

PROJECT REPORT

PRIMARY PRODUCTION OF SWARTVLEI IN  
MID-SUMMER 1980, WITH EMPHASIS ON THE  
PRODUCTION ECOLOGY OF THE LITTORAL ZONE

D. I. TAYLOR

M.Sc. Limnology

Department of Zoology and Entomology

Rhodes University

GRAHAMSTOWN

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## CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS	
1. Study area and selection of sampling sites	3
2. Water sampling and analyses	6
3. Standing stock estimation	7
4. Estimation of primary production	14
4.1. Sampling and incubation	15
4.2. Sample analyses	22
RESULTS	
1. Physico-chemical environment at time of study	30
2. Plant zonation and biomass	34
3. Primary production	46
DISCUSSION	51
SUMMARY	59
ACKNOWLEDGEMENTS	60
REFERENCES	61

## INTRODUCTION

Energy passes through an ecosystem via a multiplicity of interconnected routes, which can be broadly categorised into trophic and detrital pathways. The "metabolic activity" of most lakes will be governed predominantly at the base of these two routes; namely, the primary producer and decomposer levels, respectively (Wetzel and Allen, 1972). The importance of the littoral primary producers (especially the aquatic macrophytes) in the functioning of the Swartvlei ecosystem has been emphasised in a comprehensive report by Howard-Williams and Allanson (1978) dealing with the lake system from 1975 to 1978. They noted that although the littoral shelf (< 2m below low water level) occupies only 43% of the lake's surface area it contributed 64% of the total annual primary production during the period investigated. This was largely due to the dense Potamogeton pectinatus stands which alone accounted for 52% of the total carbon input into the lake by plants. The fact that the production/biomass ratio for P. pectinatus was only 1,2:1 suggested that its importance as a primary producer in Swartvlei was largely due to its high biomass. (Biomass, or standing stock, is used in this report as defined by Waters (1977); namely, "the amount present at a point in time, expressed best as quantity per spatial unit".)

Under "climax" conditions P. pectinatus exhibited an annual growth cycle in Swartvlei with peak biomass towards the end of summer (April) (Howard-Williams and Allanson, 1978). In 1979, however, the summer peak failed to materialize and the P. pectinatus biomass in January 1980 was only 2,4% of that recorded in January 1975 (Whitfield, 1980). These observations strongly suggested that a pronounced change in the structure and functioning of the littoral plant communities had taken place. By October (1980) the P. pectinatus stands had still not recovered and its biomass appeared

to be exceedingly low. It was, therefore, considered worthwhile to attempt to quantify the changes and so provide further insight into the production ecology of this system.

Representation of populations or communities in terms of numbers or biomass provides only limited indication of their functional importance in an ecosystem (Mann, 1969). A clearer understanding can be obtained by measuring the production of a biotic component and comparing this to that of the other components or to the production of the system as a whole (Howard-Williams and Allanson, 1978). (Production may be defined as "the rate of tissue elaboration, regardless whether it survives to the end of a given time period" (Waters, 1977). For these reasons, the present investigation, conducted from October 1980 to January 1981, aimed to determine the net production of the different plant communities in Swartvlei.

## MATERIALS AND METHODS

## 1. Study area and sampling site selection

The Swartvlei system is an oligotrophic estuarine-lake complex situated on the southern coast of South Africa (34°S 22°46'E) (Figure 1). The morphometric, hydrological and physico-chemical characteristics of this meromictic system have been comprehensively described by Robarts (1973), Liptrot (1978), and Howard-Williams and Allanson (1978). The system can be divided into two distinct regions; the upper lacustrine section (Swartvlei), and the lower estuarine section (Swartvlei estuary). Two sampling sites were established in the former region: a pelagic station (P) in the main lake basin and a littoral transect (L) on the western shore of the west basin. The former site was chosen because its physico-chemical limnology has been monitored at approximately fortnightly intervals since 1975. The latter area, however, was selected because of its proximity to laboratory facilities. The depth of the water column at the pelagic station (P) varied over the three month study period between 12,2 and 13,3m. The littoral transect (6m wide and 110m long) was positioned at right angles to the shore and extended to the edge of the littoral region (2 m below low water level) (Howard-Williams and Allanson, 1978). The location of sampling sites along the littoral transect was based on the pronounced macrophyte zonation; a station being established in the centre of each zone (except the Phragmites Zone) (Figure 2). All the in situ littoral primary production incubations, and water and plant biomass samplings, were carried out at these five stations.

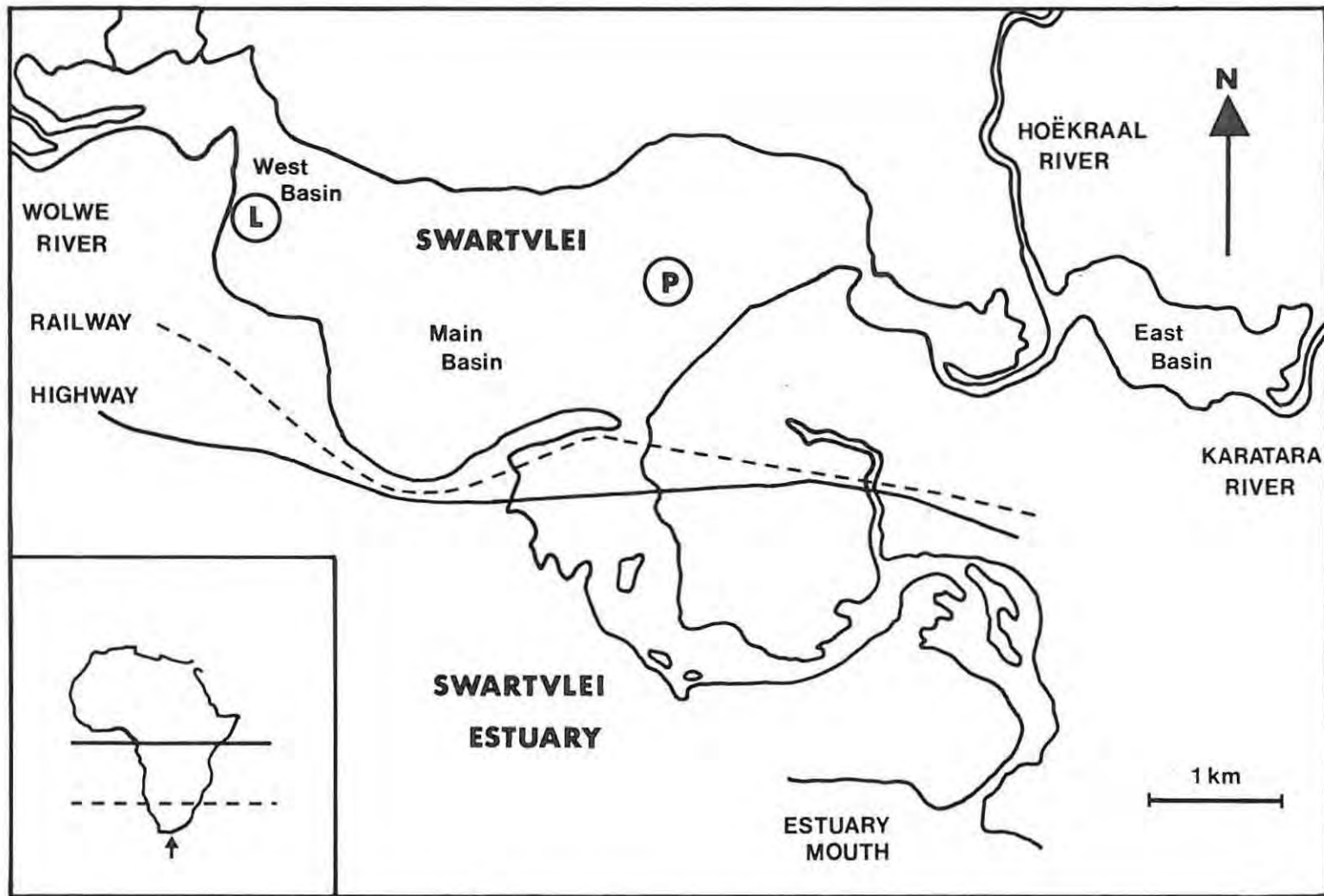
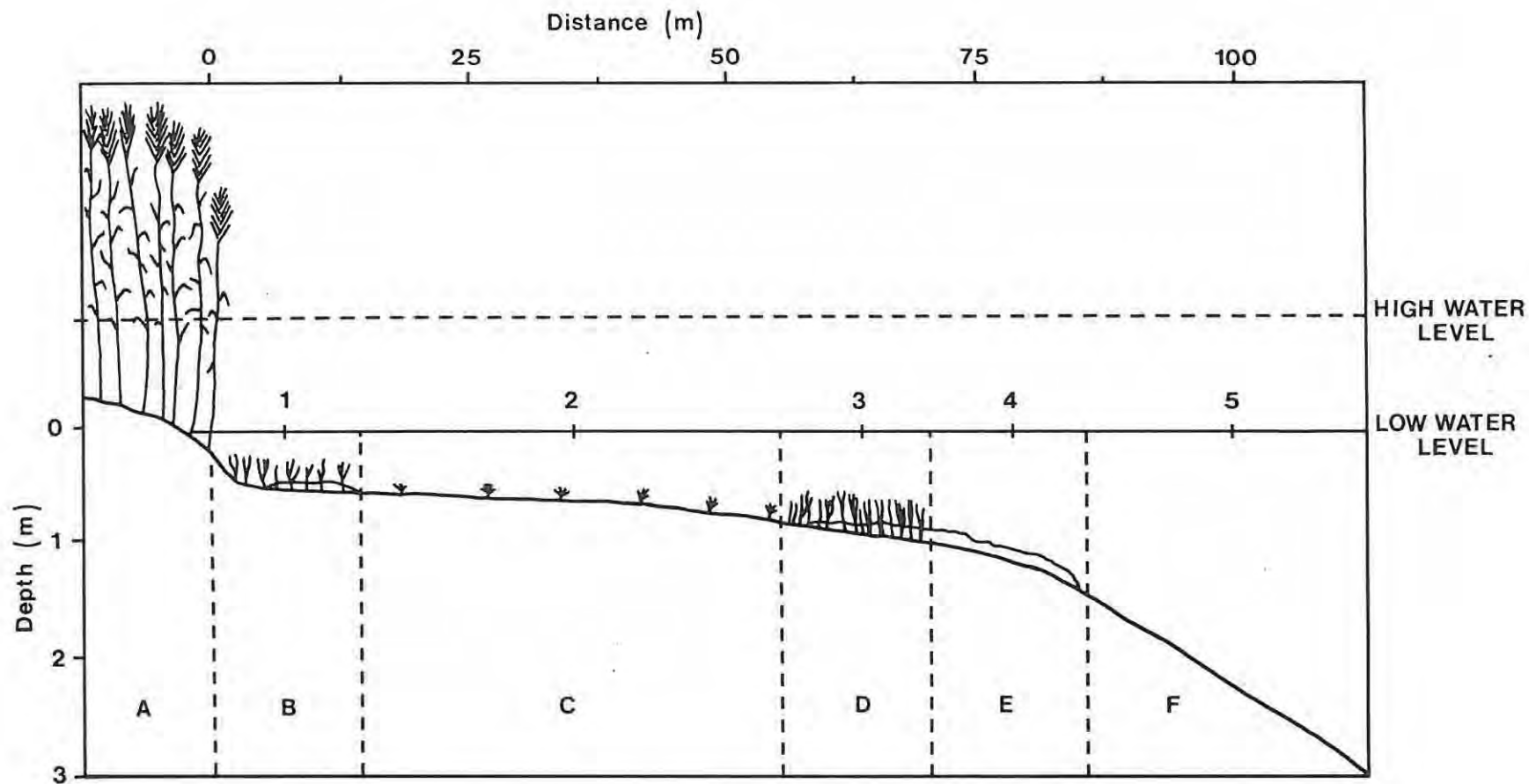


Figure 1. Map of the Swartvlei system showing the positions of the pelagic (P) and littoral (L) sampling sites (modified from contour map of Swartvlei, National Research Institute for Oceanology, Council for Scientific and Industrial Research, Pretoria).



- |   |                        |   |                        |
|---|------------------------|---|------------------------|
| A | PHRAGMITES ZONE        | D | OUTER POTAMOGETON ZONE |
| B | INNER POTAMOGETON ZONE | E | FILAMENTOUS ALGAE ZONE |
| C | CHAROPHYTA ZONE        | F | LITTORIPROFUNDAL ZONE  |

Figure 2. Profile diagram of a littoral transect on the western shore of Swartvlei showing the extent of the aquatic macrophyte communities and the location of the littoral sampling sites (1, 2, 3, 4 and 5). The high and low water levels were measured on 22.10.80 (estuary mouth closed) and 8.12.80 (estuary mouth open), respectively.

## 2. Water sampling and analyses

In order to obtain a broad indication of the physico-chemical environment in the pelagic and littoral regions of Swartvlei four sampling programmes were carried out in both the littoral and pelagic sampling areas.

Water samples were collected at metre intervals through the water column at the pelagic station (P) and at half-metre intervals at littoral stations 1, 3 and 5. They were obtained with a Ruttner bottle and stored in plastic bottles in the dark for 1 - 2 hours. Liptrot (1978) stored his samples for 2 - 4 hours and noted that this storage period did not affect pH by more than 0,02 units.

pH was measured in the laboratory using a Beckman Expandomatic pH meter and electrodes. The instrument was checked regularly with standard pH buffers (pHydrion buffer, Micro Essential Laboratories Inc.).

Salinity was measured in the field using an American Optical Instruments refractometer (temperature compensated); error of approximately 1‰ determined using aqueous sodium chloride solutions.

Temperature and dissolved oxygen were estimated using a Y.S.I. Model 51B meter. The oxygen meter was calibrated against Winkler titrations (Mackareth, Heron and Talling, 1978) and agreed to  $\pm 0,3$  at  $6,85 \text{ mg } \text{O}_2 \text{ l}^{-1}$  ( $n = 6$ ).

The total solar energy reaching the surface of the Swartvlei System was recorded by a LI-COR Integrator LI - 500. Photosynthetically active radiation (PAR) was measured using a Lambda Instruments Corporation LI - 185 meter with a LI - 192 underwater sensor. All underwater readings in  $\mu \text{ E m}^{-2} \text{ s}^{-1}$  were multiplied by a correction factor (1,4) provided by the instrument manufacturers. Secchi disc readings were also recorded.

### 3. Standing stock estimation

The aquatic macrophytes and filamentous algae were sampled using a metal quadrat (250 x 250mm) thrown randomly into a circle of three metre radius enclosing each littoral station. The above- and below-ground portions of the plants were collected manually, sorted, washed thoroughly with tap water, dried at 65°C for 36h and then weighed. A minimum of 14 samples were collected in each zone which provided a convenient compromise between precision requirements and time availability. The results obtained are expressed as g (dry weight) m<sup>-2</sup>, which enables a comparison to be made with the standing stock data presented by Howard-Williams and Allanson (1978).

However, it is logistically difficult to express standing stocks of phytoplankton, epipsammic and periphyton communities in weight units, and they are most often expressed in quantity of chlorophyll per unit area. In order to compare the standing stocks of all the plant communities in Swartvlei a common biomass "currency" was required, and the unit  $\mu\text{g chlorophyll } a \text{ m}^{-2}$  was selected. This necessitated a conversion of macrophyte and filamentous algae standing stock estimates in mg (dry weight) m<sup>-2</sup> to  $\mu\text{g chlorophyll } a \text{ m}^{-2}$ . The biomass estimates were multiplied by the appropriate wet/dry weight and chlorophyll a/wet weight ratios (see Table 1), thus:

$$\text{g (dry wt) m}^{-2} \cdot \frac{\text{g (wet wt)}}{\text{g (dry wt)}} \cdot \frac{\mu\text{g chl. } a}{\text{g (wet wt)}} = \mu\text{g chl. } a \text{ m}^{-2} \quad (1)$$

When multiplying two estimates of known confidence limits, it is incorrect to simply take the mean of the two confidence limits to determine the precision of the final estimate. The method of Bevington (1969; p63) was adopted to overcome this problem.

TABLE 1 Relationships between (a) dry weight and wet weight, and (b) wet weight and chlorophyll content, in P. pectinatus, the Charophyta, and the filamentous algal aggregate. The 95% confidence limits and number of samples (n) are indicated.

	(a) Ratio of wet weight/ dry weight (no units)	(b) Ratio of ug chlorophyll a/g wet weight
<u>P. pectinatus</u>	3.8 $\pm$ 10% ( <u>n</u> = 41)	249 $\pm$ 13% ( <u>n</u> = 10)
Charophyta	3.6 $\pm$ 29% ( <u>n</u> = 50)	186.55 $\pm$ 19% ( <u>n</u> = 9)
Filamentous Algae (Inner <u>Potamogeton</u> Zone)	5.57 $\pm$ 7% ( <u>n</u> = 51)	160.2 $\pm$ 8% ( <u>n</u> = 10)
(Outer <u>Potamogeton</u> Zone)	Assumed as for Inner <u>Potamogeton</u> Zone.	233.9 $\pm$ 24% ( <u>n</u> = 10)

Chlorophyll is a convenient and readily determined indirect measure of biomass closely linked to photosynthetic activity (Wetzel and Westlake, 1969). The pigment concentration per unit plant weight is however, highly variable and influenced by an array of environmental and internal factors. A difference in colour between the filamentous algal aggregates in the Inner and Outer Potamogeton Zones suggested a difference in their chlorophyll contents. Analysis of ten samples from each zone and application of the Student's t-test indicated a significant difference in their chlorophyll a  $g^{-1}$  (wet weight) ratios ( $P < 0, 01$ ). This spatial difference necessitated the determination of two chlorophyll a/wet weight ratios for the filamentous algal aggregate. The ratios for P. pectinatus and the Charophyta were assumed to be the same in all the zones. Since significant differences between variances will also produce a significant t value (Elliott, 1977), the t-test was always preceded by the F-test (as in Elliott, 1977).

Chlorophyll a determinations were based on the method described by Strickland and Parsons (1968) (95% C.L. =  $4,8 \pm 0,57 \mu g \text{ Chl. } a \ell^{-1}$ , C.V. = 15%,  $n = 9$ ). Certain details, precautions and procedures used for the different plant groups merit note.

1 - 2 g P. pectinatus, Charophyte and filamentous algal samples were washed, partially dried in absorbent paper, weighed and then ground for one minute in 25 ml 90% alkaline acetone with clean washed sand. As with the other chlorophyll analyses acetone extraction in a refrigerator lasted 24 hours during which time the samples were shaken occasionally. Spectrophotometric analysis, acidification with 0,1N HCl and calculation of chlorophyll a content was done according to Strickland and Parsons (1968). For all the pigment determinations the absorbance was measured in 40mm cells at 663 and 750nm in a Shimadzu 4 decimal spectrophotometer (Kyoto, Japan).

This technique provides an estimate of chlorophyll a corrected for phaeopigments. The presence of large amounts of these degradation products have been reported for periphyton extracts (Tett et al, 1978; Marker, 1972), epipsammic algae (Hickman and Round, 1970), phytoplankton, (Riemann, 1978) and aquatic macrophytes. Correction for phaeopigments is, therefore, essential.

The pelagic phytoplankton community was sampled using a Ruttner bottle, and collection was restricted to calm periods ( waves < 10cm high) in order to reduce the contribution made by epipsammic algae to the chlorophyll content of the free water. This precaution was considered necessary because preliminary investigations indicated that strong wave action in the littoral resulted in an increased chlorophyll concentration in the overlying water, probably by resuspending sediments and detrital material (Figure 3). During the first half of the study period 350 - 400 ml water samples were filtered through 0,45  $\mu$ m Millipore filter paper; subsequently this was altered and 900-1 100 ml samples were filtered through Whatman glass microfibre filters. No significant difference in chlorophyll a estimates using the two techniques was noted ( $p > 0,05$ ,  $n = 14$ ). 15 ml 90% acetone was used for extraction.

Sediment samples were obtained by gently pushing glass tubes (25 mm internal diameter, 100 mm length) approximately 10 mm into the sediments. The tube was sealed at the top with a rubber stopper, withdrawn from the sediments and then the sediment and overlying water emptied into a glass jar. At each littoral sampling site fifteen cores were taken at random positions in a 500 x 500 mm quadrat divided into 100 squares (Bowen, 1978). Considerable care was taken not to disturb the sediment during sampling. The samples were transported to the laboratory in a darkened container, filtered through Whatman glass microfibre filters and ground for one minute in a mortar with 25 ml 90% alkaline acetone.

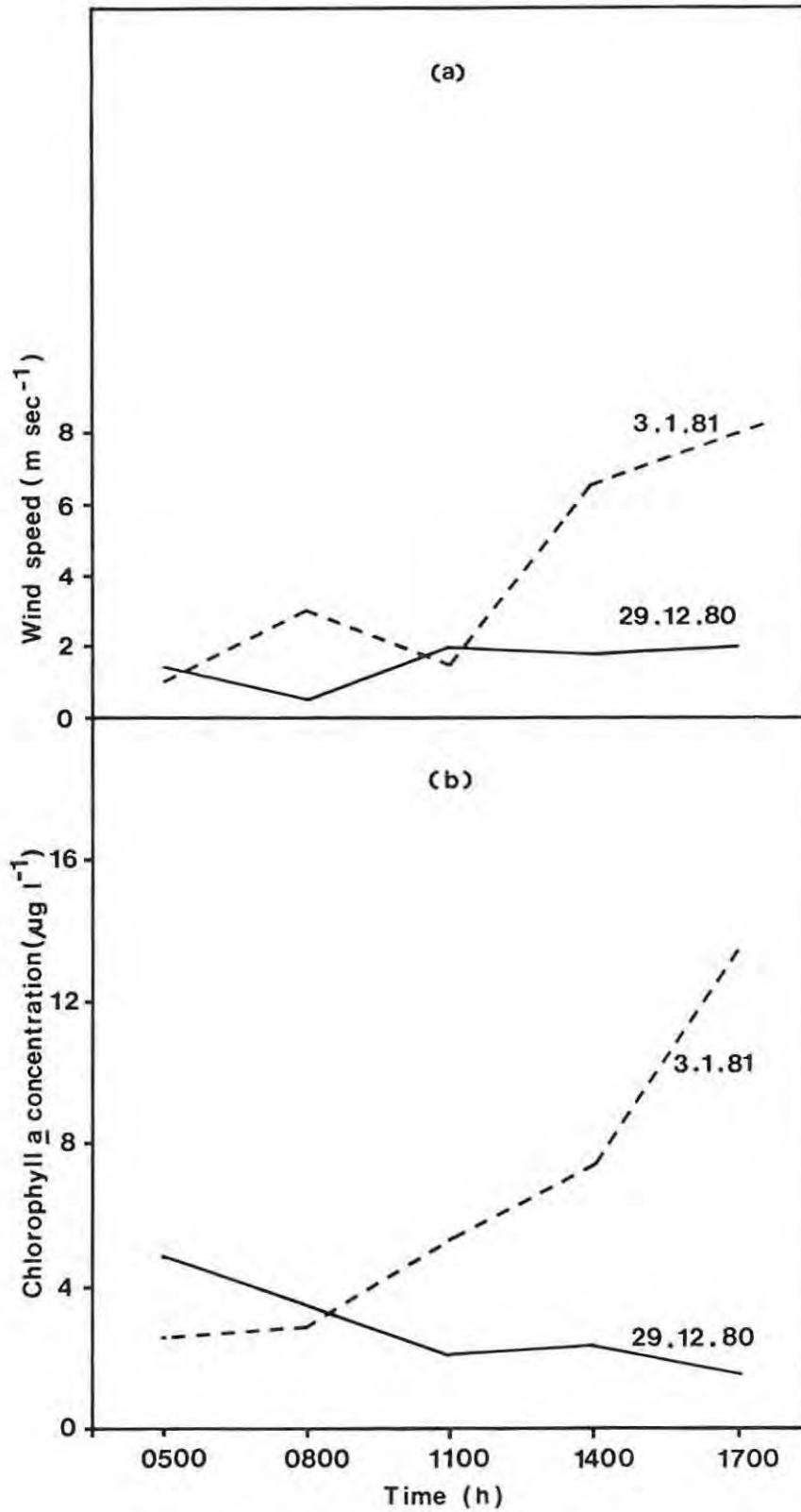


Figure 3. Diel changes in (a) wind speed and (b) chlorophyll a concentration at 1,0m depth in the Outer Potamogeton Zone on 29 December, 1980 (—) and 3 January, 1981 (---). On both dates wind was south easterly.

Filtration allows removal of the overlying water while grinding facilitates chlorophyll extraction (Fenchel and Straarup, 1971). The sediments were then dried at 65°C for 36 h and weighed to determine their exact volume. It is assumed that before disturbance the chlorophyll content of the 90 mm of overlying water is negligible in comparison to that of the sediments. The chlorophyll content of the top 10 mm of sediment is expressed in mg chlorophyll  $\underline{a}$   $\text{m}^{-2}$ .

Samples used for determining the vertical distribution of chlorophyll  $\underline{a}$  in the sediments were collected using a core apparatus similar to that of Gargas (1970) and illustrated in Figure 4. Nine incisions were made at 10 mm intervals along one side of a plexiglass tube of internal diameter 435 mm. The incisions, which extended halfway across the tube, were covered with waterproof tape. The core was gently pushed into the sediment, a rubber stopper placed in the top, the tube slowly withdrawn and then a second stopper inserted at the bottom end. In the laboratory the overlying water was carefully siphoned off and sharp metal partitions inserted into the incisions. The sections of sediment were then removed and treated as above. All sediment samples were collected on calm days (waves < 10 cm high) for the reasons discussed above. Several workers have reported rhythmic vertical migration by freshwater diatoms in sediments (for example, Round and Happey, 1965; Round and Eaton, 1966, Harper, 1969; and Round, 1978). To minimize this source of variation all sediment sampling was restricted to the period between 09h00 - 10h00.

In order to estimate epiphyton (as defined by Wetzel, 1975), approximately 100 mm portions of randomly selected P. pectinatus stems were carefully cut and placed in test tubes filled with filtered (Whatman glass microfibre filters) lake water. In the laboratory the epiphyton was

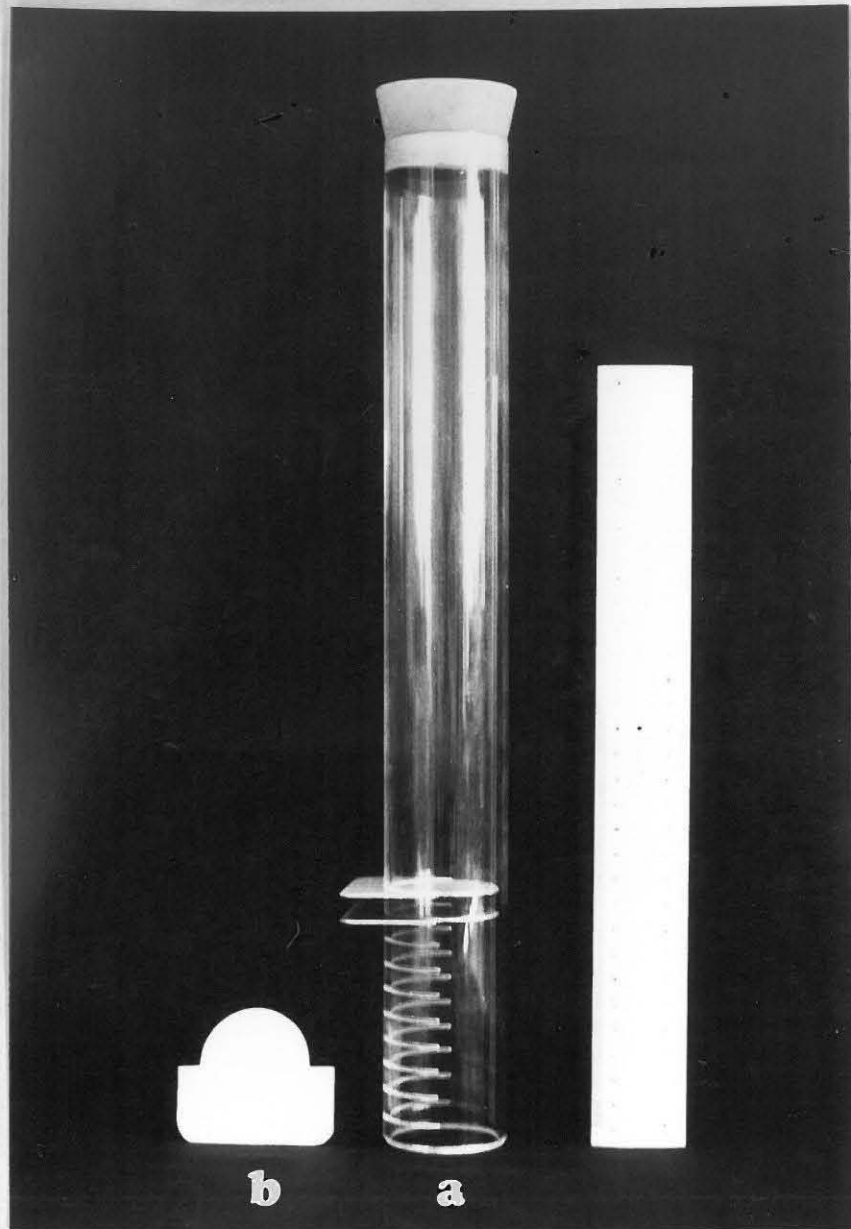


Figure 4. Core apparatus (a) with partitions (b) for collection 10mm thick sediment samples.

removed from the plant by scrubbing with a plastic brush and washing with distilled water. Microscopic examination indicated that almost all the attached microphytes were removed by this treatment.

The epiphyton suspension was filtered (Whatman glass microfibre) and the chlorophyll a determined as for phytoplankton. The surface area of the P. pectinatus stems was estimated and the epiphyton standing stock determined in  $\mu\text{g}$  chlorophyll a  $\text{m}^{-2}$  of plant surface. It was assumed that the surface area of P. pectinatus was proportional to its biomass (Titus et al, 1975) and varied from  $6\text{m}^2\text{m}^{-2}$  at minimum biomass to  $30\text{m}^2\text{m}^{-2}$  at maximum biomass (Howard-Williams and Allanson, 1978). A comparison of present P. pectinatus standing stocks with estimates obtained by the latter authors, suggested the existing biomass was at the minimum level, and as a result the epiphyton standing crop ( in  $\mu\text{g}$  chl. a  $\text{m}^{-2}$  water surface) was determined simply by multiplying the chlorophyll a value ( in  $\mu\text{g}$  chl. a  $\text{m}^{-2}$  straw surface) by  $6\text{m}^2\text{m}^{-2}$ .

#### 4. Estimation of primary production

Primary production is basically dependent on the photosynthetic activity of the autotrophic organisms present in a system. For this reason, the estimation of primary production can be based upon measures of photosynthesis; either the amount of raw material used ( e.g. carbon dioxide uptake), or the amount of by-product released ( e.g. oxygen production). The rate of  $\text{CO}_2$  uptake is usually estimated by the method of Steeman-Nielsen (1952) using labelled carbon dioxide ( $^{14}\text{CO}_2$ ). Instrumentation for measuring  $^{14}\text{C}$  activity was unavailable during the study period and in situ primary production measurements were carried out using the oxygen light and dark bottle technique. The relative merits

of this method are comprehensively outlined in Vollenweider (1969) and Golterman (1975).

#### 4.1. Sampling and incubation

P. pectinatus production was measured at stations 1 and 3, Charophyte production at station 2, and the filamentous algal production at stations 1, 3 and 4. The macrophyte samples were thoroughly, but gently washed at the collection site to remove all associated fauna, periphyton and detritus fragments. Subsamples (0,1 - 1,25g wet weight) were placed in five or six pairs of transparent and dark, 250 ml pyrex bottles filled with lake water from the sampling/incubation site. Filtered lake water has been used by other workers (e.g. Howard-Williams and Allanson, 1978) in similar experiments but the extra handling involved in filtration is likely to alter certain physico-chemical properties (e.g. pH, alkalinity, oxygen concentration) of the water which may, in turn, influence the production results. Initial investigations using controls containing lake water showed that changes in oxygen concentration due to phytoplankton production were less than the experimental errors in the epiphytic, epiphytic and macrophyte incubations. Consequently corrections for the phytoplankton contribution were considered unnecessary and were not performed. To avoid separation of shoots from roots, which may affect nutrient uptake and metabolism during incubation, whole P. pectinatus and Charophyte plants were incubated. Three bottles filled with lake water and fixed with Winkler reagents (Mackareth, Heron and Talling, 1978) were used to estimate initial oxygen concentrations. The bottles containing plant material were placed horizontally in wire trays on the sediment surface (Figure 5) and incubation lasted two hours (11h00 - 13h00) for P. pectinatus, and three hours (10h00 - 14h00) for the Charophytes and filamentous algae. It was necessary to reduce the

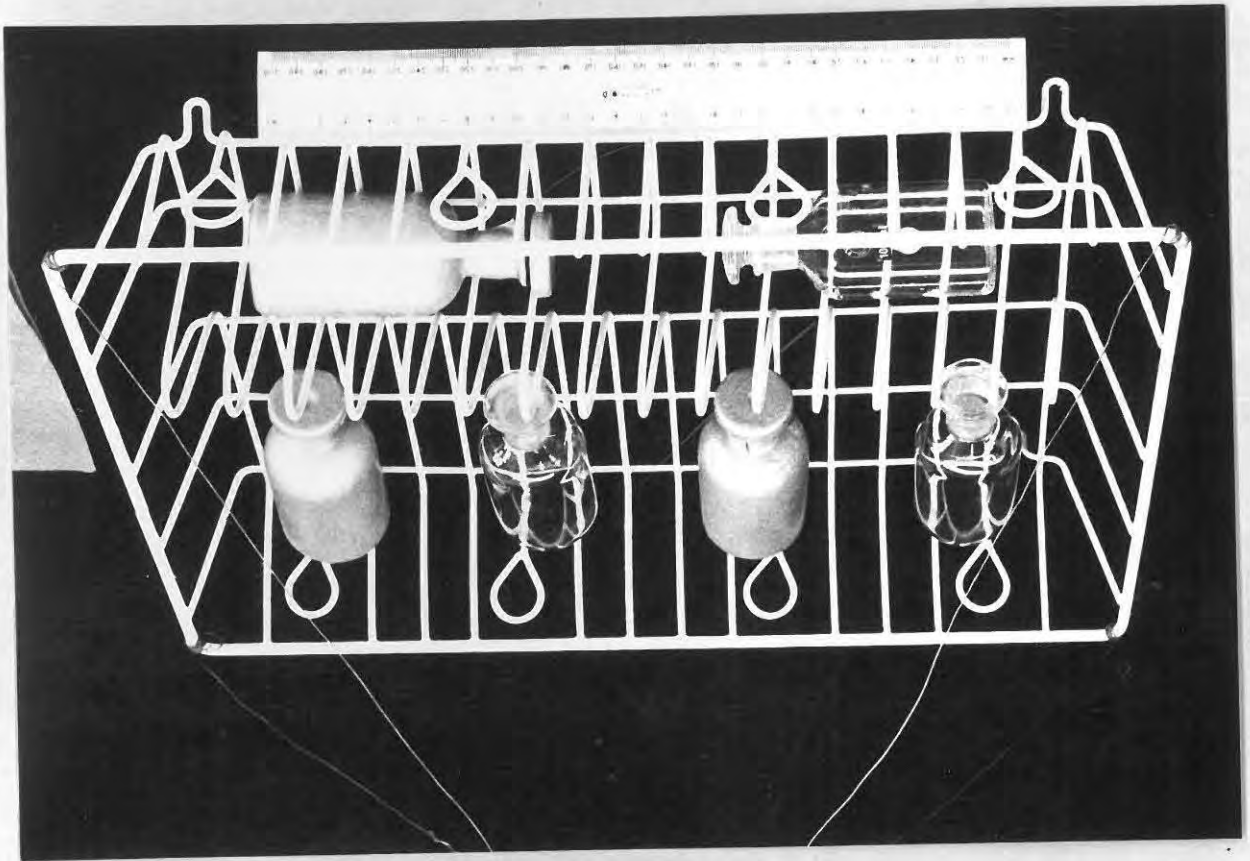


Figure 5. Wire tray containing light and dark reagent bottles used for primary production determination. Bottles shown are 100ml used for incubation of epipsammic samples; 250ml reagent bottles were used for all the other plant components.

incubation period for the macrophyte samples to 2h or 3h in order to prevent oxygen supersaturation and emission of gas bubbles, which would lead to underestimation of production. On completion of incubation and oxygen analysis the sample dry mass was determined.

The dark bottles were covered with two layers of black plastic tape painted silver to reduce heat absorption by the darkened surface. After all determinations, traces of iodine in the sample bottles were removed by rinsing with dilute (N/100) sodium thiosulphate solution.

Although a number of modifications and precautions were implemented, the application of the oxygen light and dark bottle technique to macrophytes is questionable. Reasons for this include:

1. The removal of roots from the nutrient-rich substratum may alter the plant's metabolism (Wetzel, 1969).
2. Plants may be damaged during initial washing and removal of epiphyton and attached fauna.
3. Considerable error may also be introduced by the internal storage and utilization of oxygen by macrophytes. Changes in the oxygen concentrations in the surrounding waters may not be proportional to changes in the internal oxygen concentration (Hartman and Brown, 1967).
4. Plants may require several hours to adjust to the new conditions (Wetzel, 1969). However, increased incubation time increases the effects of enclosure.
5. Isolation of plant samples introduces a number of errors commonly termed "enclosure effects". These errors include:
  - (i) growth of bacterial populations on the enclosure walls;
  - (ii) depletion of nutrients by the enclosed community; and
  - (iii) reduced mechanical disturbance (Wetzel, 1969).

Turbulence has been shown to increase metabolic rates in macrophytes (Conover, 1968), and phytoplankton (Mann et al, 1972). The present estimates of macrophyte production must therefore, be considered in the light of the above-mentioned shortcomings and difficulties.

In order to measure epiphytic algal production, algal communities were established on artificial substrata in the form of drinking straws. At the beginning of December, 1980, 200 straws in plastic containers (Figure 6) were planted at stations 1 and 3 so that each straw protruded 10 and 15 cm above ground at the two stations, respectively. Prior to planting both ends of the straws were plugged tightly with cotton wool to prevent colonization of the inner walls by algae. After 32 days five straw segments of known length were carefully placed in six pairs of transparent and dark, 250 ml pyrex bottles filled with lake water. Incubation lasted nine hours (09h00 - 15h00).

Incubation times in all the production experiments represent a compromise time between attaining a significant change in oxygen concentration and reducing the effects of enclosure.

The use of artificial substrata in epiphytic algal studies has received considerable attention in the last decade and much conflicting data have been accumulated. There are a number of inherent restrictions in the use of artificial surfaces and perhaps the major criticism is the implicit assumption that there is no interaction between the macrophyte and the epiphytic algae (Wetzel, 1975). Secondly, the nature and position

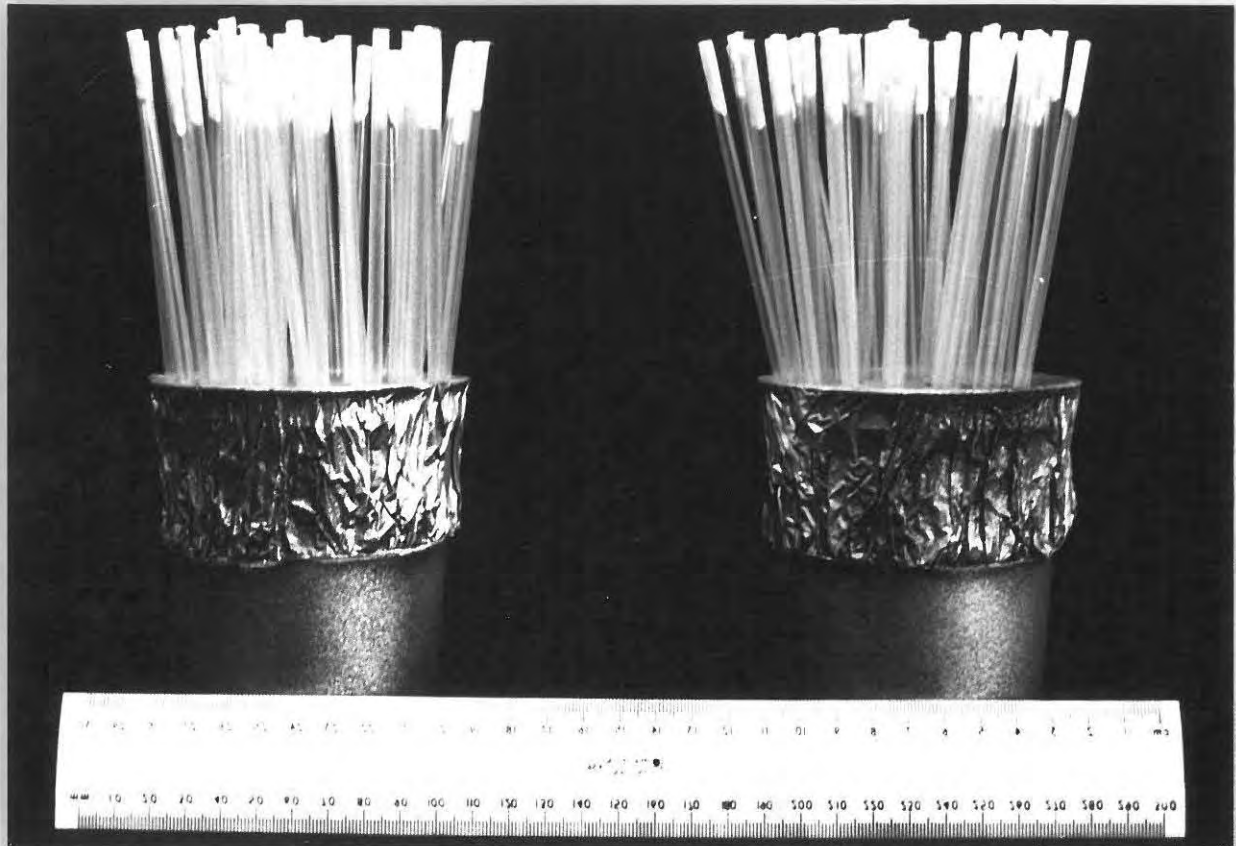


Figure 6. Plastic drinking straws in containers ; used for establishment of epiphytic algal communities.

of the substratum can markedly influence the rate of colonization, and the quantity and quality of the attached community (Wetzel and Westlake, 1969; Brown, 1976; Cattaneo and Kalff, 1979; Markošová, 1979). For these reasons, it was necessary to check the similarity between the epiphytic communities on the straws and those on the P. pectinatus stems at both stations 1 and 3. The algal colonization (measured as mg chlorophyll a m<sup>-2</sup> substrate surface) was approximately twice as great on the P. pectinatus stems than on the drinking straws at both stations (Table 2) (c.f. Howard-Williams and Allanson, 1978).

Table 2 Chlorophyll content of algal communities attached to the surface of P. pectinatus stems and plastic drinking straws at stations 1 and 3. The number of samples and 95% confidence limits are indicated.

Station	Zone	mg chlorophyll <u>a</u> m <sup>-2</sup> straw or stem surface	
		Straws	<u>P. pectinatus</u> stems
1	Inner <u>Potamogeton</u>	3.08 <sup>+</sup> <sub>-</sub> 0.53 n = 10	6.74 <sup>+</sup> <sub>-</sub> 1.9 n = 10
3	Outer <u>Potamogeton</u>	0.96 <sup>+</sup> <sub>-</sub> 0.18 n = 10	2.04 <sup>+</sup> <sub>-</sub> 0.86 n = 10

Epiphytic production estimates using straws were, therefore, multiplied by 2 assuming that self-shading would be minimal and a doubling of epiphyte biomass would provide a doubled production. Considering the straws had only been in the water for approximately one month, and the Swartvlei system is oligotrophic, this assumption is probably correct.

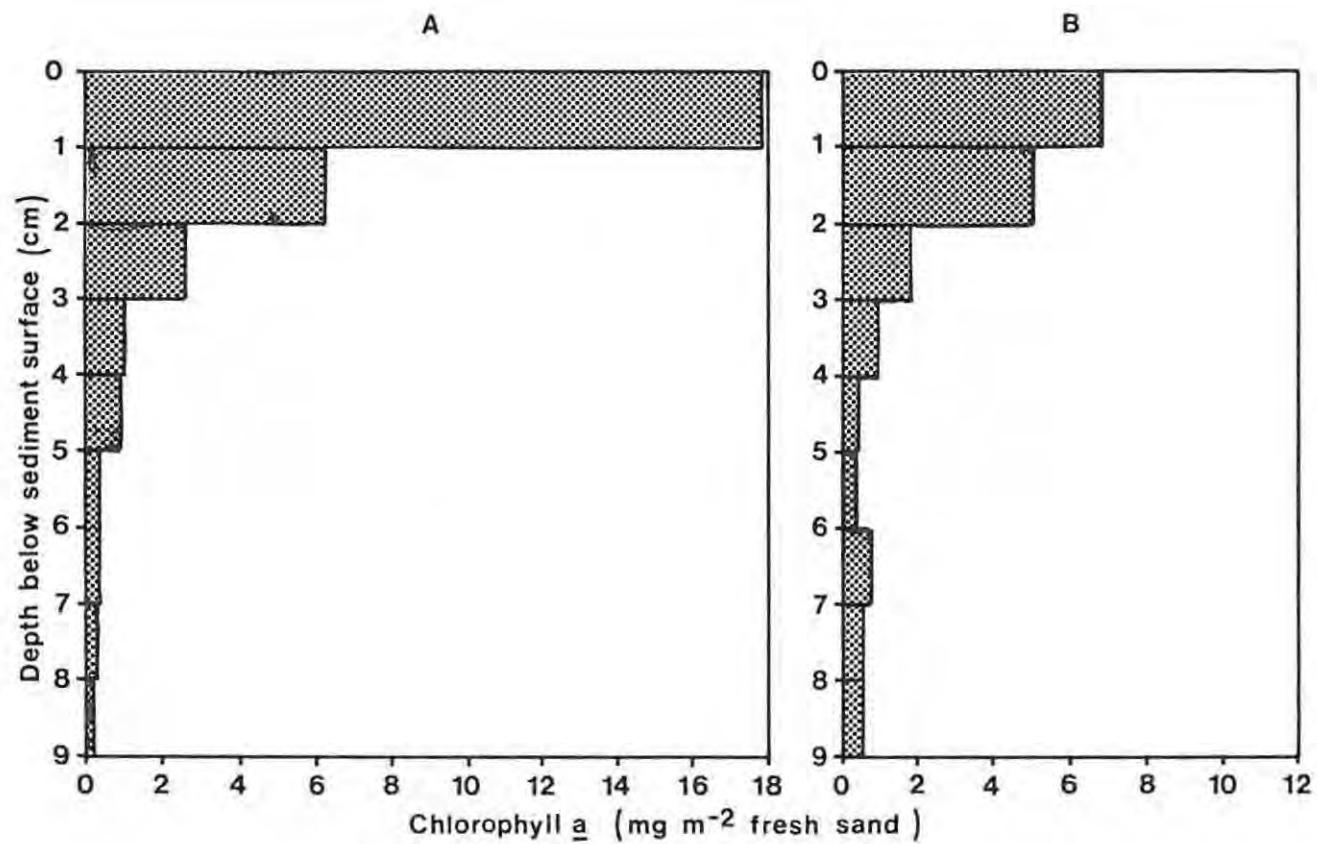


Figure 7. The vertical distribution of chlorophyll *a* in the sediment in the Charophyte (A) and Littoriprofundal (B) Zones.

(Rosemann and Gelin, 1978) noted the slow rates of colonization by algal periphyton in oligotrophic systems compared to the situation in eutrophic ones).

The production of epipsammic algal communities was measured at all five littoral stations. About 5 ml of sand, collected from the top 10 mm of the littoral shelf, were placed in five or six pairs of transparent and dark, 100 ml pyrex bottles filled with lake water. Analysis of the vertical distribution of chlorophyll a in the sediments indicated that a major proportion of the pigment occurred in the top 1 cm of sand in both the Charophyte and Littoriprofundal Zones (Figure 7). Furthermore, it has been shown that incident irradiance is reduced to less than 1% within 5 mm of the sediment surface in sandy sediments (Hargrave, 1969; Harper, 1969; Fenchel and Straarup, 1971). It is therefore probable that most of the primary production occurs in this upper layer. To obtain meaningful results it was necessary to add sediment samples to the reagent bottles used for determination of initial oxygen concentrations.

The light and dark bottles were placed horizontally in wire trays on the sediment surface and incubated for 6 h (09h00 - 16h00). After oxygen analysis the volume of settled sand was measured in a measuring cylinder.

In the filamentous algae zone sediment samples were incubated below the algal mat. As with all production experiments, care was taken to prevent trapping of air bubbles in the incubation bottles.

In order to avoid exposure of plant material to incorrect environmental (especially light) conditions all sampling and transferring of samples to incubation bottles in the littoral zone was done at the sampling/

incubation site. This was accomplished by a diver using a "Hookah" air supply. This precaution was, however, not possible for phytoplankton production estimates.

Samples were collected at 0,5 m intervals through the water column at stations 1, 3, 5 and 6, by means of a perspex Ruttner bottle. This sampler was used in preference to a metallic Friedlinger bottle since bare metal surfaces may be either detrimental or stimulating to algae (Soeder and Talling, 1969). The Ruttner bottle was encased in a PVC tube to prevent light injury to the phytoplankton (Goldman *et al*, 1963). Further precautions included rapid transfer of water samples to the reagent bottles in the shade and storage of these bottles in a light tight box until incubation.

A number of reports have shown the marked influence of container position on production estimates (Soeder and Talling, 1969). The phytoplankton bottles were therefore incubated in a horizontal position (Figure 8) to enable comparison of results with the other production estimates. Two light and two dark, 150 ml pyrex bottles were incubated at each depth for 12 hours (06h30 - 18h30). Two water samples from each depth were used for estimation of the initial oxygen concentrations. The columns of bottles were suspended between two floats which were set 1,5 m apart in order to minimize shading of bottles.

#### 4.2. Sample analyses

Analytic grade reagents and distilled water (Büchi single still) were used for all chemical analyses. The dissolved oxygen concentration was measured using the method of Mackareth, Heron and Talling (1978). (95% C.L. =  $6,56 \pm 0,17 \text{ mg O}_2 \ell^{-1}$ , C.V. = 4%,  $n = 12$ ).

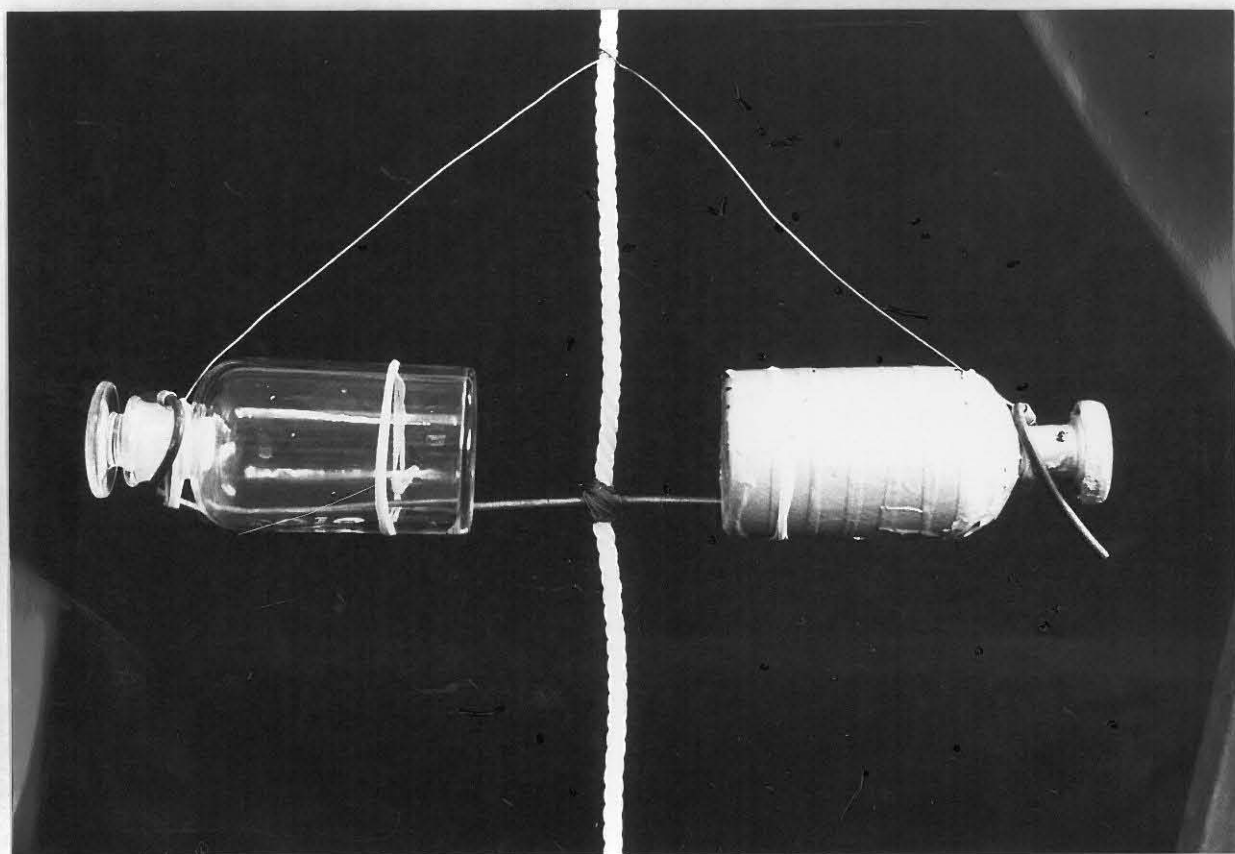


Figure 8. Reagent bottles in harness used for determination of phytoplankton net production.

Immediately placement of the light and dark containers in the incubation positions was complete, Winkler reagents were added to 3 bottles used for determination of initial oxygen concentration. At the end of the incubation period the incubation containers were treated in the same way.

The fixed samples were stored in the dark and chemical analysis completed within 24 hours. The 0,0125 N sodium thiosulphate solution (stored in the dark in a refrigerator) was standardized when required on each day of use.

All production estimates are expressed as net production per 24 hours day because this defines the material available to other trophic levels i.e. only net production per 24 h will contribute to the organic carbon pool in the long term (Howard-Williams and Allanson, 1978).

The net production of the macrophytes, filamentous, epipsammic and epiphytic algae during the incubation period was determined as follows:

$$\begin{array}{l} \text{Net production} \\ \text{during} \\ \text{incubation} \\ \text{(mg C m}^{-1}\text{)} \end{array} = \frac{\underline{A}_i \cdot \underline{S} \cdot 0,38}{\underline{V} \cdot \underline{M}} \quad (2)$$

where

$\underline{A}_i$  = increase in oxygen concentration (mg  $O_2 \ell^{-1}$ ) in the light bottle during incubation period;

$\underline{V}$  = volume of incubation bottle in litres;

$\underline{M}$  = quantity of plant material in sample (mg chlorophyll a);

$\underline{S}$  = standing stock of plant community (mg chlorophyll a  $m^{-2}$ );

and

0,38 = factor for conversion from mg  $O_2$  to mg C ( to enable comparison with the work of Howard-Williams and Allanson, 1978).

The net production ( $\text{mg C m}^{-3}$ ) of phytoplankton at each depth in the water column during the incubation period was determined as above with the modification that  $\underline{M}$  and  $\underline{S}$  were assumed to be equal and omitted from the calculation, and the result was converted to per cubic metre ( $\times 100$ ). Planimetric techniques were used to convert the results to net production per square metre of lake surface.

In all the production studies the solar energy reaching the lake surface during the incubation period was measured and used to convert the results during the incubation period to diel rates of net production, thus:

$$\begin{array}{l} \text{net production} \\ \text{(in mg C m}^{-2} \text{ daylight day}^{-1}\text{)} \end{array} = \begin{array}{l} \text{net production} \\ \text{during incubation} \\ \text{period} \end{array} \cdot \frac{\underline{R}}{3,6} \quad (3)$$

where:  $\underline{R}$  = solar radiation during incubation period ( $\text{MJm}^{-2}$ );

and, 3,6 = mean daily solar radiation for December, 1980 ( $\underline{n} = 23$ ; 95% C.L. = 0,5). This step was considered necessary because of the pronounced temporal variation in solar energy input into Swartvlei (an indication of this is provided in Figure 9). However, this extrapolation is only valid if photoinhibition of primary production at high light intensities is minimal. The extent of photoinhibition in Swartvlei is only poorly known although some surface inhibition of phytoplankton production was observed.

To convert the diel net production (over 15 hours) to net production over 24 hours, the respiration during the night had to be subtracted from the former value. The 95% confidence limits of the 24 hour

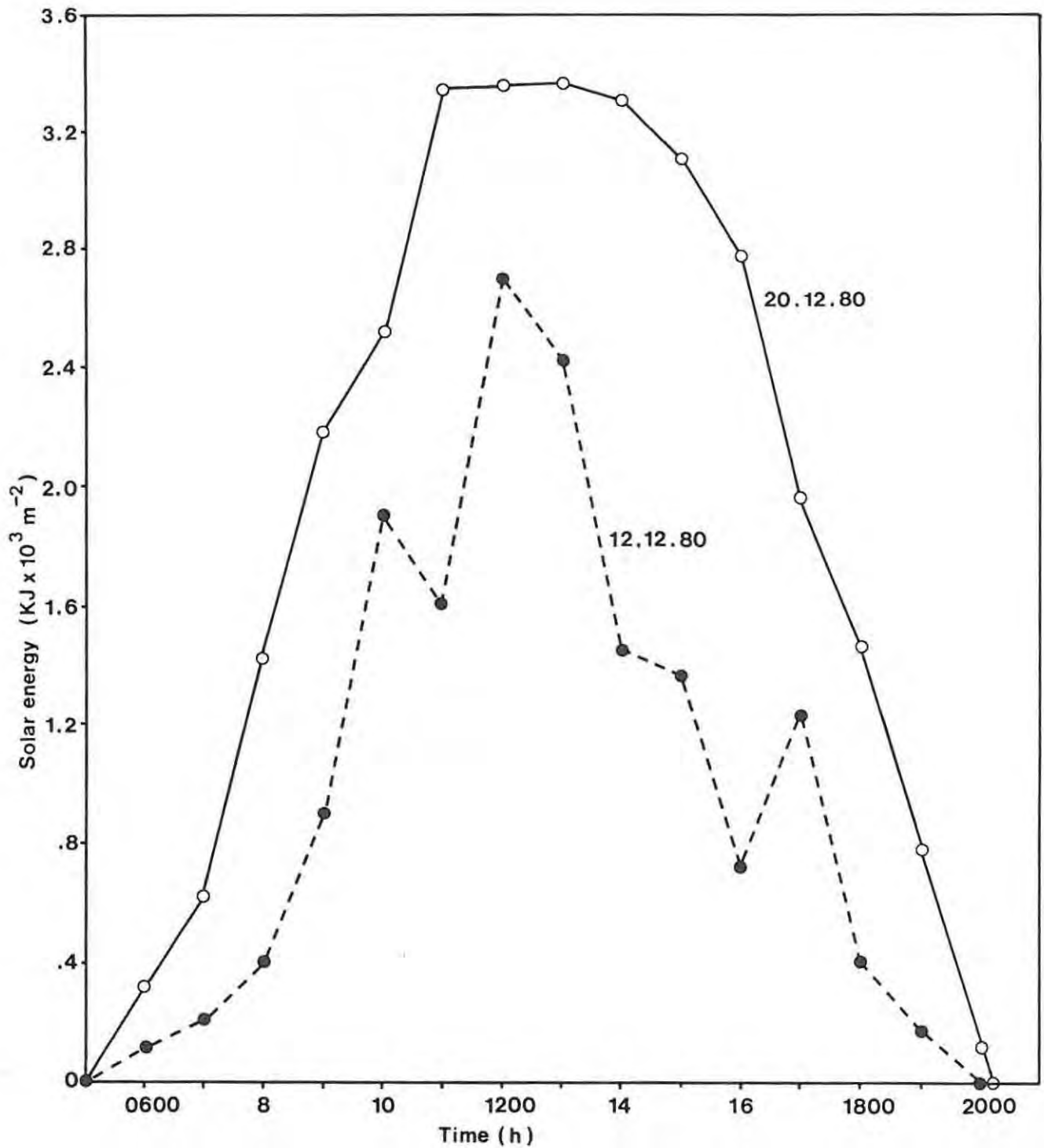


Figure 9. Diel change in the amount of solar energy reaching the surface of the Swartvlei system on a clear (o) and cloudy (●) day, December, 1980.

production estimate were determined according to Bevington (1969).

Macrophyte, filamentous algae, epipsammic and epiphytic nocturnal respiration was estimated as follows:

$$\text{Respiration during night (mg C m}^{-2}\text{)} = \frac{A_d \cdot S \cdot 0,38 \cdot 0,6 \cdot 9}{V \cdot M \cdot t} \quad (4)$$

where:  $A_d$  = decrease in oxygen concentration ( $\text{mg O}_2 \ell^{-1}$ ) in the dark bottles during incubation period;

0,6 = correction for lower temperatures ( $-3,1^\circ\text{C} \pm 0,4^\circ\text{C}$ ,  $n = 5$ ) at night  
| assuming  $Q_{10}$  of 2;

9 = number of hours darkness, December; and

$t$  = incubation time in hours.  $V$ ,  $M$ ,  $S$  and 0,38 as in equation (1).

The estimates of phytoplankton production were extremely variable and on two occasions (e.g. Figure 10) the oxygen concentrations in the dark bottles exceeded those in the transparent ones at all depths sampled. A preliminary investigation of these anomalous results was therefore considered worthwhile, and a set of experiments using 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) were conducted. DCMU can completely inhibit photosynthesis by blocking electron transport at the level of photosystem II (Fleischhacker and Senger, 1978).

Seven sets of reagent bottles were placed on a horizontal rope at 0,5 m at station 5 (Littoriprofundal Zone); each set contained two pairs of transparent and dark, 250 ml pyrex reagent bottles. These containers, plus three containers for determination of the initial oxygen concentration, were filled in the same way as for phytoplankton production estimation with the modification that 10 ml DCMU (initial concentration  $47 \text{ mg } \ell^{-1}$ ) was added to one pair of bottles in each set. Incubation lasted 10 h (07h00 - 17h00) and post-incubation treatment was as for the determination

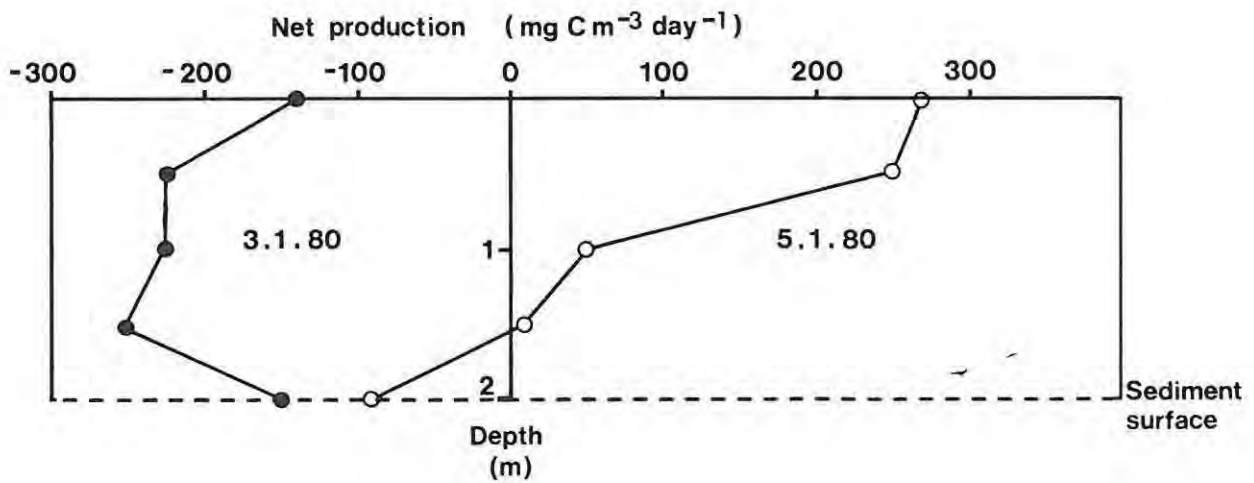


Figure 10. Vertical profile of phytoplankton production at Station 5 (Littoriprofundal Zone) on a clear day (●), which received 1153 kWh solar energy during incubation, and a cloudy day (○) which received only 493 kWh.

of phytoplankton production. The extent of the photooxidation during incubation was determined by subtracting the DCMU - treated dark bottle from the DCMU - treated light bottle in each set and taking the mean.

## RESULTS

## 1. Physico-chemical environment at time of study

Although this report is not an attempt to relate primary production to environmental conditions in Swartvlei, it is necessary to define, albeit very broadly, the physico-chemical environment in the system at the time of study.

Swartvlei exhibits a complex and dynamic salinity regime which dominates the physical and chemical processes of this meromictic lake (Robarts, 1973; Howard-Williams and Allanson, 1978). During the study period the lake system changed from the lagoon phase (estuary mouth closed) to the estuarine phase (estuary mouth open).

An indication of the physico-chemical limnology of the water column at the Pelagic Station (P) during the closed phase is shown in Figure 11. The salinity is uniform throughout the water column at  $18\text{‰}$  and the difference in temperature between the top and bottom is only  $2,0^{\circ}\text{C}$ . The dissolved oxygen concentration is approximately uniform ( $7,1 - 8,0 \text{ mg O}_2\ell^{-1}$ ) down to 10m, below which the oxygen concentration drops rapidly down to  $3,9 \text{ mg O}_2\ell^{-1}$  at 12m. Although the pH was not measured on 26 September 1980, 10 days later when very similar conditions prevailed in the lake, the pH measurements were fairly uniform through the column (between 7,38 and 7,98).

During October, November and December meromictic conditions gradually developed in Swartvlei. Initially this was brought about by flooding of the rivers flowing into the lake with the resultant input of large quantities of freshwater. At the end of October, the mouth of the estuary was artificially opened; this allows entry of seawater into Swartvlei during spring tide periods (Liptrot, 1978). By the end of

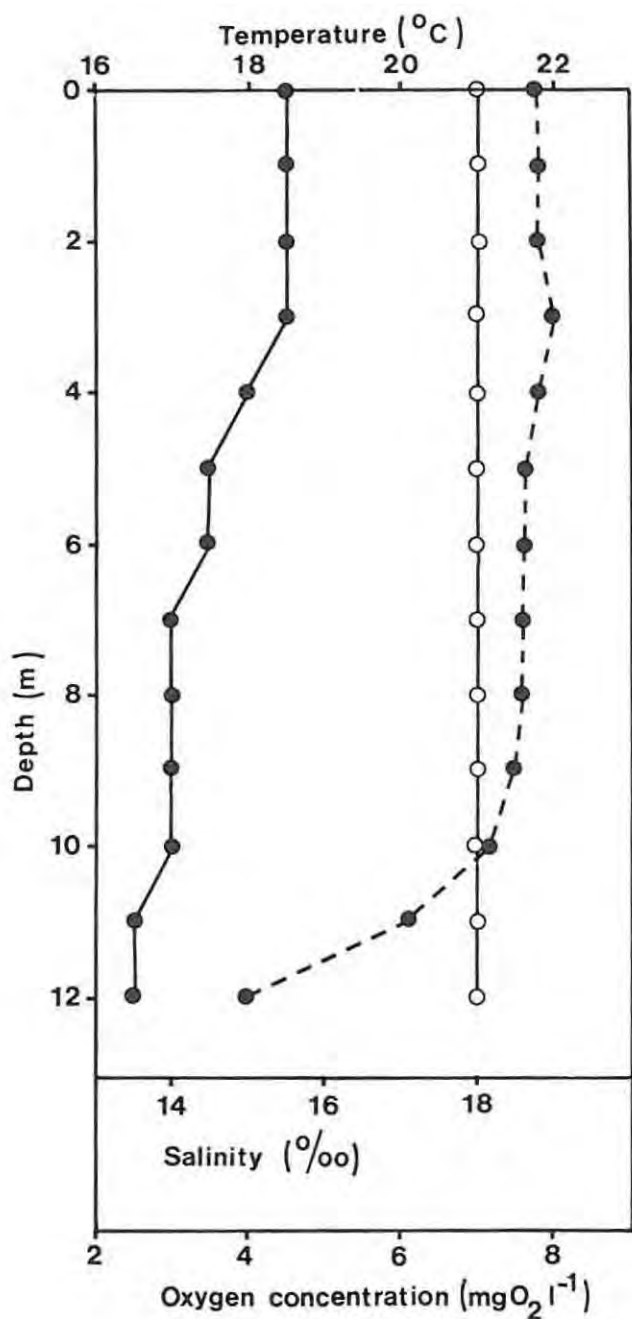


Figure 11. Vertical profiles of temperature (●—●), salinity (○—○), and dissolved oxygen (●—●) at Pelagic Station, 26 September, 1980.

December, 1980 meromictic conditions prevailed at the pelagic sampling station (Figure 12). Salinity, temperature and the dissolved oxygen content were all uniform in the top 2m of the water column but below this depth a marked increase in the former parameter and decrease in the latter two occurred. In the 13 weeks between the two sampling programs the surface salinity was reduced by 6‰ to 13‰ while at 12m it remained at 18‰. The water temperatures at the surface and at a depth of 12m below were 25,9°C (c.f. 18,5°C in September) and 11,2°C (c.f. 13,5°C in September), respectively. The oxygen concentration from 0-2m was 8 mg O<sub>2</sub>ℓ<sup>-1</sup>, by 7m this was reduced to 0,4 mg O<sub>2</sub>ℓ<sup>-1</sup>, and at 12m it was 0,2 mg O<sub>2</sub>ℓ<sup>-1</sup>.

A striking feature of the physico-chemical environment in the littoral zone is its spatial uniformity (both vertically and horizontally), which probably results from wind-induced turbulence in the region. All analyses were carried out between 10h00 and 12h00 to reduce temporal variation. The salinity never varied more than 0,5‰ from one part of the littoral zone to the next during each sampling session. It decreased from 14,5‰ at the beginning of October to 12,5‰ at the end of December. Surface water temperatures ranged from 18°C to 26°C and on only one occasion did the temperature of the deeper water fall to more than 2°C below that at the surface. Over the three month study period the dissolved oxygen content varied from 5,8 - 8,3 mg O<sub>2</sub>ℓ<sup>-1</sup> in the surface waters; while the difference in dissolved oxygen content between the surface and deeper waters never exceeded 1,5 mg O<sub>2</sub>ℓ<sup>-1</sup>. pH was also spatially very uniform never differing by more than 0,2 between the top and bottom. During the investigation the surface pH increased from 7,58 (18 October, 1980) to 7,90 (12 December, 1980).

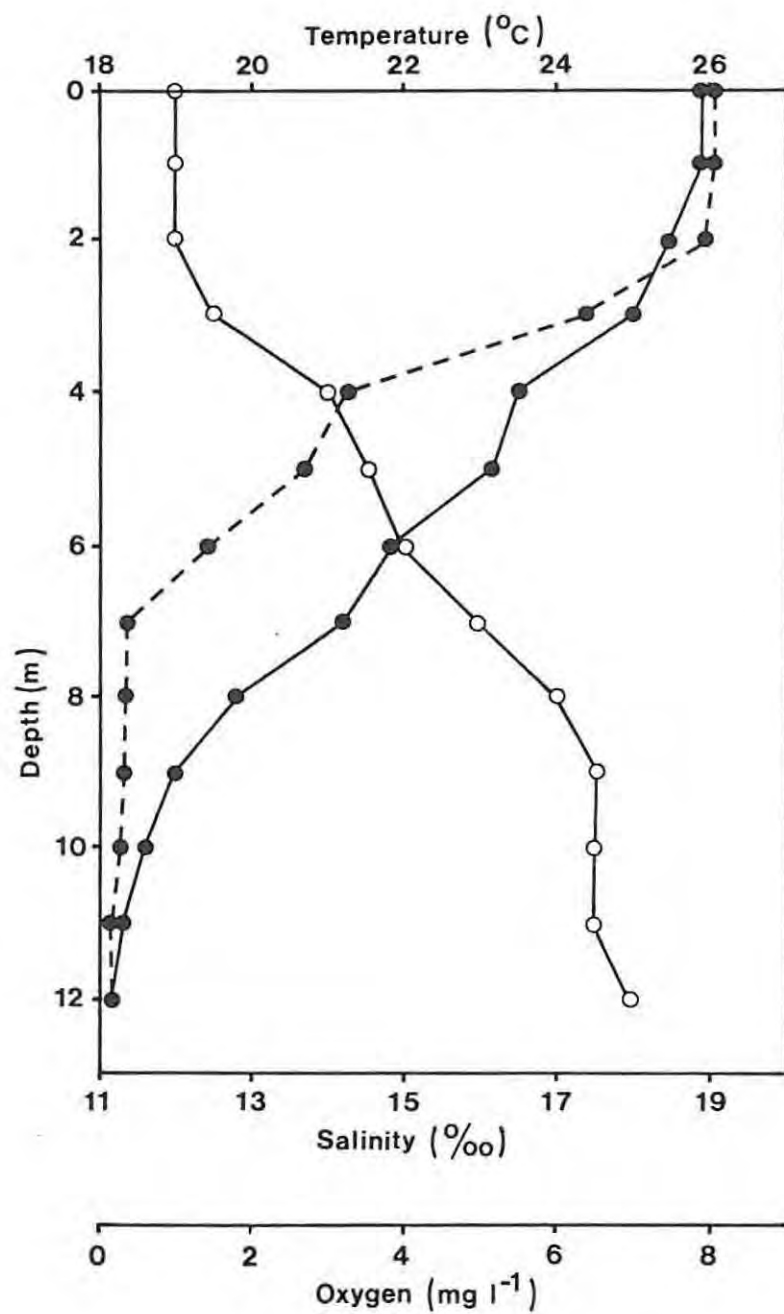


Figure 12. Vertical profiles of temperature (●-●), salinity (○-○), and dissolved oxygen (●---●), at Pelagic Station, 1 January, 1981.

The light environment in Swartvlei has been comprehensively described by Howard-Williams and Allanson (1979). During the present investigation the Secchi disc readings, which correspond to a light intensity of ca. 5-15% of that at the surface (Hutchinson, 1957), were extremely varied (1,3 - 3,9m). Inflow of large amounts of stained river water into the system caused a marked decrease in the Secchi disc values. Malfunctioning of the light meter prevented the acquisition of accurate estimates of light attenuation in the water column until the end of December. At this time the vertical extinction coefficient of the photosynthetically active irradiation (PAR) at Station P was 1,03 and the 1% level of incident PAR lay at 3,5m.

The pattern of light attenuation in the littoral region appears to be more complex than in the pelagic zone. The suspension of material from the sediments by wave action is likely to influence light attenuation and an indication of wind-induced turbidity in the littoral is shown in Figure 13. Secchi disc transparency at Station 5 (Littoriprofundal Zone) varied from 0,9m to greater than 2,0m.

## 2. Biomass and zonation

The littoral plant communities in Swartvlei can be divided into six distinct regions (Figure 2); five zones (Phragmites Zone excluded) are included in the littoral transect. The extent of these zones are shown in Table 3.



Figure 13. Wind-induced suspension of particular matter in the littoral region of Swartvlei. Wind direction south easterly and wind speed of  $8,5 \text{ m sec}^{-1}$  recorded at the time the photograph was taken.

Table 3. Magnitude of the five zones in the littoral transect, December, 1980. Total area =  $660 \pm 23\text{m}^2$  ( $n = 3$ , C.V.% = 1,4%). 95% confidence limits estimated for each zone by assuming same C.V. and number of samples.

	ZONE				
	Inner <u>Potamogeton</u>	Charophyte	Outer <u>Potamogeton</u>	Filamentous algal	Littori- profundaal
Area of zone in transect ( $\text{m}^2$ )	$85 \pm 3$	$240 \pm 8$	$89 \pm 3$	$93 \pm 3$	$153 \pm 5$
% of total transect area	13	36	14	14	23

The Inner Potamogeton Zone occurs along the lake margin of the Phragmites Zone and extends to a depth of ca. 0,5m below low water level. At the time of study the P. pectinatus and filamentous algal components contributed the bulk of the plant biomass in this region, 37% and 34% respectively (Table 4). The filamentous algal mats were dominated by two forms belonging to the genera Chaetomorpha (Chlorophyta) and Polysiphonia (Rhodophyta). Towards the end of the study these mats had been markedly reduced (Figure 14), considerable quantities of the algae having been washed into the Phragmites Zone (Figure 15). Although the Charophyta Zone (which extends from ca. 0,5 - 0,8m), occupies 36% of the transect area, it contains only 8,5% of the total living plant material (Figure 16). 89% of this plant matter is in the form epipsammic algae. The Charophyta standing stock is only  $1,1 \pm 0,5 \text{ mg chlorophyll a m}^{-2}$  and

Table 4. The standing stock (mg chlorophyll  $a\ m^{-2}$ ) of the various macro- and microphyte components at Littoral (L) and Pelagic (P) stations, December, 1980. 95% confidence limits and number of samples (in brackets) are also indicated. The horizontal dashes indicate absence or only trace of form in particular zone.

Plant component	Zone					
	Inner Potamogeton	Charophyte	Outer Potamogeton	Filamentous algal	Littoriprofundal	Pelagic
<u>P. pectinatus</u>	25 <sup>+</sup> <sub>-7</sub> (15)	-	71 <sup>+</sup> <sub>-11</sub> (16)	-	-	-
Charophyta	1,2 <sup>+</sup> <sub>-1,9</sub> (14)	1,1 <sup>+</sup> <sub>-0,55</sub> (15)	2,6 <sup>+</sup> <sub>-16,6</sub> (16)	-	-	-
Filamentous algae	23 <sup>+</sup> <sub>-6</sub> (14)	-	159 <sup>+</sup> <sub>-23</sub> (16)	241 <sup>+</sup> <sub>-73</sub> (15)	-	-
Epipsammic algae	14 <sup>+</sup> <sub>-3</sub> (15)	19 <sup>+</sup> <sub>-2</sub> (14)	10 <sup>+</sup> <sub>-2</sub> (14)	12 <sup>+</sup> <sub>-3</sub> (15)	10 <sup>+</sup> <sub>-1,6</sub> (13)	-
Epiphytic algae	4,4 <sup>+</sup> <sub>-1,3</sub> (19)	-	2,0 <sup>+</sup> <sub>-0,5</sub> (10)	-	-	-
Planktonic algae	0,8 <sup>+</sup> <sub>-0,2</sub> (5)	1,15 <sup>+</sup> <sub>-0,1</sub> (5)	2,4 <sup>+</sup> <sub>-0,7</sub> (5)	3,8 <sup>+</sup> <sub>-1,0</sub> (5)	3,8 <sup>+</sup> <sub>-1,0</sub> (5)	38 <sup>+</sup> <sub>-9</sub>
Total	68 <sup>+</sup> <sub>-10</sub>	21 <sup>+</sup> <sub>-2</sub>	247 <sup>+</sup> <sub>-30</sub>	257 <sup>+</sup> <sub>-74</sub>	14 <sup>+</sup> <sub>-2</sub>	38 <sup>+</sup> <sub>-9</sub>



Figure 14. Sparse P. pectinatus stands in the Inner Potamogeton Zone of Swartvlei. a represents aggregation of filamentous algae (Chaetomorpha sp. and Polysiphonia sp.).



Figure 15. Filamentous algal mats washed up into Phragmites beds following the opening of the stuary mouth and drop in water level.

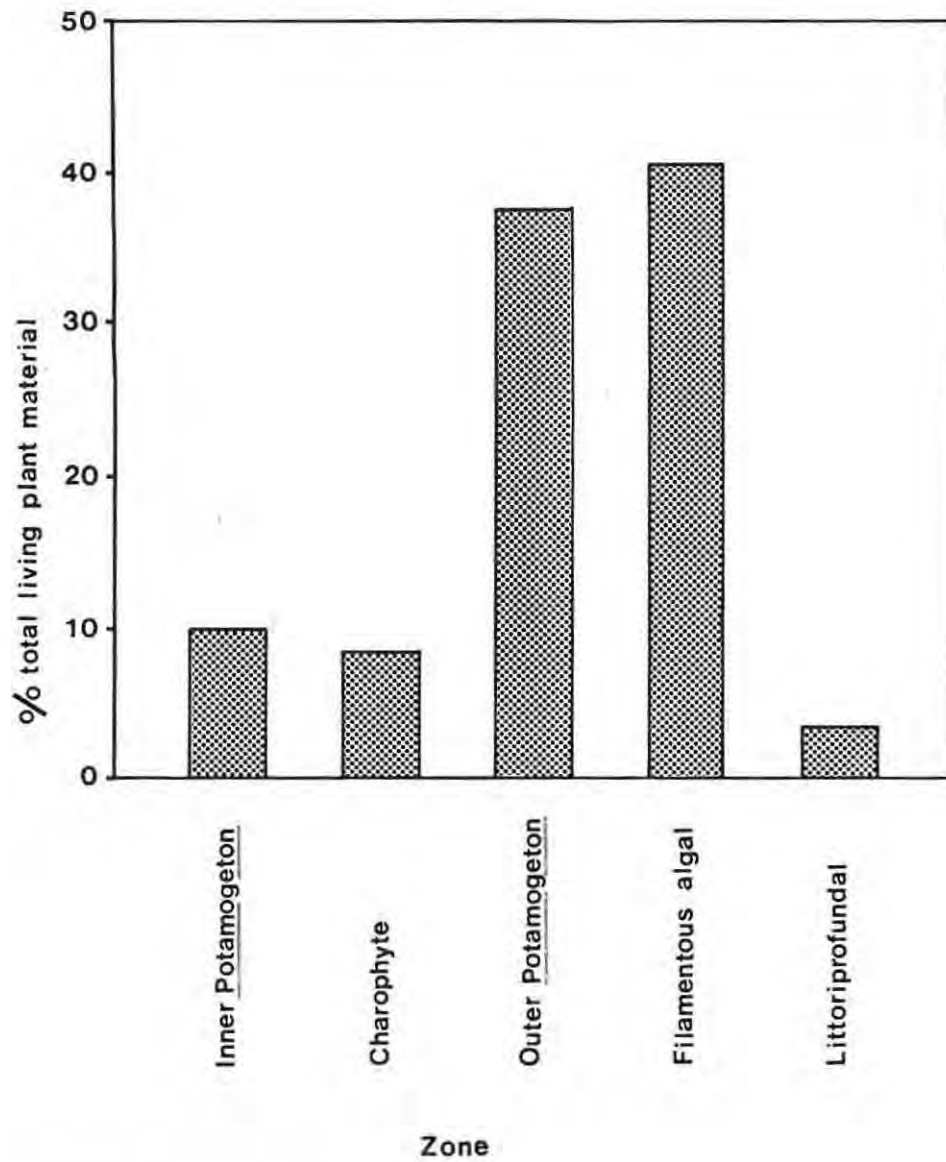


Figure 16. The quantity of living plant material in each zone expressed as a percentage of total living plant matter in the littoral transect ( $58,8 \pm 7$  g chlorophyll a ).

these macrophytes occur as small ( $\bar{x}$  height =  $15 \pm 7$ mm,  $n = 20$ ).  
isolated plants partly covered with sediment (Figure 17).

On the lake side of the Charophyte Zone, the macro-algae are replaced by a mixed region of P. pectinatus and dense algal mats (Figure 18). Approximately 37% of the living plant material in the littoral transect occurred in this zone with by far the largest contribution being made by the Chaetomorpha/Polysiphonia mats. At the time of investigation the vascular macrophytes (mean height  $150 \pm 74$ mm,  $n = 25$ ) provided only 29% of the total plant biomass in this region and the Charophyta were only a very minor component (ca. 1% total biomass in zone) characterized by an extremely heterogenous distribution, as indicated by their large coefficient of variation (1198%). This region termed the Outer Potamogeton Zone extended from ca. 0,8 - 1,2m in December, 1980.

No aquatic macrophytes were reported below a depth of 1,2m. The area beyond this, termed the Filamentous Algal Zone, was dominated by a thick (up to 300mm) Chaetomorpha/Polysiphonia mat with a biomass of  $241,4 \pm 73,3$  mg chlorophyll a  $m^{-2}$ . This standing stock figure is the largest recorded during the study for any of the plant communities in the littoral transect (ca. 24% of the total biomass in the transect). The mat extended to a depth of ca. 1,5m beyond which were exposed sands with a reduced epipsammic flora ( $10,1 \pm 1,6$  mg chlorophyll a  $m^{-2}$  at 2m and  $4,3 \pm 0,4$  mg chlorophyll a at 3m).

The contribution made to the total plant biomass in the littoral transect by the various plant components is shown in Figure 19. The significance (in terms of biomass) of the filamentous algae in the littoral zone is immediately apparent (65% of the total biomass). The next largest

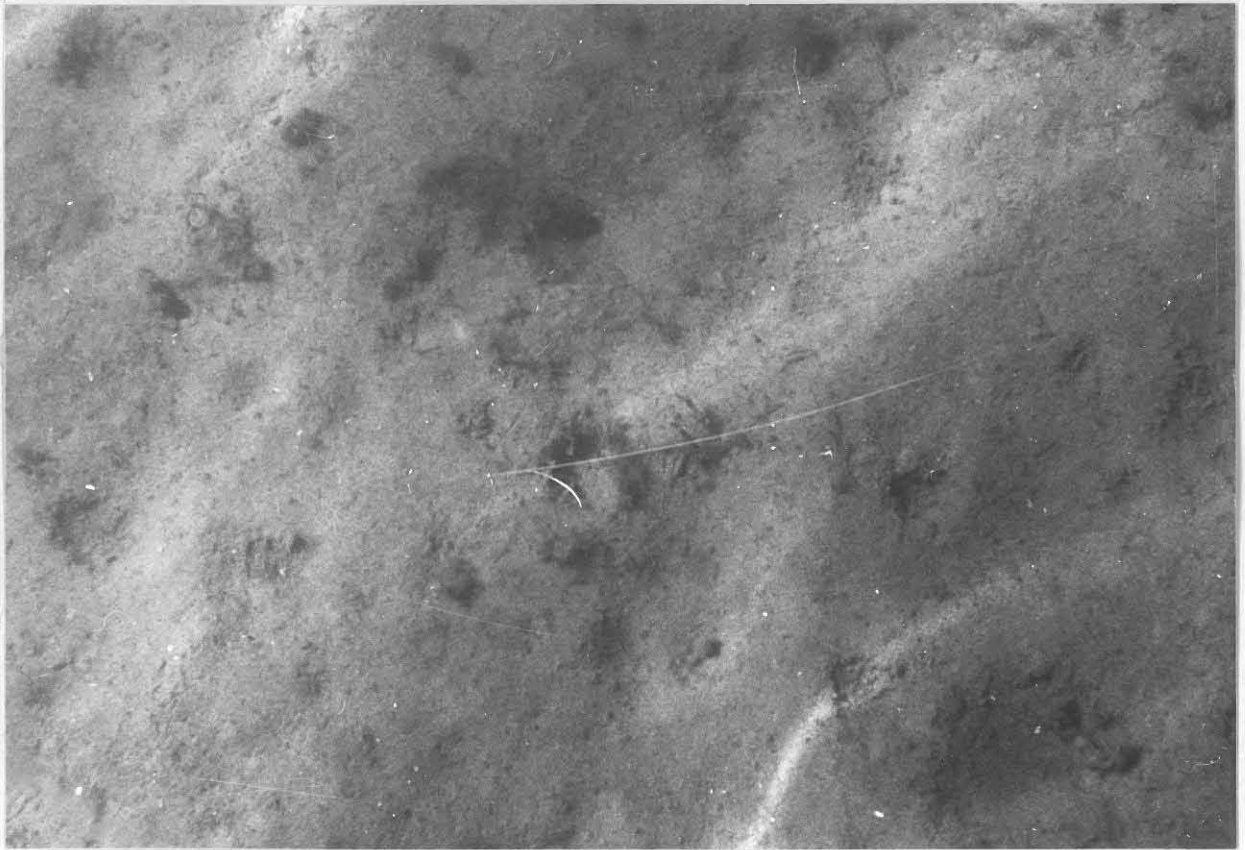


Figure 17. Charophyte Zone showing the exposed sands, isolated Charophyte plants (a) and fish foraging marks (b).

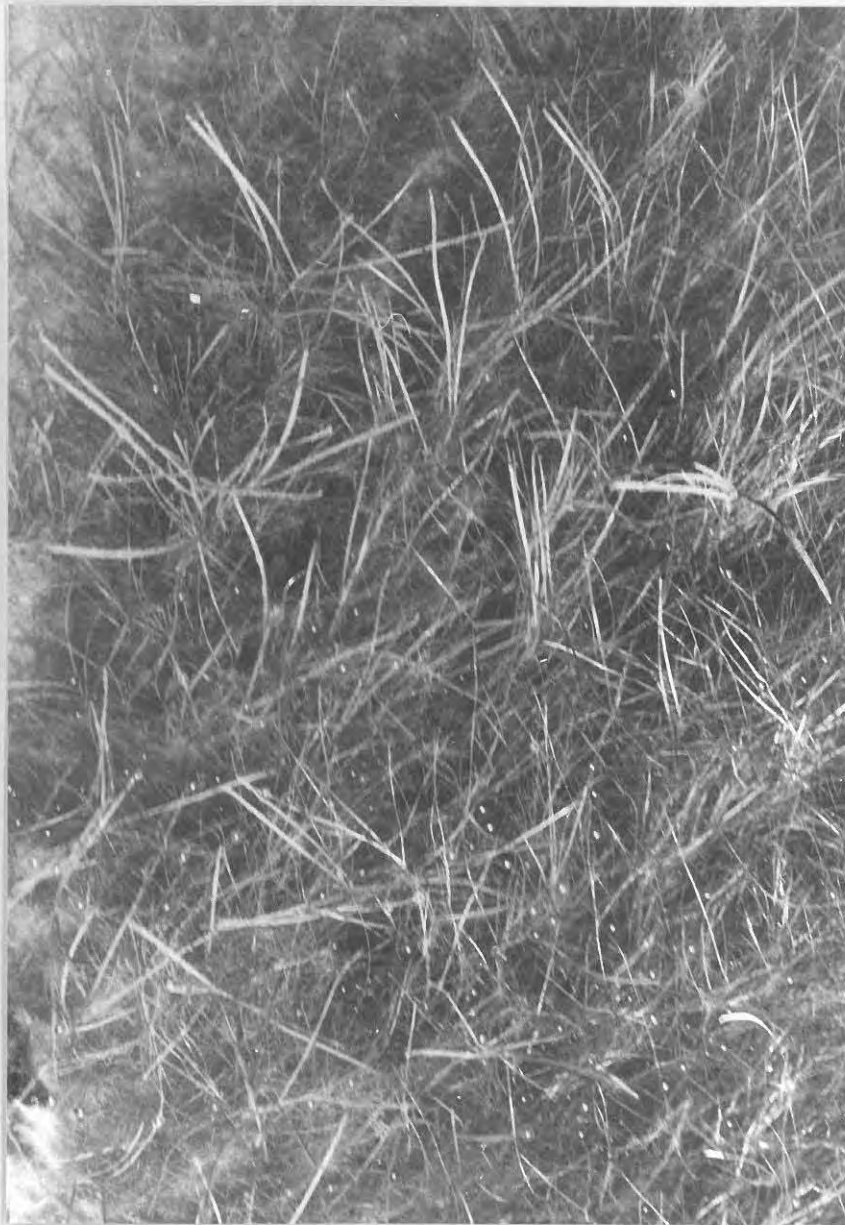


Figure 18. Dense P. pectinatus stand in the Outer Potamogeton Zone ,  
December, 1980.

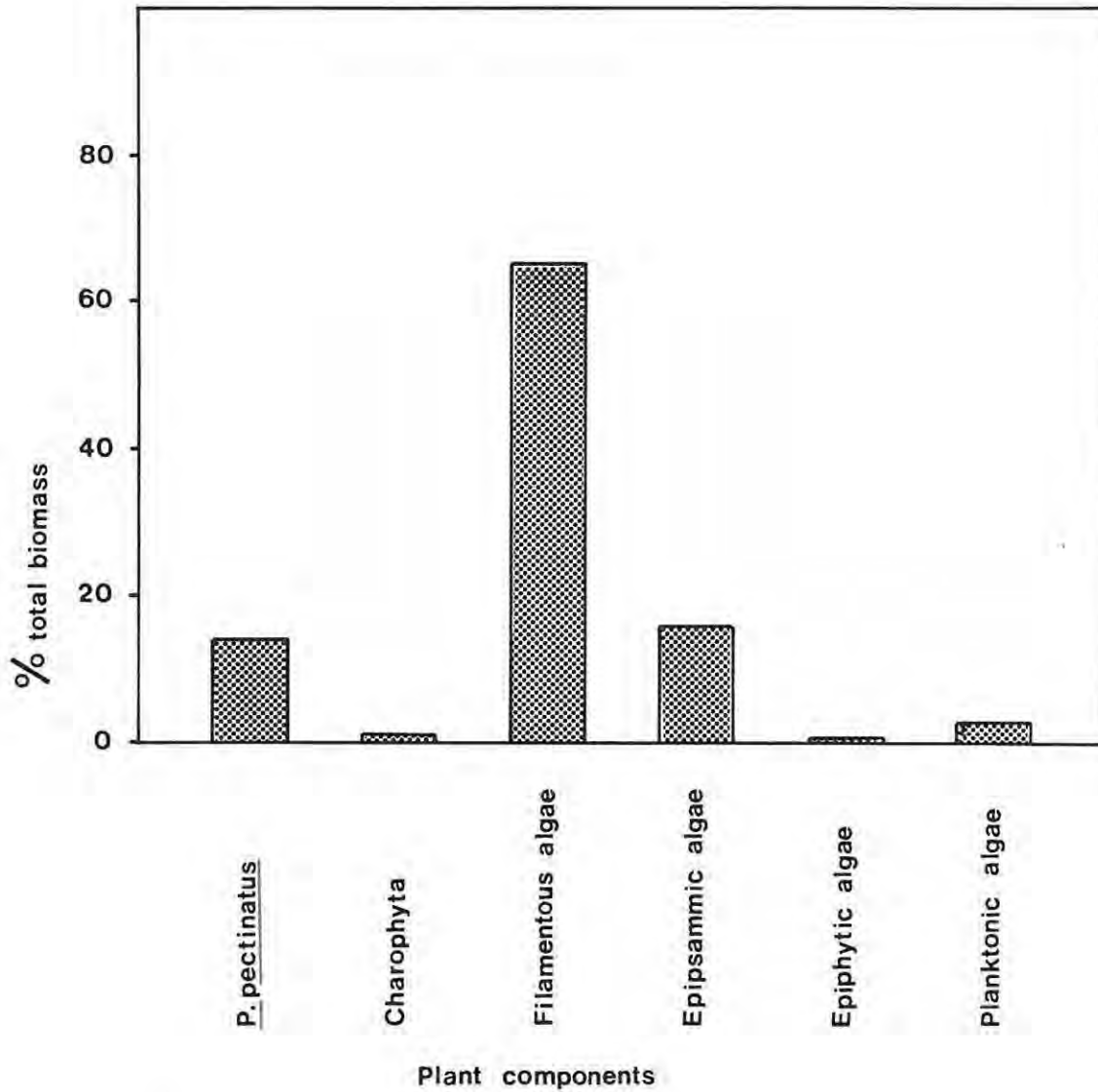


Figure 19. Contribution made by the various plant components to the total plant biomass ( $58,8 \pm 7,5$  g chlorophyll *a*) in the littoral transect, December, 1980.

contribution is that of the epipsammic algae (16%) followed closely by P. pectinatus (14%); while the Charophyta, epiphytic algae and planktonic algae contribute less than 3% of the total plant biomass in the transect.

The integral chlorophyll a content at the Pelagic Station was  $38 \pm 9$  mg chlorophyll a  $m^{-2}$  and the pigment distribution through the water column on 1 January, 1981, is shown in Figure 20. The chlorophyll content was extremely low ( $< 4 \mu\text{g}$  chlorophyll a  $l^{-1}$ ) through most of the water column but a high peak ( $12,9 \pm 3,1 \mu\text{g}$  chlorophyll a  $l^{-1}$ ) existed at 3m. By 5m, however, the pigment concentration was once again reduced to a low level ( $2,6 \pm 0,4 \mu\text{g}$  chlorophyll a  $l^{-1}$ ).

Chlorophyll a concentrations in the free water of the littoral transect were highly variable and ranged from 1,5 - 17,6  $\mu\text{g}$  chlorophyll a  $l^{-1}$ . No obvious vertical stratification of chlorophyll was evident in this region.

### 3. Primary production

The primary production in the littoral transect was estimated as  $23 \pm 5$  g C  $day^{-1}$  (phytoplankton production excluded) and the contribution made by the different plant components is shown in Table 5 and Figure 21. The major contributions included epipsammic algae (46%), filamentous algae (32%) and P. pectinatus (22%). The Charophyte and epiphytic algal production was by comparison very small ( $< 2\%$  by both components).

No reliable estimates of phytoplankton production were obtained.

Incubation of DCMU-treated phytoplankton samples on a clear day (1098 kWh during 10h incubation) showed that the light bottles had an oxygen consumption greater than that due to respiration alone (dark bottle result).

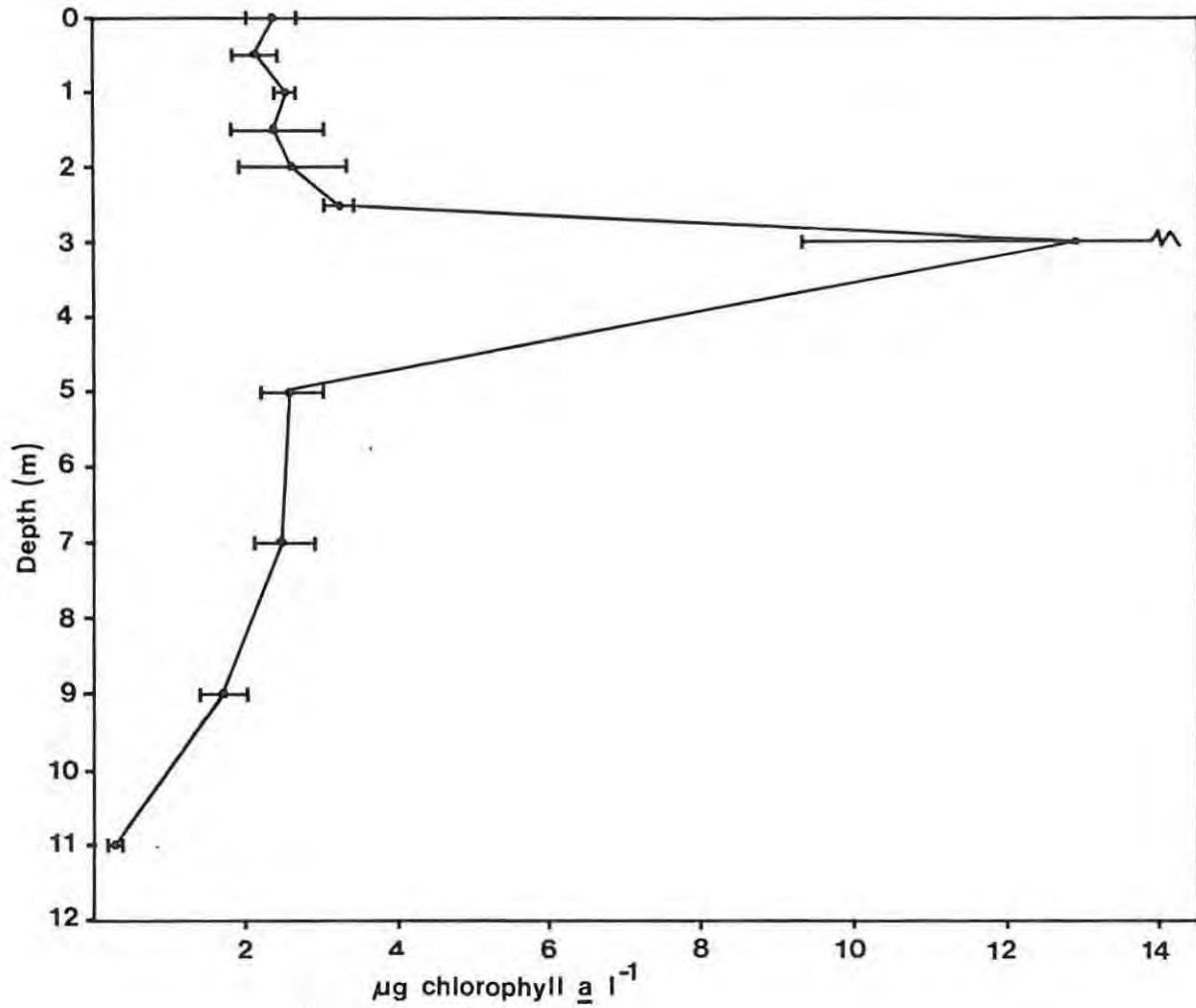


Figure 20. Vertical distribution of chlorophyll *a* at the pelagic sampling station in Swartvlei on 1 January, 1981 (09h00). Number of samples at each depth is 5 and the 95% confidence limits are indicated.

Similar results were obtained by Golterman (1971), also working with humic-rich water and it was suggested that this phenomenon was due to photocatalytic oxidation of extracellular compounds (Golterman, 1975). Photooxidation in the phytoplankton samples was estimated at ca. 35% of gross production ( $1,43 \pm 0,30 \text{ mg O}_2 \ell^{-1} 10\text{h}^{-1}$ ,  $\underline{n} = 7$ ) and 52% of net production ( $0,96 \pm 0,60 \text{ mg O}_2 \ell^{-1} 10\text{h}^{-1}$ ,  $\underline{n} = 7$ ). This value, however, is probably extremely variable (as shown in Figure 10) which therefore precluded the accurate estimation of phytoplankton net production using the oxygen light and dark bottle technique in these humic-rich waters. The oxygen consumption by photooxidation is, however, considerably less than the experimental error for the other production estimates which negated the need for photooxidation correction in these.

In an attempt to obtain an estimate of the phytoplankton net production (at best in the correct order of magnitude), the data collected on two cloudy days were utilized. It must be stressed, however, that the extent of chemical photooxidation during these periods of incubation is not known; although the data shown in Figure 10 suggests that photooxidation is markedly reduced on cloudy days. The integral phytoplankton production at Pelagic Station was estimated at  $333 \text{ mg C m}^{-2} \text{ day}^{-1}$  while that at Station 5 (Littoriprofundal Zone) was  $210 \text{ mg C m}^{-2} \text{ day}^{-1}$ .

The net production in the littoral transect was estimated at  $225 \pm 101,6 \text{ mg C m}^{-2} \text{ day}^{-1}$  (Phragmites sp. and phytoplankton production excluded). If the Phragmites sp. production is assumed to be similar to that estimated by Howard-Williams and Allanson (1978) and added to this result, the littoral net production (plankton excluded) is  $2115 \text{ mg C m}^{-2} \text{ day}^{-1}$ .

Table 5. The net production ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) of the various plant communities in the littoral transect (phytoplankton excluded), December, 1980. 95% confidence limits, and number of samples (brackets) are shown. Horizontal dashes represent no reading and are probably zero.

Plant component	Zone				
	Inner Potamogeton	Charophyte	Outer Potamogeton	Filamentous algal	Littoriprofundal
<u>P. pectinatus</u>	$35 \pm 16$ (6)	-	$24 \pm 15$ (5)	-	-
Charophyta	-	$0,1 \pm 14$ (6)	-	-	-
Filamentous algae	$14 \pm 10$ (6)	-	$59 \pm 20$ (6)	$13 \pm 9$ (6)	-
Epipsammic algae	$46 \pm 14$ (5)	$22 \pm 2$ (5)	$12 \pm 8$ (6)	$-0,02 \pm 0,01$ (6)	$-0,06 \pm 0,02$ (6)
Epiphytic algae	$0,4 \pm 1,4$ (6)	-	$0,2 \pm 1,0$ (6)	-	-
Total	$95 \pm 24$	$22 \pm 14$	$95 \pm 26$	$13 \pm 9$	$-0,06 \pm 0,02$

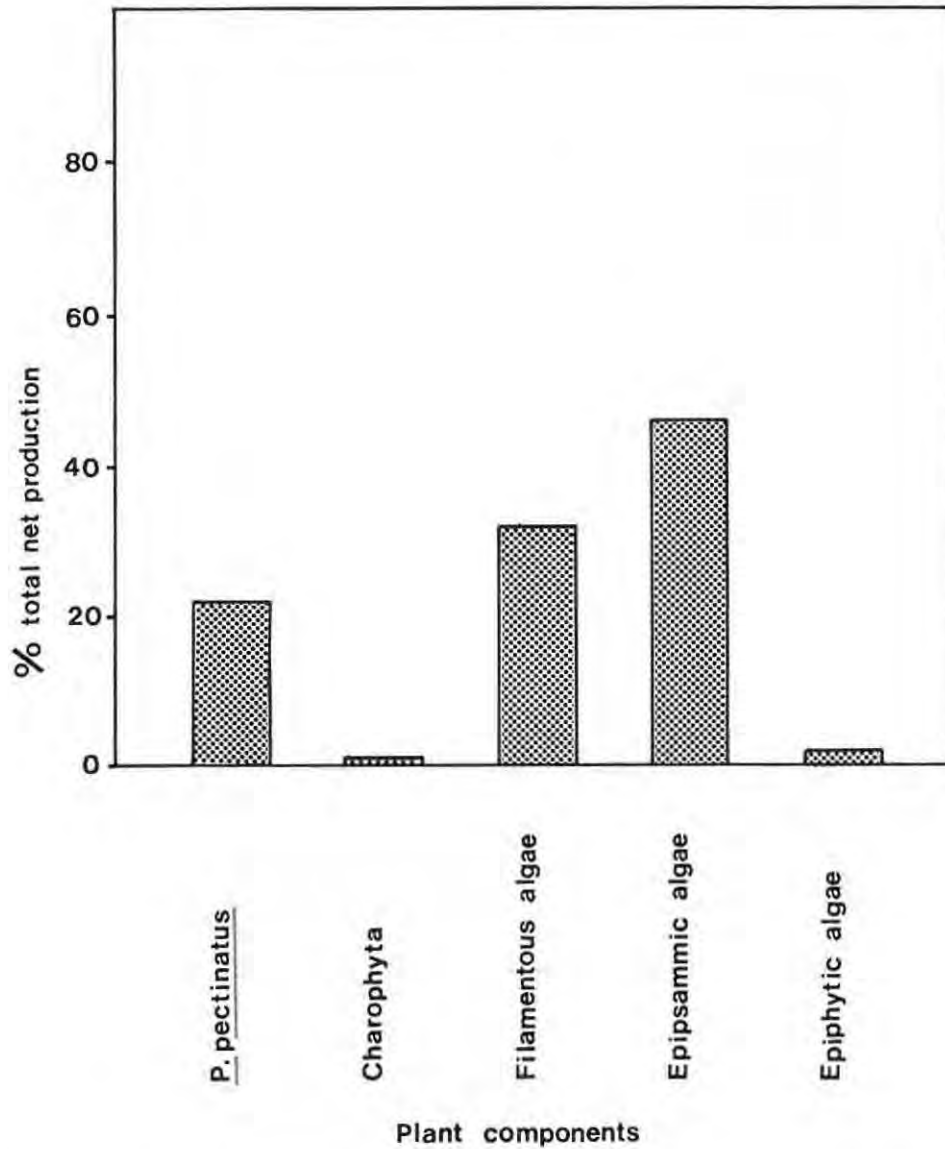


Figure 21. The net production ( $\text{g C day}^{-1}$ ) of the different plant components expressed as a percentage of the total net production in the transect ( $23 \pm 5 \text{ g C day}^{-1}$ ). Note that the *Phragmites* stands were not included in the littoral transect and are not included in the above figures.

The net primary production varied considerably from zone to zone in the littoral transect (Figure 22). Although no estimates for phytoplankton are included, their contribution would probably not have affected the overall pattern. The net production in the Inner and Outer Potamogeton Zones was very similar both as  $\text{mg C m}^{-2} \text{ day}^{-1}$  and as absolute production ( $\text{g C day}^{-1}$ ). The primary production in the Charophyte and Filamentous Algal Zones was considerably less (5,3 and 1,2  $\text{g C day}^{-1}$  respectively), while a negative production estimate was obtained for the Littoriprofundal Zone ( $-0,01 \text{ g C day}^{-1}$ ).

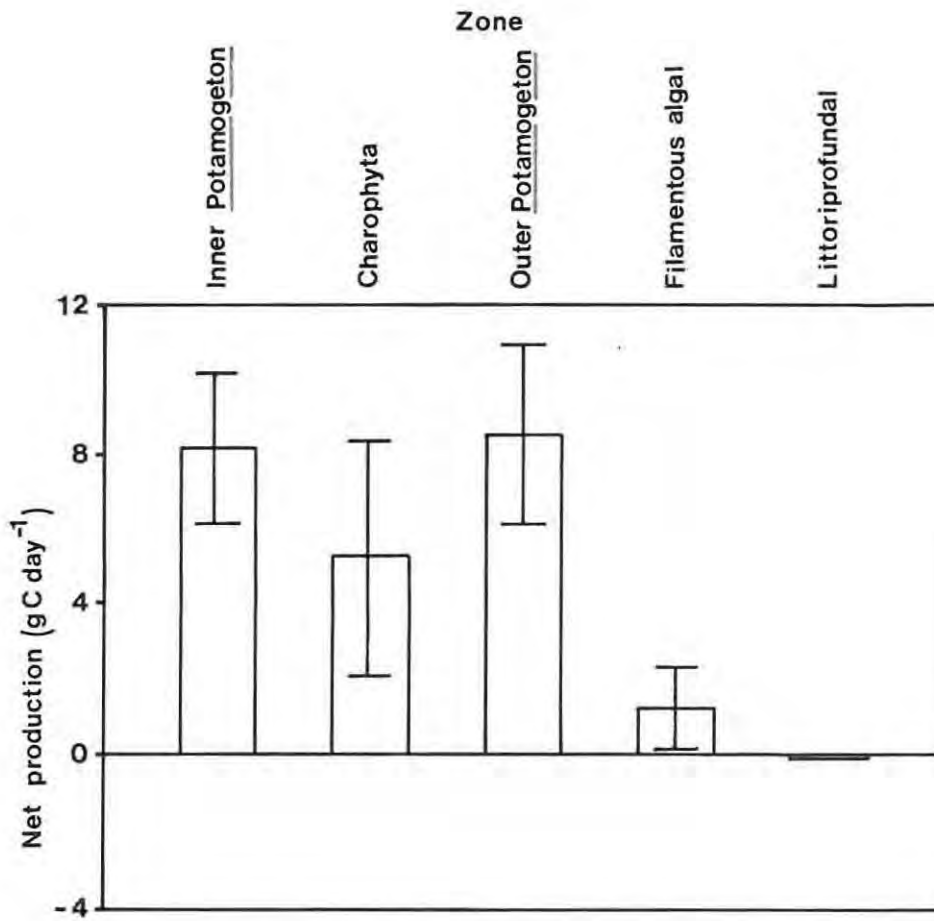


Figure 22. The actual daily net production (g C day<sup>-1</sup>) in the five littoral zones investigated (phytoplankton estimates not included).

## DISCUSSION



Since no indication of the representativeness of the sampling site or sampling period is available, the production results in this study cannot be expressed on an annual or entire-lake basis; i.e. extrapolation would be meaningless. The production estimates apply only to daily production at the sampling sites during the study period.

Although the zonation of the plant communities in the littoral transect was similar to the general zonation in Swartvlei described by Howard-Williams and Allanson (1978), several pronounced differences in the structure and functioning of these plant communities existed in December, 1980.

The importance of Swartvlei's littoral zone in terms of energy flow has been stressed by Howard-Williams and Allanson (1978). They reported that 86% of the primary production of Swartvlei is centered in the shallow littoral zone. In the present study, the significance of the littoral energy fixation is confirmed; the net production in the littoral (Phragmites sp. included) and pelagic zones being  $2115 \text{ mgC m}^{-2} \text{ day}^{-1}$  and  $333 \text{ mg C m}^{-2} \text{ day}^{-1}$ , respectively. Although the littoral primary production is considerably larger than the pelagic primary production, the former is only equivalent to 68% of the mean annual production for the littoral zone as estimated by Howard-Williams and Allanson (1978).

A major factor contributing to this difference is the markedly reduced P. pectinatus standing stock in the Outer Potamogeton Zone which was only 11,5% of that present in December, 1975. P. pectinatus stands accounted for 52% of the annual net primary production (phytoplankton production excluded) in the lake under "climax" conditions (Howard-Williams and Allanson, 1978). However, during the present investigation this aquatic macrophyte species contributed only 22% of the total daily net production

in the littoral transect (excluding Phragmites and littoral plankton production).

A further factor contributing to the low littoral primary production was the reduced Charophyte production; 0,25% of that in December, 1975. This reduction was probably largely due to the markedly lowered biomass (2% of that in December, 1975), and to the partial covering of these plants by sediments. The decrease in status of the Charophyte community is probably linked to the reduced height and standing stock of P. pectinatus in the Outer Potamogeton Zone. Howard-Williams and Allanson (1978) suggest that dense P. pectinatus stands in the Outer Potamogeton Zone protect the shallower waters from wave action and permit colonization of these regions by Chara sp. and Lamprothamnium sp.

Also related to the decreased P. pectinatus standing stock is the pronounced reduction in the epiphyte production. During the present investigation the epiphyte production (per square metre of water surface) was less than 1% of that reported by Howard-Williams and Allanson (1978). This low value, however, could also be attributed to incomplete estimation of epiphytic production. Microscopic examination of the algal mats showed that large numbers of algae (especially diatoms) were associated with these mats. Since the production of this algal component was not quantified the epiphytic production results in this report are probably markedly underestimated.

A striking feature of the littoral flora during the present study period was the dense mats of filamentous algae. It is perhaps significant to note that in 1978 a peak in filamentous algal biomass occurred and this coincided with a low P. pectinatus standing stock (Howard-Williams and Allanson, 1978); a similar situation to that prevailing in December, 1980, although different genera of algae were involved. In the present

study the algal mats were composed of two genera of filamentous algae, Polysiphonia and Chaetomorpha. Although the presence of the former genus in Swartvlei has been recorded by Howard-Williams and Allanson (1978), no previous reference has been made to Chaetomorpha sp. in this system. They noted seasonal development of filamentous algal mats but these mats were dominated by Cladophora sp. with Rhizoclonium sp. and Polysiphonia sp. being considerably less common. The occurrence of Polysiphonia sp. in the lake appears to be related to increased salinity. Both in 1976 (Howard-Williams and Allanson, 1978) and 1980 (present study) when the surface salinities rose to 16 ‰ and 18 ‰, respectively, this genus of filamentous algae increased in abundance. It is known to be common in Swartvlei estuary (Liptrot, 1978).

The algal mats accounted for 65% of the total living plant material in the littoral transect and their significance as primary producers is shown by the fact that they contribute ca. 32% of the total daily primary production in this area. The algal mats provide shelter for large numbers of small fish and invertebrates; a substrate for the attachment of epiphyton; and they are also an important food source for the herbivorous fish, Rhabdosargus holubi (A. K. Whitfield pers. comm.). The roles played by P. pectinatus under "climax" conditions appear to have been taken over, at least in part, by these extensive mats.

Although the filamentous algae standing stock was greatest in the Filamentous Algal Zone, the net production (per square metre in this particular region) was only 22% of that in the Outer Potamogeton Zone. This difference is indicated by a comparison of the relative production in the two zones; 0,4 mg C mg chlorophyll  $a^{-1}$  and 0,05 mg C mg chlorophyll  $a^{-1}$  in the Outer Potamogeton and Filamentous Algal Zones, respectively.

This reduction is possibly a result of poorer light conditions in the latter zone and self shading within the mats. It is significant to note that respiration exceeded gross production in sediments incubated below the algal mat in the Filamentous Algal Zone.

It appears likely that the accumulation of filamentous algae in the Filamentous Algal Zone was caused by the opening of the estuary mouth, lowering of the lake water level, the consequent increased wave action in the deeper parts of the littoral zone, and movement of algal mats from greater depths to the edge of the littoral shelf. A decrease in the area covered by the filamentous algal mats was observed during the study period.

Although epipsammic production has not previously been measured in Swartvlei, several studies conducted in South African estuaries have shown the important contribution made by this community to the total primary production in these estuarine ecosystems. The work of Bowen (1978) on epipsammic diatom distribution in Lake Sibaya hinted strongly that the epipsammic microflora was an important site of energy fixation in this system. This was later confirmed by Allanson (1979) who showed that the maximum summer epipsammic production almost equalled the maximum summer pelagic production. Dye (1978) measured the epipsammic algal production at different tidal levels in the Swartkops estuary in spring and autumn 1976. His daily spring production estimates ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) at 0,3m almost equal the present production estimates for the Charophyte Zone in Swartvlei.

The importance of the epipsammic production in Swartvlei has been demonstrated in the present study; it contributes 46% of the total daily net production in the littoral transect (Phragmites sp.) The epipsammic production did not exceed  $50 \text{ mg C m}^{-2} \text{ day}^{-1}$  in any of the zones and its importance (in terms of production) compared to the other plant components, can be largely explained by the wide distribution of these

algae which occur in all five biotic zones (c.f. P. pectinatus).

The primary production in the open water of Swartvlei has been studied by Robarts (1973, 1976), and Howard-Williams and Allanson (1978). The estimates presented in this report are similar to those collected by the above workers. Robarts (1973) reported that pelagic production varied from  $13 \text{ mg C m}^{-2} \text{ h}^{-1}$  in mid-winter to  $36 \text{ mg C m}^{-2} \text{ h}^{-1}$  in mid-summer; an intermediate value was obtained in the present report ( $22 \text{ mg C m}^{-2} \text{ h}^{-1}$ ). It must be stressed, however, that this particular result is approximate. Only two incubations were carried out at each depth and the error introduced by non-biological oxygen uptake is unknown. The variability of the results is likely to be high because the phytoplankton standing stocks were extremely low ( $3 \mu\text{g chlorophyll } a \ell^{-1}$  through most of the epilimnion) and the oxygen method for estimation of primary production is much less sensitive than the  $^{14}\text{C}$  technique (Vollenweider, 1969; Golterman, 1975; Wetzel, 1975).

The shape of the pelagic primary production depth profiles conform to the general pattern reported by Robarts (1973) and Howard-Williams and Allanson (1978). Surface depression of net production occurred at Station P (Pelagic Station) but not at Station 5. Maximum net production occurred at 0,5m (Station P) and at the surface (Station 5); the reason for the difference is unclear. At both stations gross production exceeded respiration to a depth of ca. 1,8m, which corresponds to the Secchi disc reading at both sites.

The low pelagic primary production in Swartvlei is a reflection of the low phytoplankton populations; chlorophyll values seldom exceed  $3 \mu\text{g chlorophyll } a \ell^{-1}$  in the epilimnion (Robarts, 1973; Howard-Williams and Allanson, 1978; Coetsee, 1979). A large peak in the chlorophyll a content existed at 3m in December, 1980. Similar deep peaks in chlorophyll a content have previously been reported in this system (Robarts, 1973; and Howard-

Williams and Allanson, 1978) and probably result from localized aggregations of flagellates ( e.g. Robarts, 1973) or green photosynthetic bacteria. Several workers ( e.g. Hutchinson, 1957) have reported the development of large bacterial populations at the junction of oxygenated and deoxygenated layers of water in meromictic conditions. If this boundary lies in the euphotic zone then large populations of green photosynthetic algae will develop with a resultant increase in pigment concentration. During the present investigation it was not possible to differentiate between bacteriochlorophylls and chlorophyll a. Extraction with acetone causes a shift in the absorption peaks of bacteriochlorophylls to very nearly 665 nm which results in an overestimation of chlorophyll a content (Fenchel and Straarup, 1971).

The present results are essentially a supplement to the already comprehensive investigations conducted in recent years on the flora of the Swartvlei system (Robarts, 1973, 1976; Howard-Williams and Allanson, 1978; Liptrot, 1978; Coetzee, 1979; Howard-Williams and Liptrot, 1980). It is, however, perhaps useful to compare the present production data with the few systems in which in situ measurements of production by the different plant components have been made simultaneously (Table 6). In all the listed lakes, with the exception of eutrophic Lake Wingra, the littoral plant communities are the major source of energy fixation. In Lake Wingra, the shallow Michigan pond and in Swartvlei (both studies), the macrophyte production exceeds the littoral algal production (c.f. Lakes Borax, Marion and Lawrence). However, such a comparison of production data from different lakes, collected under highly variable

environmental conditions over varying lengths of time, and collected using different techniques, must be considered with caution.

Table 6. A comparison of production by phytoplankton (P), littoral algae (L) and aquatic macrophytes (M) in 6 contrasting lake types. Data for Lakes Borax, Marion, Lawrence and Wingra from Wetzel (1975); for shallow Michigan lake from Barko, Murphy and Wetzel (1977); and for Swartvlei (1975 - 1978) from Howard-Williams and Allanson (1978).

Lake	Plant component	*Annual mean production (mg C m <sup>-2</sup> day <sup>-1</sup> )	Technique	Trophic status of water body
Borax (California)	P	249	<sup>14</sup> C (all components)	Oligotrophic
	L	731		
	M	76		
Marion (British Columbia)	P	22	O <sub>2</sub> , net production estimates (all components)	Oligotrophic
	L	110		
	M	49		
Lawrence (Michigan)	P	119	<sup>14</sup> C (all components)	Oligotrophic
	L	2003		
	M	241		
Wingra (Wiscconsin)	P	1200	<sup>14</sup> C (all components)	Eutrophic
	L	9		
	M	321		
Shallow pond (Michigan)	P	45	<sup>14</sup> C <sup>14</sup> C Harvest method	Oligotrophic
	L	91		
	M	212		
Swartvlei (1975-1978)	P	75	<sup>14</sup> C(phytoplankton epiphyton), O <sub>2</sub> (Charophytes, fila- mentous algae), har- vest technique, ( <u>P.</u> <u>pectinatus</u> )	Oligotrophic
	**L	621		
	M	2493		
Swartvlei (present study)	P	333	O <sub>2</sub> net production esti- mated (all components)	Oligotrophic
	**L	166		
	***M	1890		

\* Data for Swartvlei (present study) mean production during study period.

\*\* Charophyte production is included in littoral algae estimates. Littoral plankton production excluded.

\*\*\* Phragmites sp. production (Howard-Williams and Allanson, 1978) included.

## SUMMARY

The aim of the present study was to measure the primary production in a transect in the littoral region of Swartvlei and, if possible compare this with the pelagic production.

Aspects of the physico-chemical environment were monitored during the study. In order to measure the production (per unit area) it was necessary to determine the zonation and standing stock of the different plant communities.

The structure of the plant communities was compared with that described by previous workers; the major difference being a pronounced reduction in the P. pectinatus standing stocks. This reduction had a pronounced effect on the production ecology of the littoral.

The importance of the littoral zone in terms of energy fixation is confirmed in this report; the pelagic production ( in  $\text{mg C m}^{-2} \text{ day}^{-1}$ ) was only 16% of the littoral production (same units). Maximum production occurred at a depth of 0,5m in the pelagic zone. In the littoral zone most energy fixation took place in the Inner (0 - 0,5m) and Outer Potamogeton (0,8 - 1,2m) Zones. The highest daily production per unit area (Phragmites sp. excluded) was contributed by the filamentous algae in the Outer Potamogeton Zone ( $59 \text{ mg C m}^{-2} \text{ day}^{-1}$ ), while the largest contribution on a transect-area basis was by the epipsammic algae ( $10,3 \text{ g C day}^{-1}$ ). The Phragmites sp. stands were not included in the transect and their production was assumed to be equal to that determined by Howard-Williams and Allanson (1978).

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