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PRIMARY PRODUCTIVITY OF PHYTOPLANKTON IN BILLABONGS OF THE ALLIGATOR RIVERS REGION, NORTHERN AUSTRALIA (FINAL REPORT)

prepared by

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1. INTRODUCTION

Within the catchments of the South and East Alligator Rivers, Northern Territory, lie four uranium deposits - Ranger, Jabiluka, Koongar and Narbarlek. Government approval for the mining and milling of these deposits is largely dependent on adherence to environmental guidelines formulated by the Ranger Uranium Environmental Inquiry (Fox *et al.* 1977). Recognising that the waterways downstream of mining and milling operations could be subject to perturbation, this inquiry recommended the formulation of an effective biological and chemical monitoring program for these areas. It was evident that such a program must be founded on a detailed understanding of aquatic ecology of the Region. At the time of that report, little was known of aquatic ecology in tropical Australia and it was clear that considerable general limnological research would be required. The present study is part of a broadly-based investigation into the aquatic ecosystems, co-ordinated by the Supervising Scientist for the Alligator Rivers Region. This report presents the results of investigations of phytoplanktonic primary production and its measurement in billabongs of the Magela Creek.

The measurement of primary productivity in such diverse and heterogeneous water bodies as the Magela Creek billabongs poses many problems. Published work on stratification (Walker, Waterhouse & Tyler 1983), water chemistry (Walker & Tyler 1983), light climate (Walker, Kirk & Tyler 1983) and phytoplankton populations (Kessell & Tyler 1983) bear testimony to their extreme physical and biotic dynamism, and to the cardinal role of the distinctive climatic regime in the prescription of such ecological largesse.

The strict seasonality of the hydrological regime spells a protracte period of stagnancy during the months of the Dry, a period when profound changes may occur in limnological conditions in the billabongs. Of particular relevance to the present study are the progressive changes in turbidity, light penetration and nutrient concentrations as incessant evaporation concentrates the waters. At least in some billabongs, this period is marked by rapid fluctuations, in time and space, of the phytoplankton populations.

To take account of this variability it is necessary to measure productivity frequently. However, this is a detailed and time consuming exercise unless simplified procedures, based on empirical models (Brylinsky 1980; Rigler 1982), are developed to reduce such measurements to manageable proportions. It was of major concern during this study to develop and test empirical relationships permitting acceptable estimates of productivity from a minimum of *in situ* measurements. This is particularly relevant because monitoring changes in productivity offers one means of detecting ecological perturbation, by nutrient enrichment from sewage or by inhibition by pollutants, both of which are to be guarded against in the Magela system. Further, since primary production stands at the base of a pyramid of energy transfer, which governs the workings of ecosystems at all subsequent trophic levels, any proper ecological study of aquatic vertebrates or invertebrates must take account of this prime synthetic step in the whole ecological edifice.

Details of climate, geography and hydrology, together with descriptions of the billabongs, which have appeared elsewhere (Hart & McGregor 1980; Walker, Waterhouse & Tyler 1983), are summarised in Fig. 1 and Table 1.

Table 1 A classification of billabongs in the three catchments of the Alligator Rivers Region (after Walker, Waterhouse and Tyler 1983). The code name for each billabong is shown in brackets.

Billabong Classification	Catchment	Billabong Name	
Channel	Magela	Mudginberri	(MG)
		Buffalo	(BU)
	Nourlangie	Noarlanga	(NO)
	Coopers	Nimbawah	(NM)
" /Escarpment rockpool	Magela	Bowerbird	(BO)
" /Backflow	Baroalba/ Magela	Goanna	(GO)
" /Floodplain	Magela	Island	(IS)
	Nourlangie	Kulukuluku	(KK)
Backflow	Magela	Georgetown	(GT)
		Coonjimba	(CJ)
		Gulungul	(GU)
		Corndorl	(CO)
	Nourlangie	Umbungbung	(UM)
Floodplain	Magela	Ja Ja	(JA)
		Mine Valley	(MV)
		Leichhardt	(LC)
		Jabiluka	(JB)
		Nankeen	(NK)
	Nourlangie	Jingalla	(JN)
	East Alligator	Red Lily	(RL)

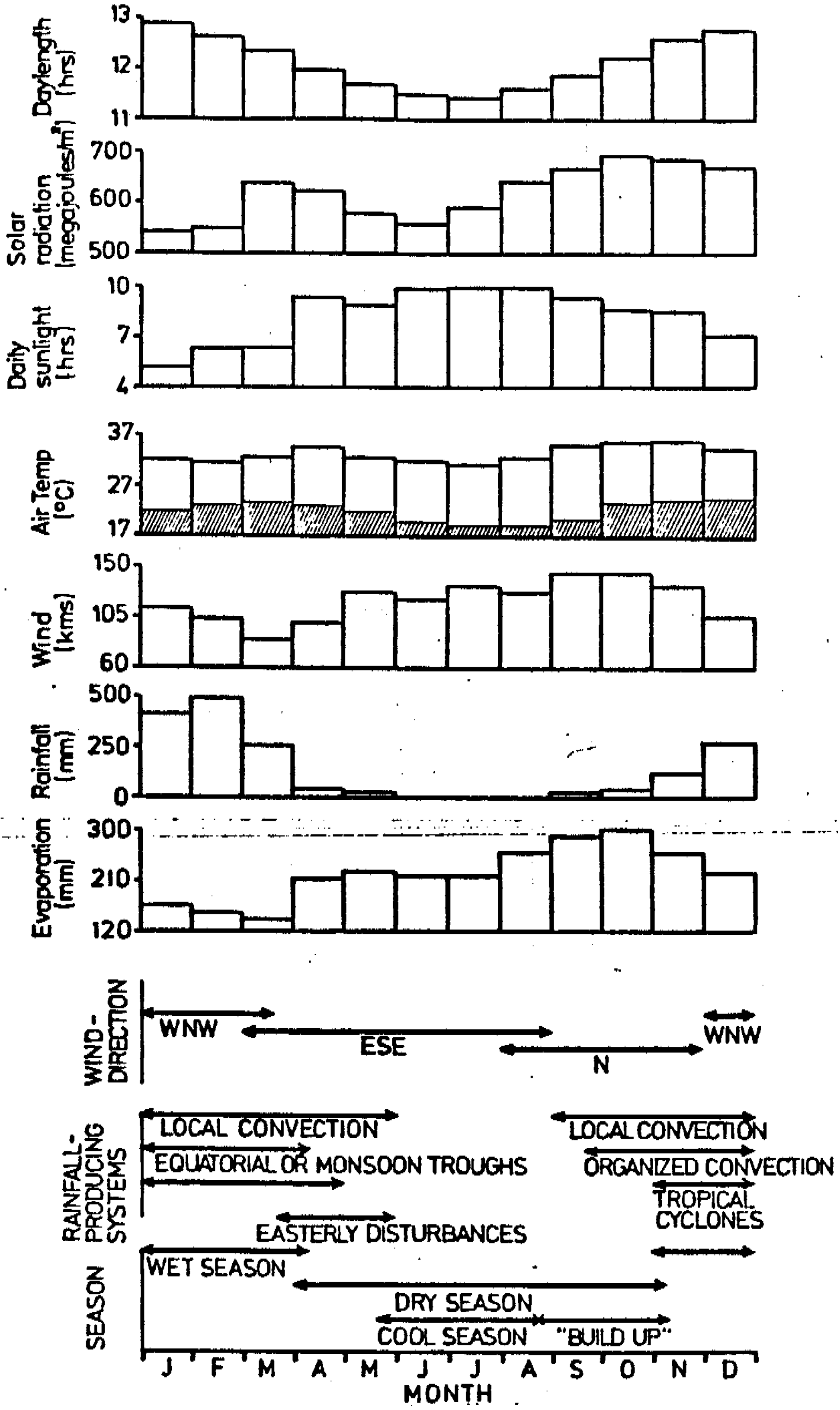

FIG. 1 SYNOPSIS OF SEASONAL METEOROLOGICAL ATTRIBUTES OF THE ALLIGATOR RIVERS REGION ~~(DATA FROM VARIOUS SOURCES)~~ (FROM WALKER, WATERHOUS + TYLER 1983)

2. THEORY

Phytoplanktonic photosynthesis, a major contributor to the synthesis of organic matter in aquatic ecosystems, is the conversion of stable inorganic compounds into energy-rich organic molecules. The process is energised by solar radiation harnessed by photoreactive chlorophylls and accessory pigments. The reaction proceeds according to the generalized equation (Wetzel 1975)

$$6\ CO_2 + 12\ H_2O \xrightarrow[\text{chlorophyll}]{\text{light}} C_6H_{12}O_6 + 6\ H_2O + 6\ O_2$$

When proceeding rapidly, as in dense phytoplankton populations, the reaction may bring about appreciable changes in aquatic chemistry. In still waters, photosynthetic evolution of oxygen may be the principal means of oxygenation of the water column, and consumption of CO_2 may cause elevation of pH during the day. The stoichiometry of the equation indicates several possible ways of measuring production - CO_2 uptake, O_2 evolution, and carbohydrate accretion.

Though photosynthesis is generally regarded as a photoautotrophic mode of nutrition, if it is to be translated into an increase in living matter (production), additional earth-inputs are necessary. It is common experience that photosynthetic production (primary production) is usually held at levels below those energetically possible, frequently by limited supplies of such nutrients as phosphorus and nitrogen. Thus, in any study of primary productivity (the rate of primary production) nutrient supply is a critical environmental variable, and several studies have shown that productivity can be predicted from nutrient loading (e.g. Imboden and Gächter 1978; Vollenweider*et al.* 1974) or nutrient concentration (Smith 1979). Since chlorophyll mediates the photosynthetic reaction which determines productivity, it is not surprising that chlorophyll concentration can also be predicted from nutrient concentrations (Nicholls & Dillon 1978).

All photosynthesis is dependent upon the availability of light, but only about 46% of the waveband of incoming solar radiation, the so-called photosynthetically-active-radiation (PAR), from 400 to 730 nm, is of use. For a forest canopy or for grasslands illumination is essentially uniform, and the available light is determined principally by daylength and meteorological conditions. By contrast, the light penetrating a body of water is progressively attenuated, and though photosynthesis may proceed throughout the water column its rate will vary with depth.

It can be shown (Walker, Kirk & Tyler 1983) that light over the PAR waveband penetrates a water body in exponential fashion (Fig. 2), such that

$$I_z = I_o e^{-kz} \qquad \ldots\ldots\ldots\ldots (1)$$

where I_z = PAR at depth z

I_o = incident PAR

k = vertical attenuation coefficient for downwelling PAR.

The euphotic depth of a lake (z_{eu}) is defined as the depth at which PAR has fallen to 1% of the value of incoming radiation (i.e. 1% I_o), and the water column so delimited is referred to as the euphotic zone. By rearrangement and substitution of equation (1) (see Walker, Kirk & Tyler 1983)

$$z_{eu} = \frac{\ln 100}{k} = \frac{4.61}{k} \qquad \ldots\ldots\ldots (2)$$

It is usual to measure primary production through the water column, to the euphotic depth. This convenience assumes that the rate of photosynthetic production of carbohydrate (gross production) at this light level (1% I_o) is just sufficient to balance its consumption by respirati For this reason the euphotic depth is also known as the compensation leve below which net gain of carbon from photosynthesis (net production = gro production minus respiration) cannot occur. It has been shown empirica that the 1% level is a good approximation of the compensation level in aquatic systems.

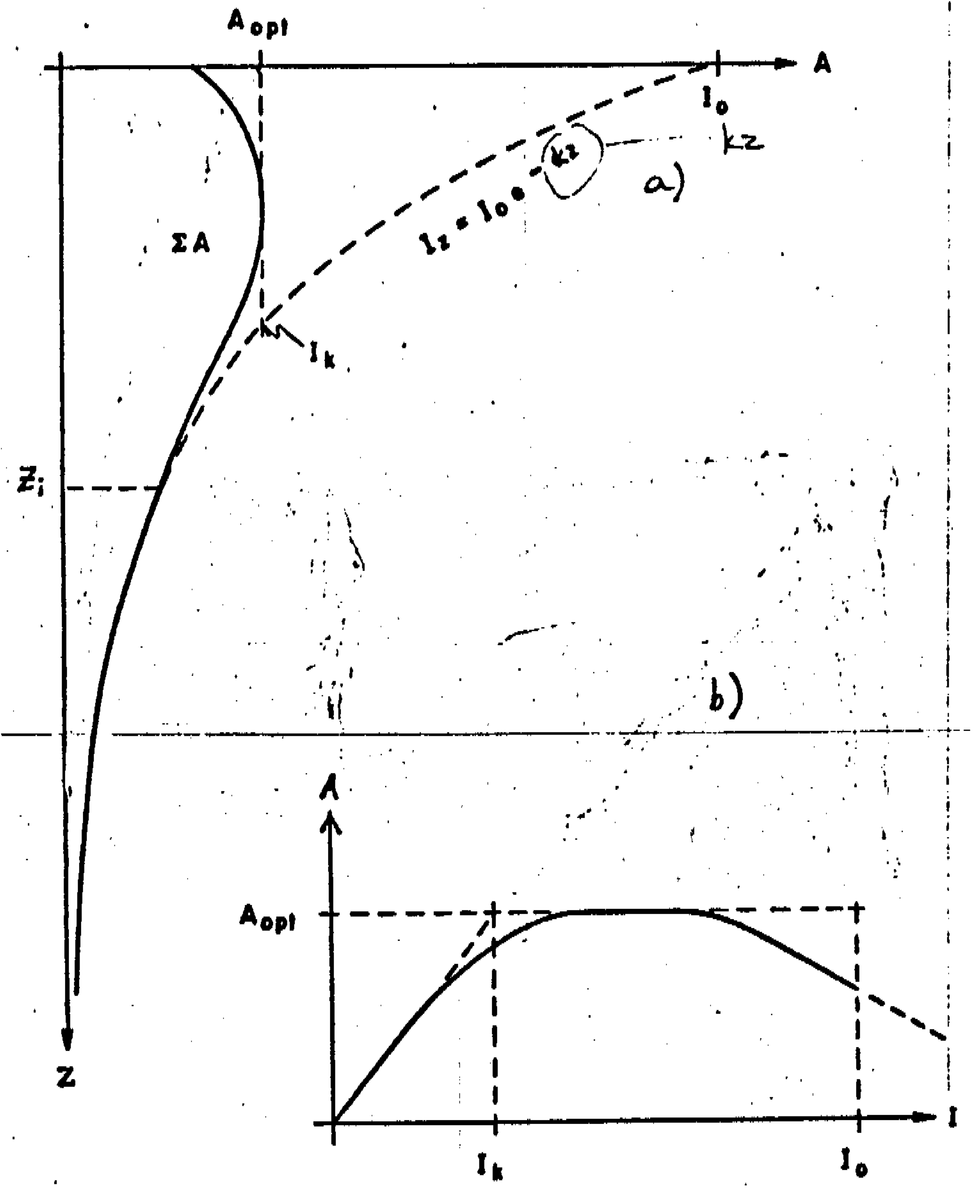

Fig. 2: Diagram depicting the usual photosynthetic profile in relation to light penetration (a), and (b) the onset of light saturation and light inhibition. (Adapted from Vollenweider (1974)).

Theoretically, in a vertically-mixed water column, where plankton is uniformly distributed, and provided that the rate of photosynthesis is linearly related to light intensity over the whole range of intensities encountered in nature, the exponential pattern of PAR should be matched by an exponential distribution of photosynthesis with depth. In practice however, light saturation and light inhibition of photosynthesis (Fig. 2) restrict production in the upper euphotic zone, substantially modifying th theoretical profile to one of the general form as shown in Fig. 2a, which is frequently encountered under bright, sunny conditions.

Examination of this photosynthesis-depth profile in vertically-mixed euphotic zones, has led to the development of production equations, such as those of Talling (1957), Vollenweider (1970) and others, which relate integral productivity, i.e. the area under the curve (ΣA), to the light saturated *in situ* rate of production (A_{opt}). These equations are of the general form (Smith 1979)

$$\Sigma A = F.\frac{A_{opt}}{k} \qquad \text{............} \; (3)$$

where the value of F varies according to various meteorological and limnological conditions (Fee 1973), and may be determined empirically. Talling (1957) has demonstrated one special, but widely applicable solution of F, namely

$$F = \ln\left(\frac{I_o}{0.5 I_k}\right) \qquad \text{............} \; (4)$$

where I_k defines the onset of light saturation (Fig. 2a,b).

3. MATERIALS AND METHODS

Primary productivity was initially measured (1978) using the familiar light and dark bottle technique for oxygen evolution (Vollenweider 1974). Samples taken from discrete depths with a 2 litre Van Dorn sampler (0.25 m in length) were enclosed in 100 ml Jena glass bottles, one light, one dark, and immediately resuspended at the sample depth. Usually sampling and incubation was at a series of standard depths, at 0.2 m intervals between 0.1 m and 0.7 m, then at 1.0 m, and at 0.5 m intervals thereafter. The middle of the sampler was used as datum for depth.

Samples were incubated for 3 hours spanning the solar noon. Oxygen concentrations at commencement and termination of incubation were measured by the azide modification of the Winkler technique (APHA 1975). Light penetration was estimated with a standard Secchi disc, occasionally supplemented by accurate measurements, with a Licor LI 185 quantameter (see Walker, Kirk & Tyler 1983).

On each occasion, and for each depth, immediately after taking the samples for incubation, additional samples were taken for chlorophyll analysis by a solvent extraction method (Vollenweider 1974). The samples were returned to Jabiru, filtered within 24 hours of sampling, extracted with cold 90% methanol and chlorophyll-a calculated using the equation of Talling and Driver (1963). Areal production (ΣA, $mgO_2m^{-2}hr^{-1}$) and areal chlorophyll (ΣB, $mgChla\ m^{-2}$) were determined from the vertical profiles by planimetry.

From 1979 onwards the dark bottle was omitted and two clear bottles incubated at each depth. Experience had cast doubt on the validity of dark bottle measurements (see Section 3.1). The time of incubation was increased to about 6 hours, commonly between 09.00 and 15.00 hrs. After May 1979, on most sampling occasions, surface samples for nutrient analysis were also taken (Walker & Tyler 1983).

For the last year of the survey (August 1980-August 1981) further methodological changes were introduced. The Van Dorn sampler was replaced by a small submersible pump (Rule 400) which draws water from a narrow stratum. Water was drawn from discrete depths through opaque tubing[†] and passed through a Turner Designs Model 10-005 fluorometer. When the fluorometer, in flow-through mode, indicated constant fluorescence, three samples were taken from the fluorometer effluent. Two were incubated, as before, at the sample depth. The third was filtered immediately and the membrane filter placed on ice and subsequently deep-frozen for later chlorophyll analysis. The precaution of sampling during constant fluorescence was dictated by the extremely rapid temporal and spatial variation in plankton populations then being recorded for some billabongs (Kessell & Tyler 1983). In addition, 90% acetone was used as the chlorophyll extractant.

Comparisons of the older and newer chlorophyll methods showed that results from the former were often serious and variable underestimates, attributable principally to degradation between sampling and filtration with the earlier method. For this reason, chlorophyll measurements prior to August 1980 were necessarily rejected.

In order to compare the productivity of the billabongs with waters elsewhere in the world day integrals (ΣΣA) were desirable. Accordingly, Licor LI 550 Integrators were installed, one permanently at Jabiru, and another on the bank of each billabong for the incubation period, to give integrals of photosynthetically-active-radiation (PAR, 400-700 nm, *Em^{-2} (Walker, Kirk & Tyler 1983)). Thus daily production (ΣΣA) could be calcul

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[†] The opaque tubing eliminated light-induced changes in fluorescence/chlorophyll relationship as the phytoplankton was drawn through a gradient of increasing irradiance.

* 1 Einstein, E, = 6.02×10^{23} quanta (or photons).

Table 4 shows the extent of the underestimate for those occasions when the 1% level was measured with a quantameter. It is evident that the underestimate is more than a few per cent only when the areal production is very low, in either clear or turbid waters, and that, therefore, Z_{eu}, which is readily measured or calculated, is the appropriate depth for integrating production. For all profiles it is possible that production of phytoplankton at depth is stimulated by the short exposures (<1-2 min) to surface irradiance at the beginning and end of incubations (cf. Tschumi *et al.* 1978). In waters where areal productivity (ΣA) in surface waters is large, slight enhancement of deepwater productivity will have little effect on total productivity, but where ΣA is low, the percentage contribut of such artifacts may be considerable. Therefore, even when there is significant proportion of integral production below Z_{eu} (in those cases whe ΣA is very low) Z_{eu} is probably still the appropriate depth.

4.2 The Amax/ΣA ratio (S)

To avoid excessive graphical representation, the form of the photosynthetic profile can be described by curve-shape statistics. Talling (1957) has shown that in a vertically-mixed euphotic zone, the area encompassed by the photosynthesis-depth curve, i.e. the integral photosynthesis, ΣA, may be set equal to a rectangle of width A_{opt}, the *in situ* light-saturated rate of photosynthesis, and depth Z_i, at which light intensity begins to be saturating for photosynthesis ($0.5I_k$) (Fig. 2). Thus

$$\Sigma A \simeq Z_i A_{opt}$$

or

$$Z_i = \frac{\Sigma A}{A_{opt}}$$

The value of Z_i is characteristic of the form of the profile (Fig. 2). authors (e.g. Lewis 1973), prefer the inverse $1/Z_i$ (=S), the Volumen/

Table 2 The methods used in this phytoplankton productivity survey, and the periods and the billabongs in which they were employed. Billabong code names as in Table 1.

Analysis	Period	Billabongs	Method	Equipment
Primary productivity	1978	BO,GT,GO,MG,IS,JA,LC	Incubation (3 hrs)	Van Dorn sampler; clear and opaque bottles
($\Sigma A, mgO_2m^{-2}hr^{-1}$)	1979	BO,GU,GO,IS,LC,JB	Incubation (6 hrs)	Rule 400 pump; clear bottles
(A, $mgO_2m^{-3}hr^{-1}$)	1980	BO,GU,GO,IS,LC,JB,RL	As in 1979	Rule 400 pump; fluorometer; clear bottles
($A_{max}, mgO_2m^{-3}hr^{-1}$)	1981	BO,GU,IS,LC,JB,RL	As in 1979	As in 1980
Daily primary productivity ($\Sigma\Sigma A, mgO_2m^{-2}d^{-1}$)	mid-1980-81	BO,GU,IS,LC,JB,RL	By calculation using ratio of incubation irradiance to daily irradiance	Licor LI 550 Integrators
Surface chlorophyll (mg Chl.a m^{-3})	1978-mid 1980	All billabongs	Filtered in laboratory; methanol extraction*	Filtration unit; spectrophotometer
	mid-1980-81	All billabongs	Filtered in field; acetone extraction	As in 1978-mid 1980
Euphotic zone chlorophyll (mg Chl.a m^{-3})	1978-mid 1980	As for "Primary productivity"	As for "Surface chlorophyll"*	As for "Surface chlorophyll"
	mid-1980-1978	As for "Primary productivity"	As for "Surface chlorophyll"	Fluorometer; filtration unit; spectrophotometer
Nutrients	mid-1978-81	All billabongs	See Walker & Tyler 1983	See Walker & Tyler 1983

* This method was shown to give serious and variable underestimates (see text [illegible] [illegible]

Table 3 Symbols used in this report

Symbol	Units	Definition
PAR	Einsteins (E)m^{-2}	Photosynthetically-active radiation
I_o	Em^{-2}	Incident PAR (no correction for reflection
k	Ln units m^{-2}	Vertical extinction coefficient for PAR
I_{inh}	Em^{-2}	Intensity of PAR indicating the onset of light-inhibition of photosynthesis
I_k	Em^{-2}	Intensity of PAR indicating the onset of light-saturation of photosynthesis
Turb.	N.T.U.	Surface turbidity
$Z_{s.d.}$	m	Secchi disk transparency
Z_{eu}	m	Depth of the euphotic zone
Z_{comp}	m	Depth at which net productivity is zero (compensation depth)
Z_i	m	Depth at which the onset of light-saturation occurs ($0.5I_k$)
PO_4-P	mg m^{-3}	Orthophosphate-phosphorus
TP	mg m^{-3}	Total phosphorus
IN	mg m^{-3}	The sum of nitrate and ammonia (inorganic nitrogen)
TN	mg m^{-3}	Total nitrogen
Temp	^oC	Early morning temperature of surface waters
ΣA	$mgO_2m^{-2}hr^{-1}$	Areal net productivity (hourly)
$\Sigma\Sigma A$	$mgO_2m^{-3}d^{-1}$	Areal net productivity (daily)
A	$mgO_2m^{-3}hr^{-1}$	Mean volumetric net productivity for the euphotic zone
A_{opt}	$mgO_2m^{-3}hr^{-1}$	Net productivity at light saturation
A_{max}	$mgO_2m^{-3}hr^{-1}$	Maximum net productivity of the photosynthetic profile
$Z_{A_{max}}$	m	Depth of A_{max}
S	-	Volümen/Oberfläche ratio of Rhode (1958) ($=A_{max}/\Sigma A = 1/Z_i$)
Q	mmol O_2E^{-1}	Efficiency of light utilization
ΣB	mg Chl a m^{-2}	Chlorophyll content of the euphotic zone
B	mg Chl a m^{-3}	Mean volumetric chlorophyll content of the euphotic zone
b_{max}	mg Chl a m^{-3}	Maximum chlorophyll content within the euphotic zone
P_{opt}	mgO_2(mg Chl a)$^{-1}hr^{-1}$	Photosynthetic capacity at light saturation (photosynthetic index).

One advantage of the oxygen evolution technique is its stated abilit to determine both gross and net production. Thus, oxygen evolution in th light bottle provides an estimate of net production, dark bottle consumpt of oxygen an estimate of phytoplanktonic respiration, and the difference between them represents gross productivity. However, in recent years, so doubt has been cast on the credibility of estimates of respiration, and hence of gross production, determined by the oxygen technique. Moss (1980 notes that the oxygen consumption in the dark bottle is more a measure of community respiration (plant, animal and bacterial) than just phytoplankton respiration. Additionally, it is evident that phytoplanktonic respiration in the dark ("dark" respiration) may not be the same as in the light. Respiration of phytoplankton in the light may involve "dark" respiration plus an additional component, photorespiration, using a different metabolic pathway (Harris 1977; Fogg 1975). Further complications arise because of the influence of previous light history on rates of "dark" respiration (Ganf 1974; Stone and Ganf 1981). Such are the theoretical difficulties. A disturbing experimental observation commonly made (e.g. Sreenivasan 1964, Tschumi *et al.* 1978), and especially during this study, is that <u>increases</u> in oxygen content of the dark bottles may occur during incubation. Due to the very low (if at all measurable) rates of community respiration during incubations in the Magela billabongs, and in recognition of the above restraints, subsequent to 1978 only light bottles were incubat and productivities computed as net productivity only.

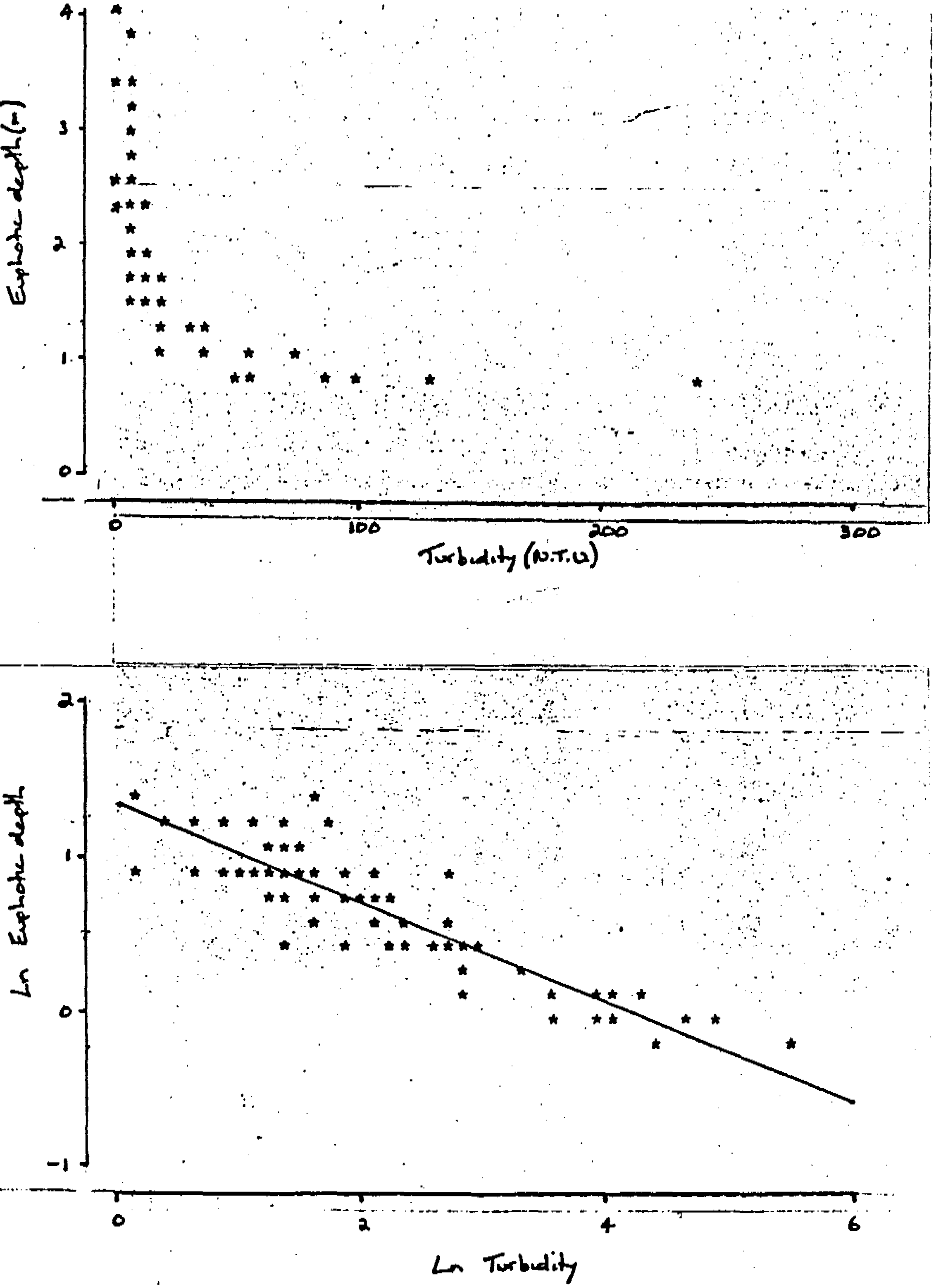

Fig. 3: The relationship between euphotic depth (Zeu) and turbidity, on arithmetic and log axes, for billabongs of the Alligator Rivers Region. The regression equation for Fig. 3b is: $Z_{eu} = 1.30-0.31$ (Turb.) $r^2 = 0.82$.

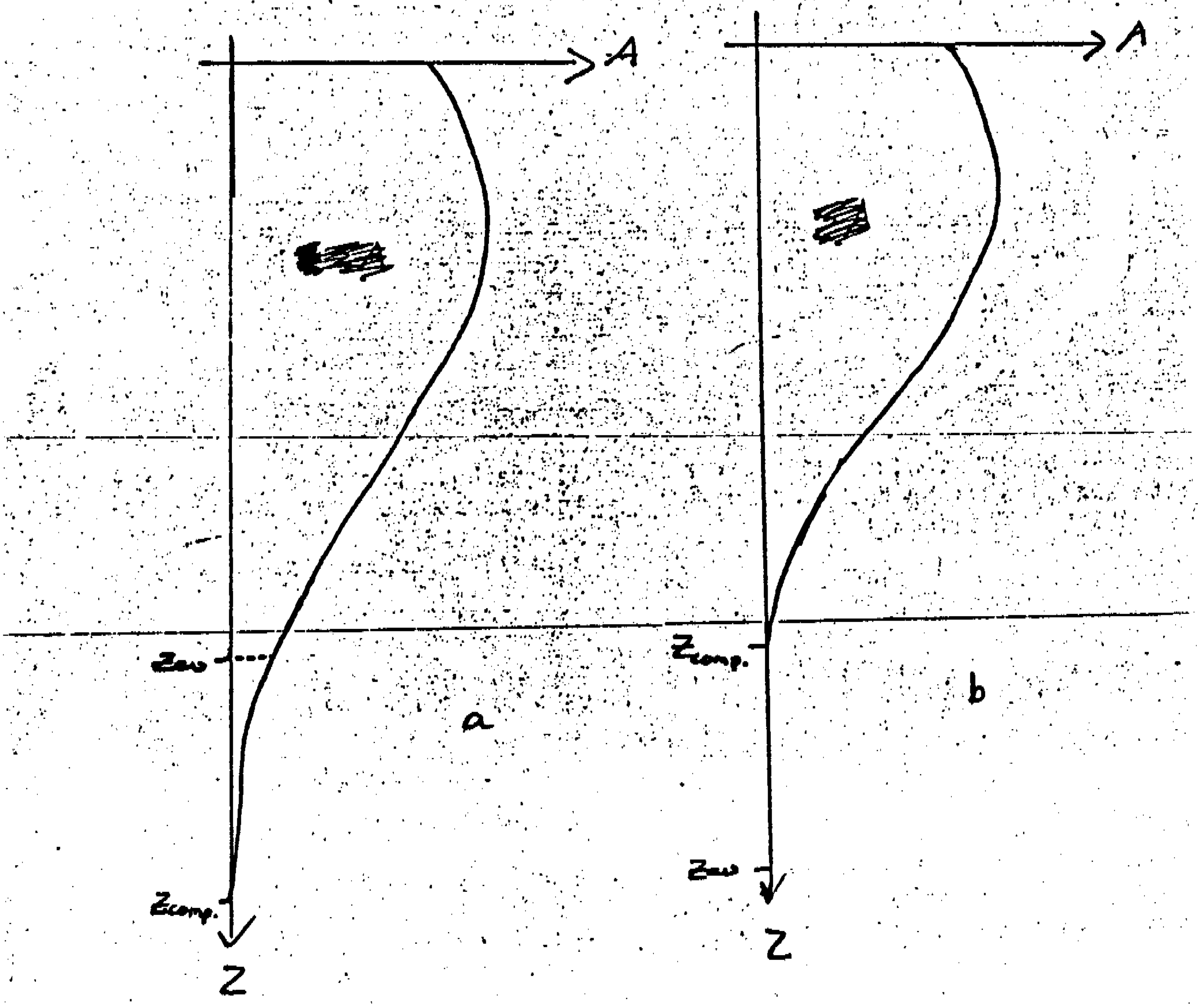

Fig. 4: Photosynthetic profiles showing possible relationships between euphotic depth (Z_{eu}) and compensation level (Z_{comp}).

4. RESULTS* - FORM OF THE PHOTOSYNTHETIC PROFILE

4.1 The euphotic zone

In almost all studies, measurements of primary production are made from a series of samples suspended at depths spanning the euphotic zone (to the 1% level). During this study, whenever possible the 1% level w determined with a quantameter. On most occasions, it was calculated fr the Secchi transparency, which was always measured, using the empirical relationship

$$Z_{eu} = 1.39\ Z_{s.d.} + 0.64$$

determined for the Magela billabongs (Walker, Kirk & Tyler 1983). The range of euphotic depth thus calculated was 0.7 - >6.5 m.

All billabongs in this survey undergo regular seasonal fluctuatio Z_{eu}, the pattern being one of decreasing euphotic depth as turbidity increases over the Dry. This is dramatic in billabongs such as Georget Gulungul, Goanna and Jabiluka following resuspension of finely-divided sediments (see Walker, Kirk & Tyler 1983), when the value of Z_{eu} may contract by as much as 3.0 m. By contrast, in the relatively clear wat of Island and Mudginberri, seasonal variation of euphotic depth is mute (usually ≈1.5 m). Regression analysis shows strong correlation between Z_{eu} and turbidity (Fig. 3).

From the incubations at chosen depths, a profile of production is obtained. To obtain areal rates this must be integrated either to the light level (Z_{eu}, (measured or calculated)), or, to the compensation le ($Z_{comp.}$) where net productivity is zero (Fig. 4). It was found during study that usually $Z_{eu}<Z_{comp.}$ (Fig. 4a) but occasionally $Z_{eu}>Z_{comp.}$ (4b). In the former case, an areal integral calculated to Z_{eu}, as is usual in production studies, would underestimate the observed producti

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* The analytical tables of the text are supplemented by tables of source data in the Appendix.

Table 4 Magnitude of underestimation of integral productivity (ΣA) when integrated to Z_{eu} not Z_{comp}. The values of Z_{eu} were measured with a quantameter.

Billabong	Date	Z_{eu} (1% I_o) (m)	Z_{comp} (m)	Productivity underestimate (%)
Island	21/ 6/79	2.0	3.0	<2
	19/ 7/79	2.8	3.0	<2
	15/ 8/79	2.5	3.0	<2
	23/11/79	2.9	3.0	<2
	26/ 8/80	2.9	2.0	0
	29/10/80	3.6	3.0	0
	8/12/80	2.4	3.5	9
	26/ 2/81	2.6	4.0	30
	26/ 3/81	3.2	4.0	5
	28/ 4/81	3.0	4.5	7
Leichhardt	8/ 6/79	3.2	4.0	5
	10/ 7/79	2.6	3.0	<2
	1/ 8/79	1.8	2.0	<2
	21/11/79	1.1	1.0	0
	15/ 8/80	2.2	3.0	15
	5/ 9/80	1.9	2.0	<2
	16/10/80	1.9	2.0	<2
	10/11/80	1.3	1.5	<2
	7/ 4/81	2.4	2.0	0
Jabiluka	12/ 6/79	1.4	2.0	5
	11/ 7/79	1.4	2.0	12
	9/ 8/79	1.3	1.5	<2
	30/ 8/80	1.1	1.5	5
	24/10/80	0.6	1.5	20
	25/11/80	0.4	1.5	50
	7/ 4/81	3.1	3.0	0

Table 4 shows the extent of the underestimate for those occasions when the 1% level was measured with a quantameter. It is evident that the underestimate is more than a few per cent only when the areal production is very low, in either clear or turbid waters, and that, therefore, Z_{eu}, which is readily measured or calculated, is the appropriate depth for integrating production. For all profiles it is possible that production of phytoplankton at depth is stimulated by the short exposures (<1-2 min) to surface irradiance at the beginning and end of incubations (cf. Tschumi *et al.* 1978). In waters where areal productivity (ΣA) in surface waters is large, slight enhancement of deepwater productivity will have little effect on total productivity, but where ΣA is low, the percentage contribut of such artifacts may be considerable. Therefore, even when there is significant proportion of integral production below Z_{eu} (in those cases when ΣA is very low) Z_{eu} is probably still the appropriate depth.

4.2 The Amax/ΣA ratio (S)

To avoid excessive graphical representation, the form of the photosynthetic profile can be described by curve-shape statistics. Talling (1957) has shown that in a vertically-mixed euphotic zone, the area encompassed by the photosynthesis-depth curve, i.e. the integral photosynthesis, ΣA, may be set equal to a rectangle of width A_{opt}, the *in situ* light-saturated rate of photosynthesis, and depth Z_i, at which light intensity begins to be saturating for photosynthesis ($0.5I_k$) (Fig. 2). Thus

$$\Sigma A \simeq Z_i A_{opt}$$

or

$$Z_i = \frac{\Sigma A}{A_{opt}}$$

The value of Z_i is characteristic of the form of the profile (Fig. 2). authors (e.g. Lewis 1973), prefer the inverse $1/Z_i$ (=S), the Volumen/

Oberfläche ratio of Rhode (1958), the value of which is lowest in waters where photosynthesis is markedly dispersed with depth (Fig. 5a), and highest in waters where production is restricted to a very narrow euphotic zone (Fig. 5d).

All the four types of profile shown in Fig. 5 were found during this study. On a few occasions, profiles displaying two productivity maxima were also encountered (Fig. 6). The values of S and Z_i varied over an order of magnitude (S = 0.43-9.43; Z_i = 2.33-0.11; Appendix tables) depending upon season and billabong.

It is usually claimed that the phytoplankton biomass, itself determin by trophic status, largely determines the shape of the production profile (Fig. 5; Wetzel 1975). However, in the Magela billabongs no relationship between S and chlorophyll-a concentration was detected (Fig. 7). On the other hand, there was strong correlation between turbidity and the value of S (Fig. 7), and billabongs which experience sustained exponential increases of triptonic turbidity during the Dry showed marked changes in S (e.g. Gulungul, S = 1.2-5.2; Jabiluka, 0.5-4.7; Goanna, 1.7-9.4; Ja Ja, 1.1-6.7). Billabongs which remain relatively clear showed little change i S despite the fact that chlorophyll concentrations changed dramatically (e.g. Island, S = 0.5-1.2; chl.a (= euphotic zone = 9.3-183 mgChla m^{-2}). Since there was good correlation (Fig. 7) between S and Z_{eu} (calculated from $Z_{s.d.}$), it appears that the shape of the profile is determined principally by light penetration which itself is principally influenced b triptonic turbidity (see Walker, Kirk & Tyler 1983).

4.3 Light inhibition

Suppression of photosynthesis near the water surface, a familiar feature of production profiles, was regularly observed in the billabongs (Fig. 6). This phenomenon may result from photoautoxidation of pigments at high irradiances (Yentsch & Lee 1966), increased photorespiration (Har

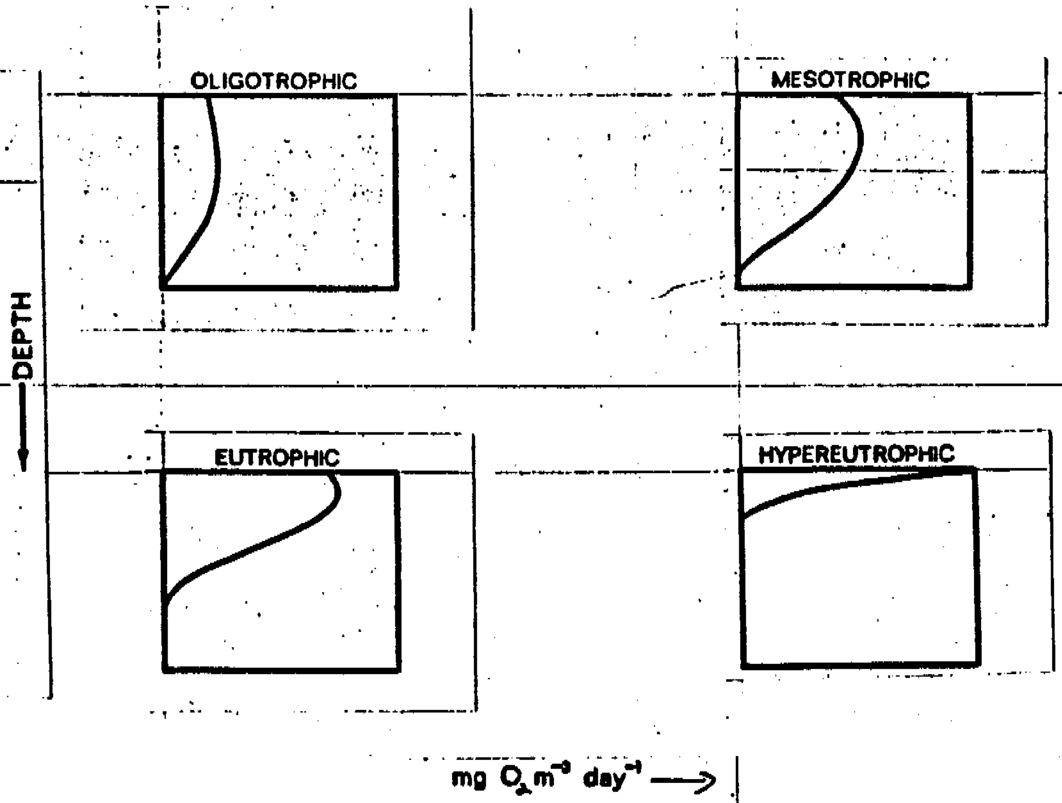

Fig. 5: Common productivity profiles in waters of different fertility. (Adapted from Wetzel (1975)).

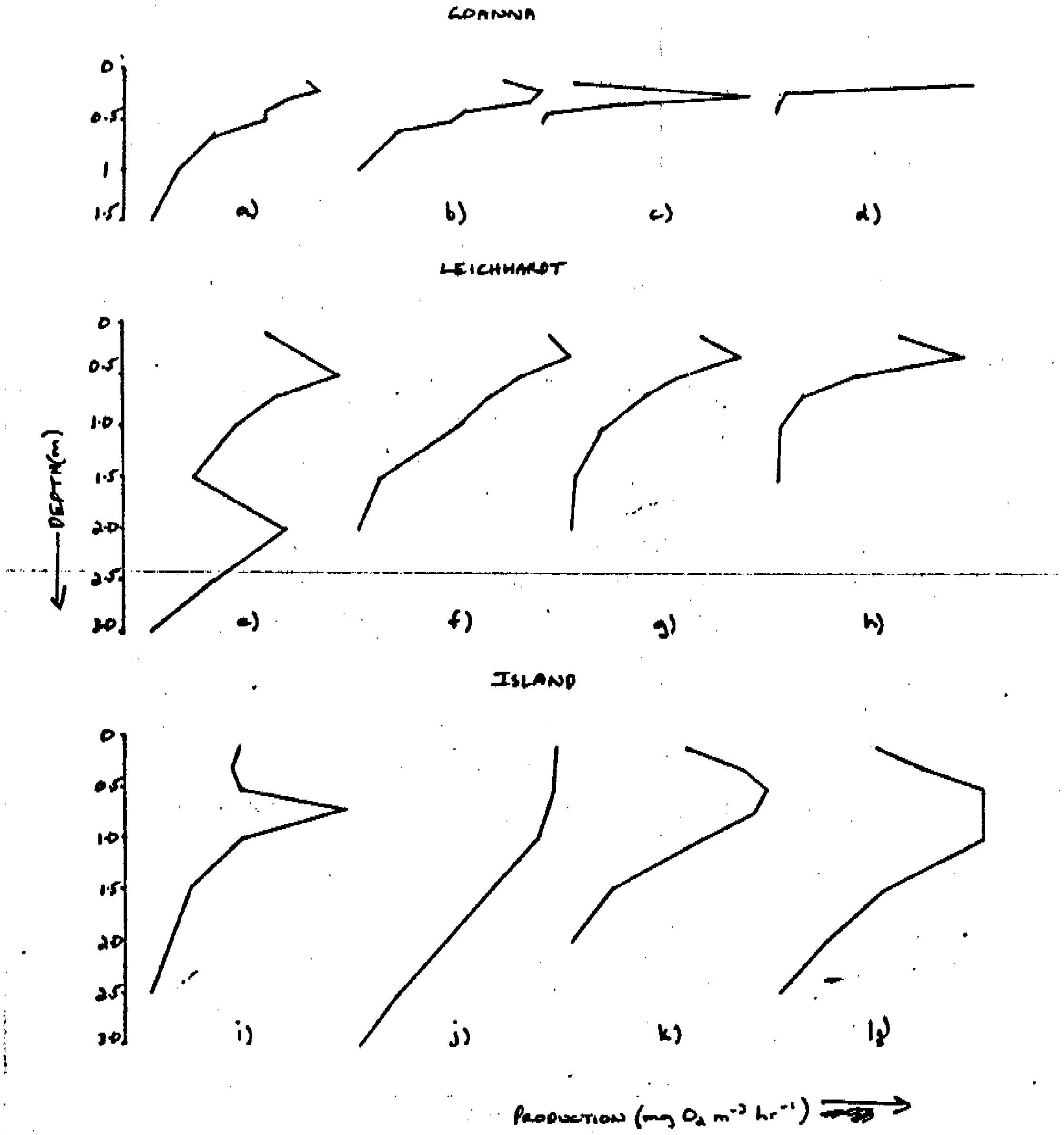

Fig. 6: Examples of productivity profiles encountered in billabongs of the Alligator Rivers Region.

Key:

a) 10/4/80
$\Sigma A = 103$
$S = 1.55$
$z_i = 0.65$

b) 12/6/80
$\Sigma A = 60$
$S = 2.33$
$z_i = 0.43$

c) 10/8/79
$\Sigma A = 49$
$S = 6.53$
$z_i = 0.15$

d) 12/10/79
$\Sigma A = 157$
$S = 9.43$
$z_i = 0.11$

e) 15/8/80
$\Sigma A = 406$
$S = 0.71$
$z_i = 1.41$

f) 5/11/80
$\Sigma A = 715$
$S = 1.16$
$z_i = 0.86$

g) 16/10/80
$\Sigma A = 839$
$S = 1.55$
$z_i = 0.65$

h) 10/11/80
$\Sigma A = 367$
$S = 2.43$
$z_i = 0.41$

(i) 2/6/80
$\Sigma A = 422$
$S = 0.73$
$z_i = 1.37$

(j) 2/7/80
$\Sigma A = 818$
$S = 0.55$
$z_i = 1.82$

k) 26/8/80
$\Sigma A = 319$
$S = 0.94$
$z_i = 1.06$

l) 22/9/80
$\Sigma A = 449$
$S = 0.69$
$z_i = 1.45$

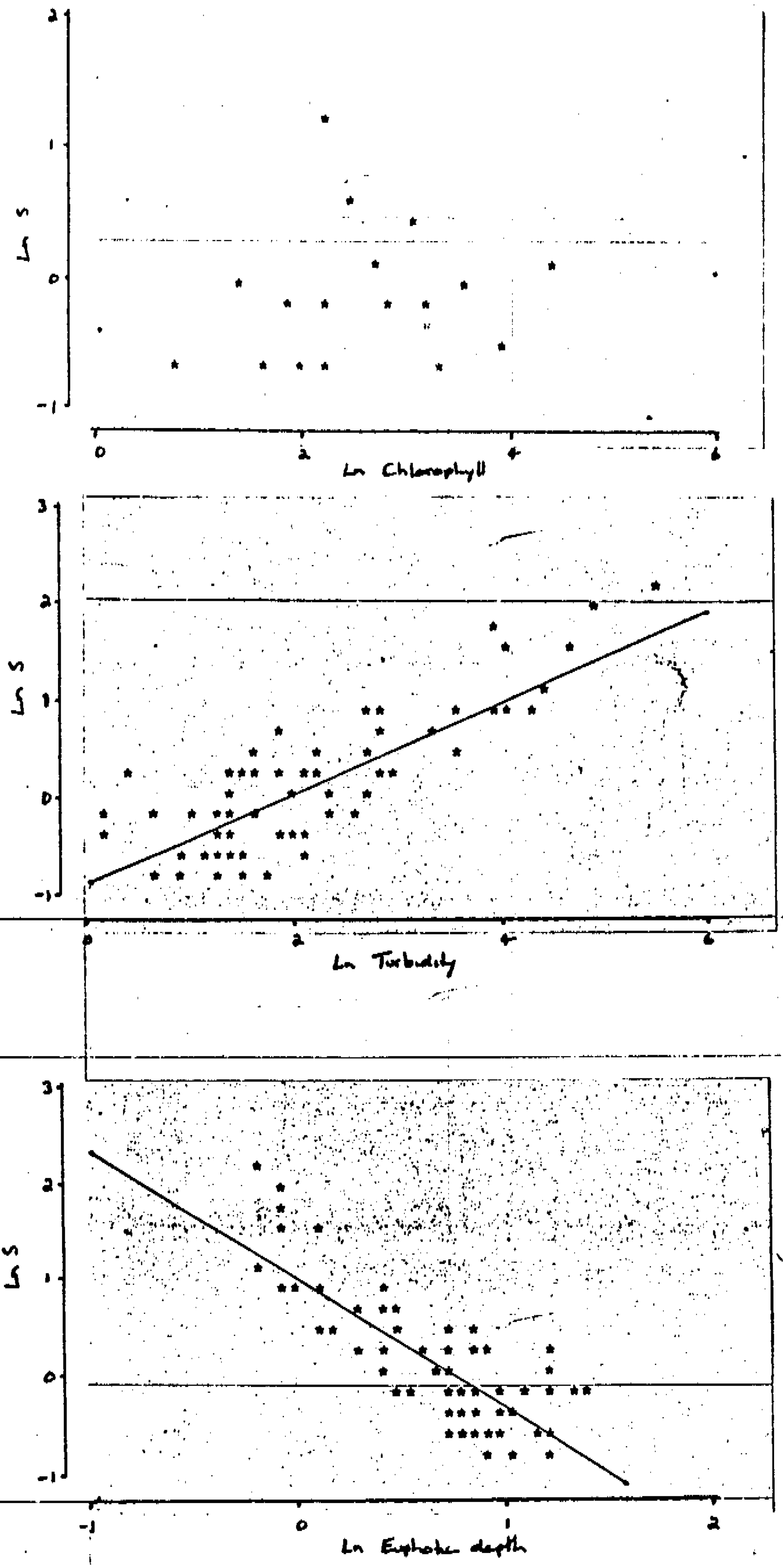

Fig. 7: The relationship between S and chlorophyll content of the euphotic zone (a), S and turbidity (b), and S and Z_{eu} (c) for billabongs of the Alligator Rivers Region.

& Lott 1973), and perhaps the inhibitory effect of excessive ultra-violet radiation (Findenegg 1966). Alternatively, Talling (1965) suggests that in many cases the "inhibition" may merely reflect depleted phytoplankton numbers in surface layers caused by sedimentation. Since vertical heterogeneity of phytoplankton is a common feature of the billabongs, profiles of productivity per unit volume (A, mgO_2m^{-3}) do not necessarily follow those of productivity per unit biomass (photosynthetic index, P, mgO_2.mg Chl a^{-1}). Thus, to test the applicability of Talling's (1965) suggestion, profiles of the photosynthetic index (P) were examined. Cle if P_{opt} occurs at some depth below the surface, photoinhibition rather than sedimentation is producing the observed inhibition. On some occasions (Table 5) P_{opt} occurred at the surface, while A_{max} occurred lower down, suggesting sedimentation, but no surface inhibition. On other occasions P_{opt} occurred further down the water column, as expected if photoinhibition were operating. From available irradiance data, measured downwelling vertical attenuation coefficients (k), and the depth of maximum photosynthetic capacity (Zp_{opt}), an estimate of the threshold of light inhibition ($I_{inh.}$) was obtained (Table 5). Lewis (1974) and Melack (1979) followed a similar procedure, using the depths of productivity maxima ($Z_{A_{max}}$) and assuming homogeneous vertical distribution of plankton.

From the limited data available (Table 5) it appears that $I_{inh.}$ varied during the Dry by about threefold, over the range 1.8 to >5.6 $Em^{-2}hr^{-1}$. However these values should be regarded as estimates only because only a limited number (1-3) of incubations can be carried out spanning the narrow stratum across which both PAR and production rates change rapidly, and $Z_{inh.}$ may be under or overestimated by 10-15 cms.

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*In a vertically homogeneous profile $A_{max} = A_{opt}$. Since heterogeneity is common for the billabongs A_{opt} is not necessarily equal to A_{max} but the latter is more easily measured, and is a reasonable estimate of A_{opt} in most cases.

Table 5 Values of the irradiance (I_{inh}) at which inhibition of photosynthesis begins for three Magela billabongs, compared with elsewhere in the world.

Lake	Date	$Z_{A_{max}}$ (m)	$Z_{P_{opt}}$ (m)	I_o $Em^{-2}hr^{-1}$	k (m^{-1}) Ln units	I_{inh} $Em^{-2}hr^{-1}$	Source
Leichhardt	5/ 9/80	0.03	0.1	6.6	2.37	>5.2	
	16/10/80	0.3	0.1	7.1	2.44	>5.6	
	13/ 5/81	0.3	0.3	4.6	-		
	20/ 6/81	0.3	0.3	5.2	-		
Jabiluka	30/ 8/80	0.3	0.3	6.2	4.17	1.8	
	25/11/80	0.1	0.1	6.2	11.72	>1.9	
	14/ 5/81	1.0	0.3	4.7	-		
	18/ 6/81	0.5	0.5	5.0	-		
Island	26/ 8/80	0.5	0.3	5.0	1.61	3.1	
	22/ 9/80	0.5	0.5	5.8	-		
	29/10/80	0.7	0.3	6.5	1.27	4.4	
	8/12/80	0.1	0.1	6.1	1.93	>5.0	
	26/ 2/81	0.5	0.3	6.5	1.80	3.8	
	26/ 3/81	0.5	0.5	5.7	1.43	2.9	
	28/ 4/81	0.1	0.1	5.5	1.54	>4.7	
	22/ 5/81	0.5	0.5	5.5	-		
	19/ 6/81	0.3	0.3	5.0	-		
Naivasha, Kenya			0.5-2.0			0.6-3.1	Melack(1979a)
Oloiden, Kenya			0.5-1.0			0.6-2.2	Melack(1979a)
Cresent Island, Kenya			2.0-3.0			0.7-1.6	Melack(1979a)
Lanao, Phillipines						0.9-2.3*	Lewis (1974)

* Calculated using the conversion 1 Einstein = 52 kilocalories and assuming that visible radiation constitutes 43% of the total incident radiation (Bannister 1974).

Nevertheless, the $I_{inh.}$ values for three Magela billabongs are generally much higher than those reported for other tropical lakes - Lake Lanao, Phillipines (Lewis 1974) and three Kenyan lakes (Melack 1979) (Table 5).

5. RESULTS - RATES OF PHOTOSYNTHESIS

5.1 Areal (ΣA), mean volumetric (A) and maximum (A_{max}) production rates

Integral productivity* (ΣA, $mgO_2m^{-2}hr^{-1}$) ranged over 3 orders of magnitude (0-1293 $mgO_2m^{-2}hr^{-1}$ - Table 6; Appendix tables), varying with season and from billabong to billabong. Bowerbird was always unproductive, as were all billabongs in the Wet and as were the highly turbid ones in the Dry. Leichhardt and Island were the most productive. For the period where appropriate irradiance records were available, daily productivity* ($\Sigma\Sigma A$, $mgO_2m^{-2}d^{-1}$) was calculated (Table 6), and this spanned 2830 to 8635 $mgO_2m^{-2}d^{-1}$. These hourly and daily rates place the billabongs at their most fertile in the middle of the range of measured productivities in tropical lakes (Table 6), and high in comparison with many temperate lakes (Table 5.19 in Westlake *et al.* 1980).

Smith (1979) has sounded a cautionary note on the use of ΣA and $\Sigma\Sigma A$ to compare lakes with different limnological characteristics, due to the possible insensitivity of both measures to changes in optical conditions. Thus, for example, the trophic status of a lake may rise due to an incre nutrient loading, triggering increases in algal biomass. The resultant self-shading may severely curtail z_{eu} and the ΣA then not truly reflect ongoing lake enrichment. Rather, Smith has demonstrated that both the productivity per unit volume of the euphotic zone (A, $mgO_2m^{-3}hr^{-1}$), and the light-saturated volumetric rate of photosynthesis (A_{opt}), are more ful measures of productivity. In this study, for convenience we have u A_{max}, the maximal rate of photosynthesis. This may not correspond exac to A_{opt} due to algal stratification (see section 4.3) but is a close approximation.

Values of A* and A_{max}* for the Magela billabongs are tabulated in Table 6 and the Appendix tables. As with ΣA, values for these two vari

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* Note that these values are for net, not gross, production.

of the Alligator Rivers Region and elsewhere in the world.

Waterbody	ΣA_2 (mgO$_2$m^{-2}hr^{-1})	$\Sigma\Sigma A$ (mgO$_2$m^{-2}d^{-1})	A (mgO$_2$m^{-3}hr^{-1})	A_{max} (mgO$_2$m^{-3}hr^{-1})	B (mgChla m^{-3})	P_{opt} (mgO$_2$(mgChla)$^{-1}$hr^{-1})	Q (mmolO$_2$E^{-1})	Source
Bowerbird B.	0-481	0-1.7		70-260				
Gulungul B.	33-309	0.2-2.0	21-160(4)	60-770				
Georgetown B.	0-20		0-25	10-70				
Goanna B.	21-267		21-199	50-1490				
Mudginberri B.	379-637		104-233	220-320				
Island B.	62-1419	1.5-8.6	35-637	50-860				
Ja Ja B.	9-633		12-323	60-650				
Leichhardt B.	40-1151	1.0-6.3	12-501	40-1360				
Jabiluka B.	66-332	1.1-1.9	34-245	60-850				
Red Lily B.	135-772	0.9-5.4	92-288	170-540				
L. Naivasha, Kenya	340-570	3.7-6.2		150-240		8-14	1.9-4.0	Melack (1979a)
L. Victoria, Kenya	340-1360	4.9-11.4		43-132	25-69	14-35	3.1-10.2	Talling (1965)
(offshore)								Melack (1979a)
L. Oloiden, Kenya	390-1120	4.2-12.1		260-750		12	3.1-5.2	Melack (1979a)
Crescent Island Crater, Kenya	280-600	4.1-6.4		80-180		12	2.0-6.1	Melack (1979a)
L. Simbi, Kenya	600-5200			950-12900		1-19		Melack (1979b)
L. Kilotes, Ethiopia	500-2400		1566-5106	4200-10000	205-402	16-34	2.4-7.7	Talling *et al.* (1973)
L. Aranguadi, Ethiopia	1400-2600		5296-17066	10000-30000	917-2170	11-18	6.0-16.0	Talling *et al.* (1973)
L. George, Uganda	1060-1740	12.3-15.7			90-292	20+	3.6-10.1	Talling (1965)
L. Mariut, Egypt		2.8-12.7*		480-5148*				Aleem & Salaam (1969)
L. Sibaya, South Africa		<2.2*						Allanson & Hart (1978)
L. Kinneret, Israel		<4.3*		<154*				Berman & Pollinger (1974)
Ooty L., India		2.2-11.3*						Sreenivasan (1964)
Yercaud L., India		1.6-4.3*						Sreenivasan (1964)
Madden L., Panama	500-800			<132				Gliwicz (1976)
Lago do Casthano, Brazil		0.4-2.6*			20-140			Schmidt (1973)

* Converted from C^{14} data assuming a photosynthetic quotient of 1.2.

\+ Mean value

span three orders of magnitude ($A = 0\text{-}637$ mgO$_2$m^{-3}hr^{-1}; $A_{max} = 10\text{-}1490$ mgO$_2$m^{-3}hr^{-1}) depending upon billabong and season, and at their most fertile, the billabongs rank with the lower-mid range of production rates noted for other tropical lakes (Table 6), but high in comparison with temperate lakes (Westlake *et al.* 1980).

5.2 Chlorophyll and the photosynthetic index (P_{opt})

During this study phytoplankton biomass was determined indirectly, a chlorophyll-a concentration. Both on areal and volumetric bases Leichha Island and Red Lily supported the highest population during the Dry (Table 7). However, late in the Dry dense surface blooms of *Microcystis aerugino* in the shallow muddy waters of Gulungul could raise surface values of chlorophyll-a above 150 mg m^{-3}. In general, though, the maximum chlorop concentrations recorded in these billabongs lie considerably below those recorded for many eutrophic lakes, regardless of latitude (Table 7).

Kessell and Tyler (1983) noted striking horizontal and vertical heterogeneity in phytoplankton biomass (as determined by chlorophyll-a concentration) in some Magela billabongs. Such horizontal heterogeneity militates against the calculation of whole billabong phytoplankton biomas or whole billabong productivity rates and production budgets from determinations at one site. This, together with the rapid changes, in t and space, of phytoplankton species composition and biomass, precludes a determination of yearly production budgets from the monthly incubations.

The rate of oxygen evolution at light saturation per unit chloroph (the photosynthetic index, P_{opt}, mgO$_2$mg Chl.a^{-1}hr^{-1}) has been widely use as an estimate of photosynthetic potential. As noted above (Section 4.3 in lakes with homogeneous vertical distributions of phytoplankton throu the euphotic zone, the depth of P_{opt} corresponds to the zone of maximum productivity (A_{max}), but this is not necessarily the case where vertical heterogeneity of the plankton is considerable. Therefore, in this study was determined for each sample depth, and the maximum value designated P

Table 7 Comparison of maximum phytoplankton biomass (as chlorophyll-a) in the Alligator Rivers billabongs, with levels attainable elsewhere in the world. Global data are taken from Table 5.1 in Westlake *et al.* (1980).

Lake	Mean depth (m)	Chlorophyll-a		
		b_{max} (mg m^{-3})	B_{max} (mg m^{-2})	B_{max} (mg m^{-2} euphotic)
Bowerbird*+	5-8	5	-	14
Gulungul*+	0-3	171	-	47
Island*	3.5-6.5	59	-	183
Leichhardt*	3.5-6	102	-	167
Jabiluka*	3.5-6	45	-	28
Red Lily*	2-4	98	-	109
L. Kilotes (Ethiopia)	2.6	412	-	194
L. Aranguadi (Ethiopia)	18.5	2170	-	325
L. George (Uganda)	2.25	440	1084	350
Jezarko Pond (Czechoslovakia)	0.7	177[a]	124[a]	-
Velky Palenec Pond (Czechoslovakia)	1.4	135[a]	190[a]	-
Velky Bezdekovsky Pond (Czechoslovakia)	1.0	1800[a]	1800[a]	-
R. Thames (UK)	2.3	199	458	-
R. Kennet (UK)	1.0	34	34	~34
L. Batorin (USSR)	3	74	222	-
L. Yunoko (Japan)	12 max	34	379	197
L. Trummen (Sweden)	1.8	173	398	351
L.Chilwa freshwater phase	2	1400	-	-
(Malawi) drying phase	<2	436	-	-
Abbot's Pond (UK)	<2	300	460	-
Loch Leven (UK) at b_{max}	3.9	217	846	260
at B_{max}		170	663	456
Lago do Casthanho (Brazil)	1-12	100	400	-
L. Biwa (Japan)	41.2	26	484	255
Corangamite L.(Australia)	2.9	226	-	-
Red Rock Tarn (Australia)	1.4	1050	-	-
L. Werowrap (Australia)	1.4	810	-	-

* This range refers to maximum, not mean, depths.

\+ Often the euphotic zone extends right down to the sediments so B_{max} will be an underestimate of that which could be attainable if the billabong were deeper.

whilst the overall value for the euphotic zone (P_{eu}) was computed from the ratio $\Sigma A/\Sigma B$, where ΣB is the areal biomass in terms of mg Chl.a m^{-2}.

Values of P_{opt} for the Magela billabongs spanned 40 units (3.4-43.8, Table 6). Except perhaps for Island, where the highest P_{opt} appears to be restricted to the clearer waters of the Wet and early Dry, a seasonal trend in the photosynthetic index cannot be demonstrated. However, from the limited data available, it is apparent that there is some relationship between P_{opt} and chlorophyll concentration (B) with some of the lowest P_{opt} values occurring at times of maximum chlorophyll content in the euphotic zone (e.g. Leichhardt 5/9/80 - P_{opt} = 7.7 mgO_2mg Chl.a^{-1}.hr^{-1}, B = 84 mg Chl.a m^{-3}; Island 8/12/80 - P_{opt} = 10.0, B = 52; Gulungul 5/10/80 - P_{opt} = 3.4, B = 150 mg Chl.a m^{-3}), and some of the highest P_{opt} values at times of minimum chlorophyll (Island 26/2/81 - P_{opt} = 43.8, B = 2; Gulungul 17/3/81 - P_{opt} = 36.4, B = 2.5). These observations agree with the common experience of decreasing P_{opt} with increasing biomass (Westlake *et al.* 1980). In general, P_{opt} in the billabongs usually fell within the range 15-30 mgO_2.mg Chl.a^{-1}.hr^{-1}.

These values of P_{opt} appear to be typical of tropical waters (Table 6), and, as a rule, much higher than those obtained in temperate waters (cf. Talling 1965 and Westlake *et al.* 1980 p.239). This is attributed to the positive influence of temperature on P_{opt} (Allanson & Hart 1975; Berman & Pollinger 1974; Talling 1965; Talling *et al.* 1973).

5.3 Efficiency of light utilization

The efficiency with which green plants use light for the production of organic matter has wide ecological significance. For phytoplankton, two indices of efficiency may be calculated. The first, light utilization or ecological efficiency (Q) relates rates of production to total available light. By contrast, the second index, photosynthetic or quantum efficiency, takes into account only that light absorbed by the algal cells themselves. In this ecological study, only the first index has been calculated.

Since only 43-46% of total incident radiation is available for photosynthesis (Bannister 1974; Talling 1957), the utilization efficiencies have been calculated only for the band of photosynthetically-active radiation (PAR, 4007-00 nm). Generally, utilization efficiencies are calculated on an energy basis, assuming an approximate calorific equivalent for either oxygen evolution (3.6 kcal/g O_2, Talling *et al.* 1973) or carbon assimilation (9.33 kcal/gC, Dubinsky and Berman 1976). Here, the efficiency (Q) was calculated on a molar basis, i.e. moles of O_2 evolved per mole of quanta of PAR (Einstein, E) incident on the water surface (after Melack 197[illegible]). The advantage with this approach is that firstly, photosynthesis, being a photochemical process, relies upon the absorption of quanta, not energy, and secondly, an energy-equivalent value for photosynthetic production (as above) need not be assumed.

Values of Q among six Magela billabongs varied between 0 and 5.1 m moles O_2 E^{-1} (Table 6). The zero value occurred in the highly transparent waters of Bowerbird billabong at the Wet/Dry interchange, when no net primary production could be measured. All other values below 0.7 were limited to shallow Gulungul and Red Lily billabongs during the late Wet and Wet/Dry interchange at a time of maximum water transparency and minimum phytoplankton biomass, and in Gulungul when turbidity is maximal (October, 75 N.T.U.). Similar to the situation in Gulungul, the lowest efficiencies (<1-1.2) in the remaining three billabongs were restricted to the transparent, oligotrophic conditions of the Wet or Wet/Dry interchange (Leichhardt, Island), and to the times of very high turbidity (>70 N.T.U., Jabiluka). In Jabiluka, Q values above 2.0 were never recorded because this billabong quickly reverts from the transparency of the early Dry to the highly turbid condition of the mid-late Dry. For most of the Dry, the waters of Leichhardt, Island and Red Lily support large standing crops of phytoplankton (Chl.A > 40 mg m^{-2}) in their euphotic zones, and then their efficiencies range between 2-4 m moles O_2 E^{-1}. The highest efficiencies (>4) appear to require chlorophyll concentrations approaching 200 mg m^{-2}.

These values for Q are in good agreement with those obtained in other tropical waters, and indicate that the Magela billabongs display moderate efficiencies on a tropical scale. For three Kenyan lakes in the Naivasha basin (Naivasha, Oloidien, Crescent Island Crater - Table 6), Q's spanned 1.9-6.1 m mol O_2 E^{-1}, usually 2-4 m mol O_2 E^{-1}. For Lake Victoria, a larger range of 3-10 (Table 6) has been noted. The highest sustained efficiencies are apparently those which characterise African soda lakes containing extremely dense crops of blue-green algae (>200 mg Chl.A m^{-2}), notably *Spirulina platensis* (Lakes Aranguadi and Kiloks - Table 6). In Lake Aranguadi, values of Q during Talling's (1965) brief survey varied from 6.0-16.0.

5.4 Seasonal changes in productivity

The often profound seasonality of such interrelated factors as nutrient status, euphotic depth, chlorophyll content, triptonic turbidi and retention time, appear likely to prescribe the character of seasonal changes in productivity of the billabongs. Retention time, directly determined by the seasonality of preciptation, plays a cardinal role, s throughflow in the billabongs, associated with low nutrient status and negligible phytoplankton stocks, results in low productivities. After cessation of throughflow early in the Dry, evapo-concentration of billa waters, often combined with sediment suspension by wind-induced or biogen (buffalo, birds) disturbance of sediments, produces a kaleidoscopic arra of limnological conditions. Similar diversity in production rates is t expected. Consideration of both areal (ΣA) and volumetric (A) producti rates together (see section 5.1) is likely to give the most accurate picture of these seasonal changes.*

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*Any seasonality due to changing limnological conditions is obviously difficult to demonstrate in billabongs where production occurs right down to the sediments, because changes in ΣA and A may merely reflect the diminishing depth of the billabong. Thus the highly transparent Bowerbi and backflow billabongs like Gulungul, which may be only a few centimetre deep by the late Dry, are excluded from this discussion.

Leichhardt displayed a great seasonal range of productivity (Fig. ; Table 4; Appendix Table 8). Walker, Kirk and Tyler (1983) have demonstrated a temporal progression during the Dry toward higher chlorophyll in the waters of this billabong, a progression matched by the seasonal increases in nutrient concentrations (Walker & Tyler 1983), with total phosphorus peaking around August-September. It is therefore not surprising to find that in most years, mean volumetric production of the euphotic zone (A) progressively increased from the low values (<30 $mgO_2m^{-3}hr^{-1}$). A slight decline in productivity was usual in the last weeks of the Dry, although a burst in production could accompany the first rains of the approaching Wet. The exception to this general pattern was in July 1979, when production fell briefly to only 10% of the figure recorded for the previous month's sampling (Appendix Table 8). It should be noted that turbidity, which in some other billabongs increases in the Dry to the extent of severely curtailing light penetration, and hence production (see below), does increase in Leichhardt but does not reach values sufficient to halt the progressive rise in productivity at least until very late in the Dry (cf. Jabiluka, Ja Ja, etc., below).

The other floodplain billabong extensively studied in this productivity survey was Jabiluka (Fig. 8; Table 4 ; Appendix Table 9), and it too exhibited a similar temporal pattern during the Dry, although one not as marked as Leichhardt. As with most billabongs, minimum productivity was recorded at the Wet/Dry interchange. Maximum productivities occurred earlier in the Dry than in nearby Leichhardt, around July-early August. An often marked decline in productivity followed, as suspended silt loads markedly rose (Walker, Kirk and Tyler 1983) and chlorophyll levels declined. As with Leichhardt, stimulation of production could result from the first rains of the Wet.

Fig. 8: Seasonal changes in turbidity, total phosphorus, surface chlorophyll and mean volumetric production for the euphotic zone (shaded) and areal production (not shaded) for three Magela billabongs in 1980 and 1981.

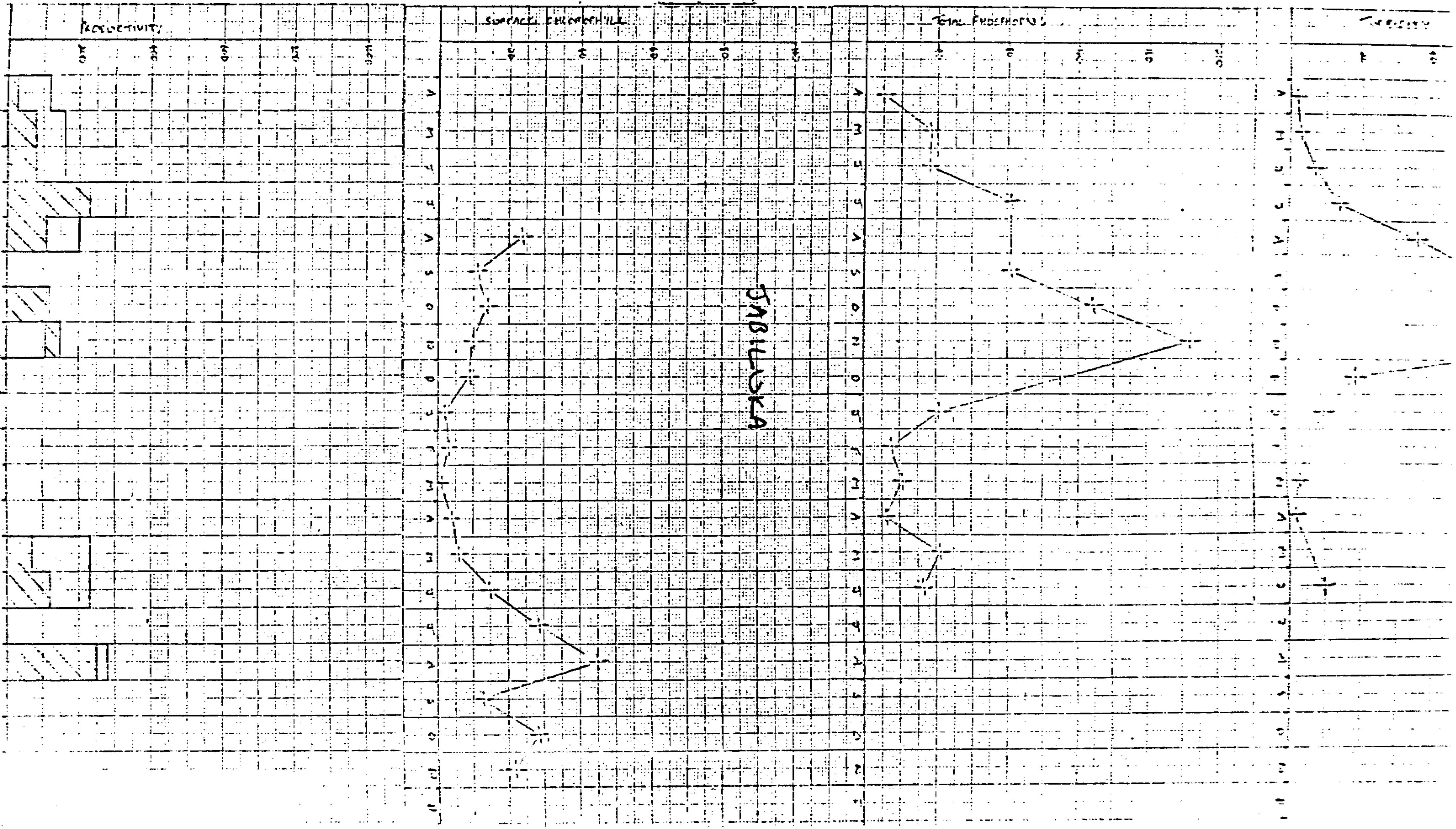


Fig 8 cont.

LEICHHARDT

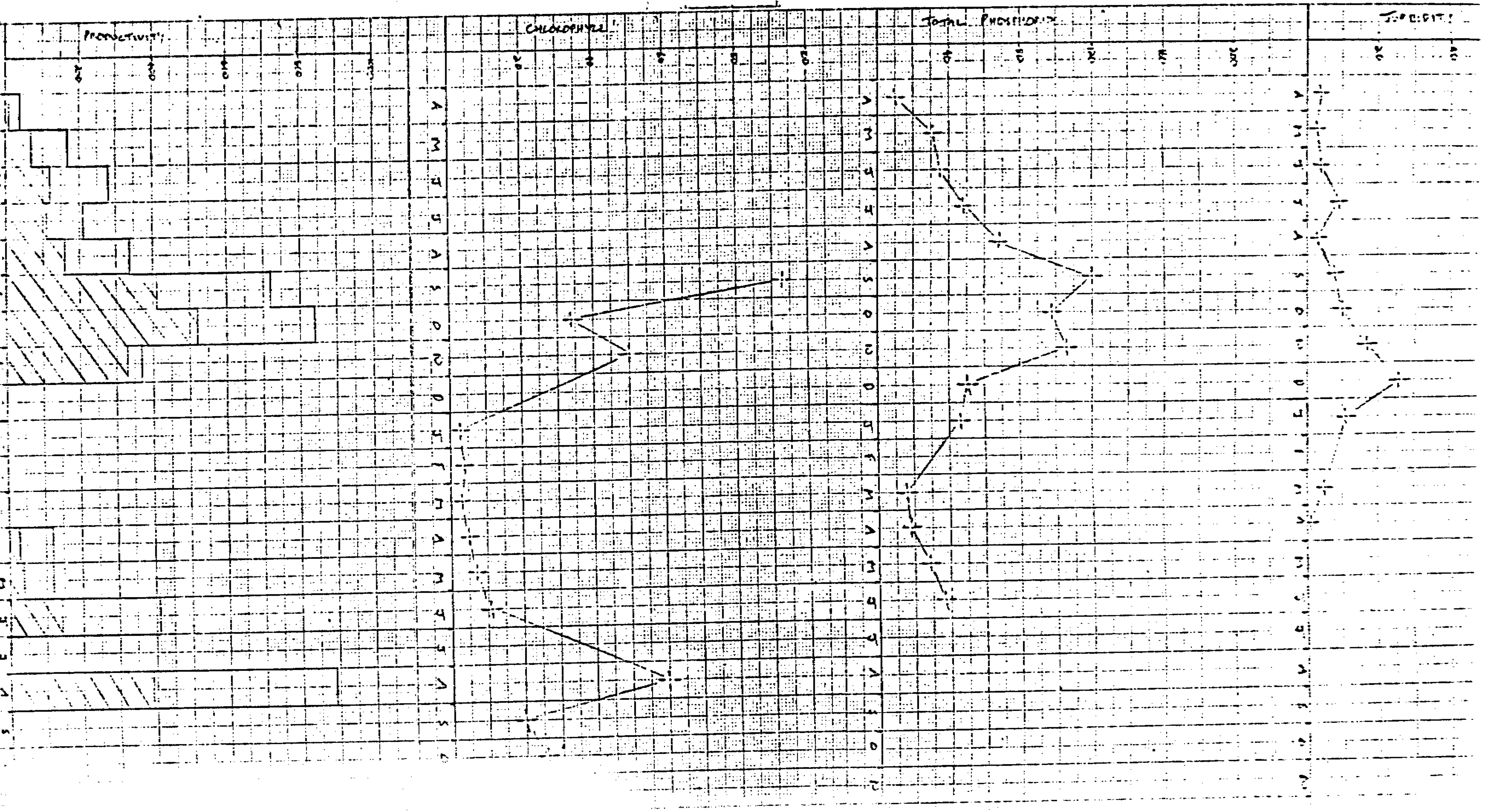
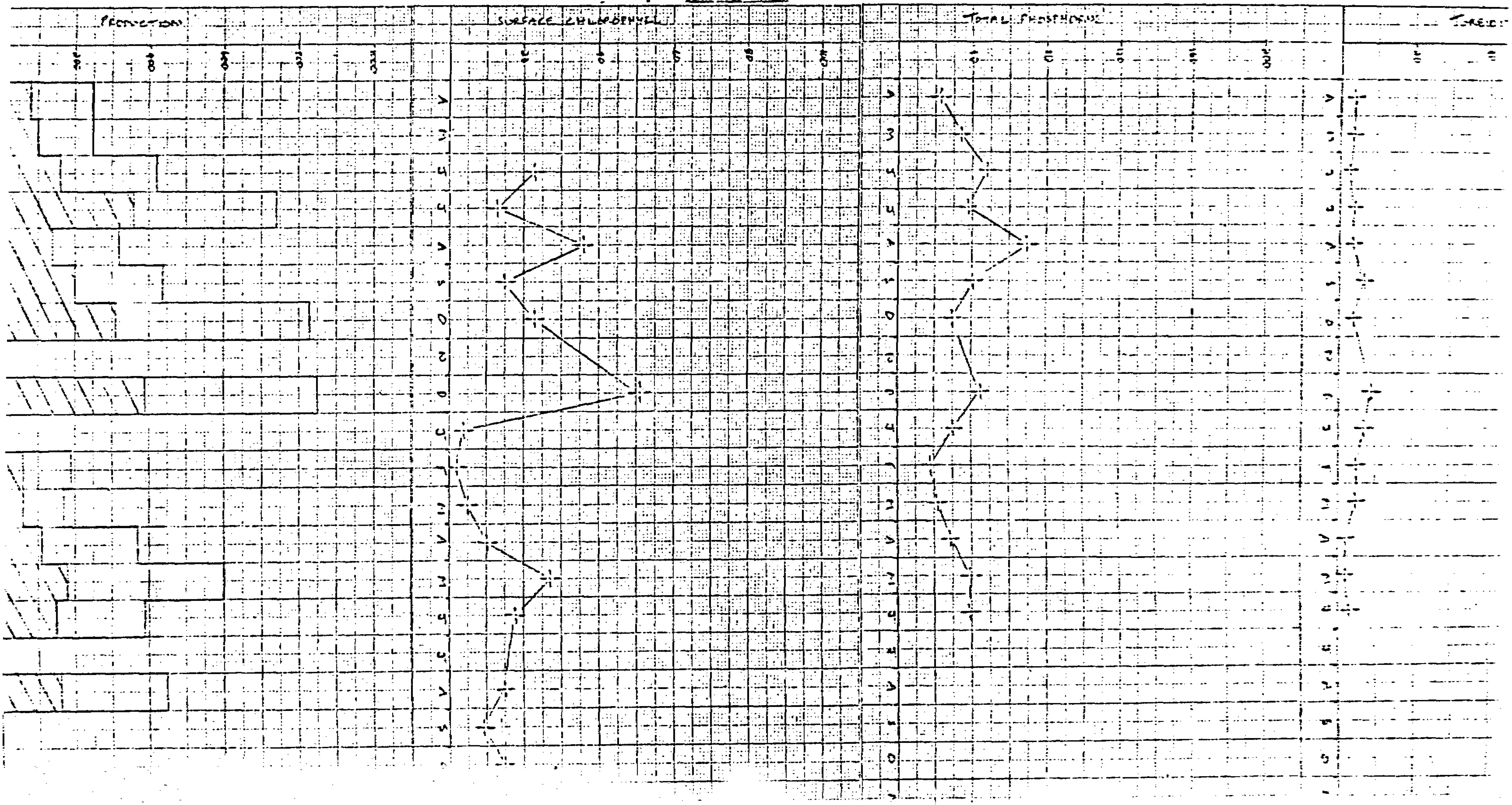


Fig 8 cont.

ISLAND.



Jabiluka's seasonal progression appears to be virtually mirrored by the much shallower Goanna (Table 4; Appendix Table 4), although in the latter, the Dry season peak of productivity may occur even earlier. Ja Ja is another billabong for which the limited data available (Table 4; Appendix Table 7) suggests similarity with the Jabiluka pattern, except that the late Dry decline in productivities is of much greater magnitude, a decline concurrent with marked increases in turbidities and decreases in chlorophyll concentrations (Walker, Kirk and Tyler 1983).

The billabong for which most information exists is Island, a large, deep and optically-transparent billabong. While it displays something of the Leichhardt-Jabiluka seasonal pattern, in that productivity increases from a low at the Wet/Dry interchange to a peak in the mid to late Dry, the seasonal change appears to be more irregular than in the above billabongs (Fig. 8; Table 4; Appendix Table 6). This may be merely a reflection of the greater sampling frequency. It is more likely however, that, in this billabong where the extent of progressive change over the Dry in turbidity and trophic status is muted (Fig. 8), the emphasis shifts from a seasonal cycle toward one with a more diurnal basis (cf. Ganf 1975; Ganf and Winer 1973). This point is amply illustrated by the strong variation in productivities (137-214 mgO_2m^3hr) measured on four occasions over a nine day period in August 1981 (Appendix Table 6). For much of the Dry, productivities of >150 $mgO_2m^{-3}hr^{-1}$ characterise these clear waters, distinguishing this billabong, with Leichhardt and Red Lily, as the most productive waters in this study. The limited data for Mudginberri (Appendix Table 5) suggests similarities with the Island pattern.

Only a year's productivity data is available for Red Lily, but this suggests remarkable constancy in production rates throughout the Dry (220-290 $mgO_2m^{-3}hr^{-1}$) until just prior to the Wet, when productivity falls, a decline which continues throughout the Wet.

In conclusion, then, most billabongs studied conform to some temporal pattern. During the Wet production is low. During the Dry it rises. In some billabongs the seasonal rise in production is reversed by massive increases in turbidity. This is the likely pattern for most floodplain and backflow billabongs. The exception of Leichhardt has already been noted. While the seasonal pattern may remain essentially the same from year to year, variations in the actual magnitude of production rates are more capricious. In other billabongs, notably Island, seasonal change in most limnological parameters is muted, and a diurnal aspect is revealed.

6. RESULTS - STATISTICAL ANALYSIS

6.1 The prediction of biomass (as chlorophyll-a)

Following the classic works of Sakamoto (1966) and particularly Vollenweider (1968), much attention has been focused on the prediction of chlorophyll concentration from nutrient concentrations in lake waters or, preferably, from nutrient loading models. Worldwide experience has shown that, in general, the concentrations of phosphorus and nitrogen hol concentrations of phytoplankton biomass below those theoretically attain from energy and other considerations. Thus, it is often feasible to predict chlorophyll concentration from a knowledge of nutrient availabil (Nicholls and Dillon 1978). Most studies indicate that it is, first, phosphorus, and second, nitrogen, which limits chlorophyll-a production natural waters, so much attention in the literature has been focused on former. However, when the TN:TP ratio (gravimetric) in lake water falls low values (e.g. TN:TP<12, Dillon & Rigler 1974), nitrogen concentration may become more critical, confusing the phosphorus-chlorophyll relations Accordingly, some authors (e.g. Smith 1982) have suggested the use of multiple regression models, incorporating both TN and TP, to account for variability in the TN:TP ratio. Table 8 gives the results of simple and multiple regression models predicting, from a variety of parameters, both surface chlorophyll concentrations and mean chlorophyll concentration of euphotic zone (B). The outstanding conclusion is that turbidity has a major influence on the chlorophyll levels attained. When all data from billabongs is included in the analysis then the predictive power for an nutrient parameter is poor. However, this is improved impressively if turbid waters are excluded from the analysis. Another way of taking acc of this "turbidity effect" is to include turbidity data, or its highly correlated stablemate Z_{eu} (Walker, Kirk & Tyler 1983), in the analysis. Prediction is thus improved for B only, but this procedure is not as effective as the exclusion of turbid waters. The unavoidable conclusion

Table 8 Efficacy of simple and multiple regression models for the prediction of surface and mean euphotic chlorophyll concentrations for Alligator Rivers billabongs. Numbers in brackets indicate number of data sets for each billabong. Billabong code names as in Table 1.

Dependent Variable	Independent Variable	All waters			Non-turbid waters		
		N	Billabongs	% variance explained	N	Billabongs	% variance explained
Surface biomass (Chl.a mg m^{-3})	PO_4-P	50	BO(1),GT(4),GU(3), GO(3),MG(4),IS(9), JA(2),LC(5),JB(4), NK(3),KK(7),NO(3), NM(2).	24	34	BO(1),GU(1),MG(3), IS(9),JA(1),LC(5), JB(2),KK(7),NO(3), NM(2).	31
	TP			14*			61
	IN			-			16
	TN			7*			16
	TP,TN			15			61
	TP,TN,Turb.			16			
Mean euphotic zone biomass (Chl.a mg m^{-3})	PO_4-P	18	IS(9), LC(5),JB(4).	28	15	IS(9),LC(5),JB(1).	40
	TP			29			67
	IN			8			26
	TN			15			31
	TP,TN			30			69
	TP,TN,Z_{eu}			36			
	TP,TN,Z_{eu},Turb.			46			

*Failed one of four tests for normality, but result included for comparison.

that the prediction of biomass from nutrient data, a technique widely used as a management tool in the abatement of eutrophication (Nicholls and Dillon 1978; Smith 1982; Smith & Shapiro 1980), is not at present possible for turbid waters of the Alligator Rivers Region, and it appears that the level of chlorophyll-a in billabong waters represents an integration of both the nutrient regime and the light climate. For clear billabongs however, or for other billabongs before they become turbid, TP is a reasonable predictor of biomass, which is not improved by inclusion of TN. This indicates that for the waters included in the analysis, phosphorus, n nitrogen, was the limiting nutrient. The inorganic forms of P and N offer no advantage over the use of TN and TP in this analysis.

Previously published phosphorus-chlorophyll relationships are compar with those obtained for non-turbid billabongs in Table 9. It appears th the predictive capability of the equations developed for the billabongs compares somewhat unfavourably with those determined elsewhere. There at least two major reasons for this:-

1) Of all the relationships reported in Table 9, only that for Lake Burragorang and the Magela billabongs has been determined from individual observations of both chlorophyll and phosphorus (Table 10 Usually, mean chlorophyll values for the growing season, stratifica period, summer, or the year are employed, with phosphorus concentr at the overturn or the winter maximum, or the mean value for eithe the circulation period or the whole year. By using mean values, i to be expected that a significant portion of the "scatter" (noise) in the phosphorus-chlorophyll relationship is removed, as fluctuatio evident from individual observations are integrated. Thus the mean value is less sensitive to short-term variation, and no doubt a more reliable indicator of the true situation. However, in most M billabongs, where chlorophyll and phosphorus concentrations may va over an order of magnitude during the Dry ("growing season"), littl meaning can be attached to an average value.

Table 9 Comparison of regression models linking chlorophyll-a with total phosphorus from the Alligator Rivers Region with those for other parts of the world.

Number	Data Set	Equation	r^2	Reference
1	31 Japanese lakes	$\log(\mathrm{Chl})=1583 \log(\mathrm{TP})-1.134$	0.95	Sakamoto (1966)
2	19 Ontario lakes + L. Washington and others worldwide	$\log(\mathrm{Chl})=1.45 \log(\mathrm{TP})-1.14$	0.90	Dillon & Rigler (1974)
3	U.S. Lakes	$\log(\mathrm{Chl})=1.18 \log(\mathrm{TP})-0.764$		Ref. in Nicholls & Dillon (1978)
4	4 Iowa lakes (3 yr)	$\log(\mathrm{Chl})=1.41 \log(\mathrm{TP})+3.24$		Jones & Bachmann (1976)
5	Turbid lakes of mid-West U.S.	$\log(\mathrm{Chl})=1.15 \log(\mathrm{TP})+0.66$	0.70	Hoyer & Jones (198)
6	143 lakes worldwide	$\log(\mathrm{Chl})=1.46 \log(\mathrm{TP})-1.09$	0.80	Jones & Bachmann (1976)
7	IBP lakes worldwide	$\log(\mathrm{Chl})=1.213 \log(\mathrm{TP})-0.848$	0.77	Schindler (1978)
8	L. Washington, U.S.	$\log(\mathrm{Chl})=1.20 \log(\mathrm{TP})-0.55$	0.94	Smith & Shapiro (1980)
9	Cline's Pond, U.S.	$\log(\mathrm{Chl})=0.96 \log(\mathrm{TP})-0.04$	0.92	Smith & Shapiro (1980)
10	Twin L., U.S.	$\log(\mathrm{Chl})=2.23 \log(\mathrm{TP})-2.41$	0.93	Smith & Shapiro (1980)
11	L. Green, U.S.	$\log(\mathrm{Chl})=2.17 \log(\mathrm{TP})-2.25$	0.99	Smith & Shapiro (1980)
12	Loch Leven, Scotland	$\log(\mathrm{Chl})=0.98 \log(\mathrm{TP})+0.01$	0.99	Smith & Shapiro (1980)
13	L. Boren, Sweden	$\log(\mathrm{Chl})=0.38 \log(\mathrm{TP})+0.32$	0.98	Smith & Shapiro (1980)
14	L. Norrviken, Sweden	$\log(\mathrm{Chl})=0.58 \log(\mathrm{TP})+0.58$	0.51	Smith & Shapiro (1980)
15	L. Burragorang, N.S.W.	$\log(\mathrm{Chl})=1.45 \log(\mathrm{TP})-0.75$	0.63	Ferris & Tyler (unpubl.)
	A.A.R. billabongs (<10 N.T.U.)			
16	a) surface	$\log(\mathrm{Chl})=1.41 \log(\mathrm{TP})-1.10$	0.61	This report
17	b) euphotic zone	$\log(\mathrm{Chl})=1.538 \log(\mathrm{TP})-1.28$	0.67	This report

Table 10 The sampling depths and periods for the data sets used in Table 9.

Number	Chlorophyll		Phosphorus	
	Period	Depth	Period	Depth
1	summer aug?	euphotic?	overturn	surface & deeper
2	summer aug.	euphotic	spring overturn	whole lake vol.wt.
3	mean annual?	?	median annual	?
4	?	?	?	?
5				
6.	?	?	?	?
7.	mean annual	?	mean annual	?
8.	mean growing season	surface?	mean growing season	surface?
9.	mean growing season	surface?	mean growing season	surface?
10.	mean growing season	surface?	mean growing season	surface?
11.	mean growing season	surface?	mean growing season	surface?
12.	mean growing season	surface?	mean growing season	surface?
13.	mean growing season	surface?	mean growing season	surface?
14.	mean growing season	surface?	mean growing season	surface?
15.	yearly maxima	surface	mean annual	surface
16.	dry season	surface	dry season	surface
17.	dry season	euphotic	dry season	surface

2) Horizontal and vertical heterogeneity of phytoplankton in the billabongs can be vast, a severe handicap in any attempt to characterise the billabong condition at any one time by a single sample. It is interesting to note that the use of integrated euphotic zone chlorophyll values, rather than surface values, did not appear to reduce the scatter of the points (Table 9). The extent of chemical heterogeneity in the billabongs is unknown.

Despite these difficulties, the equations arrived at for groups of lakes are all very similar, signifying the robustness of the phosphorus-chlorophyll relationship. For individual lakes the performance of models is considerably better (Table 7) and the equations indicate that every lake has its individual character (Smith & Shapiro 1980). It is likely, then, that models developed for individual billabongs would have improved performance.

Smith (1982) has indicated that significant improvement in the prediction of chlorophyll may be afforded by consideration of TN as well as TP, especially in those waters where the TN:TP ratio indicates nitrogen may be limiting (TN:TP<12). He found that using a multiple regression of TP and TN (which accounted for variations in this ratio) on chlorophyll significantly improved predictive capability for 127 north latitude lakes as compared to the simple regression equation of Dillon & Rigler (1974). However, for the Magela billabongs the multiple regression model offered no advantage over that of simple regression.

6.2 The prediction of production from limited *in situ* incubation data

The accurate estimation of primary production in lakes displaying considerable heterogeneity of phytoplankton populations is a time-consuming and difficult exercise. Incubation at one site may be totally insufficient to monitor accurately events throughout the lake, and it is therefore imperative to develop simpler procedures allowing the rapid assaying of production rates at a number of sites. The theoretical treatments of the light-primary production relationship by Talling (1957) and Vollenweider (1965, 1969, 1970) (see Section 2) provide a framework from which such procedures can be derived (cf. Megard 1972).

Mean volumetric production (A) is determined from areal production (ΣA) by the relation,

$$A = \frac{\Sigma A}{z_{eu}}$$

and since (Walker, Kirk & Tyler 1983)

$$z_{eu} = \frac{4.61}{k},$$

by substitution and rearrangement of equation (3) in Section 2, an equation relating A and A_{opt} is produced, i.e.,

$$A = \frac{F.A_{opt}}{4.61} = 0.22\ F.A_{opt} \qquad \text{..........} \quad (1)$$

Here, A_{max} is used as an approximation of A_{opt}, i.e.,

$$A = 0.22\ F.A_{max} \qquad \text{.........} \quad (2)$$

where the value of F is dependent upon prevailing meteorological and limnological conditions (Fee 1973). Thus in a vertically-mixed euphotic zone (an assumption upon which the production equations of Talling and colleagues are based - Section 2) ΣA and A should be linearly related to A_{max}.

Despite the facts that only net, not gross, productivity results were gained, that z_{eu} was deduced from $z_{s.d.}$ rather than measured, and that vertical heterogeneity of phytoplankton is common in these waters, overall there was a good correlation between total production and A_{max}, with the highest correlations with A rather than ΣA (Table 11). A strong correlation was evident if waters with turbidities exceeding 10 N.T.U. were excluded from the analysis.

Since A_{opt} can be expressed as the product of chlorophyll concentr in the euphotic zone (B) and the optimal photosynthetic capacity (P_{opt}),

Table 11 The efficacy of prediction of mean production in the euphotic zone (A) by various parameters derived from Talling's (1957) model. Numbers in brackets indicate numbers of data sets for each billabong. Billabong code names as in Table 1.

Dependent Variable	Independent Variable	All waters					Non-turbid waters				
		N	Billabongs	Model			N	Billabongs	Model		
				X;Y	Ln X;Y	Ln (X;Y)			X;Y	Ln X;Y	Ln (X;Y)
A	A_{max}	69	GU(4),GO(7),IS(21), JA(1),LC(17),JB(13), RL(6)	-	-	81	47	GU(2),IS(20),LC(14), JB(5),RL(6)	-	-	85
	B	18	IS(9),LC(5),JB(4).	-	-	71	15	IS(9),LC(5),JB(1)	-	-	72
	B_{opt}	18	IS(9),LC(5),JB(4).	-	-	89	15	IS(9),LC(5),JB(1)	91	83	89
ΣA	A_{max}	69	GU(4),GO(7),IS(21), JA(1),LC(17),JB(13), RL(6).	-	-	53*	47	GU(2),IS(20),LC(14), JB(5),RL(6).	-	-	81
	B	18	IS(9),LC(5),JB(4).	-	58	60	15	IS(9),LC(5),JB(1).	44	59	65
	$B.P_{opt}$	18	IS(9),LC(5),JB(4).	72	62	-	15	IS(9),LC(5),JB(4).	81	78	84

* Failed one of four tests for normality, but result included for comparison.

equation (3) of Section 2 now becomes

$$\Sigma A = \frac{F.B.P_{opt}}{k} \qquad \text{..............} \; (3)$$

or, equation (2) of this section becomes

$$A = 0.22\ F.B.P_{opt} \qquad \text{..............} \; (4)$$

and we expect, therefore, a significant relationship between production a chlorophyll, which is confirmed by regression analysis (Table 11). Again the correlation is greatest for volumetric production.

The high correlation between A and $B.P_{opt}$ (Table 11) offers excellent opportunities for a simplified incubation technique for productivity measurement. Using such a technique, only a limited number of incubation just sufficient to determine P_{opt}, are necessary at any one site in a billabong. Chlorophyll content (B) could be ascertained from a simple Lu tube (hosepipe) sample spanning the euphotic zone. With this reduced wo load it would be possible to survey several sites in any one billabong, taking account of spatial heterogeneity.

6.3 The prediction of production from multiple regression models

Many limnologists have utilized correlation and regression analysis to identify those variables most useful in estimating production, and to formulate appropriate empirical models for its prediction (e.g. Schindler 1971; Smith 1979). The analyses of Brylinsky (1980) and Schin (1978) are particularly noteworthy for extensive treatment of global data for freshwater phytoplankton production. Factors which have been identi as being of value in such empirical models are retention time, surface insolation, euphotic depth, nutrient availability, biomass, mean depth another morphometric statistic, water temperature, and a measure of the degree of mixing (e.g. thermocline depth).

In the present analysis, both volumetric (A) and areal production (are considered. The full analysis for volumetric production is reported Table 12, whilst the performance of comparable equations predicting A an

Table 12 The efficacy of prediction of mean volumetric production (A) in the euphotic zone from simple and multiple regression analysis. Numbers in brackets indicate numbers of data sets for each billabong. Billabong code names as in Table 1.

Dependent Variable	Independent Variable	All waters					Non-turbid waters				
		N	Billabongs	Model			N	Billabongs	Model		
				X;Y	Ln X;Y	Ln (X;Y)			X;Y	Ln X;Y	Ln (X;Y)
A	^{o}C	69	GU(4),GO(7),IS(21), JA(1),LC(17),JB(13), RL(6)	-	-	0.3*	47	GU(2),IS(20),LC(14), JB(5),RL(6)	6*	6*	0.2*
	Z_{eu}	69	GU(4),GO(7),IS(21), JA(1),LC(17),JB(13).	-	-	0.5	47	GU(2),IS(20),LC(14), JB(5),RL(6).	-	-	1.0
	I	18	IS(9),LC(5),JB(4).	-	-	26	15	IS(9),LC(5),JB(1).	-	-	23
	PO_4-P	26	IS(13),LC(7),JB(6).	55*	-	-	20	IS(13),LC(6),JB(1).	-	71	-
	TP	26	IS(13),LC(7),JB(6).	-	-	21	20	IS(13),LC(6),JB(1).	58	-	60
	IN	26	IS(13),LC(7),JB(6).	-	21	20	20	IS(13),LC(6),JB(1).	45	-	34
	TN	26	IS(13),LC(7),JB(6).	-	-	27	20	IS(13),LC(6),JB(1).	-	-	55
	I,PO_4-P	18	IS(9),LC(5),JB(4).	66	52	48	15	IS(9),LC(5),JB(1).	78	71	58
	I,PO_4-P,TN	18	IS(9),LC(5),JB(4).	69	53	49	15	IS(9),LC(5),JB(1).	79	80	63
	I,PO_4-P,TN, Turb.	18	IS(9),LC(5),JB(4).	78	62	51					
	B,I	18	IS(9),LC(5),JB(4).	71	-	85	15	IS(9),LC(5),JB(1).	71	-	85
	B,PO_4-P	18	IS(9),LC(5),JB(4).	-	-	79	15	IS(9),LC(5),JB(1).	-	80	72
	B,I,PO_4-P,TN	18	IS(9),LC(5),JB(4).	-	-	90	15	IS(9),LC(5),JB(1).	-	-	90

* Failed one of four tests for normality, but results included for comparison.

ΣA are contrasted in Table 13. Both linear and non-linear models have been tested.*

A strong correlation between volumetric production (A) and the concentration of chlorophyll in the euphotic zone has been previously noted (Section 6.2) for the Magela billabongs. In view of the tie between chlorophyll and nutrients (Section 6.1), it is to be expected that primary production is strongly correlated with nutrient availability. Considering only nutrient parameters (Table 12) predictive ability from simple regression is not good but multiple regression of surface insolation and nutrient concentrations improves matters. Again, the presence of turbidity confuses the issue, and when turbid waters are excluded from the analysis further improvement is apparent. The alternative of including turbidity data in the regression models was of similar assistance. Neither euphotic depth nor water temperature had effect on volumetric production. This is perhaps not surprising since Smith (1979) has indicated that A should be unresponsive to Z_{eu}, whilst Brylinsky (1980) maintains that water temperatur has little effect on adapted communities.

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* Three of the parameters mentioned above have not been included in the analysis - retention time, mean depth and mixing type. Retention time is considered to be the cardinal seasonal variable influencing primary production. During the Wet, the riverine nature of the billabongs with l throughflow, prevents the development of substantial phytoplankton stocks. The scant data for this time indicate low production. Following cessat of surface flow early in the Dry, the billabongs become endorrheic and th idea of retention time is virtually meaningless. Most data in this repo are for the Dry, and it is prediction of production during that period t is of concern here. Mean depth and mixing type could not be quantified. Sufficient bathymetric data are presently not available for the billabon especially considering the marked fluctuations in water level occurring during the year, whilst the extremely complex stratification behaviour (s Walker, Waterhouse and Tyler 1983) renders the computation of any measur of mixing near impossible.

Table 13 Comparison of multiple regression models for prediction of mean volumetric production (A) of the euphotic zone and areal production (ΣA).

Dependent variable	Case	Independent variable	All turbidities Coefficient	All turbidities r^2	All turbidities n	Turbidities <10 N.T.U. Coefficient	Turbidities <10 N.T.U. r^2	Turbidities <10 N.T.U. n
A	1	y-intercept	27.439	0.66	18	45.456	0.78	15
		I	4.086			-0.210		
		PO_4-P	10.271			12.129		
ln A	2	y-intercept	-1.164	0.85	18	-1.375	0.85	15
		ln I	2.518			2.601		
		ln B	0.654			0.669		
ln A	3	y-intercept	-5.221	0.90	18	-6.330	0.90	15
		ln I	4.023			4.790		
		ln B	0.758			0.831		
		ln PO_4-P	-0.440			-0.611		
		ln TN	0.338			0.330		
ΣA	1a	y-intercept	237.928	0.61	18	612.973	0.59	15
		I	26.282			-17.686		
		PO_4-P	16.209			16.029		
		Z_{eu}	-40.938			-91.017		
		TB	-8.447			-3.506		
ln ΣA	2a	y-intercept	-0.404	0.81	18	0.929	0.78	15
		ln I	2.219			2.089		
		ln B	0.629			0.496		
		ln Z_{eu}	0.788					
ln ΣA	3a	y-intercept	-4.734	0.87	18	-4.432	0.85	15
		ln I	4.676			5.422		
		ln B	0.790			0.778		
		ln PO_4-P	-0.518			-0.701		
		[illegible]	[illegible]			0.051		

The inclusion of a biotic index, biomass (as chlorophyll-a), in multiple regression models generally improved their effectiveness (Table 12). In addition it appears that it extends the applicability of the models to turbid waters* indicating the ability of this biological index to integrate fluctuations in the underwater light climate. That the model involving only biomass and surface insolation is only marginally poorer than one including, additionally, nutrients indicates that biomass also represents an integration of nutrient conditions.

The model employing biomass, insolation and nutrients has comparable predictivity to the model derived (Section 6.2) from *in situ* incubations. Thus, it appears that the use of time-consuming incubations offers no advantage in estimating volumetric production over more easily acquired limnological data.

Similar predictive models, developed for areal production (ΣA)**, are contrasted with those for volumetric production (A) in Table 13. When all waters are considered, ΣA can be predicted as accurately as A provided turbidity and Z_{eu} data are included. For non-turbid waters equations for ΣA are not as effective as for A, irrespective of whether Z_{eu} and turbidity data are used. Certainly, the contention of Smith (1979) that A is more responsive to changes in trophic conditions than ΣA, appears justified for the Magela billabongs.

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* Few turbid waters are included in this analysis (3 out of 18), yet these few have significant effect on all regression models which exclude biomass. Those models which include biomass, apparently suffer no loss in predictability when turbid waters are considered as well!

** Of course, there may be little point in calculating ΣA from multiple regressions since $\Sigma A = A.Z_{eu}$.

5. DISCUSSION

The traditional way of measuring primary production in the aquatic environment is the tedious and time-consuming method involving incubation of water samples in bottles suspended at various depths in the water column. For a homogeneous water column, the empirical models of Talling (1957), and others, may be used, or adapted, to reduce the number of incubations to a mimnimum (e.g. Megard 1972). Thus, in this study, the product of mean chlorophyll concentration for the euphotic zone (B) and the maximum photosynthetic capacity (P_{opt}) accounted for more than 90% of the variability in production (Table 11). This indicates that the vertical heterogeneity in phytoplankton distribution prevalent in some billabongs (Kessell & Tyler 1983) is insufficient to invalidate Talling's model for a single site. However, the considerable horizontal and temporal variability in plankton distribution, also characteristic of most billabongs, sounds a note of caution on extrapolation of events at a single site to the whole billabong (Ganf 1975). To encompass this variability, incubations at several to many sites in each billabong would be necessary, with obvious logistical implications. For this reason, empirical relationships were sought, linking production with a few, more-easily determined parameters.

Previous studies (Brylinsky 1980; Fee 1973; Schindler 1971, 1978; Smith 1979), on global or local scale, investigating a variety of parameters, had indicated both the validity of such a notion and also the variables which could be gainfully employed. Following this approach, multiple regression analysis showed that a few vicarious measurements will give an excellent estimate of phytoplanktonic production in Magela Creek billabongs during the Dry*, without the need for *in situ* incubations.

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* The special circumstances of the Wet - the high flushing rate and rapid export of phytoplankton - render any production measurements of limited relevance for a billabong's production budget. This, and the increased logistic problems militated against a concerted programme of production measurement for the Wet.

Thus, the multiple regression model, employing only mean euphotic chlorophyll concentrations, surface nutrient concentrations, and incident solar radiation (PAR), gives an excellent estimate of mean volumetric production (A) for the euphotic zone ($r^2 = 0.90$, Tables 12 and 13). Addition of euphotic depth and turbidity data to the model allows predicti of areal production with equal accuracy (Table 11). Multiple regression analysis also identifies the underwater light climate and nutrient availability as the two cardinal factors controlling phytoplanktonic production in the Magela Creek System.

Solar radiation (as light) and nutrient supplies are widely recognize in this role in both temperate and tropical aquatic environments (Brylinsky 1980; Lewis 1974). However, Lewis claims that they operate in different ways in the two latitudinal zones. In the temperate zone, in general, whil solar radiation increases markedly in summer, nutrient loading decreases as inflows dwindle. This trend will be exacerbated in the many lakes whic stratify where sedimentation may cause severe nutrient depletion of the euphotic regions. Thus, for many temperate lakes, optimal incident light conditions coincide with the least favourable nutrient concentrations. Lewis contends that in tropical lakes both nutrient supply and insolatio are distributed more equitably over the year, so that production is like to be regulated more by non-seasonal events (see also Ganf 1975). Thus, he maintains, in tropical waters maximum supply rates for light and nutr are more likely to be in phase.

Lewis' model for tropical lakes is quite inappropriate for most billabongs of the Magela system where pronounced variations in nutrient concentrations and light availability, and consequently in primary produc have a marked seasonal face, dictated by the distinctive hydrological regime. Stratification is rarely a factor to be considered in these billabongs (Walker, Waterhouse & Tyler 1983). During the Wet, for all billabongs, a combination of relatively low nutrient concentrations and flushing rates prevent establishment of substantial standing stocks of phytoplankton. The response of the billabongs to the stagnation of the Dry is anything but uniform, varying principally with light climate (Walke Kirk & Tyler 1983) and nutrient chemistry (Walker & Tyler 1983).

Soon after cessation of significant streamflow at the Wet/Dry interchange (April-May), all billabongs are at their most transparent, with euphotic zones extending 3 metres or more from the surface. However, nutrient concentrations are comparatively low, as are phytoplankton densities, and productivities are consequently low.

The channel billabongs (e.g. Island, Mudginberri), with low surface area to volume ratios and sandy substrates, unlike most other billabongs experience neither strong increases in nutrient levels from concentratio over the Dry, nor much change in triptonic turbidity and, consequently, transparency. Thus sporadic fluctuations in productivity cannot be attributed generally to seasonal events, and these billabongs at least, the Lewis model, where non-seasonal events regulating resource supply as precedence.

In most other billabongs nutrient levels rise markedly and continuo as evaporative concentration proceeds throughout the Dry. Buffalo and waterfowl congregating at these billabongs further elevate nutrient leve In response, phytoplankton stocks rise and productivity increases. Howe by the mid-Dry, in all backflow, and most floodplain billabongs, though nutrient concentrations continue to rise, the increase in chlorophyll levels and in productivity is arrested when falling water levels permit induced resuspension of fine sediments.

It has been shown earlier (Walker & Tyler 1983) that in the backflo and floodplain billabongs, much of the massive increase in nutrient concentrations towards the end of the Dry is contributed by internal loa from the high triptonic turbidity, which characterises this period. It might be supposed that the failure of both biomass and production levels reach those predicted for such nutrient concentrations, by well-tried models, stems from inability of the algae to utilize the nutrients adsorbed to the suspended load. However a number of studies (Goltermann 19 Goltermann *et al.* 1969; Healy & McColl 1974) indicate that this is unlikel since plankton can utilize adsorbed nutrients. We consider that the inhibitory effect of tripton comes from the restriction it places on anoth resource - light.

Though incident radiation is, at the mid-Dry, climbing towards its zenith the onset of a heavy load of triptonic turbidity, so characterist of these billabongs, though adding substantially to the nutrient load, causes severe deterioration of the underwater light field at this time. Thus the adverse optical conditions prevent phytoplanktonic productiviti attaining the levels they should reach on the basis of available nutrien i.e., contrary to Lewis' notion, optimal light and optimal nutrient conditions are out of phase, a circumstance with some parallels to that temperate experience (see above). In contrast, those waters which experience considerable rises in nutrient concentrations over the Dry, a more moderate rise in triptonic turbidity (e.g. Leichhardt), exhibit increasing productivities for much of the Dry, to rates exceeding 500 $mgO_2m^{-3}hr^{-1}$. In this case, deterioration of the light climate is not nearly as marked as in the backflow and other floodplain billabongs, al the phytoplankton to capitalise on the optimal nutrient conditions.

The overwhelming role of triptonic turbidity in specifying a depau underwater light field has been amply demonstrated (Walker, Kirk & Tyle 1983). That this limit on availability of solar energy exerts powerful influence on phytoplanktonic productivity is well recognised (Brylinsky Murphy 1967; Schmidt 1973), and is emphatically demonstrated statistica for the Magela system. It is the underwater light field, not the incide light field, which is the cardinal regulator of solar availability. Thu it appears that the magnitude of primary production during the Dry in th Magela billabongs is controlled principally by interactions between ligh and nutrient conditions. The way in which these two factors are determined by complex environmental interactions is shown by the hierarchical models (Fig. 9,10) developed for the Magela system.

Ecological investigations in the Alligator Rivers Region were instigated on the premise that the aquatic ecosystem was to be protected from deleterious consequences of uranium mining and associated activities. The ultimate objective of such studies was the design of a monitoring programme to allow early detection, and therefore minimisation, of any harmful effects. Two principal effluents need separate consideration - heavy metals or other toxic wastes in soluble or particulate form from the mining site, and the key nutrients of eutrophication, in sewage from urban development in the area. Hart (1980) indicates that sewage effluent will contribute about 25% of the phosphorus transported annually by the Magela past Jabiru.

The long term monitoring of phytoplanktonic productivity has an obvious part to play in the environmental programme. First, there is the possibility of detecting inhibition of plankton populations, by harmful effluents, from the depression of productivity. Second, the measurement of productivity in the long term, and even in the short term, has been a principal aid and preferred method in the detection and abatement of cultural eutrophication (Smith 1979).

The deleterious effects of heavy metals on natural phytoplankton assemblages have been well documented (e.g. Rai *et al.* 1981), and the use of natural communities as biological integrators, revealing sublethal effects of low level pollution, has been recommended (see Whitton (1982) for a review). A number of large scale experiments have demonstrated that heavy metals bring about reductions in species numbers, depressed photosynthetic activity, and major changes in community structure, with major shifts towards metal resistant species even at concentrations of metals within legally accepted limits (Gächter 1979; Gächter & Mares 1979).

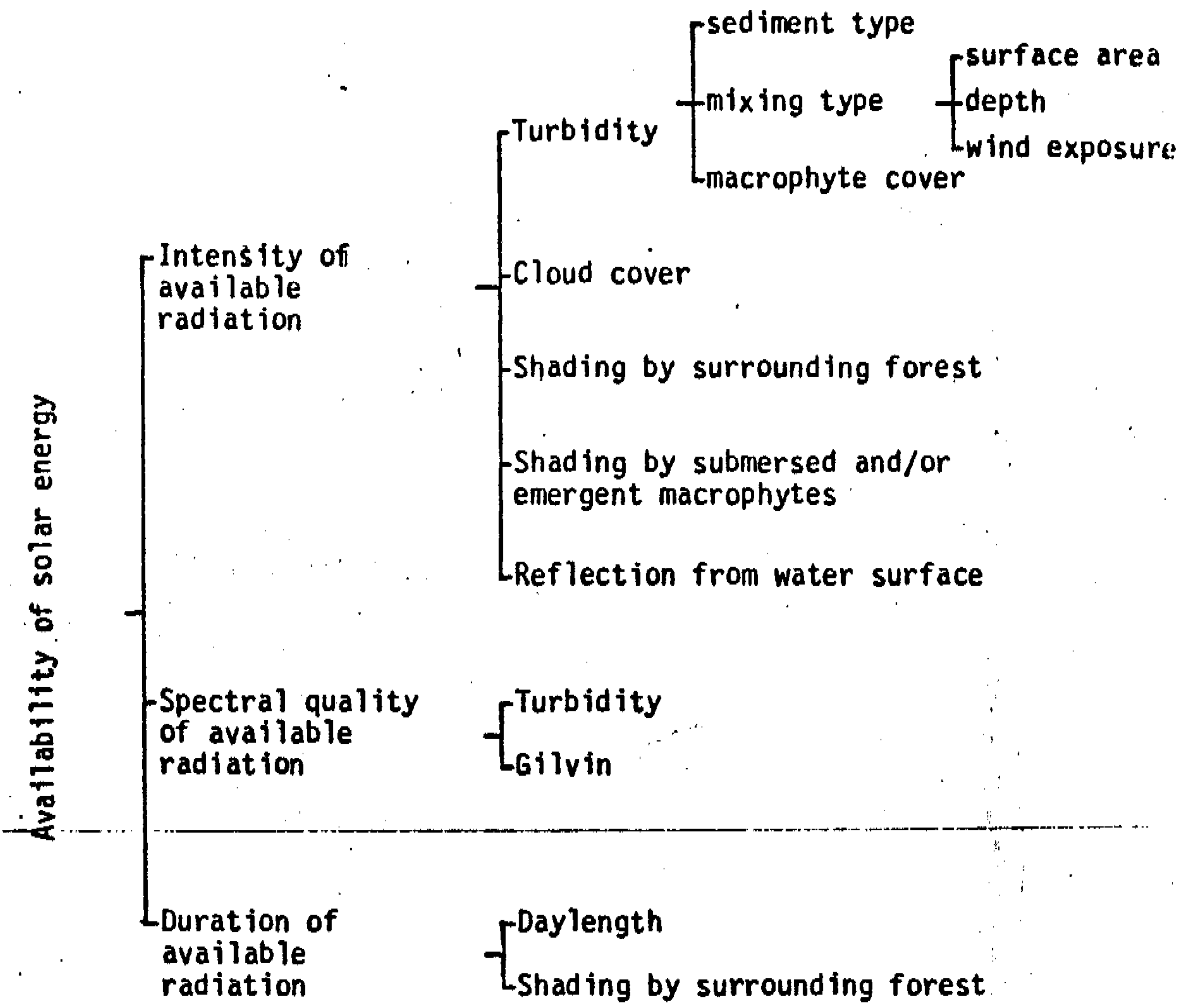

Fig. ~~10~~ 9: A Heirarchical model~~s~~ depicting the environmental interactions determining the availability of underwater solar energy ~~and nutrients~~ on billabongs of the Alligator Rivers Region. (Adapted from Brylinsky (1980)).

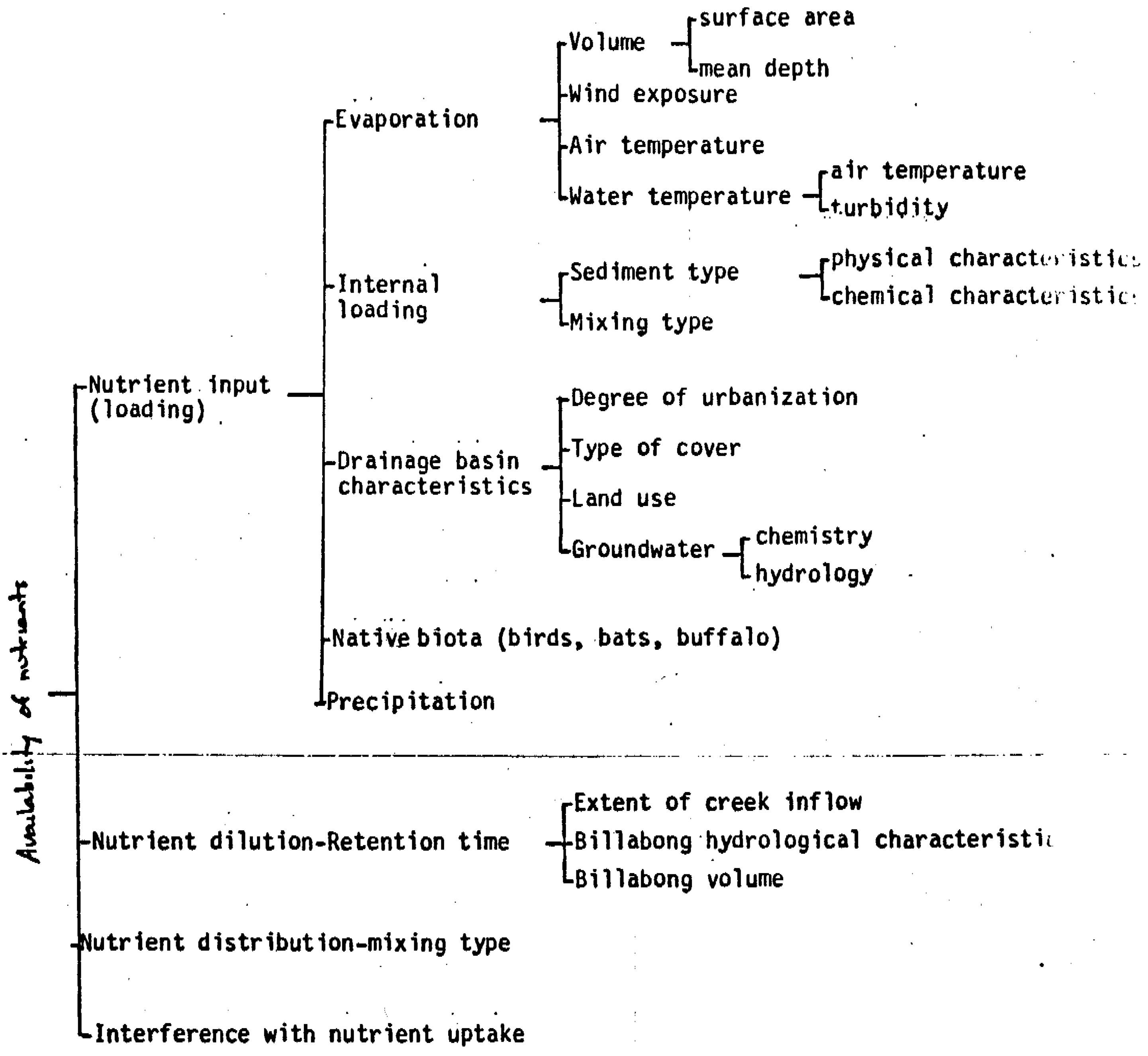

Fig 10: A Hierarchical model depicting the environmental interacti determining the availability of nutrients for billabongs of the Alligator Rivers Region. (Adapted from Brylinsky (

Preliminary studies (Kessell & Tyler 1983b) have shown that algae of the Magela Creek System are sensitive to heavy metal contamination, but recov is rapid (Hart, Jones, Bek & Kessell 1982). Any programme proposing to u productivity measurements to detect low-level metal pollution would require considerable investigation and development.

Over the last several decades the world-wide problem of eutrophicati has received massive attention. The gross impairment of water utility in cases of calamitous eutrophication has been readily apparent, but detecti of slower, insidious eutrophication, recognized by subtle but progressive changes in phytoplankton community structure or numbers, or in chlorophyl nutrients or productivity, has in all cases resulted from long term monitoring (OECD, Rohlich). It is here that we see a role for productivi monitoring in selected Magela billabongs, and for this purpose recommend mean volumetric productivity (A) for the euphotic zone as the appropriate measure (see Smith 1979). With little extra effort, areal productivity (can also be calculated. Since the primary productivity of a water body* sets the scale for secondary and tertiary production, areal productivity the starting point for other ecological investigations and for ecological modelling.

On a number of grounds, Hart (1980) has identified the billabongs, channels, and floodplains of the Mudginberri Corridor as the areas most likely to suffer deterioration from emissions of toxins or nutrients to Magela Creek at Jabiru. We concur with his findings, and recognize the critical billabongs of the Magela as those of the Corridor. First, bein immediately downstream of the town and mine, they would feel the full fo of nutrient or toxin emissions. Second, the dense macrophyte beds of th Corridor act as a filter for dissolved and suspended materials (Hart 198

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* Phytoplankton is the major component of primary production in many waterbodies but macrophytes become important in shallow lakes. They are not considered in this report.

Hart, Jones and Bek 1982)as the flood waters of the Wet, funneled down confined channels, slacken as they burst upon a wide expanse of inundated paperbark forest, which they penetrate by myriad channels to reach the main Magela floodplain. Thus much of the pollutant or nutrient load is likely to be retained and recycled within the Corridor.

The effects of nutrient or toxicant releases are unlikely to be manifested in the Corridor billabongs during the high flow period of the Wet. Concern mainly stems from the possibility of recycled contaminants finding their way to them during low flow and stagnant periods (the Dry). Quite apart from being among the first in line, the Corridor billabongs, by their nature, are particularly sensitive to both classes of contaminant. First, they retain transparent waters of relatively low nutrient status throughout the Dry, so that they have a high potential for eutrophication. Experience with floodplain billabongs indicates that dense phytoplankton populations and high production (both areal and volumetric) attends the increase in nutrient levels during each Dry, whenever and wherever the constraints imposed by suspended sediment loads on light penetration are not prohibitive. Of the Magela billabongs, those of the Corridor are highly prized for their sweet, clear waters, so that maintenance of water quality should have high priority, and long term eutrophication avoided. Second, the Corridor billabongs lack the heavy tripton loads which in other billabongs can significantly absorb heavy metal contaminants (Hart *et al.* 1981).

Thus, because of their high value and their vulnerability, the Corridor billabongs assume a critical position and warrant the closest attention. One sure watchdog on their condition would be the long term monitoring of phytoplanktonic production.

It is therefore recommended that a program to measure long term changes in biomass and production in the billabongs of the Mudginberri Corridor be instituted, based upon the simplified methods presented in this report. Regression analysis has shown how simply a good estimate of volumetric production (A) can be obtained. Euphotic depth (Z_{eu}) can be obtained simply with a Secchi disc ($Z_{eu} = 1.39\ Z_{s.d.} + 0.64$ - Walker, Kirk & Tyler 1983). From a simple Lund tube (a hosepipe!) sample spanning the euphotic zone mean chlorophyll and mean nutrient concentration can be analyzed, immediately furnishing two measures of trophic status. Addition of data from a quantameter then allows calculation of a third integrative measure of trophic status, volumetric production. Refining of the predicti equations, tailoring them to these specific billabongs, would be necessary, with an attempt to relate the various limnological parameters to daily production rather than to the hourly measure employed here. The number of sites within each billabong necessary to indicate whole billabong biomass production, together with sampling frequency, would need to be examined by further, limited, fieldwork and statistical analysis. However, the work presented here forms the basis for a rapid, pertinent and effective technique for monitoring perturbation of the aquatic environment in the Alligator Rivers Region.

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Appendix Table 1 : Some parameters of primary productivity in Bowerbird billabong (Asterisk indicates that Z_{eu} exceeded the depth of the water column).

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
25/7/78*	>3·0				320			260	1·5
20/10/78*	3·2	5·1			234			110	1·0
7/11/78	1·0	2·0		74	148	0·5	2·1	70	0·5
27/7/79*	3·6	5·6	1·1		178			100	2·5
26/5/80*	>3·6		0·7		339			200	1·0
23/7/80*			1·0		481			240	1·5
16/9/80*	>3·4		1·8		246			130	1·0
2/4/86		0			0			0	

Appendix Table 2 : Some parameters of primary productivity in Georgetown billabong.
(Asterisk indicates that Zeu exceeded depth of the water column).

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
15/7/78	0·1	0·8		25	20	3·5		70	0·1
4/10/78*	0·02	0·7			1			10	0·1
15/11/78*	0·02	0·7			0			0	

Appendix Table 3 : Some parameters of primary productivity in Gulungul billabong.
(Asterisk indicates that Z_{eu} exceeded the depth of the water column).

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	ZA_{max} (m)
5/6/79	0·85	1·8	4·8	88	160	1·2	0·8	190	0·3
9/7/79*					186			360	0·1
30/7/79	0·2	0·9	52	160	147	5·2	0·2	770	0·1
21/3/80*	0·8	1·8	9·8		72			70	0·7
16/4/80*	1·3	2·4	5·2		58			60	0·5
21/5/80*	0·9	1·9	4·3		137			160	0·5
12/6/80*	0·75	1·7	4·7		101			190	0·1
5/10/80*	0·09	0·8	75		81			510	0·1
17/2/81	0·7	1·6	16	21	33	1·8	0·5	60	0·3
17/3/81	1·3	2·4	6·6	39	95	1·2	0·9	110	0·5
16/4/81*	1·4	2·6	5·9		110			110	0·3
21/5/81*	0·9	1·9	8·0		308			370	0·5
21/6/81*					309			310	0·5
8/8/81*	0·8	1·8			241			450	0·3

Appendix Table 4 : Some parameters of primary productivity in Goanna billabong (Asterisk indicates that Zeu exceeded the depth of the water column).

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
10/7/78	0·5	1·3		199	267	1·7	0·6	460	0·4
2/10/78	0·4	1·2		104	125	3·0	0·3	380	0·1
11/11/78*	0·3	1·1			223			870	0·1
23/6/79	0·3[illegible]	1·1	58	51	58	4·7	0·2	270	0·1
10/8/79	0·15	0·9	130	58	49	6·5	0·2	320	0·2
12/10/79			240		158	9·4	0·1	1490	0·1
12/3/80	0·25	1·0	34	21	21	2·4	0·4	50	0·4
10/4/80	0·3	1·1	34	90	95	1·7	0·6	160	0·2
20/5/80	0·2	0·9	57	72	66	2·7	0·4	180	0·1
12/6/80	0·3	1·1	53	57	60	2·3	0·4	140	0·2

Appendix Table 5 : Some parameters of primary productivity in Mudginberri billabong

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
22/7/78	2·2	3·6		104	379	0·6	1·6	230	1·0
6/10/78	1·5	2·7		167	457	0·5	2·1	220	1·0
16/11/78	1·5	2·7		233	637	0·5	2·0	320	1·0

Appendix Table 6 : Some parameters of primary productivity in Island billabong.

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A ($\mathrm{mgO_2m^3hr}$)	ΣA ($\mathrm{mgO_2m^2hr}$)	S	Z_i (m)	A_{max} ($\mathrm{mgO_2m^3hr}$)	$Z_{A_{max}}$ (m)
24/7/78	1·2	2·3	3·7	235	542	1·2	0·8	660	0·7
11/10/78	1·5	2·7		221	603	0·6	1·8	330	0·1
9/11/78	1·0	2·0	7·6	264	536	0·6	1·6	390	1·0
21/6/79	2·2	3·7	5·2	118	434	0·9	1·1	390	0·1
20/7/79	1·3	2·5	4·4	188	466	0·6	1·6	300	0·5
15/8/79	1·2	2·3	5·0	231	533	0·8	1·2	450	0·7
15/10/79	1·2	2·3	4·0	211	487	0·7	1·5	330	0·7
23/11/79	1·0	2·0	7·0	637	1293	0·7	1·5	860	0·7
13/3/80	0·7	1·6	13	35	56	0·9	1·1	50	0·7
9/4/80	1·8	3·1	3·8	78	246	0·6	1·8	140	1·0
9/5/80	1·3	2·5	4·2	101	250	1·2	0·8	300	0·7
2/6/80	1·5	2·7	3·4	155	422	0·7	1·4	310	0·7
2/7/80	1·0	2·0	3·7	362	735	0·6	1·6	450	0·1
26/8/80	1·2	2·3	3·6	138	319	0·9	1·1	300	0·5
22/9/80	1·1	2·2	6·6	202	439	0·7	1·4	310	0·5
29/10/80			3·6	307	829	0·5	2·1	400	0·7
9/12/80	1·1	2·2	8·5	393	852	0·6	1·7	510	0·1
26/2/81	1·9	3·3	5·4	59	192	0·5	1·9	100	0·5
						0·5	2·1	80	0·5

Appendix Table 6 (cont.)

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
22/5/81	1·9	3·3	1·8	183	600	0·8	1·3	470	0·5
19/6/81	1·4	2·6	2·8	149	386	0·8	1·2	320	0·3
9/8/81	1·6	2·9		137	391	1·0	1·1	370	0·5
12/8/81	1·7	3·0		196	589	0·7	1·4	430	0·5
15/8/81	1·7	3·0		214	641	0·7	1·5	430	0·7
18/8/81	1·5	2·7		164	448	0·8	1·3	340	0·5

Appendix Table 7 : Some parameters of primary production in Ja Ja billabong

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
17/7/78	0·9	1·9		323	610	1·1	0·9	650	0·2
9/10/78	0·25	1·0		29	29	5·9	0·2	170	0·1
23/11/78	0·1	0·8		12	9	6·7	0·1	60	0·1

Appendix Table 8 : Some parameters of primary productivity in Leichhardt billabong.

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
9/7/78	1·4	2·6	1·1	172	446	0·7	1·4	320	0·5
14/10/78	1·1	2·2		186	404	1·9	0·5	760	0·3
24/11/78	1·2	2·3	15	302	698	1·5	0·7	1020	0·5
8/6/79	1·4	2·6	3·1	362	937	0·6	1·6	590	2·0
10/7/79	2·0	3·4	1·5	35	121	1·2	0·9	140	0·5
1/8/79	1·0	2·0	5·0	400	812	1·5	0·6	1250	0·5
19/10/79	0·5	1·3	16	500	671	1·3	0·8	870	0·3
21/11/79	0·5	1·3	29	443	562	1·9	0·5	1090	0·1
26/2/80	1·2	2·3		133	308	0·8	1·3	240	0·3
1/4/80	1·9	3·3	4·0	12	40	1·0	1·0	40	2·0
13/5/80	1·2	2·3	3·3	73	169	0·6	1·7	100	0·5
4/6/80	1·2	2·3	3·7	123	283	0·9	1·1	250	0·4
13/7/80	1·0	2·0	8·6	105	214	1·2	0·9	250	0·1
15/8/80	1·1	2·2	3·3	157	341	0·9	1·2	290	0·5
5/9/80	0·8	1·8	7·8	469	715	1·2	0·9	830	0·3
16/10/80	0·7	1·6	9·5	521	839	1·6	0·6	1300	0·3
10/11/80	0·4	1·1	17	325	367	2·4	0·4	890	0·3
7/4/81	2·4	4·0	1·2	31	123	0·9	1·1	110	0·5
13/5/81	1·9	3·3		39	126	0·8	1·3	100	[illegible]
20/6/81	1·7	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			

Appendix Table 9 : Some parameters of primary productivity in Jabiluka billabong.

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A (mgO_2m^3hr)	ΣA (mgO_2m^2hr)	S	Z_i (m)	A_{max} (mgO_2m^3hr)	$Z_{A_{max}}$ (m)
12/6/79	0·5	1·3	16	206	261	1·2	0·8	320	0·3
11/7/79	0·6	1·5	19	137	202	1·4	0·7	280	0·1
9/8/79	0·5	1·3	28	174	233	1·9	0·5	430	0·1
16/10/79	0·2	0·9	100	72	66	4·7	0·2	310	0·2
6/3/80	1·9	3·3	3·2	67	221	0·6	1·6	140	0·3
2/4/80	2·0	3·4	2·3	34	117	0·5	2·0	60	1·5
14/5/80	1·0	2·0	3·3	79	160	0·8	1·2	130	0·7
5/6/80	1·0	2·0	7·2	84	164	1·6	1·0	160	0·1
10/7/80	0·6	1·5	14	226	332	2·6	0·4	850	0·1
30/8/80	0·4	1·2	36	163	195	1·7	0·6	330	0·3
24/10/80	0·3	1·1	74	115	122	2·5	0·4	310	0·1
25/11/80	0·08	0·8	85	145	109	3·1	0·3	340	0·1
14/5/81	1·9	3·3		71	233	0·5	1·9	120	0·1
18/6/81	0·9	1·9	9·8	123	233	1·0	1·0	240	0·5
7/8/81	0·4	1·1		245	277	1·6	0·6	430	0·3

Appendix Table 10 : Some parameters of primary productivity in Red Lily billabong.

Date	$Z_{s.d.}$ (m)	Z_{eu} (m)	Turb. N.T.U.	A $(\mathrm{mgO_2m^3hr})$	ΣA $(\mathrm{mgO_2m^2hr})$	S	Z_i (m)	A_{max} $(\mathrm{mgO_2m^3hr})$	ZA_{max} (m)
22/4/80	0·7	1·6	3·8	248	399	0·9	1·1	350	0·1
29/5/80	0·6	1·5	10·5	227	333	1·0	1·0	340	0·5
6/8/80	1·2	2·3	2·5	288	666	0·6	1·6	410	2·0
13/10/80	0·~~8~~75	1·7	10·6	288	484	0·8	1·2	400	0·3
3/12/80	0·9	1·9		193	364	1·5	0·7	540	0·3
29/1/81	1·2	2·3	8·3	104	241	0·7	1·4	170	2·0
13/3/81	0·6	1·5	6·1	92	135	1·9	0·5	260	0·1