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10.—Primary Productivity of Phytoplankton in Loch Leven, Kinross.
By Margaret E. Bindloss,* The Nature Conservancy, Edinburgh.
(With 14 text-figures and 1 table)

SYNOPSIS

Photosynthetic productivity of phytoplankton in Loch Leven was studied over a 4-year period (1968–71), using the oxygen light and dark bottle technique. Marked seasonal changes in hourly and daily rates of gross photosynthetic productivity are described within the range 0.02 to 1.59 g O₂/m².h and 0.4 to 21.0 g O₂/m².day respectively. Hourly rates are shown to be relatively insensitive to variations in surface light intensity, whereas daily rates are influenced to a considerable extent by the duration of incident radiation (daylength).

The phytoplankton itself exerts a dominant influence on underwater light penetration, accounting for *ca* 75 per cent of light extinction at highest crop densities. This self-shading effect contributes to the poor correlation observed between crop density and areal gross productivity. The chlorophyll *a* content per unit area in the euphotic zone often approached its estimated theoretical limit of 430 mg/m².

In general, increase in photosynthetic capacity (per unit content of chlorophyll *a*) accompanied increase in water temperature. During certain periods an inverse relationship between photosynthetic capacity and population density was evident. Reduction in photosynthetic capacity is attributed, in part, to the high pH values (>9.5) with concomitant CO₂-depletion associated with dense phytoplankton crops.

Estimates of net photosynthetic productivity were frequently zero or negative, even over periods when algal populations were increasing and dissolved oxygen and pH values were above their respective air-equilibrium values. Underestimation of gross photosynthesis due to photochemical oxidation, photorespiration or the use of stationary bottles could not account for this apparent anomaly. The most probable sources of error in the estimates of net photosynthetic productivity are discussed.

INTRODUCTION

Loch Leven is a shallow, nutrient-rich freshwater lake in lowland Scotland. A general description of the loch, its history, fauna and flora is given by Morgan (1970, 1972).

Phytoplankton are considered to make a significant, probably dominant, contribution to total primary production at the loch. Macrophytes were sparse during the study period (1968–71). Considerable quantities of benthic algae do occur (Bailey-Watts 1974) but their productivity has not been measured.

This paper describes seasonal changes in productivity of phytoplankton in relation to some controlling factors. Species composition of the phytoplankton is given by Bailey-Watts (1974). The work forms part of a comprehensive study of productivity and energy flow at Loch Leven and is a contribution to the International Biological Programme.

METHODS

Gross primary productivity was measured by the oxygen light and dark bottle method using *ca* 3 h exposures near midday and Winkler oxygen determinations. In principle the procedure used was similar to that described by Talling (1957*a*). Water taken from 0.5 m depth was siphoned into 190 ml 'Monax' borosilicate glass bottles which were suspended, in pairs, at depths distributed over the euphotic zone. Pairs of dark bottles (covered with black cloth) were suspended at only two depths

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(0.6 m and 1.6 m). Photosynthesis-depth profiles obtained using 0.5 m water differed very little from those obtained using a 0–3 m integrated tube sample or when bottles were filled with water taken from the depth of exposure. This reflects the efficiency of vertical mixing at Loch Leven which generally maintains a uniform depth distribution of phytoplankton, temperature and chemical characteristics throughout the water column and is rapid enough to prevent any physiological adaptation of the phytoplankton to a particular underwater light intensity.

Oxygen uptake in the dark bottles was used as a measure of community respiration.

Gross production rates per m^2 were estimated by planimetric integration of the depth-profiles of photosynthesis.

Daily rates were calculated from hourly using equation 5 of Talling (1965).

In the laboratory photosynthesis was measured in an illuminated, constant temperature water bath. A bank of 7 closely spaced 'daylight' fluorescent tubes (65/80W) with internal reflectors, placed immediately below the glass base of the bath, provided a maximum light intensity of 23.7 klux (120 kerg/cm².sec). This light intensity proved sufficient for light-saturation of photosynthesis to be realised at the temperatures studied. Lower light intensities were obtained by placing various thicknesses of black plastic gauze on the bottom of the bath in compartments optically isolated from each other by partitions of black plastic.

Phytoplankton density was estimated as chlorophyll *a* essentially as described by Vollenweider (1969). Water samples were filtered on to Whatman GF/C glass fibre filters and pigments were extracted in 90 per cent aqueous methanol. Optical densities of the centrifuged extracts were measured at 665 nm and 750 nm and the concentration of chlorophyll *a* was calculated from the equation of Talling and Driver (1963). Ninety per cent aqueous acetone extracts were used to obtain a relative index of pigment degradation products according to the methods of Moss (1967*a, b*) and Lorenzen (1967).

Total incident solar radiation during exposures was determined planimetrically from the mV chart records of a Kipp and Zonen solarimeter.

Ten-day mean daily radiation values were provided by Mr I. R. Smith. These were determined from records of bright sunshine taken from a Campbell-Stokes recorder (Smith 1974). Energy available for photosynthesis, in the spectral region 400–700 nm, was assumed to be 46 per cent of total incoming solar energy (Talling 1957*a*).

Underwater light penetration was measured with a Secchi disc and with a selenium photocell, microammeter and red (RG 1), green (VG 9), blue (BG 12) and orange (OG 2+BG 18) Schott filters. The vertical extinction coefficients of red, blue and green light, together with the measurement of incident light intensity, were used to calculate absolute irradiation at various depths according to the procedure described by Talling (1957*a*). I_k , the photosynthetic characteristic introduced by Talling (1957*a*) to express the onset of light-saturation of photosynthesis in relation to light intensity, was calculated as the light intensity at which photosynthetic rate reached 0.75 of the light-saturated rate (Talling 1965).

pH was measured using a model 30C portable pH meter (Electronic Instruments Limited, Richmond, England), with an accuracy of approx. ± 0.05 unit.

Alkalinity was measured by titration with N/100 hydrochloric acid to pH 4.5 using B.D.H. 4.5 indicator.

RESULTS AND DISCUSSION

Distribution of Gross Photosynthetic Activity with Depth

Depth-profiles of gross photosynthetic activity per unit volume of water (nP , mg O₂/m³.h) for 1971 are presented in text-fig. 1. The range of profile shapes represented is typical of that encountered in earlier years. An inhibition of photosynthesis near the surface was recorded on most occasions. Maximum (light-saturated) rates of photosynthesis occupied a very narrow depth zone, often no greater than 10 cm (the depth covered by the experimental bottles). Beneath the zone of light-saturation photosynthetic rates declined rapidly, reaching very low values below 3 m. The narrow zone of optimum light and the sharp decrease of photosynthetic rate with depth reflect the generally rapid extinction of light in this lake which in turn, as shown later, is influenced largely by the density of the phytoplankton crop it supports.

GROSS PHOTOSYNTHESIS PER UNIT AREA AND THE COMPONENT VARIABLES OF THE PHOTOSYNTHESIS-DEPTH PROFILE

Midday hourly rates of gross photosynthesis per unit area (ΣnP), determined by planimetric integration of the photosynthesis-depth profiles, are given in text-fig. 2. Values of ΣnP determined in this way were in good agreement (text-fig. 3) with those obtained using the following formulation, devised by Talling (1957*b* equation 3), to describe integral photosynthesis in an unstratified water column:

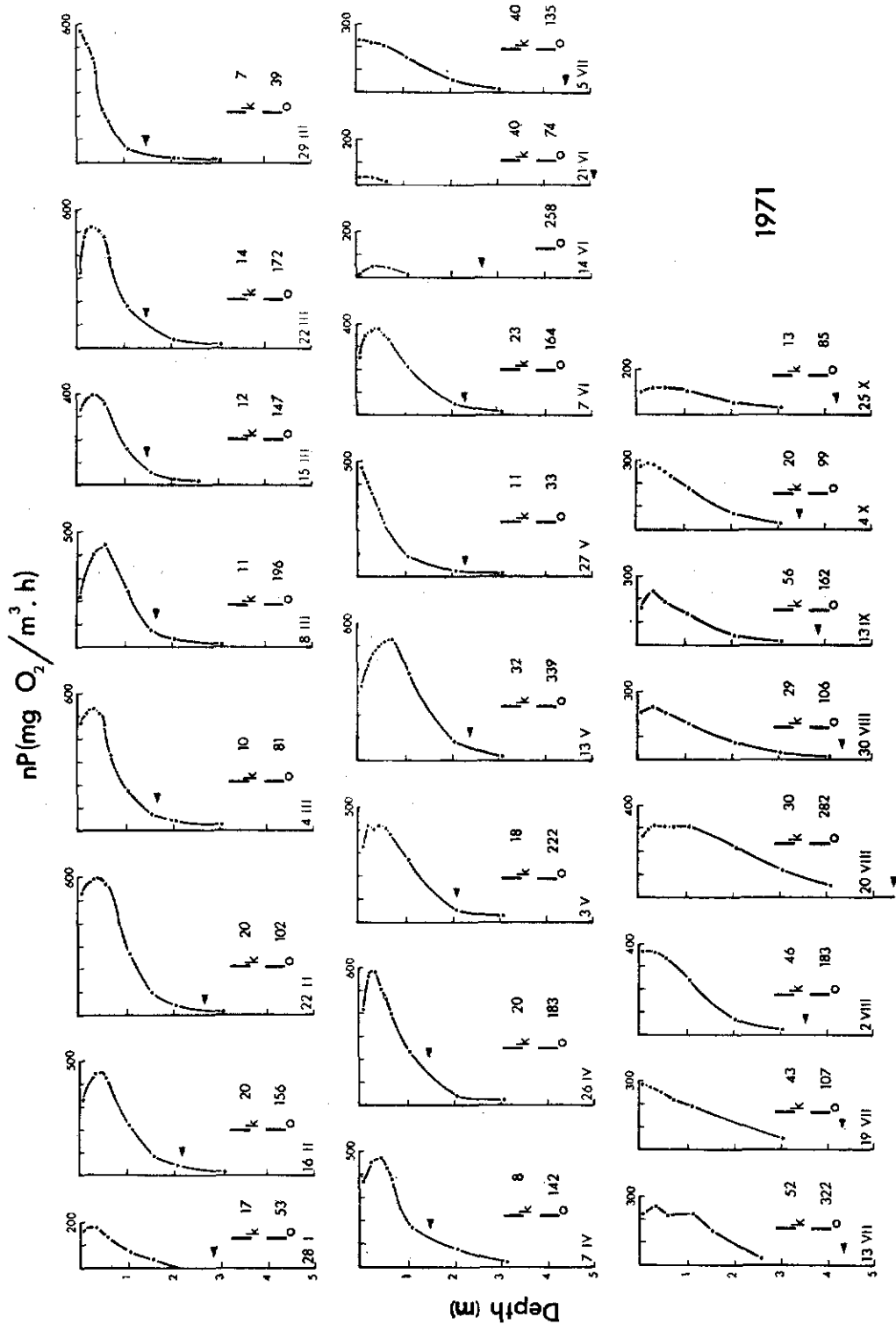
$$\Sigma nP = \frac{nP_{\max}}{1.33k_{\min}} \ln 2 \left\{ \frac{\log I'_0 - \log 0.5 I_k}{\log 2} \right\}. \quad (1)$$

This expression can be reduced to:

$$\Sigma nP = \frac{nP_{\max}}{1.33k_{\min}} \ln \left\{ \frac{I'_0}{0.5 I_k} \right\}. \quad (2)$$

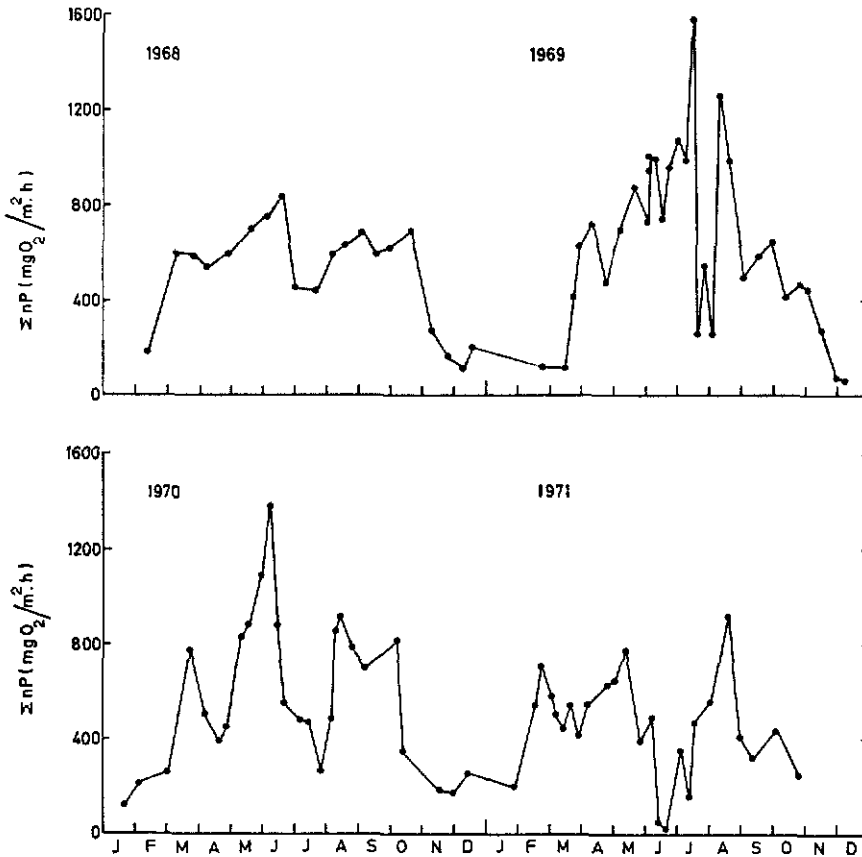
The symbols in the above equations, and in the text and figures, are those used by Talling; in the following key equivalent symbols, recommended in Winberg (1971), are given in parentheses:

- $\Sigma nP(\Sigma A)$ = hourly rate of gross photosynthesis per unit area (mg O₂/m².h)
- $n(B)$ = population density per unit volume of water, as mg chlorophyll *a*/m³
- $k_{\min}(\epsilon_{\min})$ = the minimum value (over the visible spectrum) of the vertical extinction coefficient (ln units/m)
- $P_{\max}(A_{\max}/B)$ = light-saturated rate of gross photosynthesis per unit population, in mg O₂/mg chlorophyll *a*.h (photosynthetic capacity)
- $nP_{\max}(A_{\max})$ = light-saturated rate of gross photosynthesis per unit water volume (mg O₂/m³.h)
- I'_0 = light intensity immediately below the water surface (i.e. surface light intensity, I_0 , corrected for surface loss of 10 per cent), in kerg/cm².sec (400–700 nm)
- I_k = light intensity indicating onset of light-saturation of photosynthesis, in kerg/cm².sec (400–700 nm). Characteristic introduced by Talling (1957*a*) and equivalent to the light intensity at which an extrapolation of the initial linear region of the rate-intensity curve would reach the light-saturated rate.



TEXT-FIG. 1.—Depth-profiles of rates of gross photosynthesis per unit water volume for 1971. The mean surface-incident light intensity (I_0) and the value of I_k are given where available, in $\text{ker}/\text{cm}^2 \cdot \text{sec}$ (spectral region 400–700 nm). Arrows indicate the depth of the euphotic zone.

Talling's mathematical model usefully identifies the components of the photosynthesis-depth profile and illustrates their relative influence on the area-based integral rate (ΣnP). Seasonal variations in ΣnP may therefore be interpreted in terms of variation in these components, their interaction and their response to environmental factors. The indirect calculation of integral photosynthesis also works if the I_k value was obtained independently in the laboratory.



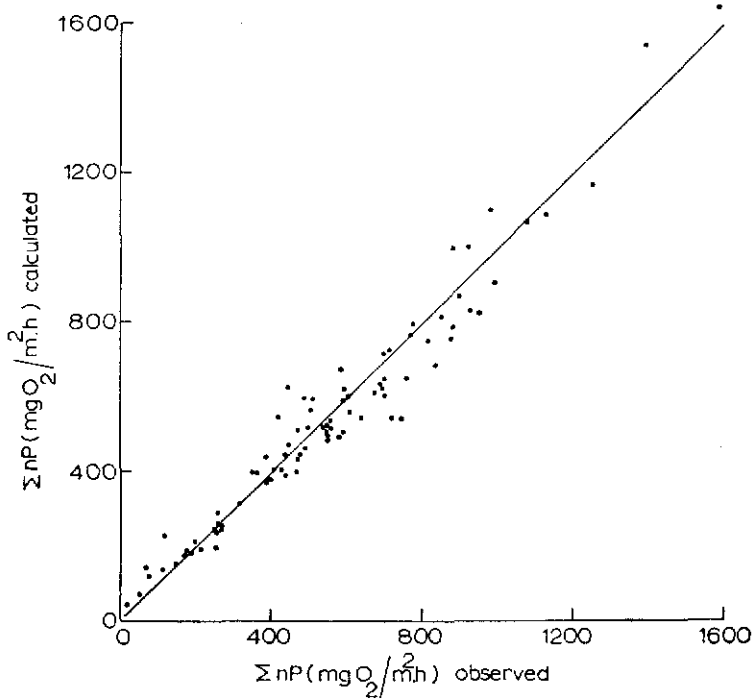
TEXT-FIG. 2.—Midday hourly rates of gross photosynthesis per unit area (ΣnP) 1968–71.

Most of the variation in the measured hourly rates of gross photosynthesis per unit area (ΣnP) at Loch Leven was accounted for by variation in the ratio nP_{\max}/k_{\min} (text-fig. 4). The following average relationship was observed between ΣnP and nP_{\max}/k_{\min} and is indicated as a broken line in text-fig. 4.

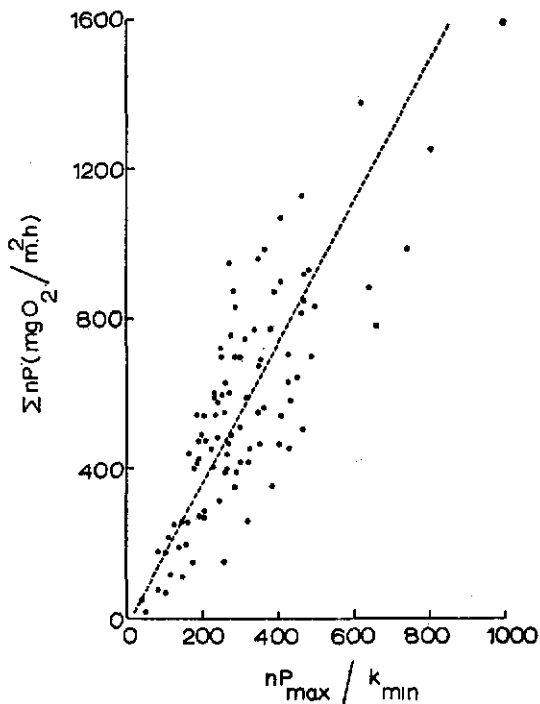
$$\Sigma nP = \frac{nP_{\max}}{k_{\min}} 1.9.$$

Multiplication of the minimum extinction coefficient, k_{\min} , by 1.33 yields a measure of the effective vertical extinction (k_e) of total visible light (Talling 1957*b*, 1971 p. 222). Substituting k_e in the above equation gives:

$$\Sigma nP = \frac{nP_{\max}}{k_e} 2.5.$$



TEXT-FIG. 3.—Midday hourly rates of gross photosynthesis per unit area (ΣnP) as observed in *in situ* exposures and as calculated from equation 3 of Talling (1957b). The inserted line corresponds to a 1 : 1 relationship.

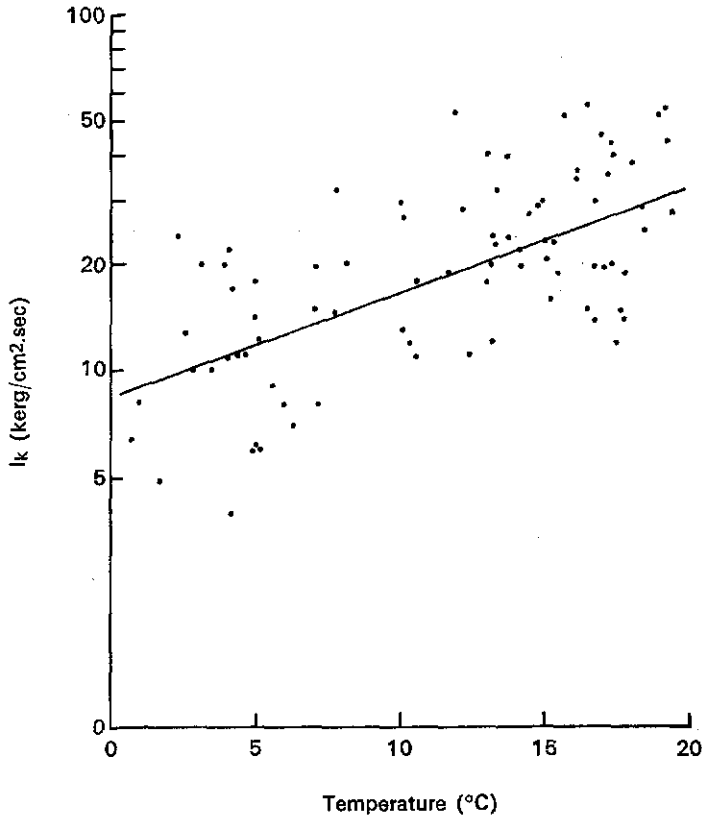


TEXT-FIG. 4.—Gross photosynthesis per unit area (ΣnP) as a function of the ratio $nP_{\text{max}}/k_{\text{min}}$. The dashed line indicates the average relationship between ΣnP and $nP_{\text{max}}/k_{\text{min}}$.

The factor 2.5 is equivalent to the function $F(I)$ of various authors and is equal to $\ln(I_0/0.5 I_k)$; similar values for $F(I)$ have been reported by Rodhe, Vollenweider and Nauwerck (1958) and Wright (1959). A rather higher value of 3.5 may be calculated from the data of Talling (1965 p. 20).

Surface Incident Light Intensity (I_0) during Exposure Periods and Light-Saturation Behaviour (I_k)

Talling's model (equation 2 above) predicts that areal hourly gross productivity (ΣnP) will be relatively insensitive to changes in instantaneous surface light intensity



TEXT-FIG. 5.—Values of I_k (logarithmic scale) measured at Loch Leven at the ambient temperatures indicated. The correlation coefficient is 0.65. $Q_{10} = 1.98$.

I_0 —or its subsurface derivative I'_0 —to which it is related as a logarithmic function of $I_0/0.5 I_k$. This prediction is fulfilled in that most of the variation in ΣnP could be accounted for, without reference to I_0 by the ratio nP_{\max}/k_{\min} .

I_k showed an increase with temperature (text-fig. 5) similar to that described later for P_{\max} (text-fig. 12). Because of the temperature dependence of I_k , lower winter I_0 values tend to be associated with lower I_k values. Consequently the ratio $I_0/0.5 I_k$ shows less marked seasonal fluctuation than either of its components thereby reducing

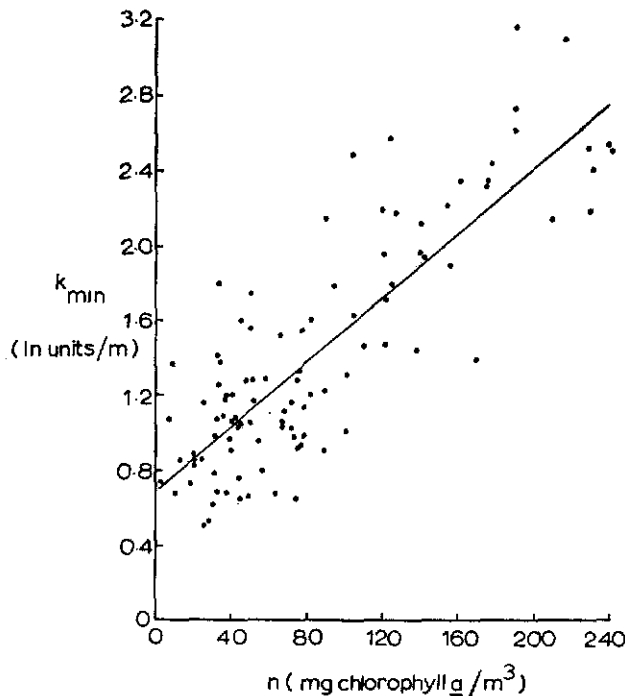
the potential influence of these components (I_0 and I_k) on hourly gross productivity per unit area. The *duration* of incident radiation, on the other hand, will be shown later to exert a relatively large influence on *daily* gross productivity per unit area.

Underwater Light Penetration

The minimum vertical extinction coefficient (k_{\min}) normally lay in the orange spectral region (at ca 590 nm) and varied seasonally between 0.5 and 3.1 ln units/m. The depth of the euphotic zone (z_{eu}), calculated as the depth corresponding to 1 per cent available surface radiation, was found to be inversely proportional to k_{\min} such that $z_{eu} \approx 3.7/k_{\min}$. This relationship was found by Talling (1965, 1971) to apply to a range of lakes in Africa and England. Euphotic depth (z_{eu}) showed marked seasonal variation within the range 1.2–7.4 m, with a strong tendency for lower values to be associated with higher densities.

On average the depth of the euphotic zone was about 3 times the depth of disappearance of the Secchi disc. The relationship between euphotic depth and Secchi disc transparency became more variable as water clarity increased.

Self-shading (the influence of phytoplankton density on light penetration). A positive correlation between population density (as mg chlorophyll *a*/m³) and the minimum vertical extinction (k_{\min}) is indicated in text-fig. 6. The correlation coefficient is 0.84. From the calculated linear regression line in text-fig. 6, the mean increment in k_{\min}



TEXT-FIG. 6.—The relationship between the minimum vertical extinction coefficient (k_{\min}) and the concentration of chlorophyll *a* in the water column (n). The correlation coefficient is 0.84.

associated with unit increase in population density (i.e. the k_s value of Talling 1960) is 0.0086 ± 0.0011 ln units per mg chlorophyll a/m^2 . This value is lower than some published values of k_s (of the order of 0.02) found by Talling (1960) and Ganf (1972). Lower k_s values (of the order of 0.01) were found by Talling (1971) and Steel (1972) and attributed to the relatively large cell size of the phytoplankton species concerned. This seems an unlikely explanation for the low k_s at Loch Leven where the phytoplankton was dominated by 'ultra' and 'nanno' algae (Bailey-Watts 1974).

The average background level of non-algal light extinction, indicated in text-fig. 6 by the intercept of the regression line on the y axis, is low relative to light extinction by phytoplankton at high crop densities. On average, a crop density equivalent to 240 mg chlorophyll a/m^3 accounts, at Loch Leven, for 75 per cent of total light extinction in the water column. The low background light extinction of Loch Leven water is also illustrated by the laboratory spectroradiometer measurements made by Talling (1970 fig. 5). Day-to-day variation in the amount of background light extinction, due mainly to non-algal particulate material, probably accounts for much of the scatter in text-fig. 6. Little seasonal variation in the background colour of the water itself, imparted by dissolved substances, was revealed in routine spectrophotometer measurements of filtered lake water in the 400–700 nm spectral range. Seasonal variation in pigmentation and cell size characteristics of component algal species may affect the increment in k_{min} per unit chlorophyll a and thus contribute to the scatter of points in text-fig. 6.

Standing Crop (Biomass) of Phytoplankton in Relation to Gross Production Rates

The relationship between population density per unit volume of water and gross productivity per unit area. In text-fig. 7 rates of gross areal production (ΣnP) have been plotted against corresponding measurements of phytoplankton density (as mg chlorophyll a/m^3). A wide scatter of points exists suggesting that in this lake biomass, expressed per unit volume of water, is a poor index of productivity per unit area.

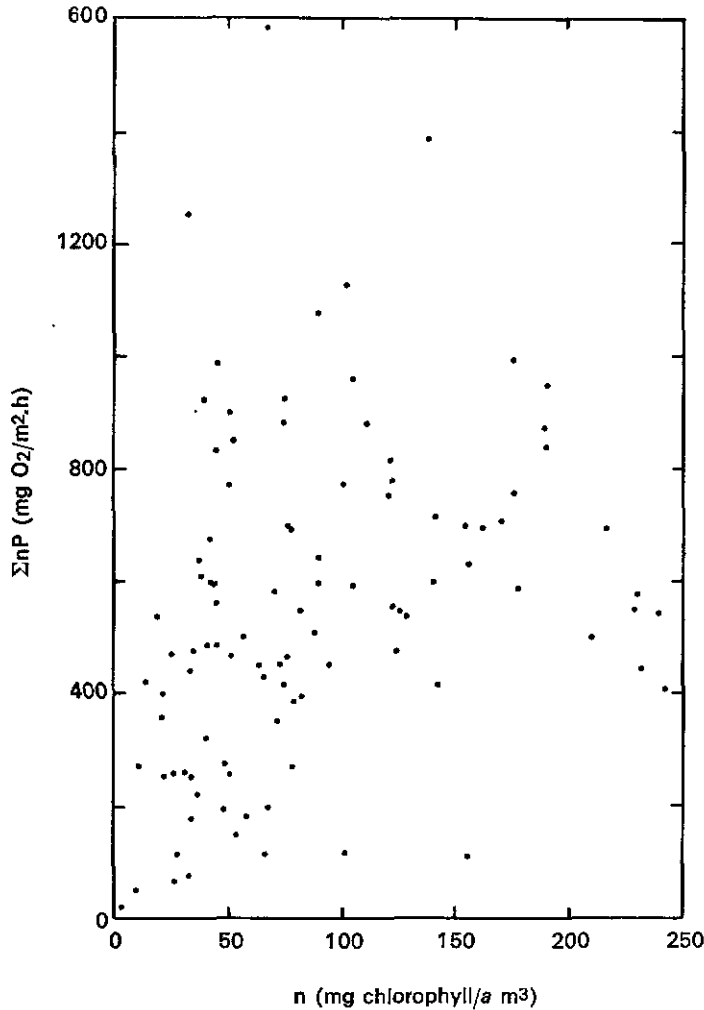
Because of self-shading, population density (n) influences both the horizontal and vertical components of the photosynthesis-depth profile as follows:

- (1) as one of the determinants of the light-saturated rate of photosynthesis per unit volume of water (nP_{max}), population density influences the maximum horizontal extent of the profile;
- (2) as a major determinant of underwater light penetration, expressed in terms of k_{min} , population density also influences the vertical extent of the profile.

Thus, population density affects both components of the ratio nP_{max}/k_{min} shown earlier to be the chief determinant of areal productivity. Increase in population density (n) leads to an increase in both nP_{max} and k_{min} with the result that nP_{max}/k_{min} (and consequently ΣnP) can be expected to show less marked variation than n itself. In other words, increase in population density, whilst tending to increase the horizontal extent of the profile, also decreases its vertical extent so that changes in the area of the profile are not likely to be linearly related to those of population density.

The extent to which population density determines the light-saturated rate of photosynthesis (nP_{max}) is shown in text-fig. 8. Clearly the relationship is not close, implying relatively wide variation in the light-saturated rate of photosynthesis per unit population (P_{max}) and providing an additional explanation for the poor relationship between productivity per unit area and standing crop of phytoplankton.

The amount of chlorophyll *a* in the euphotic zone in relation to gross productivity per unit area. The phytoplankton at Loch Leven is normally distributed uniformly with depth (Bailey-Watts 1974). The total amount of chlorophyll *a* in the euphotic zone under a square metre of water surface (Σn) was therefore calculated as the concen-

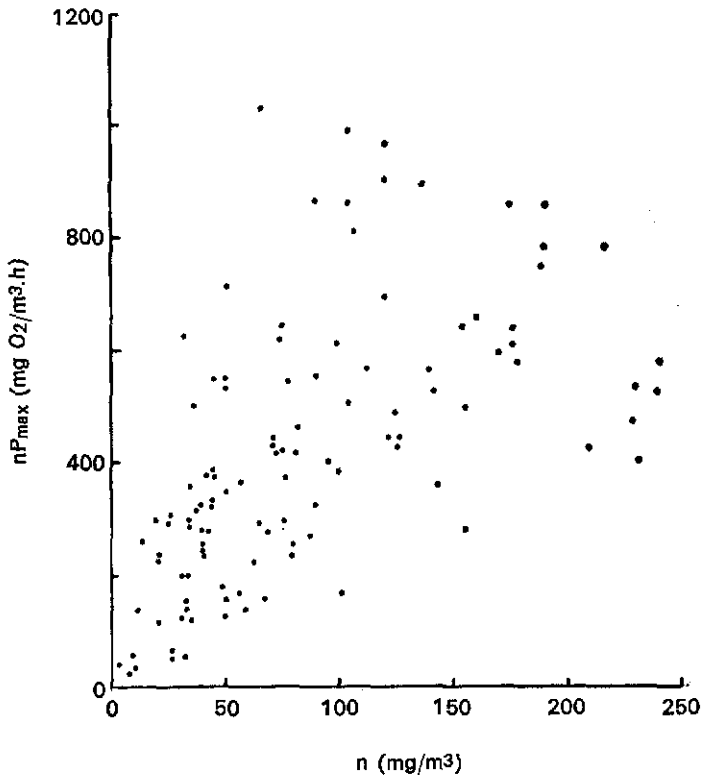


TEXT-FIG. 7.—Gross photosynthesis per unit area (ΣnP) in relation to chlorophyll *a* concentration (n).

tration of chlorophyll *a* per m³ multiplied by the depth (in metres) of the euphotic zone.

Over the 4-year period the chlorophyll *a* content of the euphotic zone (Σn) ranged from 15 to 456 mg/m². Seasonal fluctuations of Σn were usually less marked than those of n , particularly at higher population densities (above about 100 mg chlorophyll *a*/m³). This is because increase in population density (n) reduces the depth of the euphotic zone through self-shading, and consequently brings about a less than pro-

portionate increase in Σn . This feature is illustrated in text-fig. 9 using data from 1969. Essentially similar patterns were observed in other years. As a consequence of self-shading, the pigment content of the euphotic zone (Σn) cannot theoretically exceed an upper limiting value, which will be achieved when the algae reach densities where they are the dominant cause of light extinction in the water column. This potential



TEXT-FIG. 8.—Relationship between light-saturated rate of photosynthesis per unit volume of water (nP_{max}) and population density (n) estimated as chlorophyll *a*.

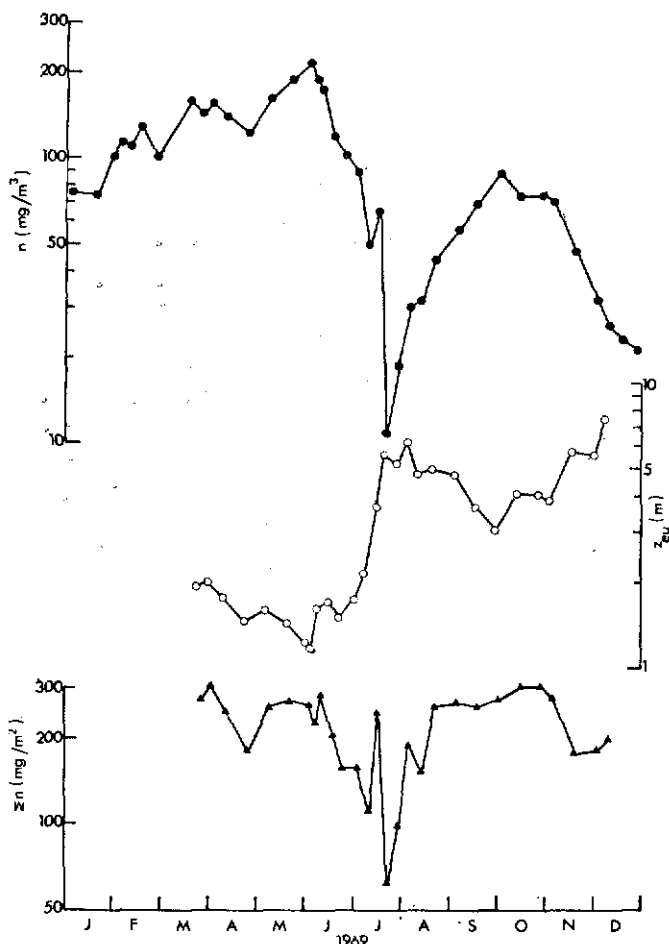
upper limit to Σn depends on the effect on light extinction of unit increase in population density (i.e. on the value of k_s). When light extinction is due solely to algae, k_{min} will be equal to the product of population density (n) and k_s (the increase in k_{min} for unit increase in population density), i.e. $k_{min} = nk_s$.

If the euphotic zone is defined in terms of k_{min} as $3.7/k_{min}$, Σn will be given by $3.7n/k_{min}$ and the theoretical upper limit of Σn will be equal to $3.7/k_s$. For Loch Leven with an average k_s of 0.0086, the theoretical upper limit for Σn is therefore 430 mg chlorophyll *a*/m². Estimates of Σn have often approached (and on one occasion exceeded) this theoretical upper limit. The fact that many of the values of Σn measured at Loch Leven are considerably higher than the theoretical upper limit of Σn of 185 mg chlorophyll *a*/m² possible with a k_s of 0.02 provides additional evidence that, despite the small-celled nature of Loch Leven phytoplankton, it is nevertheless characterised by a relatively low k_s value.

An important implication of a low k_s value is that potentially it allows a higher

euphotic population to be reached and therefore favours higher productivity per unit area.

The chlorophyll *a* content of the euphotic zone (Σn), because it incorporates the self-shading effect, might be expected to show a closer relationship with productivity



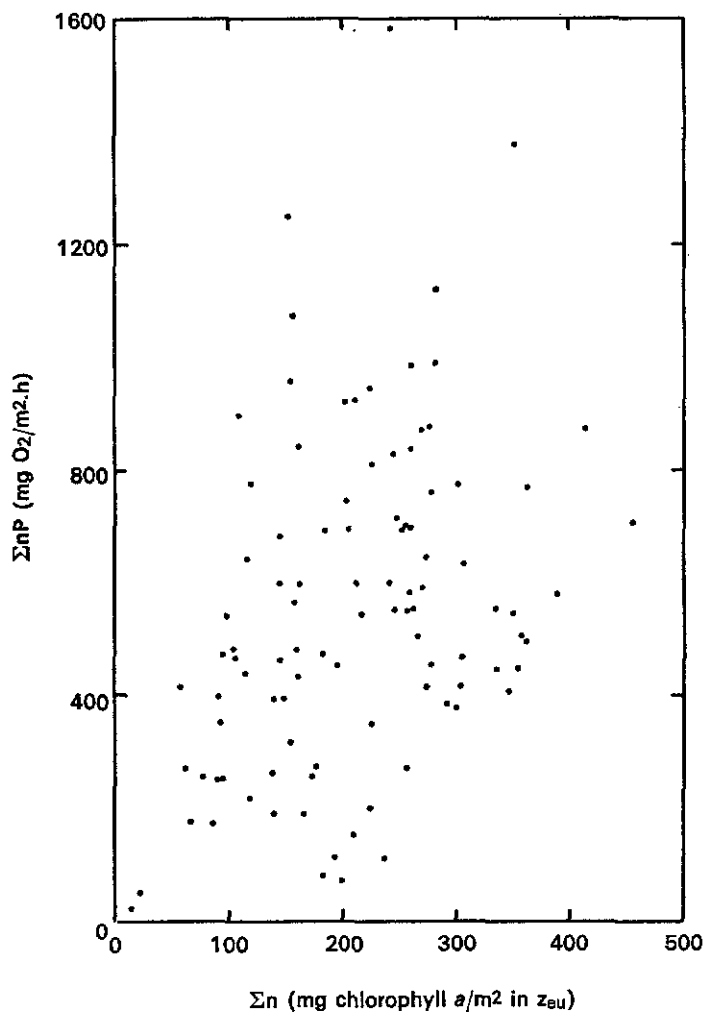
TEXT-FIG. 9.—Seasonal changes during 1969 of chlorophyll *a* concentration (n), euphotic depth (z_{eu}) and chlorophyll *a* content per unit area of the euphotic zone (Σn).

per unit area than does population density (n). However, the poor correlation between ΣnP and Σn , illustrated in text-fig. 10, shows that even when self-shading is taken into account biomass remains an unreliable index of gross productivity per unit area. A further cause of 'uncoupling' of ΣnP and n at Loch Leven is the variation (discussed below) in photosynthetic capacity (P_{max}) per unit of population.

The Specific Rate of Photosynthesis per Unit Population measured at Light-Saturation (Photosynthetic Capacity, P_{max})

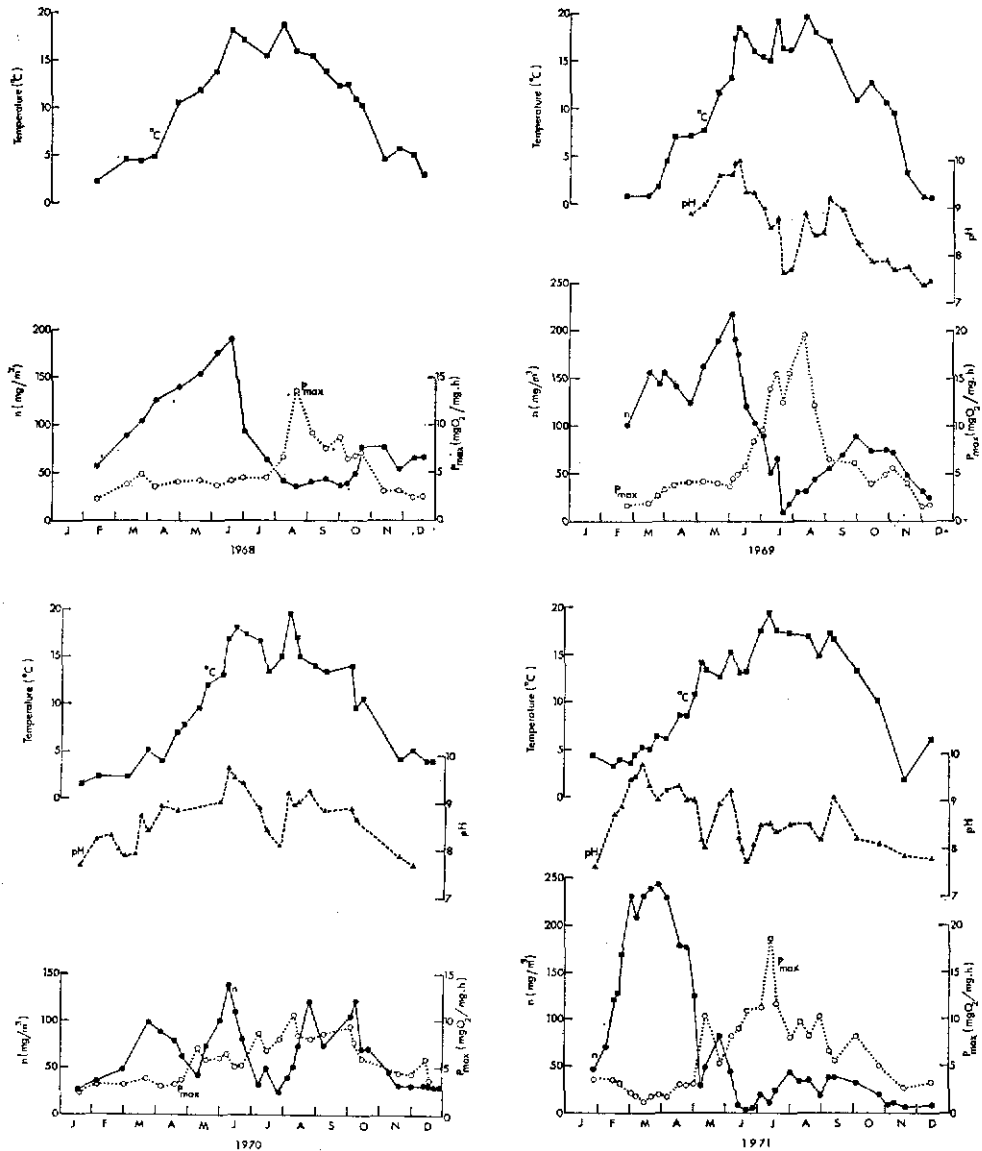
Seasonal changes in photosynthetic capacity (P_{max}) as $\text{mg O}_2/\text{mg chlorophyll } a \cdot \text{h}$ are shown in text-fig. 11. Over the 4-year period, values covered an approximately

tenfold range from 1.6 to 19.6 mg O₂/mg.h. Photosynthetically inactive populations were never observed. Variations in P_{\max} were broadly correlated with those of water temperature (text-fig. 12). The correlation coefficient between $\log P_{\max}$ and temperature is 0.79 and the calculated linear regression line indicates an average temperature



TEXT-FIG. 10.—Gross photosynthesis per unit area (ΣnP) in relation to the chlorophyll *a* content per unit area of the euphotic zone (Σn).

coefficient (Q_{10}) of 2.2. Departure from the overall trend of increase in P_{\max} with increase in temperature was observed during certain periods which may be identified from text-fig. 11. Between April and July 1968 and between April and early June 1969 P_{\max} remained more or less constant despite a temperature increase of ca 14°C. During May and June 1970 P_{\max} showed little change as temperature increased from 8°C to 17°C. In February and March 1971 P_{\max} declined whilst temperature remained constant and continued to decline when temperature increase began during March.

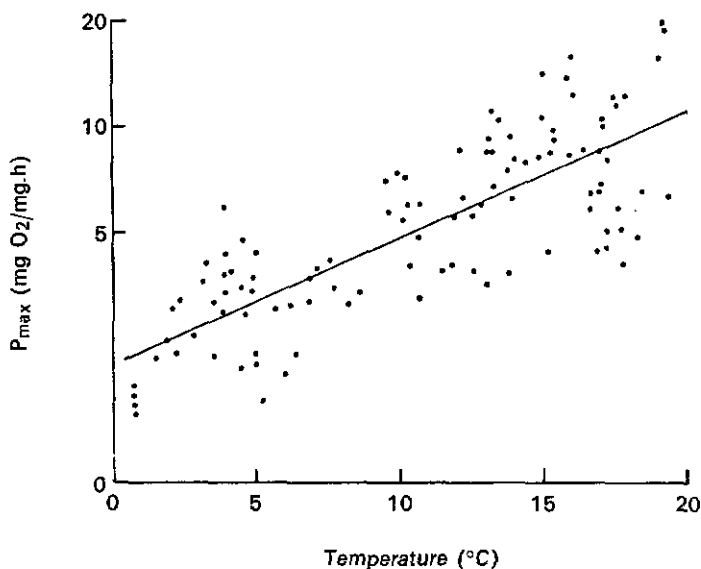


TEXT-FIG. 11.—Seasonal changes in population density (n) estimated as chlorophyll a , light-saturated rate of photosynthesis per mg chlorophyll a (P_{max}), pH and water temperature. 1968–71.

During all four periods when P_{max} did not behave as expected on temperature grounds, population density was increasing (text-fig. 11). This suggests that the factors depressing P_{max} at constant temperature (in 1971) or preventing its increase with temperature (in 1968, 1969 and 1970) are population density-dependent factors. This suggestion is further supported by the observation that subsequent decline in population density (n) is accompanied by an increase in photosynthetic capacity (P_{max}), the clearest example being that of 1969. Except in 1971 this increase in P_{max}

as population density declined occurred over periods of relatively constant temperature. The increase in rate appears to be due to removal of a depressive factor rather than to temperature enhancement. The algae themselves, when growing at high population density, appear to be producing conditions unfavourable to their own photosynthetic activity.

The resulting inverse relationship, between population density and photosynthetic capacity, tends to oppose the expected decrease in productivity per unit area (ΣnP) with decrease in standing crop and thus tends to reinforce the self-shading effect in reducing variation in areal gross production.



TEXT-FIG. 12.—Values of photosynthetic capacity (P_{\max} , logarithmic scale) measured in Loch Leven at the ambient temperatures indicated. The correlation coefficient is 0.79. $Q_{10} = 2.2$.

Difficulties were encountered in the use of published methods (Lorenzen 1967; Moss 1967*a, b*) for the estimation of absolute concentrations of pheopigments. These problems have been described elsewhere (Bindloss *et al.* 1972). The chlorophyll *a* values presented here, and used in the calculations of photosynthetic rates per unit chlorophyll, are therefore uncorrected for pheophytin interference. In general, results obtained using the above methods indicated that degraded chlorophyll was relatively more abundant when crops were low. Any correction for pheophytin interference would therefore tend to accentuate the observed inverse relationships between population density and photosynthetic capacity.

Various factors associated with increase in population density may be responsible for limiting photosynthetic capacity. These include nutrient depletion, decrease in water clarity leading to 'shade' adaptation, and build up of pH and oxygen to inhibitory levels.

Of these factors pH appeared to play a dominant role at Loch Leven and will be discussed here in detail. Oxygen saturation values in the euphotic zone varied over the four years from 68 to 169 per cent. Values below 85 per cent and above

120 per cent were comparatively rare. Due to a small amount of aeration during sampling, the 'initial' oxygen concentration of the sample used to fill the light and dark bottles was usually closer to air equilibrium than was the *in situ* oxygen concentration. Oxygen tension did not appear to be a significant factor determining photosynthetic capacity.

The relative importance of other population density dependent factors, and of species composition, in controlling photosynthetic capacity, was less clearly established and will be discussed elsewhere (Bindloss in prep.).

Influence of pH on photosynthetic capacity (P_{max}). The pH of the water in the euphotic zone, measured near midday, varied seasonally between 7.5 and 10.0 (text-fig. 11). Titration alkalinity showed relatively little seasonal variation, within the range 1.0–1.6 m-equiv./l. Air equilibration at 17°C of samples of alkalinity 1.1 and 1.5 m-equiv./l produced final pH values of 8.1 and 8.3 respectively. Change in alkalinity is not therefore sufficient to account for the observed pH changes; these are largely a consequence of the biological activities occurring in the water column and at the sediment-water interface.

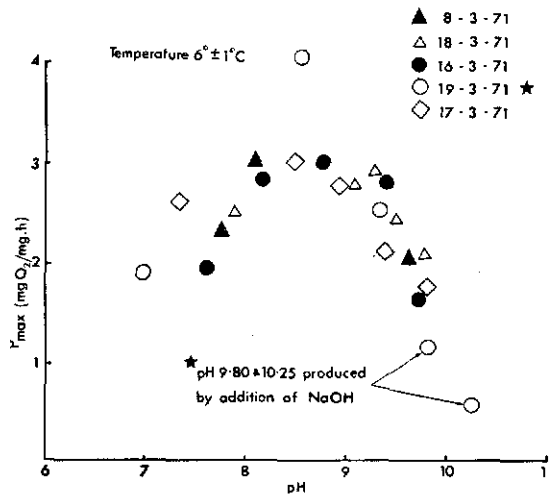
Increase in pH generally accompanied increase in population density (text-fig. 11). The photosynthetic removal of inorganic carbon from the natural bicarbonate-carbonate buffer system, at a rate faster than it can be replaced by community respiration and atmospheric equilibration, is reflected in a rise in pH. Utilisation of $\text{NO}_3\text{-N}$ will also cause pH to rise. As population density declined, the pH of the water decreased. Four periods were identified earlier from text-fig. 11, during which an inverse relationship between population density (n) and photosynthetic capacity (P_{max}) could be recognised. The general parallelism between seasonal changes of population density and those of pH suggests that the limitation of photosynthetic capacity observed at high population densities may reflect an adverse influence of the associated high pH values. Experimental support for this idea was obtained in March 1971. Prior to the experiments, water temperature had remained relatively constant but photosynthetic capacity (P_{max}) had been declining as population density (n) and pH increased. The effect on P_{max} of lowering pH (by blowing in CO_2 -rich lung air) was measured in the laboratory. The results of five experiments are shown in text-fig. 13. P_{max} increased with reduction in pH from 9.8 to 8.0 in each experiment. Further reduction in pH, below 8.0, produced no further increase in P_{max} . When pH was increased in one experiment (19 March 1971) from 9.30 to 9.80 and 10.25 (by addition of NaOH) P_{max} was reduced.

There is thus a reasonable amount of evidence, based on seasonal observations and laboratory experiments, that pH values above *ca* 9.0 reduce the photosynthetic capacity of Loch Leven phytoplankton. Similar results were obtained for benthic algae (Bindloss in prep.).

A rise in pH could affect algal metabolism in a number of ways. These include:

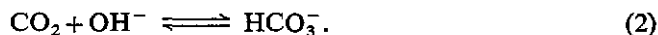
1. Increase in pH resulting from photosynthetic CO_2 uptake causes a decline in total CO_2 concentration (i.e. free $\text{CO}_2 + \text{HCO}_3^- + \text{CO}_3^{2-}$). Also as pH rises there is a shift in the molecular proportions of the remaining inorganic carbon away from free CO_2 towards a predominance of HCO_3^- and CO_3^{2-} . The $\text{CO}_2 - \text{HCO}_3^- - \text{CO}_3^{2-}$ equilibrium system and its pH relationships are discussed in detail by Hutchinson (1957) and more recently by Stumm and Morgan (1970). Concentrations of free CO_2 at different

pH values were calculated from pH, alkalinity and temperature data using nomographs constructed by Dr R. B. Wood from the tables of Dye (1952) and Karlgren (1962). It was assumed that titration alkalinity was predominantly due to the anions of carbonic acid plus OH^- . At 1.22 m-equiv./l alkalinity and 5°C the concentration of free CO_2 is $0.41 \mu\text{mol/l}$ at pH 9.75 and $97.05 \mu\text{mol/l}$ at pH 7.60. If an alga is an



TEXT-FIG. 13.—Results of five laboratory experiments on the effect of lowering pH (by CO_2 in lung air) or increasing pH for two points only on 19/3/71 on light-saturated rate of photosynthesis per mg chlorophyll *a* (P_{max}).

obligate free CO_2 user, reduction in the concentration of free CO_2 ($\text{CO}_{2\text{aq}} + \text{H}_2\text{CO}_3$), because of increase in pH, could limit its rate of photosynthesis: CO_2 is supplied via the dehydration of carbonic acid and/or bicarbonate:



These reactions are not instantaneous. Kern (1960) has reviewed work on the rate constants. Reaction (1) occurs at pH values below 8 whilst at pH values above 10 reaction (2) is dominant. Between pH values of 8 and 10 (which is approximately the pH range at Loch Leven) both reactions may occur and their relative importance cannot be distinguished. For this (and for other reasons to be discussed elsewhere) it is difficult to determine the rate of photosynthesis theoretically possible when only free CO_2 is utilised. Some algae (see reviews by Raven 1970 and Goldman *et al.* 1972) may be able to take up bicarbonate ions and use them in photosynthesis, either directly or after enzyme-catalysed dehydration to CO_2 . Such algae would therefore be able to continue photosynthesis even after the supply of free CO_2 became virtually exhausted. However there is evidence, for at least one freshwater alga, that the rate of photosynthesis at light and carbon-source saturation is lower when bicarbonate is being used than when free CO_2 is being used (Raven 1968). Thus, even if Loch Leven phytoplankton are capable of utilising bicarbonate, the observed high pH effect could still reflect a form of carbon limitation.

2. The availability of phosphorus may be affected by pH in two ways:
 - (a) As pH increases HPO_4^- increases at the expense of H_2PO_4^- . There is still doubt about the ionic form of phosphate most readily taken up by algae. Ullrich-Eberius and Simonis (1970) found that *Ankistrodesmus* absorbed actively only the monovalent ion. If this is generally true of algae, higher pH values would certainly depress phosphate uptake: this might ultimately lead to a reduced capacity for photosynthesis.
 - (b) At higher pH values phosphate ions may precipitate, e.g. as calcium phosphate or hydroxyapatite.
3. High pH values may affect adversely membrane permeability and active uptake mechanisms, or may inhibit internal cell metabolism.
4. Photorespiration in *Anabaena cylindrica* is reported to be stimulated by conditions of low pCO_2 and high pO_2 (Lex, Silvester and Stewart 1972). It may be that such enhanced photorespiration causes the apparent reduction in gross photosynthetic capacity at high pH at Loch Leven.

Extrapolation of Measured Hourly Rates of Gross Photosynthesis to Longer Time Periods

Daily gross productivity. Laboratory experiments showed that photosynthetic capacity of Loch Leven phytoplankton began to decline in exposures >6 hours. Direct measurement of daily integral photosynthesis per unit area, using whole day exposures, was therefore considered undesirable in this lake.

Daily rates were calculated from hourly rates, measured in 3-hour exposures, using the following equation (No. 5 of Talling 1965):

$$\frac{\Sigma\Sigma nP}{\Sigma nP} = 0.9 \Delta t \frac{(\log \bar{I}'_0 - \log 0.5 I_k)}{(\log I'_0 - \log 0.5 I_k)}$$

where $\Sigma\Sigma nP$ = daily integral photosynthesis per unit area

ΣnP = hourly integral photosynthesis per unit area

\bar{I}'_0 = mean sub-surface light intensity over the daylength (Δt)

I'_0 = mean sub-surface light intensity over 3-hour exposure period

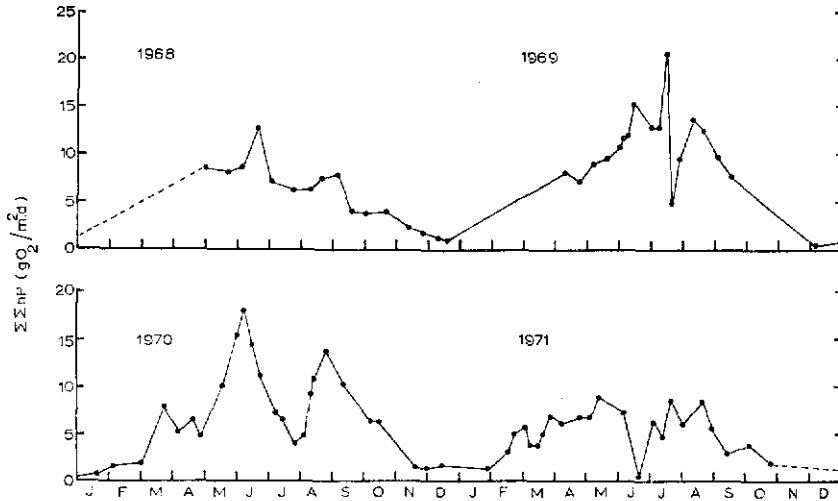
Δt = daylength (in hours)

I_k = photosynthetic characteristic expressing the onset of light-saturation, as defined earlier.

The derivation and limitations of this equation are described by Talling (1957b); implicit in its use is the assumption that photosynthetic activity at a given light intensity remains constant throughout the day. No evidence of significant diurnal variation in photosynthetic capacity, or in two of the factors (pH and oxygen level) likely to induce such variation, was found at Loch Leven on the 5 occasions when this was examined. Diurnal variation is reported to be enhanced by strong illumination and poor nutrient conditions (Saijo and Ichimura 1962). The efficiency of turbulent mixing in this lake, in preventing the residence of algal cells for long periods at inhibitory light intensities and in accelerating gaseous exchange with the atmosphere

and gaseous and nutrient exchange with the aphotic zone, may well reduce the chance of significant diurnal changes developing.

Calculated values of daily gross photosynthesis per unit area (ΣnP), in $\text{g O}_2/\text{m}^2\cdot\text{day}$, are shown in text-fig. 14. Carbon-based equivalents, given below, were derived from a photosynthetic quotient of 1.0. Marked seasonal changes in daily gross productivity were recorded, within the range $0.4\text{--}21.0 \text{ g O}_2/\text{m}^2\cdot\text{day}$ ($0.1\text{--}7.9 \text{ g C}/\text{m}^2\cdot\text{day}$). The highest value recorded represents an isolated measurement but rates of $10.0\text{--}15.0 \text{ g O}_2/\text{m}^2\cdot\text{day}$ ($3.8\text{--}5.6 \text{ g C}/\text{m}^2\cdot\text{day}$) are fairly common. During most of the year rates



TEXT-FIG. 14.—Seasonal changes in computed daily gross photosynthetic productivity (ΣnP), 1968–71.

of gross production $>5.0 \text{ g O}_2$ (1.9 g C)/ $\text{m}^2\cdot\text{day}$ were maintained. Values $<5.0 \text{ g O}_2$ (1.9 g C)/ $\text{m}^2\cdot\text{day}$ were restricted mainly to autumn and winter months (September–March), with the exception of a midsummer minimum, of short duration, observed in 1970 and 1971.

Annual mean daily gross productivity (assessed over the 4 years) is 5.8 g O_2 (2.2 g C)/ $\text{m}^2\cdot\text{day}$.

At the latitude of Loch Leven, 56°N , daylength varies between 17.6 hours in June and 6.9 hours in December (Smithsonian Meteorological Tables 1951). Clearly, from equation 5 of Talling (1965), reproduced above, seasonal variation in daylength (Δt) exerts a direct influence on the amount of daily gross production (ΣnP) possible for any given hourly value (nP). As a determinant of water temperature, daily incident radiation exerts further control of ΣnP , by virtue of the influence of temperature on photosynthetic capacity (P_{max}). Thus low daily light intensities and temperatures are major factors limiting daily gross productivity in winter months in Loch Leven, as in many other temperate lakes. However, other factors being equal, the limitations which low winter light intensities impose on daily gross productivity are likely to be reflected in a less severe limitation of net production (and therefore of potential biomass accumulation) in a shallow lake than in a deeper lake. This is because shallowness, in reducing respiration losses, can partly compensate for low winter

illumination. The relative shallowness of Loch Leven is one of the factors which may contribute to the higher winter crops and earlier spring rises encountered here as compared with other deeper temperate lakes like Windermere (Talling 1971). Within the limits of incident light intensity and temperature imposed largely by latitude, daily rates are determined by the influence of 'local' conditions on the ratio nP_{\max}/k_{\min} discussed earlier and shown to be the chief determinant of hourly photosynthesis per unit area (ΣnP). 'Local' factors are clearly important in restricting gross daily production to low levels in midsummer, when daylength and water temperature are close to maximal. The midsummer minima found at Loch Leven coincide with periods of particularly low crop densities. This observation does not invalidate the overall absence of a correlation between population density (n) and areal productivity (ΣnP) described earlier (text-fig. 7). 'Uncoupling' of n and ΣnP variations is more severe at higher population densities owing to (i) self-shading, (ii) inverse relationships between phytoplankton density (n) and photosynthetic capacity (P_{\max}).

The highest values of daily gross productivity recorded for Loch Leven lie towards the upper end of the range of values so far encountered in natural waters. According to Steemann Nielsen (1954), the most productive tropical and sub-tropical oceans yield between 0.5–3.0 g C/m².day. Of the 35 lakes in Europe and North America listed by Vollenweider (1968), only one has a maximum daily production as high as the maximum found at Loch Leven and only five have rates > 10.0 g O₂ (3.8 g C)/m².day—a fairly common upper value at Loch Leven. The annual mean daily gross production rate at Loch Leven is higher than that of any of the lakes listed by Vollenweider (1968), and according to the classification scheme of Rodhe (1969) places Loch Leven in the 'eutrophic polluted' category.

Daily rates between 10.5 and 16.0 g O₂ (4–6 g C)/m² were recorded by Talling (1965) in a number of African lakes. Similarly high values have been measured in fertilised fish ponds in Israel (Hepher 1962) and in impoundments and ponds in India (Sreenivasan 1972). Such rates approach the maximum rates of net production (ca 14 g C/m².day) which have been achieved in outdoor mass cultures of algae (Tamiya 1957).

Daily rates of gross production will clearly approach an upper limiting value as the amount of phytoplankton in the euphotic zone approaches its theoretical maximum. As discussed earlier this upper limit to 'photosynthetic cover' is at times closely approached at Loch Leven and is an important factor contributing to the high daily rates observed. Once this upper limit to the size of the euphotic crop is reached, the maximum daily production limit is set essentially by the photosynthetic capacity of the algae and by daylength. Based on such considerations Vollenweider (1968) estimates that the theoretical upper limit to daily production is of the order of 10–20 g C/m².day.

Annual gross productivity. Annual production values (table 1) were determined by planimetry of the areas under the curves of daily rates in text-fig. 14. Carbon-based values were calculated assuming a photosynthetic quotient of 1.0. Table 1 also shows annual incoming radiation totals and percentage energy conversion estimates (calculated assuming 1 g O₂ evolved in photosynthesis is equivalent to 15841 joules fixed). In order to obtain a figure for annual production for each calendar year studied the values for the beginning of 1968 and the end of 1971, which were not actually measured, have been taken as equal to the mean of the three intervening December/January values determined from the continuous curve in text-fig. 14.

Mean annual gross productivity over the 4 years was estimated as 2100 g O₂ (785 g C)/m².year. On the basis of this value Loch Leven would be considered 'polytrophic' in the classification scheme of Vollenweider (1968), and 'eutrophic polluted' in that of Rodhe (1969).

TABLE 1

Total incident radiation, annual gross phytoplankton production and percentage energy conversion estimates for 1968-71

Year	Total incident radiation (J/m ² .y)	Gross productivity			Percentage of total energy converted in photosynthesis
		g O ₂ /m ² .y	g C/m ² .y	J/m ² .y	
1968	372 × 10 ⁷	1918	720	30 × 10 ⁶	0.8
1969	397 × 10 ⁷	2590	971	40 × 10 ⁶	1.0
1970	387 × 10 ⁷	2310	853	36 × 10 ⁶	0.9
1971	395 × 10 ⁷	1590	597	25 × 10 ⁶	0.6

Respiration Rates and Net Daily Photosynthetic Productivity

If measured rates of community respiration are assumed to be due to phytoplankton alone, they are equivalent to values ranging from 0.1 to 3.9 mg O₂/mg chlorophyll *a*.hour. Values greater than 2.0 mg O₂/mg chlorophyll *a*.hour were uncommon and generally restricted to summer months (June-August). Overall no clearly defined relationship was apparent between respiration rates and water temperature. The ratio (*r*) of respiratory rate to light-saturated photosynthetic rate (both expressed per unit volume of water) varied from 1 : 2 to 1 : 14.

Daily respiratory oxygen consumption per m² over 4.8 m (the effective mean depth) was calculated on the assumption that hourly respiration rates remained constant over 24 hours and were the same throughout the water column. Effective mean depth was used in these calculations in preference to the mean depth, for the reasons discussed by Talling (1957*b*). Effective mean depth was calculated according to Talling (1957*b*). The estimates of daily respiratory loss frequently equalled or exceeded estimated daily photosynthetic gain. Zero or negative values for net photosynthetic productivity were found even over periods when algal population densities were increasing.

Uptake and utilisation of organic carbon compounds by the phytoplankton could contribute to this discrepancy but it is not known if this occurs at Loch Leven.

Underestimation of gross photosynthetic productivity, another possible reason for the discrepancy, was attributed by Golterman (1971) to the occurrence photochemical oxidation and by Kowalczewski and Lack (1971) to the use of stationary bottles. These two sources of error were investigated and found to be unimportant at Loch Leven (Bindloss in prep.). Photorespiration was not investigated. If it occurs, it could lead to underestimation of gross rates of oxygen evolution. At present it is uncertain whether photorespiratory oxygen uptake is accompanied by carbon dioxide release in algae (Lex, Silvester and Stewart 1972). If carbon dioxide is evolved with an R.Q. of 1, then although photorespiration would cause underestimation of gross production, it could not explain the discrepancy between estimates of net photosynthetic productivity and observed algal crop changes.

The use of community (rather than algal) respiration rates in the calculations of

net photosynthesis is probably a major cause of underestimation of net productivity. It was not possible to separate the phytoplankton from all zooplankton and bacteria and therefore the contribution of non-algal respiration is not known. It is interesting to note, however, that most of the measured respiration rates, when expressed per unit of chlorophyll, fall within the range of values reported by Ryther and Guillard (1962) for bacteria-free cultures of marine planktonic diatoms.

Dissolved oxygen concentrations below saturation were recorded in the euphotic zone on several occasions confirming that a negative community oxygen balance does sometimes exist. However, dissolved oxygen levels and pH values were frequently above their respective air-equilibrium values when estimates of net daily oxygen production were negative. This additional anomaly suggests that community respiration rates may themselves be overestimates. Underestimation of gross photosynthesis by photorespiration could not account for this anomaly since photorespiratory oxygen uptake would occur in the open water as well as in the experimental bottles.

The assumption that dark respiration rate is constant over 24 hours may be in error and may have led to overestimation of daily respiratory losses. Thus Kok (1952) found with *Chlorella* cultures that after a period of illumination, the rate of O₂ uptake declined slowly reaching a low and steady endogenous level after *ca* 20 hours.

Community respiration rates in 3-hour exposures yield very small changes in oxygen concentration which are sometimes almost at the limit of sensitivity of the Winkler method. Respiration rates as measured in this study are therefore subject to relatively greater inaccuracies than are the measurement of gross photosynthesis. Even small errors assume greater importance when hourly respiratory rates per unit volume are extrapolated to a 24-hour areal basis. Such experimental errors may account, at least in part, for the discrepancies described above. Measurement of respiration rates from longer exposures was inconvenient for routine use and of debatable value since bacterial activity is likely to be enhanced, particularly in longer exposures, by the provision of solid bottle surfaces (Zobell and Anderson 1936).

Because of these as yet unresolved uncertainties, it is not possible to offer a reliable estimate of net photosynthetic productivity.

In pure cultures of algae, and in some natural populations where respiration due to bacteria and zooplankton is negligible, the rate of respiration of actively growing healthy cells is often found to be a more or less constant function (5–15 per cent) of the light-saturated photosynthetic rate (Ryther 1954, 1959; Steemann Nielsen and Hansen 1959; McAllister, Shah and Strickland 1964).

Daily net photosynthetic production rates, calculated assuming a relative respiration rate (*r*) of 0.05, ranged from 0.3 to 14.7 g O₂/m².day. Annual net production values, estimated from the areas under the seasonal curves of net daily rates (not shown), are 1132 g O₂ (18 × 10⁶ J)/m².year in 1968, 1643 g O₂ (25 × 10⁶ J)/m².year in 1969, 1424 g O₂ (22 × 10⁶ J)/m².year in 1970 and 913 g O₂ (14 × 10⁶ J)/m².year in 1971. Estimates of net production are extremely sensitive to the value assumed for the relative respiration rate, the variability of which is largely unknown. Consequently the accuracy of the above net production values is also unknown. In fact, all that can be said with any confidence is that net annual production must be less than gross annual production. The latter value is not completely useless in the study of food chain dynamics: if the food demands of the secondary producers are in excess even of gross primary production by phytoplankton, then this would indicate that these

animals must also be utilising non-phytoplankton material (e.g. benthic algae or allochthonous material).

Because of self-shading, gross daily photosynthesis per m^2 does not increase as a direct result of increase in population density. Unless the self-shading limitation is offset by parallel increases in daily irradiance and/or photosynthetic capacity, 24-hour column respiration losses are likely to increase in relation to daily gross photosynthesis as population density increases. Thus self-shading tends to push the population towards a position of zero net production. The above net production values calculated for a relative respiration rate (r) of 0.05 are all greater than zero. Thus, under Loch Leven conditions, light-limitation of net production, due to self-shading, would never be sufficient to preclude further increase in population density if relative respiration rate (r) remained constant at 0.05. However, respiration rate is likely to become a relatively greater fraction of the light-saturated photosynthetic rate when the latter is inhibited by high pH or other population density-dependent factors. High pH is thus likely to reinforce the self-shading effect in limiting net production and hence the rate of biomass accumulation.

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