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Dr. LOTHAR KALBE,
Dr. HEINZ WERNER,
Institut für Hygiene
der Universität Rostock,
DDR – 25 Rostock,
Leninallee 70

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DON T. WAITE and H. C. DUTHIE

Department of Biology, University of Saskatchewan, (Regina Campus), Saskatchewan
Department of Biology, University of Waterloo, Ontario

An Analysis of the Nutrient Contribution by Phytoplankton Primary Production to the Food Web of a Small Lake[1]

Abstract

Phytoplankton primary production was measured for 148 days, from May 31 to October 2... in Sunfish Lake, Ontario, using the ^{14}C light and dark bottle technique. The purpose of the ... ment was not only to measure the rate of production but also to give some indication of t... of the material produced by the algae.

The following data were calculated for the sampling season: total gross production 57,7... C m^{-2}; algal respiration 31.74% of gross production; total net production 39,895.4 mg ... extracellular production 9.2% of total net production. The efficiencies of both gross and n... production were inversely correlated with light intensity. The rate of extracellular product... directly correlated with the rate of total production. The rate of respiration was not signif... correlated with either the rate of gross production or with the algal biomass as calculated from ... tial cell counts. The weekly rate of phytoplankton turnover was calculated by combining ... ments of algal biomass with net particulate production measurements. The turnover rate... phototrophic zone ranged from plus 6,788.5 mg C m^{-2} to minus 1,104.4 mg C m^{-2}. The ... figure indicates an increase in algal biomass which can not be accounted for by primary prod... The rate of phytoplankton turnover was compared with fluctuations in the standing crop... plankton but the correlation was not significant. Gross and net rates of extracellular pr... were estimated and compared. There was no significant difference between the two measu... and the implications of this are discussed with respect to other work in the field.

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1. Introduction . . . . . .
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4. Summary . . . . . .
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1. Introduction

Dynamic measurements of phytoplankton primary production have been rel... common in the literature. Presumably the purpose of most of these studies h... to evaluate the contribution of phytoplankton fixed carbon compounds to t... web of aquatic systems. A thorough evaluation of the food producing role of p... plankton should, however, involve more than a simple measurement of photosy... rates.

The ^{14}C light and dark bottle technique was chosen for this present study ... allows easy measurement of extracellular production (Fogg, 1969) a...

[1] Research supported by a grant from the National Research Council of Canada to H. C. Duthi...

articulate) fixation. By manipulation of incubation times it is possible to estimate oth gross and net rates of primary production as long-term (in this case 24 hours) cubations permit a considerable amount of respiration of photosynthetically fixed rbon (Vollenweider and Nauwerck, 1961). Gross production can be calculated om short-term (4 hour) incubations by referring to the daily light curve (Goldman, 961). Subtraction of net from gross production provides an estimation of respiration hich is not affected by the potential problems of photorespiration as outlined by och, Owens and Kok (1963) and Lex, Sylvester and Stewart (1972). From a oduction point of view it would seem preferable to talk of respiration in terms of rbon utilized (or CO_2 produced) rather than in terms of O_2 uptake.

When discussing production it is necessary to differentiate between extracellular d cellular or particulate production as these may be considered to enter the food web a two different pathways. The extracellular products enter the dissolved organic aterial pool of the system while the cells themselves might be considered part of the rticulate material pool. The fate of extracellular products is somewhat difficult to aluate. The loss of cells from the system through sedimentation, grazing or death ay be estimated by calculating the rate of phytoplankton turnover. This, in fact, ight provide an even better estimate than photosynthesis of the contribution of ytoplankton to the food web as it indicates the removal of algae from the system d could be compared with zooplankton grazing rates, algal sedimentation rates, c. to indicate the immediate fate of phytoplankton metabolites. There seems, however, to be little use of this technique.

It was our intention, in this paper, to provide a fairly complete estimation, for a full mmer season, of the production role of phytoplankton of Sunfish Lake, Southstern Ontario. Sunfish Lake is a small meromictic body of water with a very tricted circulation (Duthie and Carter, 1970). It was thought that the input of ochthonous material would be relatively small as the main inlet flows only periodily and the incoming water has been seen to move directly to the adjacent outlet. cause of this, phytoplankton production could contribute significantly to the lake od web and the data in this paper could provide important baseline data for future trition studies on the lake.

2. Methods

Gross and net primary production were measured using the light and dark bottle ^{14}C technique. s method has been extensively reviewed in the literature since its introduction by Steemann lsen (1952) and the procedure followed was essentially the same as that described by Goldman, emann Nielsen, Vollenweider and Wetzel (1969). Net primary production was measured using a twenty-four hour, sunrise to sunrise incubation period. Enrichment bioassays indicated t the common nutrients did not become limiting in the bottles during the incubation time. ss primary production measurements were based on a four hour incubation period from 10:30 to 2:30 p. m. The daily gross production was calculated by comparing the light energy during incubation period with the total day's light energy using the following equation:

$$\text{Gross production day}^{-1} = \frac{(A)\,(B)}{(C)}$$

e A = production for 4 hours
B = light intensity (cal cm $^{-2}$ day $^{-1}$) for the day
C = light intensity (cal cm $^{-2}$) for the incubation period.

e use of this calculation was based on Goldman's (1961) report of little asymmetry in the response of phytoplankton to light. For logistical reasons it was not possible to measure production by a day-long series of four-hour incubations as suggested by Vollenweider

Water samples for production experiments were taken, with an opaque, ...te Kemmerer bottle, at the surface, 0.5, 1, 2, 4, 6, 8, and 10 m depths. Four subsamples were taken in 125 ml, ground glass stoppered bottles from each sample. $NaH^{14}CO_3$ was injected and the bottles (two dark and two light) were suspended in the lake for the incubation period. To reduce the problems of light inhibition (Goldman, 1961) all sample manipulation was done under a black plastic tent on the boat. At the end of the incubation period the samples were transported to the laboratory in light-proof boxes for immediate filtration.

Before filtration the samples were agitated and 0.5 ml of the liquid was removed. This was counted in a Triton-X-100 and toluene liquid scintillation fluor (Waite, Duthie and Matthews, 1973) to determine added radioactivity. A 10 ml aliquot from each bottle was filtered on 2.5 cm, 0.45 μ pore, millipore filters. The filters were washed with 5 ml of 0.01 N HCl and counted in a 2-methoxyethanol and toluene liquid scintillation fluor (Waite, Duthie and Matthews, 1973). The filtrate was used to measure extracellular production according to the technique of Fogg (1969). The radioactivity of the extracellular products was measured using the Triton-X-100 and toluene scintillation fluor.

During filtration, pressures never exceeded 10.2 cm (4 inches) Hg. The cell breakage problems reported by Arthur and Rigler (1967) and Schindler and Holmgren (1971) as occurring during vacuum filtration were not evident for Sunfish Lake phytoplankton (Waite, 1973).

Both the four and twenty-four hour incubations were carried out in the same area of the lake each Monday during the sampling season from May 31 to October 25, 1971.

Incident light as Langleys (cal cm^{-2} min^{-1}) was measured with a direct reading Y. S. I. pyranometer connected to a recorder. The curves produced were integrated planimetrically. Recordings were made, with the light cell located on the roof of a building less than eight km from the lake, every day during the entire sampling season. Light penetration curves were measured on each sampling day with a G. M. model submarine photometer. By combining these readings with the incident light measurements it was possible to calculate the light energy present at that depth. The calculations are outlined below:

$$E_{xy} = E_{iy}\,[y\,(1 - L_x) + L_{x1}]$$

where the lake was sampled on days 1 and n:

y represents the y^{th} day between days 1 and n;
E_{xy} is the light energy at depth x on day y;
E_{iy} is the incident light energy on day y;
L_{x1} is the percent incident light on day 1;
$\Delta L_x = [L_{xn} - L_{x1}]\,[(n-1)^{-1}]$, the change in percent incident light, at depth x, from day 1 to day n;
L_{xn} is the percent surface light at depth x on day n.

Weekly production rates were calculated as follows. Production efficiency was calculated for each sampling depth on the basis of the measured light intensity at that depth and the production rates of the bottles at that level using the following equation:

$$K_x = \frac{E_x}{P_x}$$

where K_x is the production efficiency at depth x;
E_x is the light energy at depth x;
P_x is the rate of production at depth x.

The efficiencies on two successive sampling days were integrated to calculate the efficiencies, for depth, for each day between the two sampling days. For example, if the lake were sampled on days 1 and n, the equation to calculate the production efficiencies for a day between would be

$$K_{xy} = K_{x1} + \left[\frac{K_{xn} - K_{x1}}{n-1}\right] y$$

where K_{xy} is the efficiency at depth x on the y_{th} day between the sampling days 1 and n:

K_{x1} is the efficiency at depth x on day 1;
K_{xn} is the efficiency at depth x on day n;
y is the day, between 1 and n, for which efficiency is being calculated.

Combining this efficiency factor for each day and each sampling depth with the calculated light intensity for that depth it is possible to estimate the rate of primary production for days not sampled. The calculation is:

$$P_{xy} = (E_{xy})\,(K_{xy})$$

where P_{xy} is the rate of primary production (ppm C time^{-1}) at depth x on day y.

This method of calculation was used for both gross and net rates of production.

Certain terminology should be defined at this time. Extracellular production refers to organic material, fixed by the phytoplankton cells during photosynthesis and then released into the lake. Particulate production is material fixed by the cells and retained within them. Following the practice of Hellebust (1965) total production represents the sum of particulate and extracellular production.

Differential phytoplankton cell counts were made at each production sampling depth on each sampling day. Water samples were prepared in Lugol's solution and enumerated with an inverted microscope (Utermöhl, 1958 from Margalef, 1969). Cell volumes were calculated and converted to weight as mg C using a factor of 10% of the volume (Vollenweider, 1969a).

The zooplankton standing crop was measured on most sampling days. Three total vertical hauls were made with a 10 mesh plankton net with a mouth area of 163.4 cm^2. The average dry organic weight (60 °C) of these samples was determined and the standing crop expressed as g m^{-2}. The zooplankton samples were taken at the same station as the primary production measurements.

3. Results and Discussion

The total gross and net primary production calculated for the sampling season of 148 days is shown in Table 1. Of the 40 different types of phytoplankton identified from the lake about 11 species were present for most of the summer (Table 2). The biomass data (Table 3) represents the conversion of volumetric data to carbon content for all species within the euphotic zone (Vollenweider, 1969a). The actual measured rates of total gross and net primary production are shown in Figure 1. The space between the two lines of Figure 1 represents the quantity of inorganic carbon released after fixation as organic material. It is, in effect, and estimation of phytoplankton respiration although it could also include algal material respired by herbivores. Based on the calculations for seasonal production (Table 1) it appears that 31.74% of the total gross production was released as inorganic carbon, leaving 68.26% of the total fixed carbon as organic material to be utilized by other trophic levels. The potential problems of photorespiration (Hoch, Owens and Kok, 1963 from Forti, 1965; and Lex, Westlake and Stewart, 1972) make it unwise to compare respiration rates measured by oxygen uptake with those measured by CO_2 formation. The figure of 31.74% is not, however, out of line with Steele's (1965) mean results from the North Sea of 26% respiration at the level of maximum photosynthesis.

Table 1. Some production data for Sunfish Lake for the sampling season (148 days)

Total gross production	57,770.6 mg C m^{-2}
Respiration	17,875.2 mg C m^{-2}
Total net production	39,895.4 mg C m^{-2}
Net extracellular production	3,670.4 mg C m^{-2}
Total incident light energy	43,792 × 10^4 cal m^{-2}

Table 2. Phytoplankton species list and dates of occurrence within the phototrophic zone

	May		June			July			August				September				October		
	31	7	14	21	28	5	12	19	26	2	9	16	23	30	6	13	20	27	4	11	18	25
DIVISION CYANOPHYTA																						
Anabaena sp.		×																				
Aphanothece nidulans			×	×																		
Chroococcus sp.					×																	
Chroococcus dispersus																						
Chroococcus limneticus																						
Chroococcus pallidus																						
Chroococcus turgidus						×																
Coelosphaerium Kutzingianum																						
Coelosphaerium Naegelianum																						
Dactylococcopsis acicularis																						
Dactylococcopsis raphidioides																						
Gloeopsa punctata																						
Gleothece linearis																						
Gomphosphaeria aponina																						
Gomphosphaeria lacustris																						
Gomphosphaeria lacustris var. *compacta*																						
Microcystis aeruginosa																						
Oscillatoria Agardhii																						
DIVISION CHLOROPHYTA																						
Ankistrodesmus falcatus																						
Cosmarium depressum																						
Cosmarium subtumidum																						
Crucigenia quadrata																						
Kirchneriella sp.																						
Mougeotia sp.																						
Oocystis sp.																						
Pandorina morum																						

no data

Fortsetzung Tabelle 2

	May 31	7	June 14	21	28	5	July 12	19	26	2	August 9	16	23	30	6	September 13	20	27	4	October 11	18
DIVISION CHRYSOPHYTA																					
Class Bacillariophyta																					
Cyclotella bodanica																					
Fragillaria crotonensis		×																			
Nitzschia sp.	×		×																		
Stephanodiscus hantzschii		×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×
Synedra sp.						×															
Synedra tenera		×	×	×	×		×		×	×											
Synedra ulna		×																			
Class Chrysophyceae								no data													
Chrysosphaerella sp.																					
Mallomonas sp.		×				×					×		×								
Rhizochrysis limnetica	×																				
Synura sp.																					
DIVISION PYRRHOPHYTA																					
Class Cryptophyceae																					
Cryptomonas erosa	×	×	×	×			×		×	×	×	×	×			×	×		×	×	
Rhodomonas minuta	×	×	×	×		×	×		×	×	×	×	×			×	×		×	×	

Table 3. Phytoplankton standing crop (mg C m^{-2}) calculated to 11 m) of the phototrophic zone as calculated from differential volumetric sp[illegible] counts

Date		Mg C m^{-2} (to 11 m)
May	10	16,156.2
	17	9,674.8
	31	9,925.7
June	7	4,800.1
	14	656.6
	21	2,077.6
	28	2,214.2
July	5	2,631.1
	12	2,032.1
	19	2,067.0
	26	2,101.8
Aug.	2	2,800.3
	9	3,720.4
	16	1,409.0
	23	1,958.3
	30	4,388.0
Sept.	6	6,817.7
	13	3,218.7
	20	5,088.8
	27	4,145.8
Oct.	4	3,202.8
	11	3,548.7
	18	2,863.5
	25	1,589.4

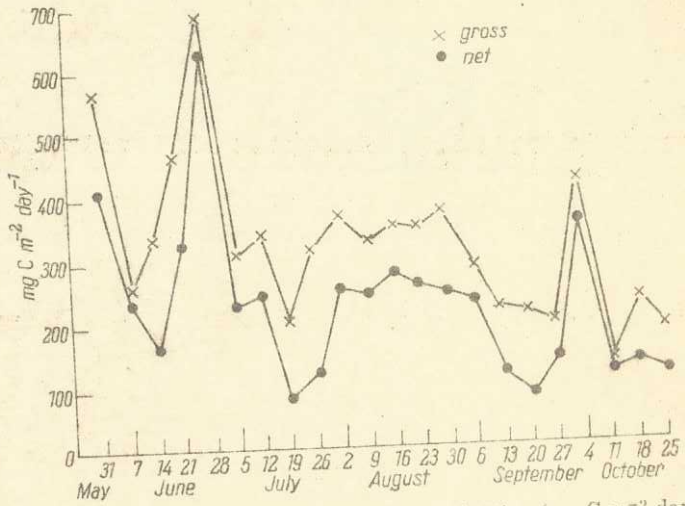

Fig. 1. Total gross and total net primary production (mg C m^{-2} day^{-1}).

The rate of respiration varied throughout the season and did not correlate w either the total gross rate of production or with changes of the phytoplankton stand crop. It may be that changes in the physiological state of the phytoplankton c

...ELE, 1965) or ...he species composition of the algal community masked any ...lations.

The daily production efficiency of the phototrophic zone was calculated for the ...pling days using the following equation:

$$\text{Efficiency} = \frac{P}{(E)\ (B)}$$

...ere

P is the rate of primary production (gross or net) as mg C m^{-2} day^{-1};
E is the light energy immediately below the water surface (cal cm^{-2} day^{-1});
B is the algal biomass as mg C m^{-2}.

The above equation does not provide a true efficiency factor as efficiency is con...ered dimensionless (PLATT, 1969). To convert our efficiency factor to a dimension...s quantity it would be necessary to substitute energy data in place of the carbon ...ntities for factors P and B. The factor of 13.3 kcal (g carbon)$^{-1}$ has been suggested PLATT and IRWIN (1968 from PLATT, 1969) to convert primary phytoplankton ...duction to energy fixation but it was felt that use of this constant would provide ...le information that could not be obtained from the above equation. For proper ...sideration the energy content of the phytoplankton population and of the photo...thate must be measured on each sampling day as these factors can be expected to ...y throughout the year (PLATT, 1969).

The regression of production efficiency, corrected for biomass, against the light ...ensity immediately below the water surface (subsurface light intensity) was calcu...ed for both gross and net rates of total primary production. The regression with ...ss production efficiency (Figure 2) was significant at the level of $p = 0.05$. The ...ression coefficient was negative indicating that phytoplankton production effi...ncy decreased as the light intensity increased. This may reflect the effect of light ...ibition or saturation on primary production noted in the literature (GOLDMAN, ...1; EL...TER, 1965; VOLLENWEIDER, 1965). A decrease in the amount of surface light

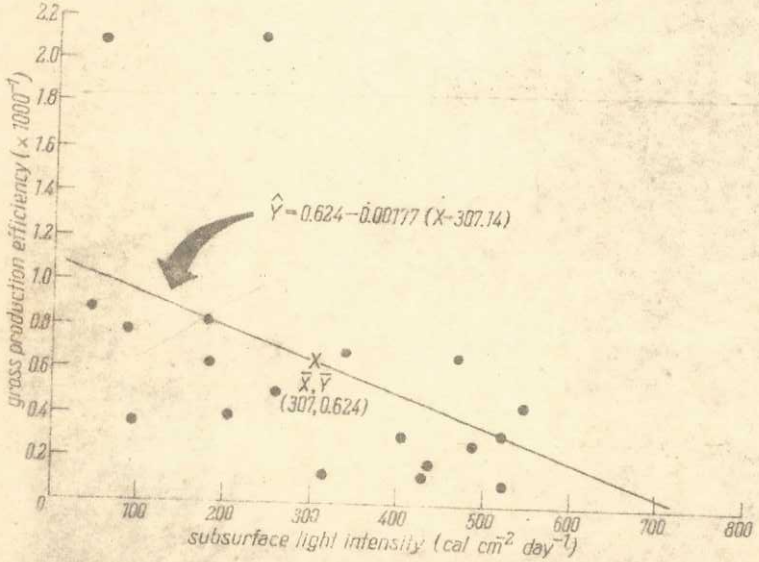

Fig. 2. Regression of total gross production efficiency against subsurface light intensity. $\hat{y} = 0.624 - 0.00177\ (x - 307.14)$; $p = 0.05$.

inhibition was noted by WAITE (1970) on cloudy days of ver...w light intensity. A negative correlation between incident light intensity and ... rate of primary production was also reported although the level of significance was low ($p = 0.22$) (WAITE, 1970).

The regression of net production efficiency on light energy was also negative (Figure 3) but of a lower level of significance ($p = 0.10$). The lower level of significance

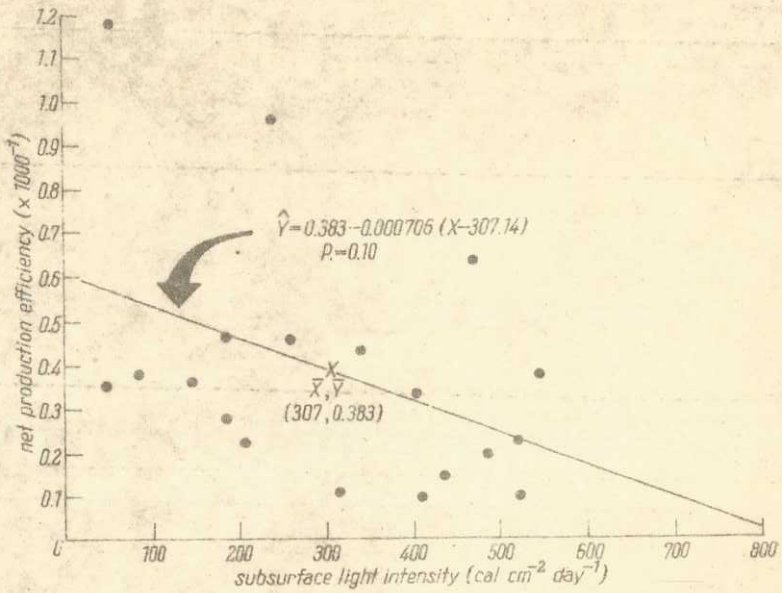

Fig. 3. Regression of total net production efficiency against subsurface light intensity.

may result from a differential effect of respiration on the production data. It wa... noted, at the beginning of this section, that the rate of phytoplankton respiration wa... not significantly correlated with either the rate of gross production or with the phyto... plankton biomass.

Extracellular production was measured during both four and twenty-four hour in... cubations, using the equations presented in the Methods section, and was assumed t... estimate gross and net production, respectively. The rationale behind this calculatio... is as follows. The majority of extracellular production is associated with photo... synthesis and occurs in lighted conditions. The dark bottles in Sunfish Lake produ... tion experiments generally produced radioactive extracellular products which we... barely distinguishable from background counts. Glycollic acid has been identified ... one of the major constituents of the extracellular products of some algae and its pr... duction related to the formation of an intermediate in the photosynthetic pathwa... (FOGG, NALEWAJKO and WATT, 1965; TOLBERT and ZILL, 1956; and FOGG and WA... 1965). Other investigators (LEWIN, 1956; HELLEBUST, 1965) have shown that a lar... variety of other compounds may be released by photosynthesizing algal cells. Regar... less of the type of compounds liberated from the cells it seems that this process occ... under light conditions. During the night period in the twenty-four hour *in situ* i... cubations there should be little production of extracellular products but, if the... compounds do provide a nutrient source for the microbial population, heterotrop... assimilation should continue. This assimilation should, then, result in a lower appare... rate of extracellular production in the twenty-four hour incubated bottles than in t...

ur hour incubati[illegible] This is not to say that some assimilation could not have occurred in the four hour incubations, but that this uptake of radioactive organic material would be proportionately greater in the twenty-four hour incubated bottles.

The measured gross and net rates of total production and extracellular production are shown in Figures 4 and 5. It may be seen that the rate of extracellular production seems correlated with the rate of total production in both figures. The linear regressions of extracellular production on total production were calculated for both gross

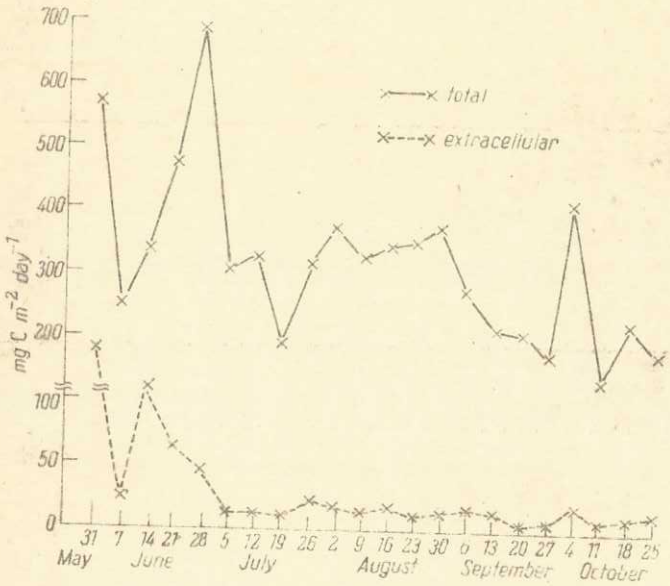

Fig. 4. Total gross and gross extracellular production.

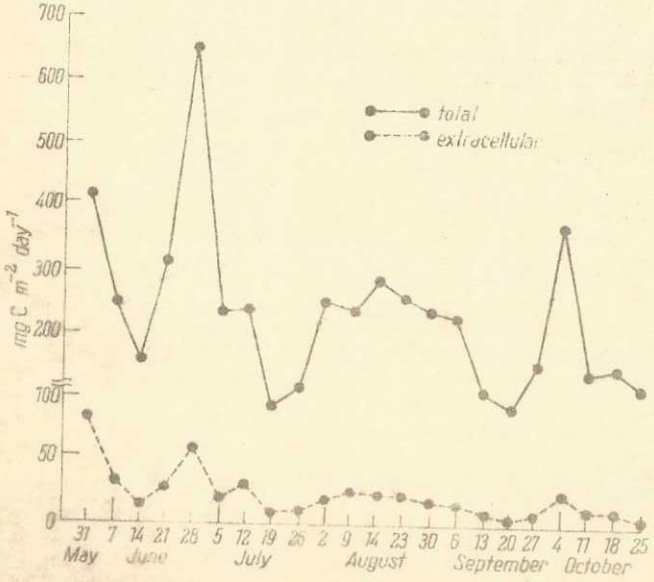

Fig. 5. Total net and net extracellular production.

and net production (Figures 6 and 7). Both regressions were found to be significant at greater than 0.005 level of probability. For Sunfish Lake, then[illegible] rate of extracellular production seems directly related to the rate of primary production when the total

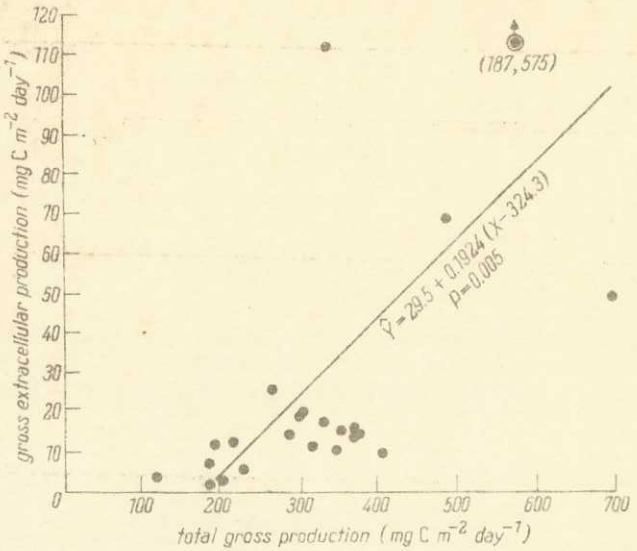

Fig. 6. Regression of gross extracellular production against total gross production.

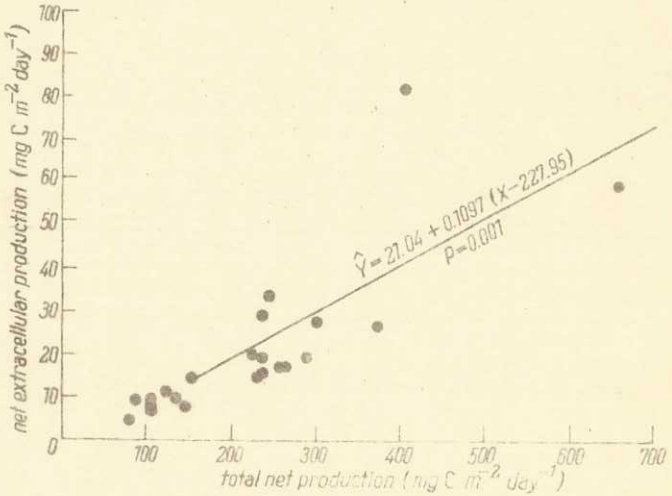

Fig. 7. Regression of net extracellular production against total net production.

column of the euphotic zone is considered. It was calculated that about 9.2% of th[illegible] total net production was released as extracellular products. This is within the rang[illegible] of the results of other investigators (Fogg, Nalewajko and Watt, 1965).

The gross and net rates of extracellular production were then compared (Figure 8). Except for two days at the start of the sampling season there appeared to be litt[illegible] difference between the calculated gross and measured net extracellular productio[illegible]

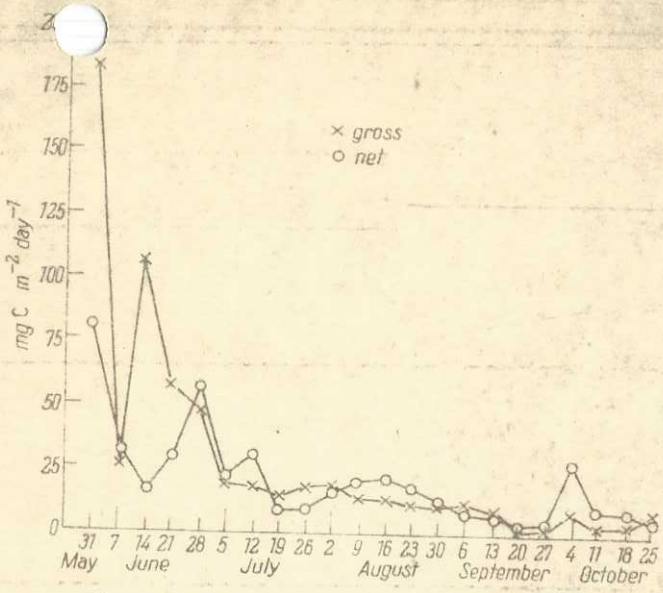

Fig. 8. Gross and net extracellular production.

ates. When the gross and net rates of extracellular production are statistically treated s paired data the two rates can be shown different at only the level of significance of $.4 > p > 0.2$. Furthermore, if the two days, May 31 and June 14, when the rates of roduction are extremely different, are removed from the calculation the level of ignificance decreases to $p > 0.5$. Statistically, then, there seems to be little, if any, ifference between the rate of extracellular production measured in the four hour and enty-four hour production experiments for Sunfish Lake. This would seem to imply hat little immediate use is made of the extracellular phytoplankton products by the icrobiota of Sunfish Lake.

ALLEN (1971) showed that extracellular products of some littoral macrophytes ould be utilized by epiphytic algae and bacteria. FOGG, NALEWAJKO and WATT (1965) ostulated that some phytoplankton extracellular products would be utilized by the quatic microbiota as a nutrient source. WRIGHT and HOBBIE (1965) and VACCARO and ANNASCH (1966) showed that heterotrophic uptake of dissolved organic material DOM) occurred both in lakes and in the ocean. Both bacteria and algae have been plicated as agents of this uptake. The formation of particulate material from DOM s been shown in marine systems at least (BAYLOR and SUTCLIFFE, 1963; RILEY, 963; BARBER, 1966) and it seems likely that similar mechanisms occur in freshwater stems. Such particulate formation involving radioactive extracellular products ould result in the deposition of this material on the filters used in production mea rements. It was most unexpected, then, that there was no apparent or statistical ifference between the rates of extracellular production from the four hour and the enty-four hour incubations.

It should be noted, however, that SAUNDERS (1972) has shown the rate of algal xtracellular production to be asymmetric with the daily particulate production rve. It is possible, that our calculations of gross extracellular production somewhat derestimated the actual production. Unfortunately SAUNDERS does not present any ta on the daily light curves of his sampling days and it is therefore difficult to ate his findings with our data. As periodic cloudyness is common in the area where

Table 4. Phytoplankton turnover rates, as mg C m $^{-2}$, calcula[ted] to 6 and 11 m, fo[r] the periods between and including the dates ind[icated]

Date	To 6 m	To 11 m
May 31 – June 6	2,833.3	6,788.5
June 7 – June 13	1,525.7	5,616.1
June 14 – June 20	439.9	477.3
June 21 – June 27	2,726.1	2,797.2
June 28 – July 4	3,398.7	3,595.9
July 5 – July 11	2,541.4	2,830.1
July 12 – July 18	1,543.4	1,342.8
July 19 – July 25	1,317.1	1,123.7
July 26 – Aug. 1	882.4	733.7
Aug. 2 – Aug. 8	872.2	826.5
Aug. 9 – Aug. 15	2,444.1	3,814.6
Aug. 16 – Aug. 22	778.8	1,174.4
Aug. 23 – Aug. 29	455.5	1,104.4
Aug. 30 – Sept. 5	473.1	1,040.3
Sept. 6 – Sept. 12	2,739.6	5,518.4
Sept. 13 – Sept. 19	645.8	338.2
Sept. 20 – Sept. 26	2,160.4	2,864.6
Sept. 27 – Oct. 3	2,073.4	2,815.0
Oct. 4 – Oct. 10	986.2	1,108.8
Oct. 11 – Oct. 17	1,441.5	1,573.2
Oct. 18 – Oct. 24	1,292.7	2,116.9

our study was carried out symmetrical daily light curves seldom occur. The fluctuatin light levels might reduce the discrepancies caused by a lag in extracellular productio

The turnover rate of the phytoplankton population was calculated (Table 4) usin both standing crop and primary production measurements, as follows:

$$T_{a-b} = [S_a + P_{a-(b-1)}] - S_b$$

Where T_{a-b} is the turnover (mg C m $^{-2}$) from day a to day b
S_a is the standing crop of phytoplankton on day a (mg C m $^{-2}$)
S_b is the standing crop of phytoplankton on day b (mg C m $^{-2}$)
$P_{a-(b-1)}$ is the net particulate primary production for the period from day to day $(b-1)$.

In terms of the above equation, then, the rate of phytoplankton turnover, as used the paper, may be described as follows. The standing crop of phytoplankton w measured as mg C m $^{-2}$ on the first day of the week (for this purpose, on Monday). T rate of primary production was measured, as mg C m $^{-2}$, for the week and the total the carbon fixed was added to the standing crop present on the first day of the wee This total, standing crop plus carbon fixed, represents the quantity of carbon whi should be present on the last day of the week if there is no loss of phytoplankton fro the system. By subtracting the actual standing crop present on the first day of t next week the quantity of phytoplankton carbon removed from, or lost from, the la may be calculated. The turnover rate, then, represents the amount of phytoplankt fixed carbon which has been either removed by grazing or lost through precipitation the bottom.

Turnover rates have been used in bacterial work (SOROKIN, 1969) and zooplankt studies (WINBERG *et al.*, 1971) but little use has been made of this measurement

phytoplankton wo[illegible] The I.B.P. Handbook on Primary Production Methods (Vollenweider, 1969b), for example, makes no mention of this technique for phytoplankton studies. It would seem, though, that this measurement should provide some basic and important estimate of the fate of photosynthetically fixed carbon. It should be realized, however, that the method outlined herein does not consider heterotrophic assimilation by phytoplankton.

The rates were calculated to 6 m and to 11 m, representing the upper half and the total of the phototrophic zone (Figure 9). The majority of the weekly turnover rates

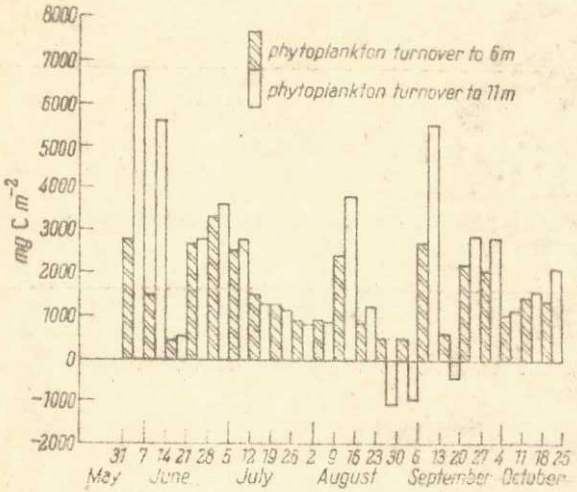

Fig. 9. Phytoplankton turnover rates (mg C m^{-2}) calculated to 6 and 11 m.

were positive indicating that carbon was photosynthetically fixed in excess of that represented by the phytoplankton biomass at the end of the week. Of special interest are the rates of the weeks 23 to 30 August, 30 August to 6 September, and 13 to 20 September. The turnover rates calculated to 11 m were negative for these 3 weeks. This would indicate that the rate of accumulation of algal biomass was in excess of that which can be accounted for by primary production.

The turnover rate to 6 m was positive. The unexplained phytoplankton biomass, then, occurred in the lower part of the phototrophic zone. It seems unlikely that the total increase resulted from an unexpected increase in the rate of primary production at this depth. A high rate of heterotrophic activity by the algae could account for at least some of this material.

The turnover rate calculated to 6 m was rather low for those 3 weeks. Possibly the rate of primary production was underestimated for those weeks. An underestimate of the primary production rate coupled with a relatively high rate of cell sedimentation could also contribute to a negative turnover rate in the lower phototrophic zone.

We attempted to use phytoplankton turnover rates as an indicator of the fate of phytoplankton metabolites by correlating these with the zooplankton standing crop expressed as dry weight [illegible] (Table 5). The rationale behind this comparison was as follows. Some studies have shown that zooplankton can utilize phytoplankton by grazing (Arnold, 1971, Conover, 1966a and 1966b, McAllister, 1969). The degree of utilization of a phytoplankton population would, of course, depend on the species composition of the two groups. If, however, the zooplankton population was directly dependent on phytoplankton for food there should be a correlation between the size

Table 5. Zooplankton standing crop, as g dry organic weight [illegible] for sampling days

Date		Dry Organic Weight (g C m^{-2})
May	31	1.4950
June	7	1.3219
	14	3.1971
	21	9.0387
	28	3.0153
July	5	2.7668
	12	2.0004
	19	No Data
	26	1.9949
Aug.	2	No Data
	9	2.0928
	16	1.6141
	23	No Data
	30	No Data
Sept.	6	1.5786
	13	1.4629
	20	1.2707
	27	0.6053
Oct.	4	No Data
	11	0.6702
	18	0.6580
	25	0.2399

of the zooplankton population and the rate of turnover of the phytoplankton popu[illegible] lation.

This relationship was tested by linear regression. The x values were zooplankto[illegible] dry organic weight as g m^{-2} and the y values the phytoplankton turnover (mg C m^{-2} rate to 11 m for the week preceeding the zooplankton measurement. The correlatio[illegible] was insignificant ($p > 0.50$). The rate of phytoplankton turnover, then, would no[illegible] seem to be related to the size of the zooplankton standing crop. From this either of th[illegible] following may be inferred:

1. The zooplankton of Sunfish Lake do not directly utilize phytoplankton as [illegible] source of food; or

2. There is sufficient food material of another nature present in the lake that th[illegible] dependence of zooplankton on phytoplankton is proportionately reduced.

There is evidence in the literature which suggests that some species of zooplankto[illegible] can survive on a diet of particulate but non cellular organic material (Riley, 196[illegible] Baylor and Sutcliffe, 1963). Unfortunately we have no evidence to either suppor[illegible] or refute this hypothesis for Sunfish Lake. It seems reasonable to suggest, however that, in this lake, the zooplankton do not significantly affect the phytoplankto[illegible] population. The value of phytoplankton turnover rates will, though, have to be mo[illegible] critically examined before any strong conclusions can be drawn from this type [illegible] data.

4. Summary

The primary production measurements on Sunfish Lake covered a period of 148 days, from May 31 to October 25, 1971. During this period the total gross primary production was 57,770.6 mg C m^{-2}. Of this 31.74% was respired by the phytoplankton leaving 39,895.4 mg C m^{-2} available as food for other trophic levels. Of the total net production 9.2% or 3,670.4 mg C m^{-2} was released as extracellular products.

The calculated efficiency rate of total gross primary production, corrected for biomass, was inversely correlated with the subsurface light intensity at a significance of $p = 0.05$. The calculated efficiency rate of net production, corrected for algal biomass, was correlated with the subsurface light intensity at a lower level of significance ($p = 0.10$). The lower significance of the second regression may have resulted from changing rates of algal respiration throughout the summer. The rate of respiration was not significantly correlated with either the gross production or the standing crop of phytoplankton.

The rate of gross extracellular production was significantly correlated with the total gross production. The rate of net extracellular production was directly correlated with the total net rate of production. There was, however, no significant difference between the gross and net rates of extracellular production.

The phytoplankton turnover rate, calculated for all of the phototrophic zone (0–11 m), varied from 6,788.5 to minus 1,104.4 mg C m^{-2}. Variations in the rate of phytoplankton turnover were not significantly correlated with changes in the standing crop of zooplankton.

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Dr. DON T. WAITE
Saskatchewan Department of Environment
Water Pollution Control Branch
11th Floor, SPC Building
Regina, Saskatchewan S4T 2V8, Canada

Dr. H. C. DUTHIE
Associate Professor
Department of Biology
University of Waterloo
Waterloo, Ontario N2L 3G1, Canada

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AKIRA YABE[1] and HIDEO TAKADA

Biology Department, Science Education Institute
of Osaka Prefecture
Biology Department, Faculty of Science, Osaka
City University, Osaka

Light-dependent Synthesis of δ-aminolaevulinic Acid Dehydratase During the Developmental Period of *Trapella* Seedlings

Abstract

Mature seeds of *Trapella sinensis*, after removal of receptacles, were germinated for 10 da at 23 °C in the dark and then were illuminated. After illumination, the activity of δ-aminola vulinic acid (ALA) dehydratase was determined in relation to chlorophyll synthesis, and increas in dry weight of the whole or of parts of a developing seedling. Internal programming of develo ment was related to changes in ALA dehydratase activity on the basis of porphobilinogen synthes Exogenously added ALA as well as an extract of *Chlorella* cells promoted this activity. There w an enhancement of chlorophyll formation resulting in an enhancement of the photosynthet rate and in an increase of growth promotion by addition of *Chlorella* extract.

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1. Introduction

In a series of developmental and physiological studies on the growth of seedlings *Trapella sinensis* OLIV. just after germination, there was good evidence that growt regulators such as gibberellin, kinetin, and an extract of light grown *Chlorella* cel can accelerate growth differently if they are applied to seedlings after 10 days of ge mination, as compared to earlier stages. Because of this, it has been suggested tha growth of seedling in developing and differentiating stages can be divided into tw stages – an initial one being not responsive to regulators and a second which may b promoted by regulators and *Chlorella* extract. Among regulators used, only *Chlorel* extract promoted growth as a result of an activated rate of photosynthesis throug increased chlorophyll formation, as well as an increased respiratory rate through a increased cytochrome oxidase activity (YABE *et al.* 1974 a and b). *Chlorella* extra appears to play a very important role in the differentiation and growth in the secon stage of developing *Trapella* seedlings.

On the other hand, it is obviously of interest to investigate whether the porphyri ring of chlorophylls and cytochromes was constructed in the aquatic plant on the sam

[1] Formerly AKIRA KAWAHARA.