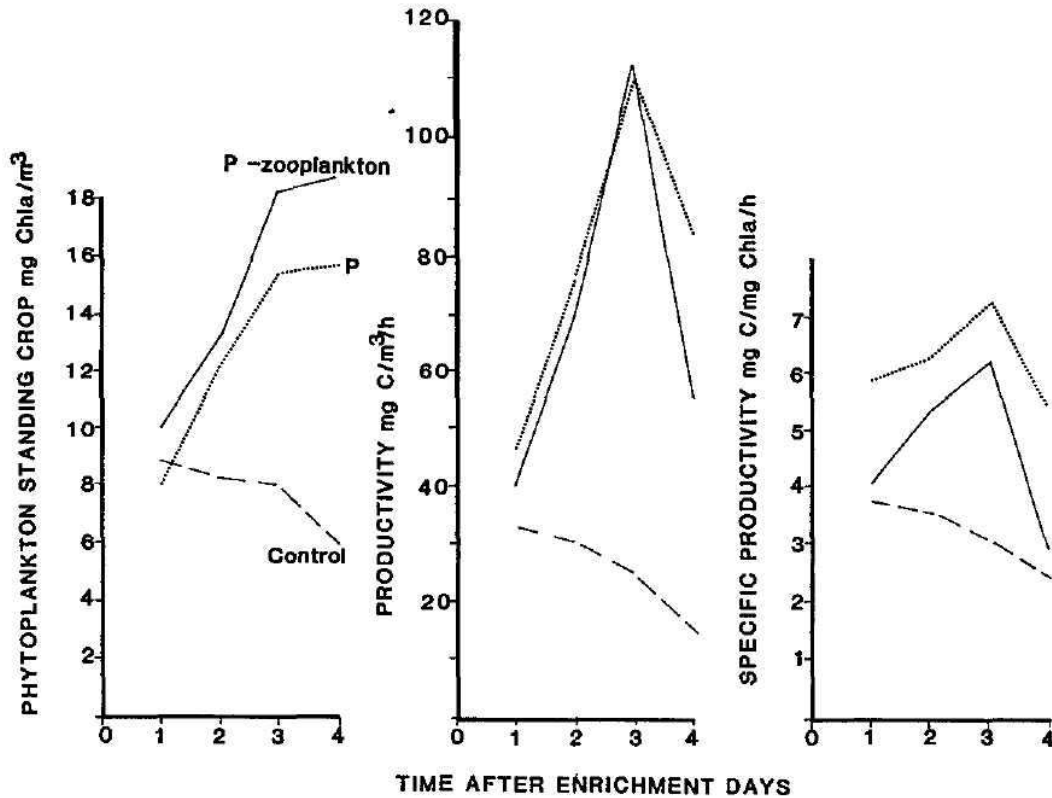


Figure 45 Patterns of response to nutrient enrichment in Control, no nutrients, + phosphorus and + phosphorus without zooplankton.

Conclusions

Phytoplankton are the major food source for the zooplankton and because grazing is a selective process, there is a dynamic interaction between the zooplankton and phytoplankton communities. Food availability regulates the size of zooplankton populations as evidenced by the results of the enrichment studies in which stimulated phytoplankton growth effected changes in both the size and reproductive potential of the zooplankton community. This response was strongly influenced by water temperature and the species composition of the phytoplankton.

The zooplankton, through grazing, are an important factor regulating both the size and species composition of the phytoplankton standing crop throughout the year, but particularly during the summer months when the

ambient water temperature is most favourable for their growth. In summer the zooplankton contain the size of the diatom population allowing the blue-green algae to dominate. Because the blue-green algae have a lower specific productivity than the diatoms, productivity does not show a summer peak despite the large numbers of blue-green algal cells. If the diatoms were more numerous in summer the rates of production measured during this period would be much higher. This can be seen by comparing the values of EA measured during the spring period of 1980 and 1981, when water temperatures and phytoplankton numbers were the same, in October 1980 EA = 60,5 and October 1981 EA = 24,2 mg C/m²/hr. The difference between the two years can be accounted for by the differences in phytoplankton species composition at these times. In 1980 the diatom MELOSIRA GRANULATA accounted for 61% of the total whereas in 1981 M. GRANULATA accounted for only 5% of the total species composition.

The restriction of the development of large diatom populations, particularly of MELOSIRA GRANULATA, during the summer months when water temperatures are most favourable for algal growth has implications for the costs of producing high quality potable water since large diatom populations tend to block filters used in the treatment of water for human consumption.

Grazing by zooplankton also plays an important role in the cycling of nutrients within a system like Lake Midmar by increasing the rates of mineralization of nutrients bound within the cells of certain algal species, but no attempt has as yet been made to quantify this role.

6. SECONDARY PRODUCTION

INVERTEBRATES

J. Heeg

Introduction

Primary production within any lake is utilized by animals at the primary consumer level. These animals are, of necessity, small invertebrates, and are, in turn, preyed upon by larger animals including fish. Productivity of the lake is, therefore, important in determining its angling potential which, in the case of Midmar with its secondary recreational function, merits some consideration.

The invertebrate fauna of the lake comprises two components, a bottom or benthonic fauna and a planktonic component which utilizes the water column. Both are almost entirely dependent upon autochthonous primary production, as allochthonous inputs are seasonal and appear to be highly erratic.

The benthic fauna

Fluctuations in lake level due to variable seasonal inflow and constant drawdown give rise to a very unstable and ill defined littoral zone, with negligible development of a littoral flora. Periodic inundation of encroaching terrestrial vegetation after prolonged periods of low lake levels does create favourable conditions for the development of a littoral benthonic fauna, but such conditions are transient, unpredictable and, during the course of this investigation, were of short duration. Studies on the benthonic fauna were, therefore, largely confined to the limnetic zone.

The only organisms collected in a sampling programme carried out in November/December 1980 were tubificid oligochaetes (*BRANCHIURA SOWERBYI* and two unidentified species), dipterous larvae (*CHAOBORUS PUNCTIPENNIS* and a *CHIRONOMUS* species) and Nematoda. The latter occurred in such small numbers as not to merit further mention, and *C. PUNCTIPENNIS* as a predator in the plankton, can more appropriately be considered part of the plankton community.

Table 22 shows the standing stock of those benthonic animals associated with organic detritus. It can be seen that their density is extremely low, with a mean density of one organism per 40 cm². Such low numbers did not warrant continuation of this investigation.

A qualitative study of the benthonic fauna of the littoral was carried out following inundation of a considerable stand of terrestrial plants in March 1982. Mayfly nymphs (Ephemeroptera, family Baetidae) and the larvae of chironomid midges were the most abundant animals recorded, with a variety of other aquatic insects also being present. Such habitats, even if only temporary in nature, constitute important fish feeding grounds.

Zooplankton

Zooplankton was collected weekly from three sampling Stations. To date a total of 65 species have been identified from Lake Midmar compared with 40 species from Hartbeespoort (Rayner, 1982). Crustacea constitute the dominant component of the zooplankton. Although all recorded species

Table 22 Standing stock of Oligochaeta and larval Chironomidae during the period 28.10.1980 to 9.12.1980

Taxon	No. of Stations sampled	Mean density (no./m ²) ± S.E.	Range (no./m ²)	
			minimum	maximum
Oligochaeta	20	218 ± 39,6	0	733
Chironomidae	20	35 ± 8,6	0	100
Total	20	253 ± 38,6	67	733

will ultimately be included in a full analysis, only the most important species are considered here.

The main grazers in the zooplankton are the cladocerans DAPHNIA LONGISPINA, DAPHNIA PULEX, DAPHNIA LAEVIS and DIAPHANOSOMA EXCISUM, and the calanoid copepods TROPODIAPTOMUS SPECTABILIS and METADIAPTOMUS TRANSVAALENSIS. Of the cladocerans D. EXCISUM is seasonal, with numbers only becoming significant in the summer months, particularly after substantial inflows. All other species occur in reasonable abundance throughout the year. T. SPECTABILIS was the dominant calanoid up to the winter of 1981, when it was replaced by M. TRANSVAALENSIS, a species considered by Hutchinson et al. (1932) to be characteristic of alkaline waters. The change coincided with the establishing of a higher pH range in the lake.

Figure 46 shows the fluctuations in total zooplankton numbers per cubic metre of water for Main Basin Station, together with the numbers of grazers, which have been divided into calanoid Copepoda and Cladocera. These plankton densities and fluctuations are largely representative of those of the other two stations as well. Cyclopoid copepods and the larvae of the phantom midge CHAOBORUS PUNCTIPENNIS are the predatory component of the plankton. Figure 47 shows the fluctuations in numbers of these predators compared with the total numbers of grazers. The former follow the trends of the latter fairly closely, particularly in the case of the cyclopoids, which prey mainly on the juvenile stages of the grazers.

Studies on the feeding of the grazers show that METADIAPTOMUS TRANSVAALENSIS feeds on the larger planktonic algae. It has been observed ingesting chains of the diatom MELOSIRA GRANULATA, and diatom frustules are frequently present in the gut. The cladocera, being true filter feeders, are equipped to collect smaller particles, including bacteria and other nanoplankton. Wherever a green alga has been seen in the gut of these animals, it has shown no signs of being digested. The relationship between zooplankton numbers and algal production will be discussed elsewhere.

Population sizes in and species diversity of the zooplankton community of

a lake both reflect its trophic status. A comparison between Lake Midmar and Hartbeespoort illustrates this well, particularly in a comparison between the population sizes of the major crustacean assemblages, as shown in Table 23. The only comparable figures are those for calanoid Copepoda. Calanoids are numerically the dominant grazers among the Crustacea of the Midmar zooplankton, comprising 69% of the grazing component, whereas in Hartbeespoort they constitute only 4%. This discrepancy is most likely a reflection of a difference in the composition of the algal community. Figures 46 and 47 show marked differences between the zooplankton densities recorded in 1981 and 1982. These differences are summarised in the mean densities for the respective years in Table 24. The difference in calanoid numbers appears, at least in part, to be due to a difference in the food supply. The amount of MELOSIRA GRANULATA and other diatoms was low during 1981, with blue-green algae dominating the phytoplankton. Although the phytoplankton collected in 1982 had not yet been analysed, it was apparent from that which was incidentally collected with the zooplankton, that a considerable bloom of MELOSIRA occurred in * April/May 1982, and that this persisted through winter. Consistently high densities of the calanoid METADIPTOMUS TRANSVAALENSIS were recorded from January to well into June, when a normal winter fall in numbers was apparent. The Cladocera were less affected, but in the absence of detailed phytoplankton data, nothing further can be said about this at this stage.

Table 23 Comparison between zooplankton populations at Station 1 in Lake Midmar during 1981/82 and a Station of comparable depth (Station 4) Lake Hartbeespoort 1973/74. Hartbeespoort data from Seaman 1977

	Midmar			Hartbeespoort		Midmar as % of Hartbeespoort
	Mean No./m ³	S.E.	Maximum No./m ³	Mean No./m ³	Maximum No./m ³	
<u>Grazers</u>						
Calanoids	1520	39	12085	2714	11880	56%
Cladocera	694	26	3958	63290	482000	1,1%
<u>Predators</u>						
Cyclopoids	1703	41	7084	35950	226500	4,7%
Chaoborids	22	3,4	244	165	838	13,3%

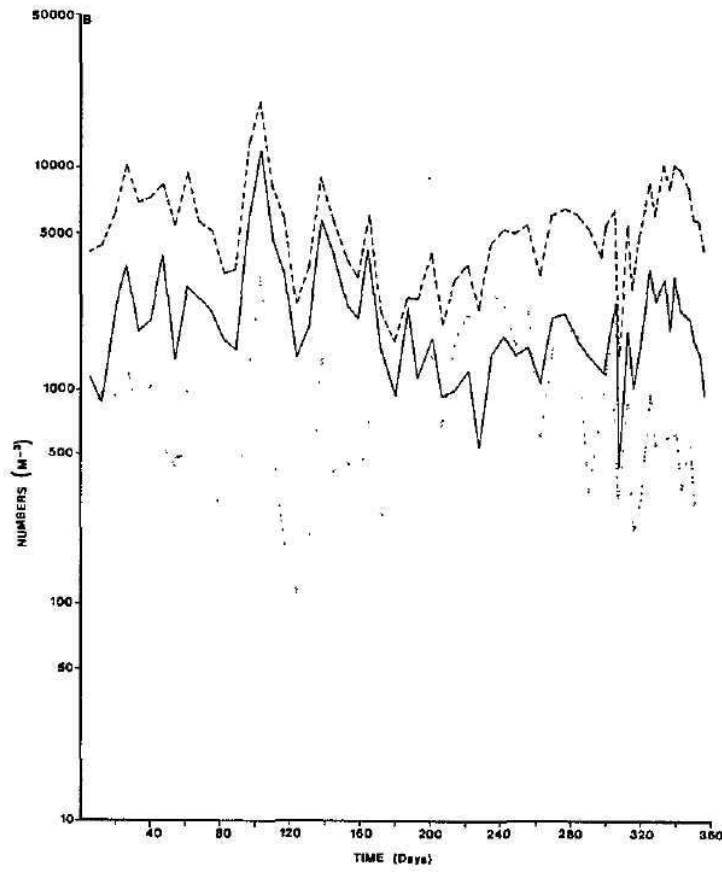
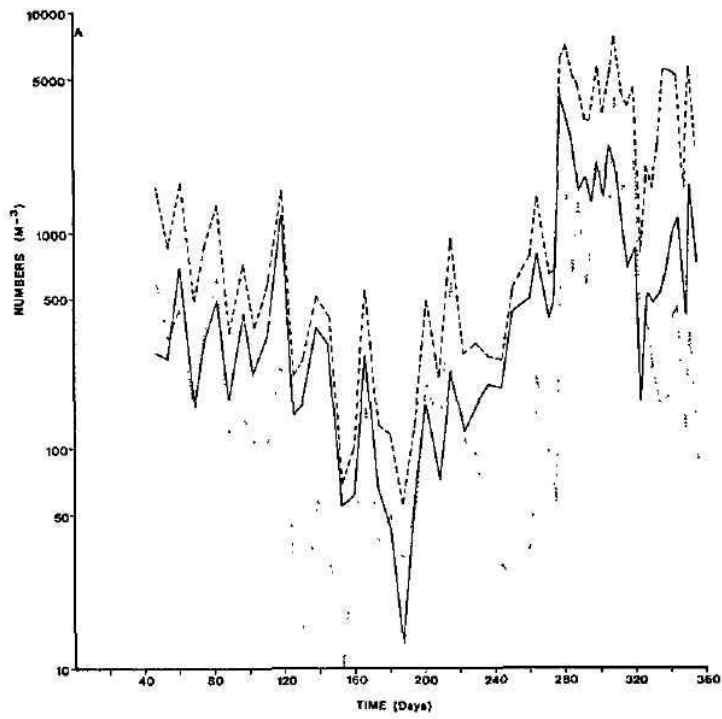


Figure 46A and B Fluctuations in total zooplankton numbers.

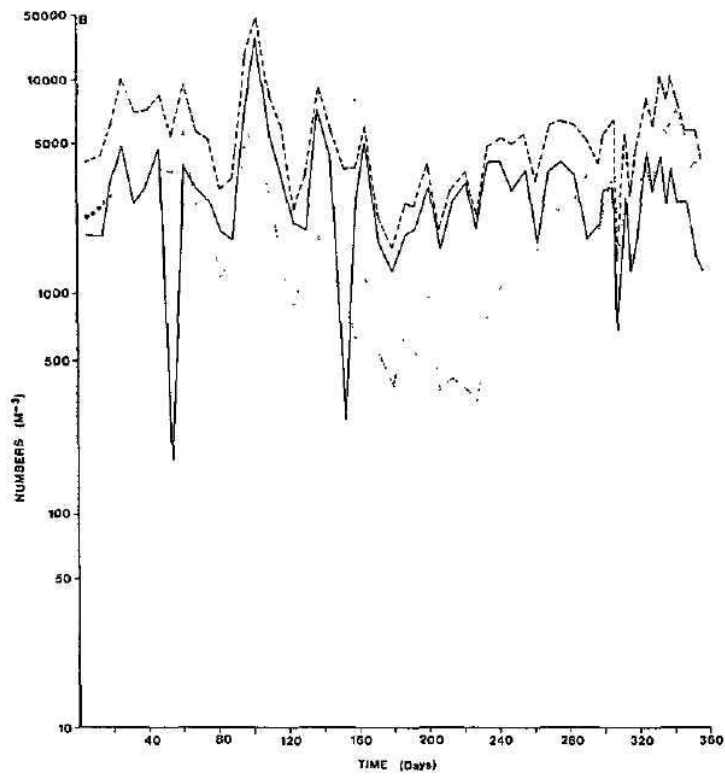
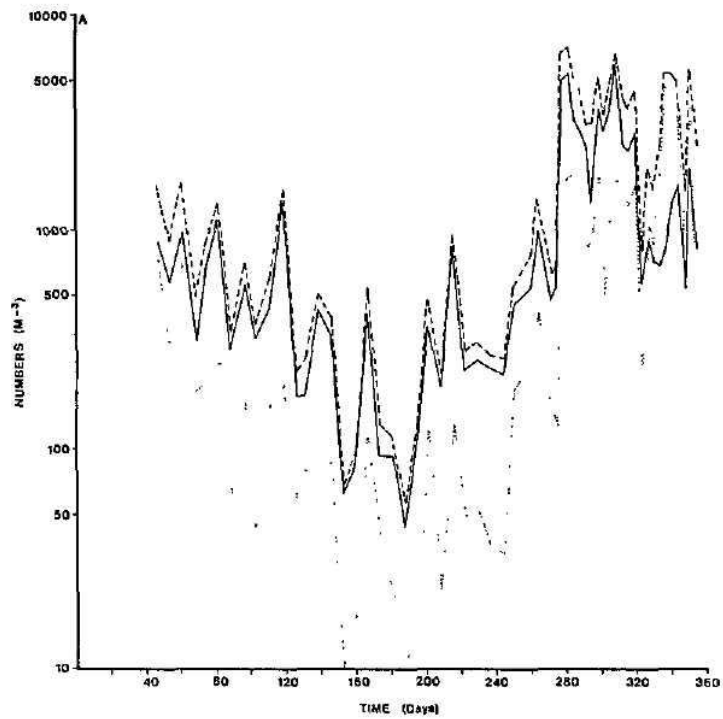


Figure 47A and B Fluctuations in the numbers of predatory zooplankton.

Table 24 Comparison between zooplankton populations at Station 1 in Lake Midmar during 1981 and 1982

Component	1981			1982			1981 as % of 1982
	Mean No./m ³	S.E.	Maximum No./m ³	Mean No./m ³	S.E.	Maximum No./m ³	
<u>Grazers</u>							
Calanoids	756	28	4222	2247	47	12085	33,6%
Cladocera	789	22	3958	695	26	2225	70,4%
<u>Predators</u>							
Cyclopoids	799	28	3997	1704	41	7084	46,9%
Chaoborids	12	2,3	93	31	6,0	244	38,7%

Utilization of Invertebrates

Zooplankton is a major component of the diet of many fish species, and is probably the most important dietary constituent of juvenile fish of all species.

Nine fish species are known to occur in Lake Midmar. These derive from fish present in the Mgeni River, and from those present in farm dams prior to inundation. The fish fauna includes a number of exotics, only three indigenous species, the scaly (BARBUS NATALENSIS), chubby head barb (BARBUS ANOPLUS) and common eel (ANGUILLA MOSSAMBICA) having been recorded from the river above the Howick Falls and from the lake prior to the introduction of the large mouth tilapia (OREOCHROMIS MOSSAMBICUS). Based on angler's catch returns (Table 25), the most important angling fishes are bluegill sunfish (LEPOMIS MACROCHIRUS), usually introduced as a food source for bass (MICROPTERUS species), carp (CYPRINUS CARPIO), scaly (BARBUS NATALENSIS) and tilapia (OREOCHROMIS MOSSAMBICUS).

Sufficient specimens of these species, (with the exception of the scaly), were collected during the investigation to allow for a meaningful analysis of the stomach contents. Figure 48 shows the percentage of the volume of the stomach contents contributed by different food items. The fish were, with the exception of the bass, mainly juveniles, with modal lengths varying between 20-29 mm (carp) and 40-49 mm (tilapia). While zooplankton was found in the stomachs of all species, its importance to bluegill sunfish, carp and tilapia was considerable. The insect remains recorded from fish stomachs were largely mayfly nymphs, with the larvae of chironomid midges, the nymphs of dragonflies and water bugs (Heteroptera) making a significant, though smaller, contribution. On the basis of identifiable remains, however, zooplankton is the most important component of the diets of young non-piscivorous fish, and, through them, makes a considerable contribution towards sustaining populations of bass, which are the most sought after angling fish in the lake.

Table 25 Numbers of fish caught in Lake Midmar based on angler's returns over the period February 1978 to July 1982

Species	Number of fish caught
Bluegill sunfish (Lepomis macrochirus)	12 694
Bass (Micropterus species)	259
Scaly (Barbus natalensis)	187
Carp (Cyprinus carpio)	5 998
Tilapia (Oreochromis mossambicus)	119
Brown trout (Salmo trutta)	2
Common barbel (Clarias gariepinus)	96
Common eel (Anguilla mossambica)	126

A permanent summer stratification of the lake could conceivably reduce zooplankton availability during late summer and early autumn, while spring, early summer and late autumn may see substantially greater zooplankton densities than recorded to date. A three metre increase in the overall depth of the lake could give rise to such a plankton cycle, which seems to have been an incipient trend during 1978/79 when water levels in the lake were considerably higher than during the present investigation. An increase in zooplankton production coincident with fish spawning during spring is certain to favour the survival of young fish, and provided that sufficient littoral feeding areas are available during the period of stratification, fish populations should benefit. However, nutrient limitation in an oligotrophic system such as Midmar will remain the ultimate determining factor of its angling potential, thus the lake is not likely to develop into an angling resort per se.

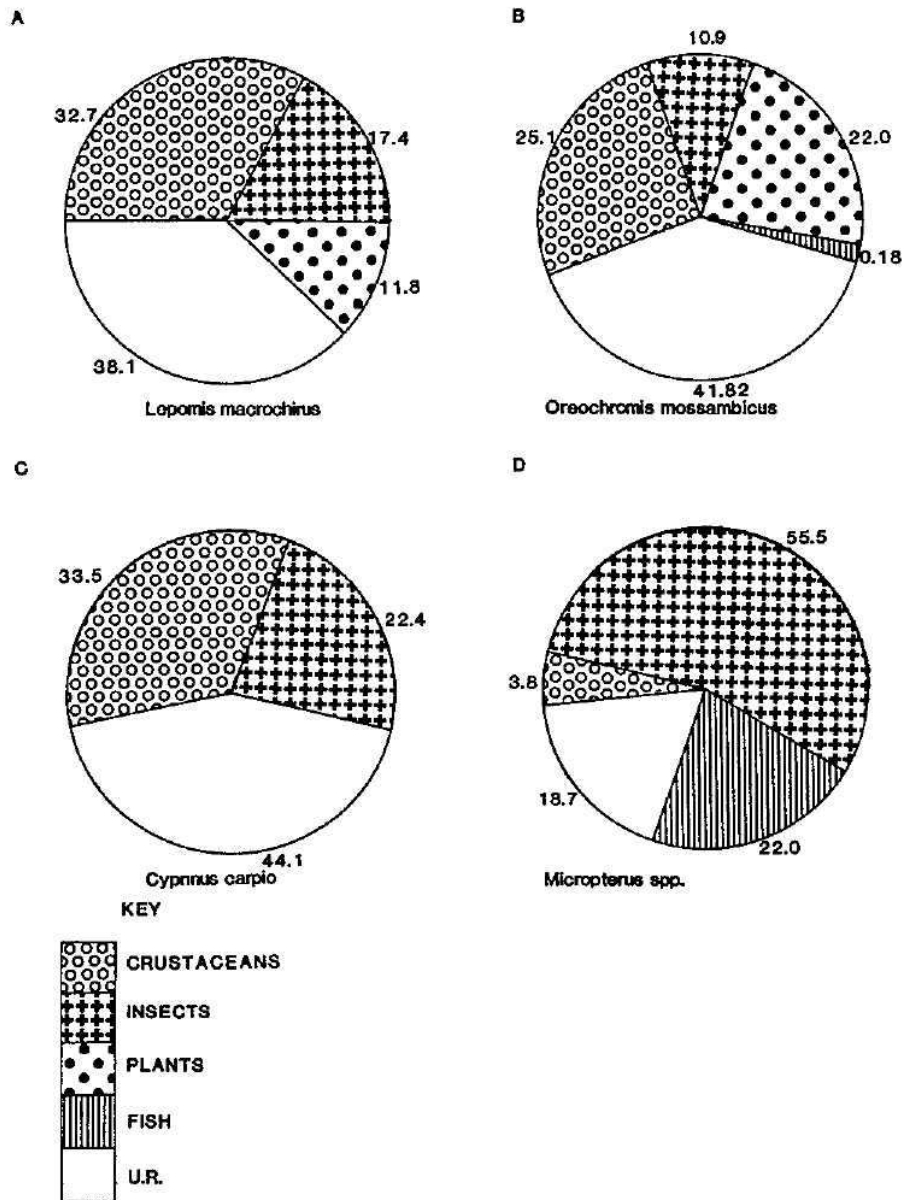


Figure 48 Composition by volume of the gut contents of Lake Midmar fish species.

7. DISCUSSION

The Mgeni river is currently operated as a cascade system, with water being stored in the highest-lying impoundment (Midmar) and supplied to lower-lying impoundments from which the demand is greatest (Kroger, pers. comm.). A particular advantage of this policy is that the high quality water emanating from the upper Mgeni catchment can be used to improve water quality downstream. Considerable importance can therefore be attached to maintenance of water quality in the catchment of Midmar and Albert Falls lakes.

Although water quality is largely determined by nutrient loading, the relationship between loading and response cannot be accurately defined at the present time. This is because each system is structurally and functionally unique and the response is modified by both structure and function. Thus whilst general trends in response may be predicted using currently available empirical models, the wide confidence limits detract from the usefulness of these models in the management of aquatic systems.

In this discussion we assess the applicability of empirical water quality models in prediction of the response of Lake Midmar to changing conditions of nutrient loading and hydrology. To facilitate understanding of the pattern of response, the structure and functioning of the lake is also discussed.

7.1 NUTRIENT LOADING AND EUTROPHICATION MODELLING

C.G.M Archibald and C.M. Breen

Introduction

Simple empirical eutrophication models of the Vollenweider type have been developed to predict the consequences of nutrient loads on aquatic systems in terms of algal growth responses, and to evaluate external control options. The philosophy is based on the relationship between phosphorus load and water quality. The significance of this lies in the fact that phosphorus is considered the growth rate limiting nutrient and that substantial effective reduction from point sources, at least, can be achieved with current technology within financial reason. Jones and Lee (1982) have indicated that even if it is not the primary rate limiting nutrient, a substantial reduction in the external load will improve water quality and may even induce phosphorus-limiting conditions.

Hydrological budget

A necessary prerequisite for the determination of nutrient loading:system reponse relationships is an adequate water balance for the system. This was derived from Equation 1 and the relevant data are provided in Table 26.

Table 26 An analysis of the hydrological budget of Lake Midmar between 1979 and 1982. All values as $m^3 \times 10^6$ *

IMPORTS		1979/80	1980/81	1981/82
Total surface inflow from Rivers	R_c	36,20	103,18	80,31
Direct precipitation on lake surface	P, d	9,77	10,69	11,03
Perimetral seepage	$S_$	-	-	-
TOTAL	Q_i	45,97	113,87	91,34
EXPORTS				
Discharge of compensation Water	D, a	47,35	43,58	79,33
Abstraction*	A, d	19,77	26,36	25,74
Evaporation	E	21,52	20,65	20,87
Seepage	L	-	-	-
TOTAL	Q_{out}	86,64	90,64	125,94
CHANGE IN LAKE				
Volume	AW, d	-42,67	+23,28	-34,26

* Calculated from Equation 1 in text Basic

Hydrological relationships:

$$R + P + S = D + E + L + A_d + A_w \quad \text{Equation 1}$$

where

R = Total surface inflow ($m^3 \times 10^6$) from catchment rivers

P = direct precipitation on the lake surface ($m^3 \times 10^6$)

S = perimetral seepage gain ($m^3 \times 10^6$)

D = discharge of compensation water ($m^3 \times 10^6$)

E = evaporation from the lake ($m^3 \times 10^6$)

L = seepage loss

A_d = abstraction volume via pipeline ($m^3 \times 10^6$)

A_w = change in water storage in the lake

Seepage losses out of the lake and perimetral seepages into the lake were not measured and were considered to be small and of the same order. They therefore do not influence the hydrological budget significantly- The abstraction volume was calculated for each year since data were not available. Subsequent confirmation of the accuracy of the budget was provided by comparison with daily average abstraction rates (Thorn - Mgeni Water Board : personal communication). There was an apparent increase from $0,05 \text{ m}_3 \times 10^6/\text{d}$ to $0,07 \text{ m}_3 \times 10^6/\text{d}$ in the abstraction rate between 1979 - 1982 and these data were used to calculate the nutrient discharge (losses) from the system via the pipeline.

Data used in the application of models

The data necessary for application of the empirical models are provided in Table 27. They span three successive years from October 1979 to September 1982. During the period of investigation Lake Midmar was exposed to severe drawdown effects and therefore never really approached a steady state condition which is a necessary precondition for the modelling approach used by Vollenweider. Mean values of morphometric characteristics such as surface area, volume and mean depth have therefore been calculated from weekly observations made by staff of the Directorate of Water Affairs as inputs to the model.

Problems related to the application of empirical eutrophication models

A guide to the degree of eutrophy of lakes formulated by Vollenweider (1975) in a nutrient budget model for phosphorus has been widely used and modified, but it has not been accepted without qualification. Jones and Lee (1982) have recently reviewed the Vollenweider approach and have developed the OECD load-response models from a very wide data base. Modifications of the Vollenweider approach have been made, for example, by Dillon and Rigler (1974), Larsen and Mercier (1976) and Jones and Bachman (1976) to accommodate the imprecision in the nutrient load:system response relationship. Jones and Lee (1982) have pointed out, however, that although technically similar in foundation, these adjusted models have not been developed on as broad a data base as the OECD load:response system relationship nor over long enough periods of time, and therefore are unlikely to be as robust as the more recent model. This is particularly true of the Walmsley & Butty (1980) derivations which were based on data for a single year collected from 21 South African impoundments.

The cause-effect coupling between nutrient loading (phosphorus input) and system response (trophic state as indicated by chlorophyll a) is unlikely to be linear because the relationship is influenced by a number of competitive/alternative processes. These processes all serve collectively or individually to reduce the effective phosphorus concentration in producing direct short term responses manifested as algal growth.

The Vollenweider approach to developing load-response models was developed on the basis of theoretical nutrient utilization in a completely mixed system, with negligible internal loading, a balance between resuspension and sedimentation, little inorganic turbidity and loss only through discharge. The evidence from Lake Midmar indicates that even in oligotrophic systems, internal loading may provide

Table 27 Data used in application of eutrophication of models to Lake Midmar

SYMBOL	PARAMETER		UNIT	Condition - refer to text							
				A	B	C	D	E	F	G	H
				1979-80	1980-81	1981-82	1980-81		1980-81		
A	SURFACE AREA		Ha	1471	1424	1463	712	1424	1424	1851	1424
\bar{V}	VOLUME		$m^3 \times 10^6$	154,70	142,31	152,60	21,62	142,31	142,3	255,26	142,3
\bar{z}	MEAN DEPTH	V/A	m	10,52	9,99	10,43	3,04	9,99	9,99	13,79	9,99
Q	TOTAL INFLOW		$m^3 \times 10^6$	45,97	113,84	91,34	113,84	76,17	76,17	113,84	113,84
	HYDRAULIC LOAD	Q/A	myr^{-1}	3,13	7,99	6,24	15,99	5,35	5,35	6,15	7,99
	HYDRAULIC RESIDENCE TIME	V/Q	yrs	3,37	1,25	1,67	0,19	1,87	1,87	2,24	1,25
M	TOTAL EXTERNAL PHOSPHORUS LOAD		$kg yr^{-1}$	1714	6244	5426	6244	11130	3524	6244	12488
L_P	AREAL PHOSPHORUS LOADING RATE	MP/A	$gm^{-2} yr^{-1}$	0,117	0,438	0,371	0,877	0,782	0,247	0,337	0,877
P	FLUSHING RATE	$1/r_w$	yr^{-1}	0,296	0,800	0,598	5,263	0,534	0,534	0,446	0,800

significant sources of phosphorus for algal growth.

Three categories of load:response models have been used with Lake Midmar data, namely nutrient loading versus trophic state, nutrient loading versus nutrient concentrations and nutrient loading versus chlorophyll a. concentrations (Table 28). Comparison of predicted values with observed data indicates good agreement in some cases but very often there is a wide divergence from the measured value. Jones & Lee (1982) recommended that technically appropriate alterations must be made to account for deviations from the OECD load:response relationship, and that data should be collected on a site specific basis, the accuracy of which will maximize the uniqueness of the relationship.

The characteristics of Midmar dam which may have an influence on the nutrient loading:system response relationship are:

Patterns of inflow of nutrient are highly irregular in magnitude and seasonal (Chapter 4.3), and therefore constant input is not a realistic assumption;

The unequal horizontal distribution of nutrients in a dendritic (multicompartiment) lake where two major compartments contribute approximately 30% of the surface area at F.S.L. and may intercept the flow and cause a time lag in the measured response;

The complete mixing assumption is violated by the morphometric and stratification characteristics of the lake which tend to compartmentalise the system;

- The biologically available component of total phosphorus varies seasonally with the load and with in-situ conditions. Furthermore, chemical analyses may not accurately indicate the soluble available phosphorus fraction (Twinch & Breen, 1982).

Eutrophication modelling

It is difficult to define the complex interactions that occur in a reservoir such that accurate assessments can be made of the impact of management strategies. The empirical eutrophication models of the Vollenweider - OECD type offer a compromise between very expensive ecosystem modelling and desk top calculations, providing the parameters of the model have been measured and appropriate modifications have been made.

The approach adopted in this study involved accurate measurement of the nutrient input on a daily basis from the major source (Mgeni catchment) and measurement of in situ response (chlorophyll a) on a weekly basis over a 2-3 year period. Unfortunately the period of investigation was apparently unique in the extreme dry conditions which have been experienced in the catchment, and therefore the hydrological regime and its associated nutrient load does not reflect the situation which might prevail under high flow conditions of wetter periods.

Projection of demands for stored water and of development in the Mgeni catchment permit formulation of a range of probable future conditions of loading hydrology. These conditions have been used in the Vollenweider (Figure 49) and OECD (Figure 50) models to predict lake response. They are also used to assess sensitivity of the models to accuracy of

Table 28 Nutrient loading and system response relationships in Lake Midmar

<u>A. Nutrient loading vs. trophic state</u>		1979/80	1980/81	1981/82
<u>Source</u>				
1. Vollenweider (1975)	$L_{TP} = 0,020qs(1+\sqrt{\frac{2}{qs}})$	0,178	0,338	0,286
2. Toerien & Walmsley (1977)	$L_{TP} = 0,025qs(1+\sqrt{\frac{2}{qs}})$	0,223	0,423	0,358
3. Observed values	g/m ² /yr	0,117	0,428	0,371
<u>B. Nutrient Load vs. nutrient concentration</u>				
1. Jones and Backman (1976)	$\frac{0,84 L_{TP}}{\bar{z}(0,65+\rho)}$	10	25	24
2. Dillon & Rigler (1974)	$[P] = \frac{L_{TP}(1-R)}{\bar{z}\rho}$	25	21	19
3. Observed values	(µgP/L)	18	23	19
<u>C. Nutrient load vs. Chlorophyll concentration</u>				
1. Walmsley and Butty (1980)	Chlo = 0,83 L _{TP} + 2,97 when Secchi disc > 0,2m N: Pratio > 5 : 1	3,1	3,3	3,3
2. Jones and Lee 1982	log Chlo = $0,75 \log \left[\frac{L_{TP}}{qs(1+\sqrt{\frac{2}{qs}})} \right] - 0,259$	3,9	6,5	6,5
3. Observed values	µg Chlo/L	2,5	2,3	3,4

Table 29 Data used for the determination of the phosphorus loading term, the observed and predicted chlorophyll concentrations

Condition Refer to text		$L_{(P)}$	q_s	$\frac{L}{q_s}$	τ_w	$\sqrt{\tau_w}$	$\frac{L/q_s}{1 + \sqrt{\tau_w}}$	Phosphorus Loading mg/m^3	Mean Chlorophyll "a" conc. $\mu g/L$	
									Measured	Predicted
A	1979-1980	0,117	3,13	0,037	3,37	1,836	$\frac{0,037}{1 + 1,836}$	13,0	2,5	3,9
B	1980-1981	0,438	7,99	0,055	1,25	1,118	$\frac{0,055}{1 + 1,118}$	26,0	2,4	6,6
C	1981-1982	0,371	6,24	0,059	1,67	1,292	$\frac{0,059}{1 + 1,292}$	25,7	3,4	6,6
D		0,877	15,99	0,055	0,189	0,436	$\frac{0,055}{1 + 0,436}$	38,3		8,8
E	1980-1981	0,780	5,35	0,146	1,868	1,367	$\frac{0,146}{1 + 1,367}$	61,7	2,4	12,6
F	1980-1981	0,247	5,35	0,046	1,868	1,367	$\frac{0,046}{1 + 1,367}$	19,4	2,4	5,2
G		0,337	6,15	0,055	2,242	1,497	$\frac{0,055}{1 + 1,497}$	22,0	-	5,8
H		0,877	7,99	0,109	1,25	1,118	$\frac{0,109}{1 + 1,118}$	51,5	-	11,0

estimation of nutrient loading. The conditions chosen were as follows:

- Conditions A,B and C. These represent the observed values of those twelve month periods (i.e. October - September of 1979-1980, 1980-1981, 1981-1982). Nutrient loads, nutrient loading rates, chlorophyll a measurements and the associated hydrological characteristics of the system were measured and derived from the data provided (Tables 27 and 29).

Conditions D and E. These represent the extremes which were measured between overestimation and underestimation of the annual nutrient input using the product of a fortnightly sampling strategy of spot-flow and spot-concentration. The flow data are therefore different but the morphometric characteristics of the lake remain unchanged from Condition B.

Condition F. A hypothetical situation in which the effects of drawdown to 50% surface area can be evaluated. Data for Condition B were used as an example. The nutrient load and inflow were held constant but a 50% reduction of surface area results in doubling of the loading rate and an 88% reduction in volume with a consequent change in the hydraulic residence time.

- Condition G. A hypothetical situation which would exist if Midmar dam wall was raised to give a maximum depth of 26,82 metres (Olivier, 1980), i.e. an increase in depth of 20,5%. A corresponding increase in surface area to 1851 hectares (18,6%) and volume to $255,26 \text{ m}^3 \times 10^6$ (43,7%) would result. Using the inflow and nutrient load characteristics of Condition B, as an example, the effects of raising the wall can be evaluated using the two models.

Condition H. A hypothetical situation in which the nutrient load is doubled without a significant change in the hydrology or morphometric characteristics of the dam. Condition B was used to provide hydrological data and in this example therefore, loading rate is similar to that in Condition B but both water inflow and hydraulic residence time are different.

Sensitivity to annual variation in flow and load

When the three years were compared using the Vollenweider model (A, B and C in Figure 49) it was evident that during the 1979/80 period loading rate was within 'permissible' limits, but for the other two years, although not 'excessive', loads exceeded the 'permissible' limit. The OECD model was less sensitive to annual variations and all three years gave similar results which were within the 95% confidence limits (A, B and C in Figure 50). Because the points fell below the line of best fit for the OECD model, it can be assumed that chlorophyll values in Lake Midmar are lower than might be expected on the basis of phosphorus load. This confirms the view that Midmar is either buffered to some extent against phosphorus enrichment or that measured phosphorus load is not representative of effective phosphorus load. Present understanding of lake functioning implicates both of these in depressing response.

Sensitivity to accuracy of load estimation

Comparison of the highest and lowest estimates of nutrient loading obtained by changing sampling strategy, show that in the Vollenweider model it can alter the condition from 'excessive¹ to 'permissible' (D and E in Figure 49). In contrast, because the 'Y' axis in the OECD model is the chlorophyll concentration in the lake, variation in load estimation influences the position of the point relative to the 'x' axis only (D and E in Figure 50). Because the OECD model is quite sensitive in this regard, it reduces confidence in the prediction that may be made. Predictions based on the Vollenweider model are, however, less acceptable because they predict a situation which did not arise and which is quite out of context for Lake Midmar.

It can also be concluded that effort should be directed to ensure that load estimation is as accurate as practicable.

Sensitivity to a. reduction in lake volume

Increasing demand for stored water will accentuate annual drawdown so that the load is effectively applied to a smaller volume than at present. In the Vollenweider model halving the surface area enhances the response to current loading to the extent that it approaches the 'excessive¹ level (F in Figure 49). From the OECD model it is predicted that chlorophyll would increase about threefold and the lake might more closely resemble the mean trend from a large number of lakes (F in Figure 50).

These observations emphasise that water quality may be expected to deteriorate as demand increases and obviously this will be greatly aggravated by any development which results in a steady input of nutrients (a point source) even if concentrations are not elevated to any great degree. The Mpophomeni and Howick urban developments must be viewed in this light.

It is interesting to note that during the current drought both load and lake volume decreased. This was associated with an increase in the rate of production but not in the concentration of chlorophyll, implying that zooplankton grazing controlled the standing crop of phytoplankton.

Sensitivity to increasing storage capacity

Using the Vollenweider model it can be predicted that raising the wall and increasing the storage capacity will not significantly affect the trophic status (G in Figure 49). In the OECD model Lake Midmar would, under these conditions, fall slightly higher on the line of best fit (G in Figure 50). Neither of these observations are surprising because the results of this study have repeatedly indicated that the shallow depth and frequent mixing are important determinants of lake functioning, and that increasing the depth would make Midmar more 'typical¹ of lakes used in the development of these models (Figure 51).

Vertical stratification, arising from the greater stability of the water column consequent upon raising the wall, will persist for longer periods allowing epilimnetic nutrient depletion and accumulation in the hypolimnion, particularly if anoxic conditions prevail. At overturn nutrients in the hypolimnion will become available to algae and growth will be stimulated. Although this will occur at the onset of winter,

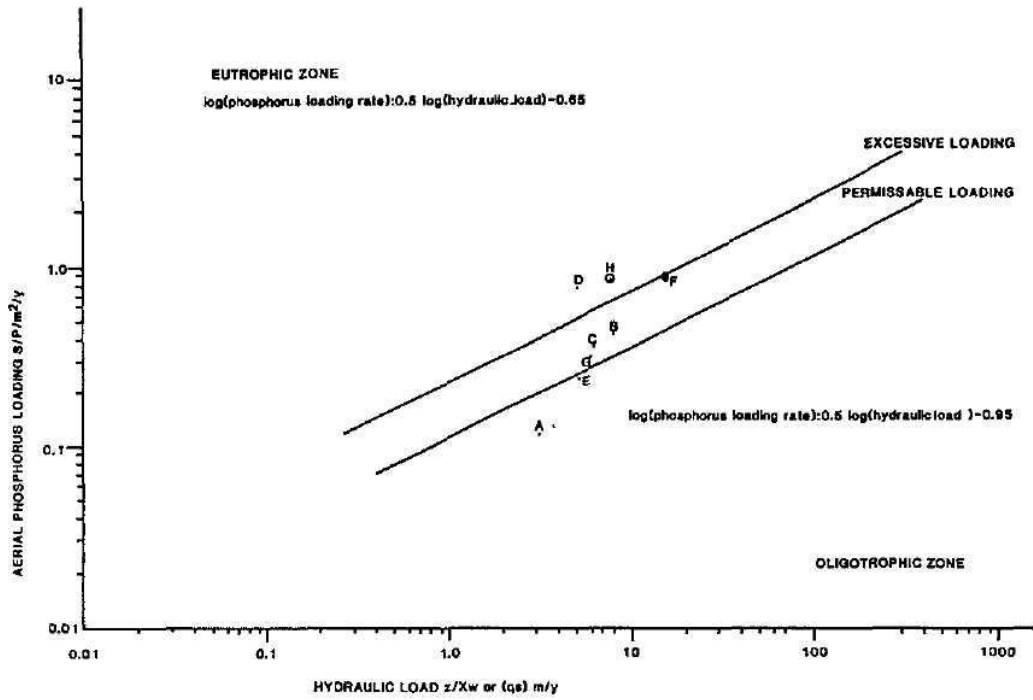


Figure 49 Vollenweider phosphorus loading - mean depth/ hydraulic residence time relationships applied to Lake Midmar.

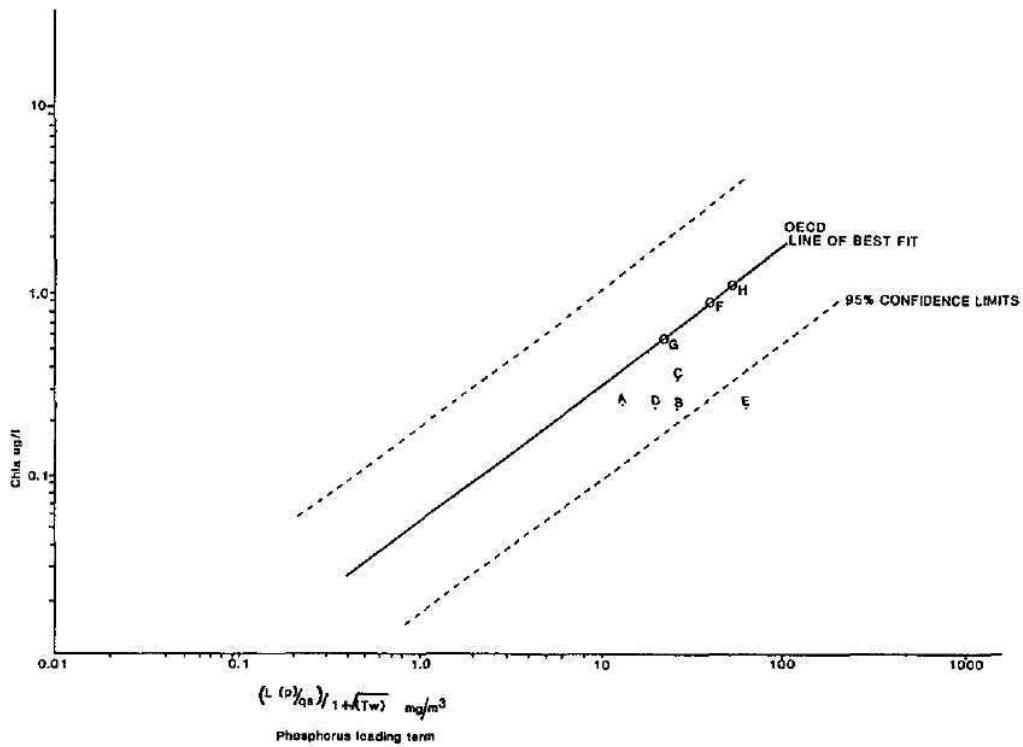


Figure 50 Phosphorus load - chlorophyll concentration relationship applied to Lake Midmar.

luxury uptake will prolong the consequences until the next spring. Thus greater water column stability will enhance the seasonal variability of the phytoplankton, creating unfavourable conditions in spring and early summer. This will be aggravated if the load is increased.

Horizontal compartmentalisation results from the dendritic form of the lake and it will be more strongly developed if the wall height is raised. At the present time although each 'arm' of the lake at times behaves differently, it is still reasonable to base prediction on a single compartment model. This will be less satisfactory when the wall is raised but, without a better understanding of the pattern of mixing in the lake, it is not possible to predict what will happen with any confidence.

Raising the wall height will make the system more complex and will therefore demand more sophisticated management. Advantages accruing from increasing the wall height must be weighed against those deriving from construction of another impoundment. It is desirable that all aspects of water use in the Mgeni system are based on predictive impact assessment.

Sensitivity to doubling the nutrient load

The nutrient load to Lake Midmar is not high and even when doubled, it would be regarded as low. Despite this, prediction based on the Vollenweider model indicates that the load would be unacceptably high (H in Figure 49). Because chlorophyll concentration is predicted in the OECD model, the predicted response to doubling the load must lie on the line of best fit (H in Figure 50). Its position indicates that chlorophyll concentration might be expected to increase four-fold, to a level at which serious water quality problems would be expected. However, because the OECD model appears to overestimate the response in Lake Midmar, the position of the point (H in Figure 50) could lie below the line of best fit. If the response line (track) of Lake Midmar is assumed to parallel the line of best fit, then chlorophyll concentrations might only double, at which level water quality problems would not be expected. If the response line does not track along the line of best fit, prediction could be wrong and the greater the deviation from parallel the greater the potential error. The best response line for Lake Midmar is obtained by joining the loading data from 1979/80 (A in Figure 50) with H, but inspection of the hydrological data in Table 26 shows that 1979/80 was unusual in that it experienced the greatest change in lake volume. At present we do not have a sound theoretical basis for predicting how a particular lake will track, and the examples given by Lee and Jones (1982) only show tendencies to track parallel to the line of best fit. Predictions based on the OECD model should therefore be interpreted with caution.

These observations support the view that as more of the stored water is used each year, the lake will become increasingly responsive to nutrient loading, but there is sufficient evidence to postulate that the response of Lake Midmar will be buffered against increased nutrient loading (Figures 51 and 52). However, since loading has not increased significantly over the past few years, it has not been possible to validate the hypothesis. Circumstantial support is provided by studies of the response of other shallow, well-mixed lakes : Lake Shagawa for example, in the OECD study (Jones and Lee 1982), does not track along the predicted course in response to a reduction in nutrient loading.

Under increased loading the equilibrium concentration for phosphorus is exceeded and there is a net adsorption of phosphorus. With phosphorus being continuously removed, response to load is depressed. If anoxic conditions prevail periodically, the solubility of sediment phosphorus is enhanced and, although there will still be a net adsorption if the equilibrium concentration is exceeded, more phosphorus will remain in solution and response to load will be depressed less than under aerobic conditions. Since raising the wall height by even two or three metres will greatly increase vertical and horizontal compartmentalisation of the lake water, it will have negative consequences for management particularly if the loading rate increased. Until the pattern of mixing in Lake Midmar is better understood, it is not possible to predict the extent of compartmentalisation and hence the response.

Buffered response to* increased nutrient loading is not justification for complacency in management. It implies only that the lake will be responsive to controlled loading; it does not mean that higher loading should be permissible here, or that ameliorative management procedures (hypolimnetic discharge, catchment management etc.) should be ignored. Every effort should therefore be made to ensure compatibility between catchment development and nutrient export to the lake.

This discussion has highlighted both the advantages and disadvantages of these models. The OECD model seems to be the better of the two but because it is quite sensitive to accuracy of load estimation and because no consensus has yet been reached on how to measure load and which fraction/s to include, predictions remain tentative. In general terms, however, the predictions are consistent with our understanding of the functioning of Lake Midmar.

7.2 THE STRUCTURE AND FUNCTIONING OF LAKE MIDMAR C. M. Breen and J. Heeg

Introduction

The biota of ecosystems can be allocated to groups (communities) on the basis of the positions they occupy and the roles they play in the ecosystem. The presence or absence of groups and their interrelationships, the trophic structure, greatly influences the response of the system to changing conditions, and is therefore central to our ability to predict the behaviour of the system.

Trophic structure

The most significant determinants of trophic structure in Lake Midmar are instability of the water level and the water column. Both have direct effects on the representation of trophic levels in the system and indirect effects on processes and the rates at which they occur (Figure 51).

Unstable water levels: Three sources of primary production can be recognized in aquatic systems: algae and higher plants growing suspended in or on the water; algae and rooted or emergent plants growing in the shallow water; and plant material transported into the system from outside. Fluctuating water levels have their greatest effects on the last two.

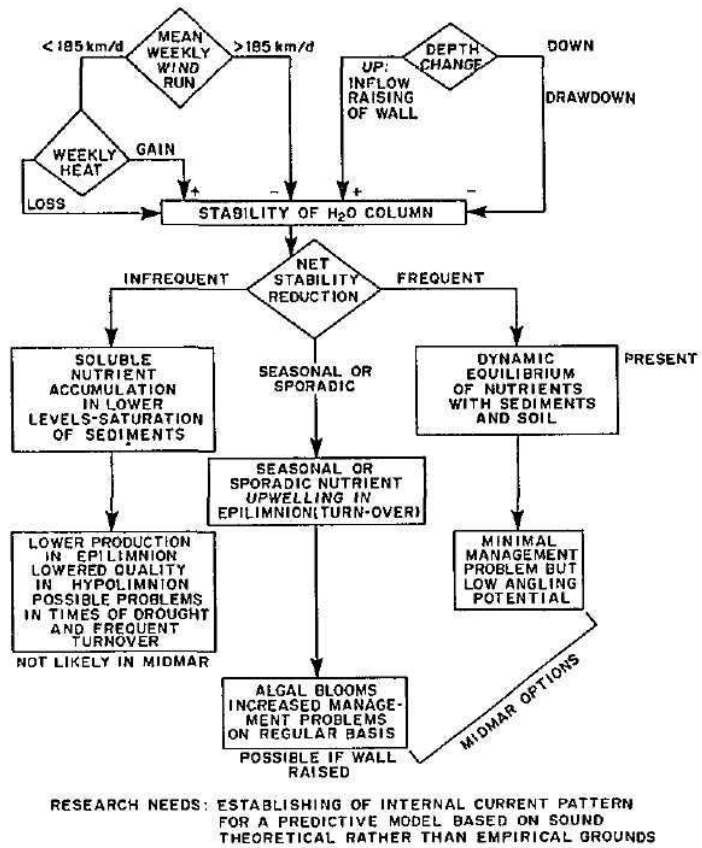


Figure 51 Effect of drawdown and/or change of wall height on biological processes in Lake Midmar.

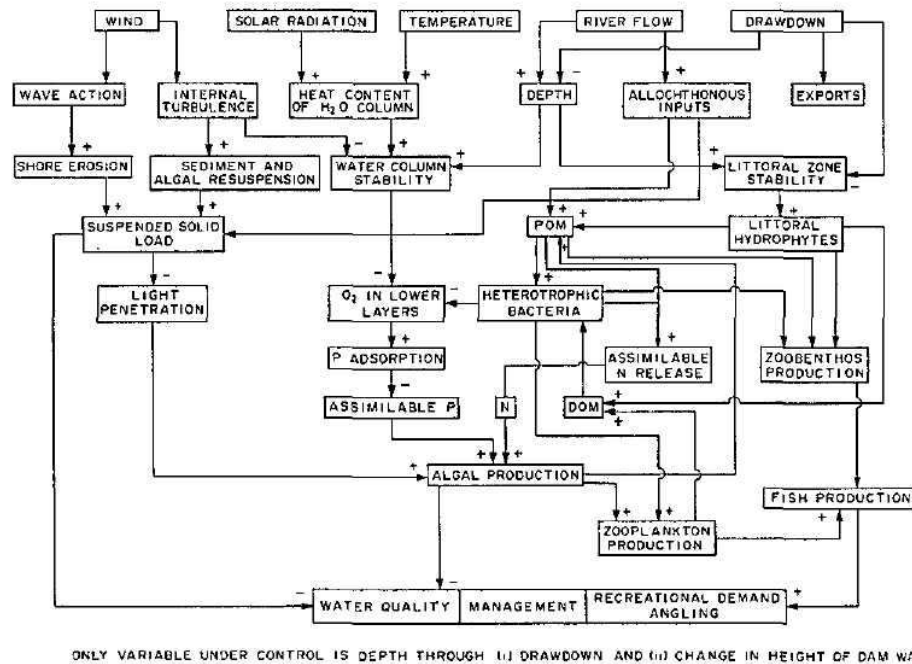


Figure 52 A conceptual model showing interactions between climatic and management variables on biological processes in lake Midmar.

Although most, if not all, hydrophytes have adaptations which allow them to survive periods of exposure, the negative effects increase with the period of exposure. In systems such as Midmar where water levels fluctuate considerably each year, the period of exposure is sufficiently long to suppress the development of a littoral plant community. That this is not the only factor responsible for the weak development of hydrophytes is evidenced by the restricted distribution of reed (PHRAGMITES) communities to the delta areas of streams entering the lake. The structure and stability of the substratum favour hydrophyte growth in these areas whereas on the more exposed shorelines, wind induced wave action continually erodes the substratum, material being transported into deep water where hydrophyte growth is impossible. Fluctuating water levels therefore directly affect the establishment of these communities and indirectly affect system function by restricting their roles in the transfer of nutrients from the sediments to other components of the system and in energy fixation.

In many shallow lakes the zone of periodic inundation (eulittoral zone) may provide the major source of energy for system functioning. This is not the case in Lake Midmar (Chapter 4.4), and the most likely explanations are: that exposure occurs mainly during the winter period when dry conditions, low temperatures and periodic frost limit plant establishment and growth, and erosion and removal of organic material and silt during periods of high water, prevent the development of a suitable substratum in the shallow areas.

Unstable water column: The direct effects of water column instability may be positive or negative depending on the specific adaptations of the organism (Figure 52). Thus turbulence effecting periodic entrainment of bottom sediments and their removal from the shallow waters create unfavourable conditions for benthic organisms, and the zoobenthos community in Lake Midmar is therefore poorly developed. In contrast, water column instability (turbulence) creates favourable conditions for certain phytoplankton species such as MELOSIRA which may have low light requirements or which sink below the euphotic zone when calm conditions prevail (Chapter 5.3).

The depauperate trophic structure of Lake Midmar reflects the instability of both the water level and the water column. This structure helps to maintain the current low levels of production in the system with beneficial effects for provision of potable water, boating and swimming but negatively affects the angling potential.

Community dynamics

Community dynamics reflect many interacting components and processes but, within this complex picture, it is possible to identify the major controlling functions. It is evident from the trophic structure that secondary production is largely dependent upon two sources of organic matter (energy sources): allochthonous material introduced principally by the Mgeni and Lions rivers, and organic matter produced in the system by the phytoplankton.

Allochthonous sources: The amount and nature of the allochthonous material entering the lake is greatly influenced by the floodplain immediately upstream. Much of the heavier inorganic material is deposited before the water enters the lake leaving the finer inorganic and lighter organic material as the major part of the load.

The evidence indicates that, with the probable exception of nitrogenous compounds, allochthonous loads of both particulate and soluble inorganic material are relatively minor determinants of community dynamics. This is because within-lake processes are dominant: more inorganic suspensoids derive from shoreline erosion and resuspension than from river input and sediment: water phosphorus fluxes frequently override those attributable to allochthonous loading. Although current low water levels have resulted in greater turbidity from resuspension and therefore have enhanced within-lake processes, Lake Midmar is sufficiently shallow for internal processes to predominate even at full supply level.

Allochthonous organic material raises bacterial production significantly (Figure 52), as evidenced by elevated CO₂ concentrations which persist for a few days after high flow events. This pulse of production is then transferred to other trophic levels through filter feeding zooplankton and their predators. Under present allochthonous loading rates the amount of energy entering the system in this way is insufficient to maintain elevated levels of production, and secondary production is thus largely dependent on zooplankton which graze phytoplankton.

Autochthonous sources: Phytoplankton forms the basis of primary production within the lake. The overriding determinant of the rate of production is nutrient (phosphorus and nitrogen) limitation and this is reflected in the extremely low rates of carbon fixation. Production levels are lower than would be predicted from the loading rate. Three factors may contribute: inaccurate load estimation; basing prediction on the wrong fractions of phosphorus, and internal processes favouring phosphorus removal from the water column. Although temperature can also control the rate of production in individual species, there is no marked evidence of seasonality in carbon fixation because the phytoplankton community dominants change. In winter colder temperatures and lower net radiation favour MELOSIRA, whereas in summer other species including blue-green algae predominate.

The zooplankton standing crop is very much controlled by the nature and quantity of the phytoplankton, and it is therefore generally low. Like the phytoplankton, it shows distinct seasonal shifts in species composition according to the temperature tolerances of individual species, and composition of the phytoplankton food source. As the zooplankton are the major energy source for predators (other species of zooplankton and fish) they in turn have low rates of production

Seasonal variation in the water column stability can, particularly in more productive systems, result in distinct peaks of phytoplankton production which are then translocated through the trophic levels to the top producer. This does not occur to a significant degree in Lake Midmar principally because the water column is unstable, and nutrients released by mineralisation are continually mixed into the whole water column.

The community dynamics in Lake Midmar reflect intense competition for the available resources so that overall production remains remarkably constant despite changing conditions. This is accomplished largely by changing community structure as each species gains or loses advantages.

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