

PLANKTONIC AND BENTHIC METABOLISM
IN GLADFELTER POND

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TABLE OF CONTENTS

	Page
I. LIST OF TABLES	v
II. LIST OF FIGURES	vi
III. INTRODUCTION	1
IV. MATERIALS AND METHODS	4
V. RESULTS AND DISCUSSION	17
Diffusion	17
Insolation and Productivity	20
Planktonic Productivity	20
Benthic Productivity	24
Photosynthetic Efficiency	27
Metabolic Ratio and Community Respiration	31
VI. SUMMARY	34
VII. LITERATURE CITED	36

LIST OF TABLES

Table		Page
I.	Computer and manually calculated planktonic gross primary production (GPP), and community respiration (RESP) based on computer calculated oxygen rate-of-change curves which were corrected for diffusion by utilization of the diffusion constant (k) indicated	19
II.	Computer calculated and corrected areal gross primary production (GPP) and community respiration (RESP) for the benthic littoral community.	26
III.	A comparison of primary productivity by different communities in various aquatic systems	30

LIST OF FIGURES

Figure	Page
1. Topographic map of Gladfelter Pond showing locations of Stations A and B	6
2. Graphs of typical dissolved oxygen variation (above) and corresponding percent oxygen saturation (below) in Gladfelter Pond	9
3. Graphs of oxygen rate-of-change (above) and oxygen rate-of-change corrected for diffusion (below) in Gladfelter Pond	11
4. Diagram showing the assumed inverse linear relationship between depth and benthic productivity	15
5. Linear regression showing the relationship between planktonic productivity and available insolation	22
6. Linear regression showing the relationship between benthic littoral productivity and available insolation	29

INTRODUCTION

Primary production is the transformation of inorganic structural elements into organic matter by autotrophic organisms, and it results in accumulation of producer biomass which serves as the energy source for primary consumers. Primary production may result from photosynthesis which utilizes radiant solar energy, or from chemosynthesis which utilizes the energy in inorganic compounds. In aquatic systems, photosynthesis is generally regarded as the most important of these two modes of energy fixation. The net effect of this biosynthetic activity is to increase organic matter and, hence, energy within the system. The producer community is of great consequence to the system because it is upon this trophic level that the entire trophic structure ultimately depends.

The synecological approach to the study of aquatic community metabolism has facilitated the accumulation of a large amount of literature regarding primary production. The majority of this literature deals with the planktonic community, which frequently is the only component of the producer community considered in production studies (Eley, 1970; Osborne, 1968; 1972; Prophet, 1966; Thomas, 1964; Weedon, 1970).

It is not uncommon for phytoplankton primary production to be reported as representing total primary production for a lake or pond. In marine environments and large, deep lakes this is a reasonable assumption. However, in lotic environ-

ments, estuaries, shallow lakes, and ponds benthic producers often play a major role in energy fixation. In his study of Marion Lake, which is a large, shallow lake in British Columbia, Hargrave (1969) found that benthic littoral primary production accounted for 62.2 % of the primary production for the lake.

The benthic littoral producers consist primarily of periphyton and macrophyton. Literature regarding in situ measurements of macrophytic primary productivity and methods used for its quantification is voluminous. Penfound (1956) presented an extensive review of macrophytic production and related subjects. Although there is an abundance of literature on periphytic primary productivity, results based on in situ measurements are limited (Wetzel, 1963; 1964; 1965; and 1970). Sladeckova (1962) and Wetzel (1964) have reviewed studies of periphyton productivity, but most of the studies cited were based on measurements of temporal changes in biomass. In addition, artificial substrates used for periphyton colonization, which has numerous inherent sources of error (Wetzel, 1964), was employed almost exclusively to determine changes in biomass.

The current study was designed to make in situ estimates of both planktonic and benthic littoral community metabolism and to determine the relative significance of these two components of the producer community in Gladfelter Pond. An understanding of the rate at which solar energy is fixed and made available to higher trophic levels is essential to a comprehension of energy flow within this system.

The limnological features of Gladfelter Pond have been well documented by previous studies. Griffith (1961) conducted a study of physicochemical characteristics and occurrence of fauna when the pond was newly impounded. Subsequent studies include Osborne's (1968) investigation of limnological features and primary productivity, which was conducted in 1965-66, and Perez's (1970) study of limnological and biological characteristics conducted in 1969-70.

Recently, the filter-feeding rates of two species of zooplankters in Gladfelter Pond were studied by Waite (1975). His data are pertinent to the quantification of the energy flux between planktonic producers and primary consumers and provides information which is fundamental to an understanding of planktonic secondary productivity in the pond. Studies such as this and the above are accumulating integral bioenergetics data which will culminate in a more thorough knowledge of the fate of energy in aquatic food webs.

MATERIALS AND METHODS

Gladfelter Pond is a man-made impoundment located on the Emporia Kansas State College Ross Natural History Reservation approximately 22.5 km northwest of Emporia. The early history of the Ross Natural History Reservation and descriptions of its vegetation and topography, have been reported by Hartman (1960) and Wilson (1963).

The pond (Figure 1) attains a maximum depth of 5.0 m and has a surface area of 1.0 hectare at spillway level. It is relatively turbid with a euphotic zone that rarely exceeds 1.6 m in depth and a littoral zone with an area of approximately 0.55 hectare. The pond has a total volume of 18,000 m³, of which roughly 11,500 m³ is in the trophogenic portion.

The watershed for Gladfelter Pond is approximately 32.3 hectares in area, consisting almost entirely of grassland with few trees and no land under cultivation.

After preliminary investigations in July and August 1973, two permanent sampling stations were established (Figure 1). Station A was located in a portion of the pond where water depth was 2.5 m and which was considered representative of the photosynthetically active portion of the pond. Station B was located along a 5.0 m length of the 0.33 m bottom contour and was considered representative of the benthic littoral community at that depth.

The daily oxygen variation method described by Odum (1956), modified for use in lentic environments by Odum and

Figure 1. Topographic map of Gladfelter Pond showing locations of Stations A and B



Gladfeller Pond, R.A.H.R.
Limnology Class
June 1968

Hoskins (1958), and later adapted to computer usage by Eley (1970), was employed to estimate community metabolism in the pond. The method uses oxygen concentration measurements and simultaneous percent oxygen saturation at intervals not to exceed three hours over a 24 hour period. Figure 2 shows these two parameters plotted on the same horizontal time scale. From the oxygen concentration curve the average rate-of change for each interval between observations is calculated and then plotted (Figure 3). A calculated diffusion constant is multiplied by the oxygen saturation deficit and the product is added to the rate-of-change value to compensate for the oxygen change due to diffusion. The corrected rate-of-change curve is presumably due to the metabolic activity of the biota of the pond. A hypothetical daytime respiration line based on average nighttime respiration rates is drawn from a pre-sunrise point on the corrected rate-of-change curve to a post-sunset point on the curve. The accuracy of the daily oxygen variation method is a function of the accuracy in determination of the end points of this line (Odum and Hoskins, 1958).

The area under the corrected rate-of-change curve and above the hypothetical daytime respiration line is gross primary production. The area bounded on the top by the zero rate-of-change line and on the bottom by the continual respiration line represents average community respiration.

A computer program (Eley, 1970) punched on an IBM 026 keypunch and compiled on an IBM 370 Fortran compiler was used to calculate the diffusion constant and corrected rate-of-

Figure 2. Graphs of typical dissolved oxygen variation (above) and corresponding percent oxygen saturation (below) in Gladfelter Pond

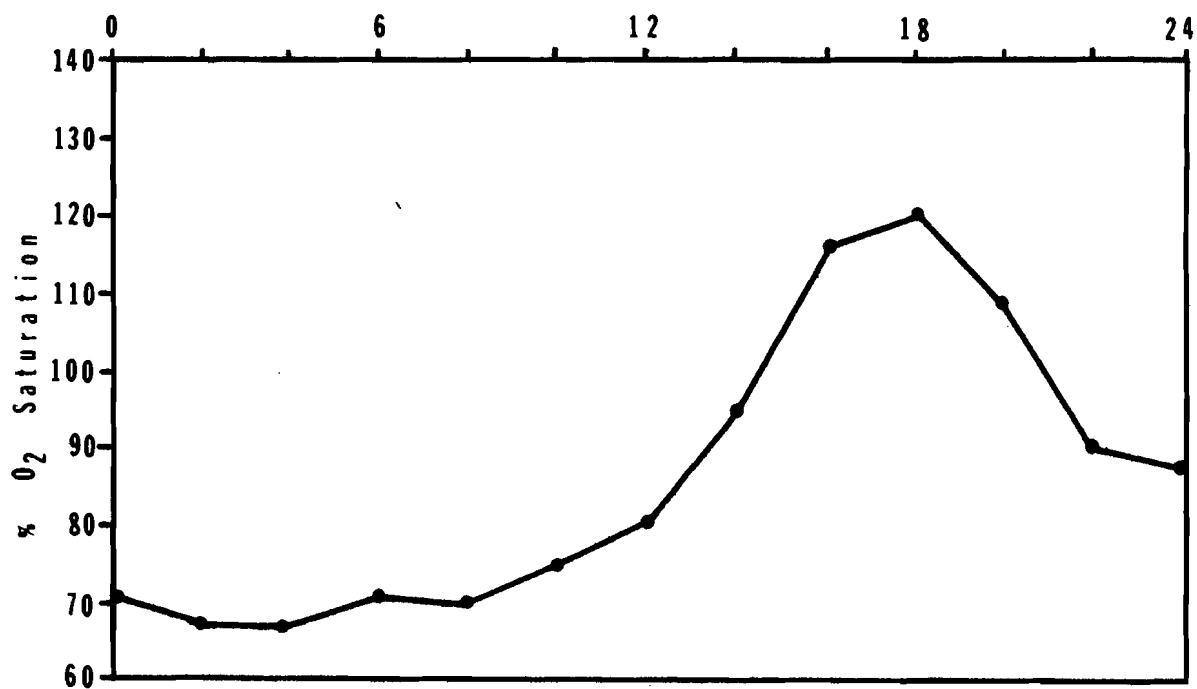
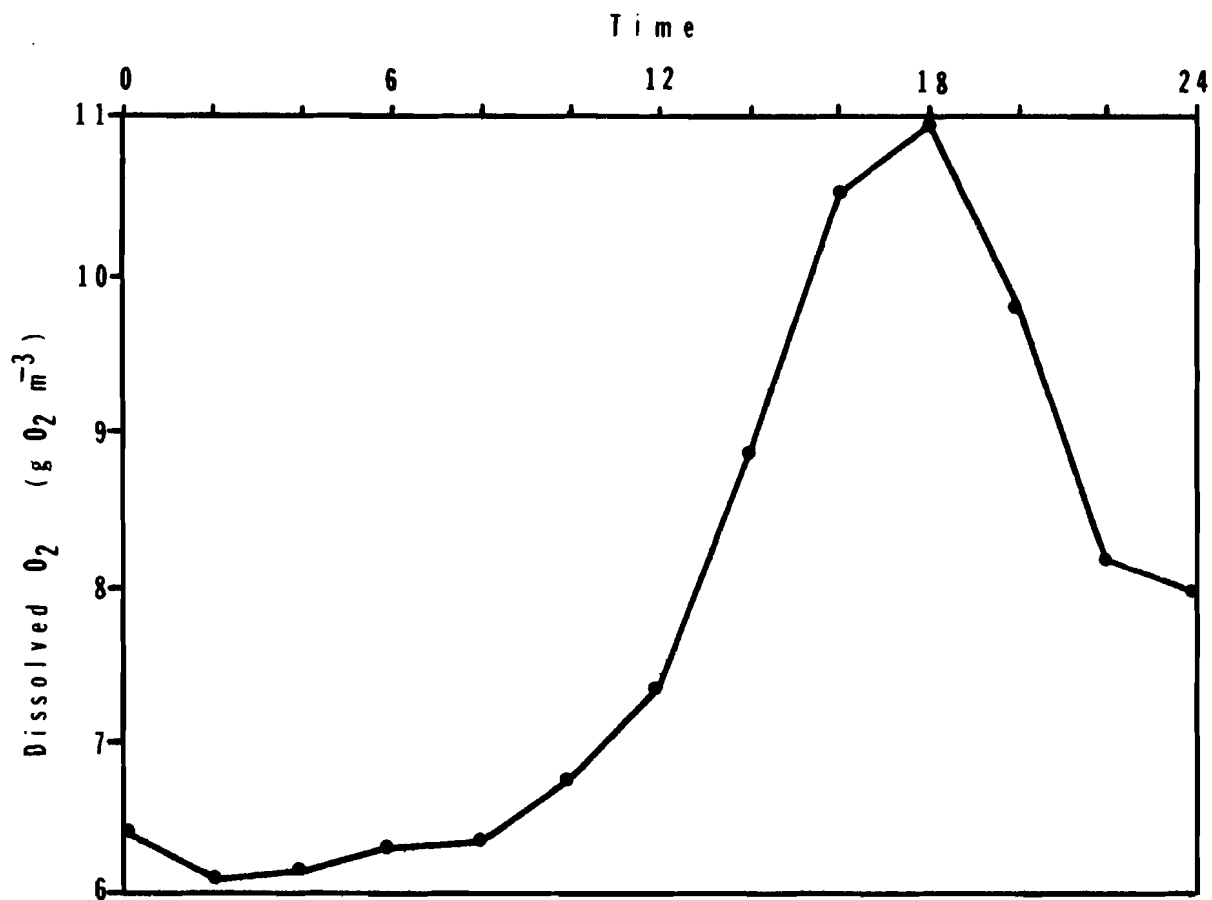
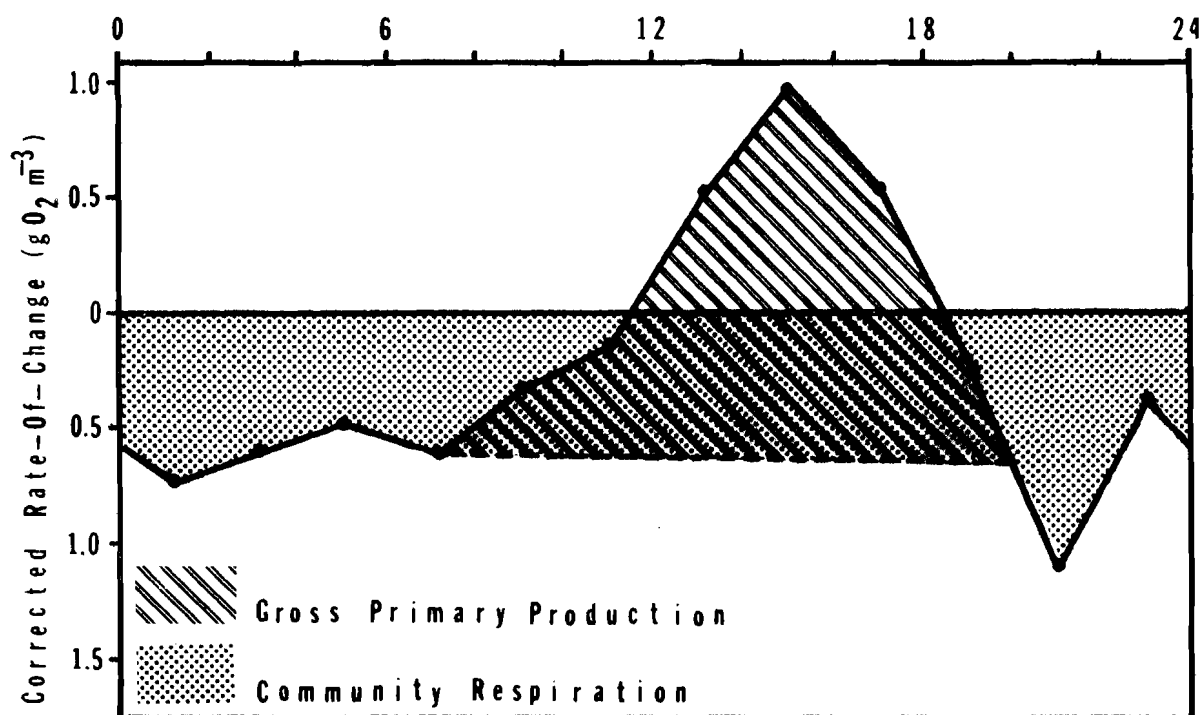
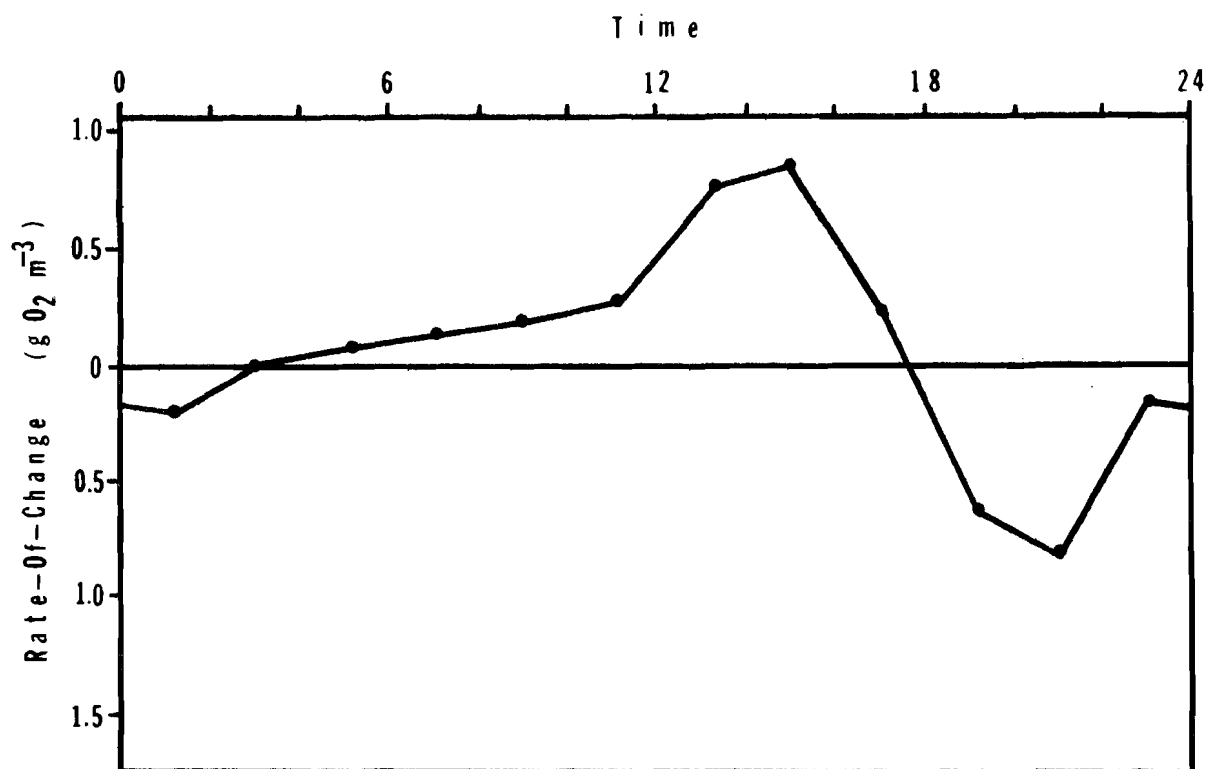


Figure 3. Graphs of oxygen rate-of-change (above) and oxygen rate-of-change corrected for diffusion (below) in Gladfelter Pond



change values. From the corrected daily oxygen rate-of-change curve the computer program also calculated gross primary production, community respiration, net primary production, and productivity/respiration ratios. From the computer calculated corrected daily rate-of-change curve, gross primary production and community respiration were also calculated manually using the graphical method described by Odum and Hoskins (1958).

A Rustrak Model 192 dissolved oxygen and temperature recorder was used to monitor and continuously record dissolved oxygen and temperature.

A pumping device was necessary to circulate water past the dissolved oxygen probe in order to prevent oxygen depletion in the area of the probe membrane. This device utilized a Little Giant Model 1-42AA circulating pump and 0.64 cm inside diameter rigid plastic tubing for intake and return. The maximum capacity of the pump was 8.0 liters per minute, but this was somewhat reduced by restricting the intake and return from 1.67 and 0.95 cm, respectively, to 0.64 cm.

Station A was sampled by pumping water from the 0.8 m depth, the median depth of the euphotic zone, through the pumping device past the oxygen probe and returning it to the edge of the pond.

A clear plastic dome measuring 0.62 m in diameter and 0.31 m in height with a volume of 59.3 liters was used to isolate 3019 cm² of the littoral benthic community at Station B. Water was pumped from one side of the dome, circulated

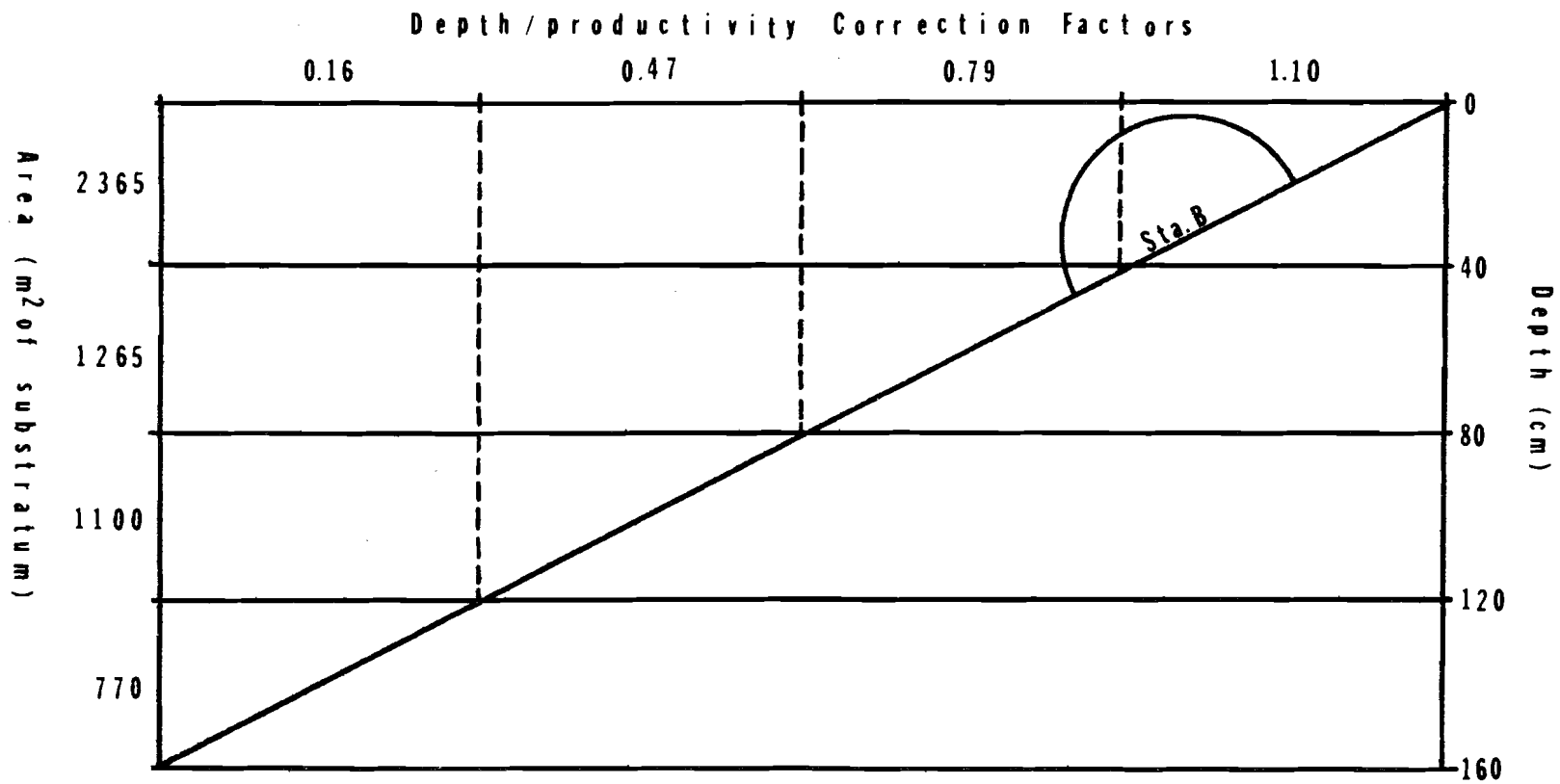
past the dissolved oxygen probe and returned through the opposite side of the dome, thus forming a closed system.

Because input oxygen data were entered in grams per cubic meter, the computer program calculated metabolism in like units. Conversion of volumetric data to metabolism per unit area of substratum necessitated a correction for the 59.3 liters isolated by the plastic dome, which was effected by multiplying by 0.0593. Secondly, the product, which represented metabolism of the 3019 cm² of benthic substratum isolated by the dome, was multiplied by 3.31 to get metabolism per square meter of benthic littoral substratum.

The settling of silt on the surface of the dome and ensuing attenuation of light within the dome was a source of error in estimating photosynthesis under the dome. The dome was cleared of silt as frequently as possible to minimize any error due to siltation.

To facilitate calculation of gross primary production at all depths of the littoral zone a linear relationship between depth and productivity was assumed. This assumption was based on Fogg's (1965) report that in algal cultures with heavy biogenic turbidity photosynthesis decreased linearly with depth below the area of light saturation. Figure 4 is a diagram showing the correction factors derived from a straight line which intersects the lower limit of the euphotic zone at 160 cm where, presumably, there would be zero photosynthesis, and at 33 cm which is Station B. From the topographic map of Gladfelter Pond (Figure 1) it was determined

Figure 4. Diagram showing the assumed inverse linear relationship between depth and benthic productivity



that approximately 43 % of the littoral zone was from 0 - 40 cm in depth, 23 % was 40 - 80 cm deep, 20 % was 80 - 120 cm deep and 14 % was 120 - 180 cm deep. A benthic depth/productivity constant of 4241 was calculated by summing the products of the correction factors and areas within the corresponding depth range. Observed areal gross primary production (m^{-2} of substratum) was multiplied by the depth/productivity constant to ascertain benthic gross primary production for the entire littoral zone.

Intensity ($\text{g cal cm}^{-2} \text{ min}^{-1}$) and daily accrued insolation ($\text{g cal cm}^{-2} \text{ da}^{-1}$) were recorded on a Bristol recorder using an Eppley pyroheliometer, which was located atop Breukelman Hall on the Emporia Kansas State College campus. According to Talling (1957) 47 % of total solar irradiance is within the photosynthetically active portion of the spectrum (from Vollenweider, 1969), and Hutchinson (1957) reported that an average of 7 % of total solar irradiation incident at the surface of a body of water is reflected. Accordingly, recorded total irradiance was multiplied by a factor of 0.4 to correct for the quantity of photosynthetically active radiation available to aquatic producers.

RESULTS AND DISCUSSION

There are three major phenomena, photosynthesis, respiration, and diffusion, which affect the dissolved oxygen concentration in aquatic systems. Continuous monitoring of dissolved oxygen in the field is a relatively simple and direct process. Analysis of dissolved oxygen fluctuation by the daily oxygen variation method previously described allows the partitioning of oxygen change into the three causal phenomena and allows indirect estimates of each. It is imperative that accurate estimates of diffusion, which is determined by derivation of a concise diffusion constant, and respiration, which is dependent upon proper placement of the hypothetical daytime respiration line, be made.

Diffusion

The quantity of oxygen that a volume of water is capable of dissolving is dependent upon the temperature of the water and the partial pressure of the gas at the air/water interface. In general, the direction and rate of diffusion depends upon the extent to which the water is undersaturated or supersaturated with oxygen. This is an over simplification of a complex mechanism but space and the scope of this paper does not permit a detailed discussion beyond quantification.

Theoretical oxygen diffusion rates of $5.0 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (100 % saturation deficit) or greater can be calculated, but

the maximum rate possible under given conditions is not known. Odum and Hoskins (1958) reported that in quiet, shallow, or stratified water, diffusion rates of less than $1.0 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ are usual, while a rate of $3.0 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ or more could occur in turbulent waters. Copeland and Duffer (1964) measured oxygen diffusion rates under a plastic dome and found rates in concrete ponds to vary from zero to $0.5 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ and from approximately 1.5 to $2.6 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ in an Oklahoma stream.

The computer program (Eley, 1970) calculated a daily mean diffusion constant by averaging diffusion constants calculated for each interval between observations. There was, however, an input argument which allowed limitation of the absolute value of any interval diffusion constant to a desired maximum. When a limit of $10.0 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ was used, the computer-calculated daily mean diffusion constants varied between 3.37 and $10.0 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ which exceeded those found in the literature. This also produced gross primary production and community respiration values which were unreasonably high.

Based on the observations of Odum and Hoskins (1958) and Copeland and Duffer (1964) a limit of $2.0 \text{ g O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ was selected as the maximum interval diffusion constant for Gladfelter Pond. The resultant computer-calculated diffusion rates, as expected, were lowered and, likewise, gross primary production values were reduced to an admissible level (Table I).

It should be noted that the use of the clear plastic

Table I. Computer and manually calculated planktonic gross primary production (GPP), and community respiration (RESP) based on computer calculated oxygen rate-of-change curves which were corrected for diffusion by utilization of the diffusion constant (k) indicated.

Date	k	COMPUTER CALCULATED		MANUALLY CALCULATED		AREAL PLANKTONIC METABOLISM	
		(g O ₂ m ⁻³ da ⁻¹)		(g O ₂ m ⁻³ da ⁻¹)		(g O ₂ m ⁻² da ⁻¹)	
		GPP	RESP	GPP	RESP	GPP**	RESP***
5-12	1.60	5.48	-1.02	5.08	7.83	8.77	12.53
5-13	1.50	2.56	9.67	*		4.10	
5-14	2.00	1.55	-1.64	1.79	13.22	2.48	21.15
5-15	2.00	0.30	9.75	2.31	13.76	0.48	22.02
5-16	1.50	2.56	9.67	2.20	9.21	4.10	14.74
5-20	2.00	5.13	1.57	1.89	4.23	8.21	6.77
5-21	2.00	10.24	5.54	*		16.38	
5-22	1.60	11.38	17.64	10.38	17.76	18.21	28.42
5-23	2.00	3.55	5.61	*		5.68	
5-24	1.84	5.39	0.74	4.38	5.27	8.62	8.43
5-25	1.61	2.21	2.05	3.59	3.57	3.54	5.71
5-31	2.00	5.13	-2.80	5.02	18.87	8.21	30.19
6-1	2.00	8.07	5.15	7.70	16.38	12.91	26.21
6-2	2.00	10.01	10.14	7.41	11.36	16.02	18.18
6-3	2.00	0.90	9.36	*		1.44	
6-4	2.00	3.28	3.11	2.52	12.64	5.25	20.22
6-5	2.00	1.55	8.46	1.78	9.37	2.48	14.99
6-6	1.50	6.20	1.41	6.00	9.50	9.92	15.20
6-7	2.00	4.04	3.06	3.77	7.23	6.46	11.57
6-8	1.60	0.77	3.72	*		1.23	
6-9	2.00	2.75	16.39	1.51	12.57	4.40	20.11
6-13	1.96	14.43	10.46	9.06	18.48	23.09	29.57
6-14	2.00	23.10	8.10	18.02	36.80	36.96	58.88
6-15	2.00	25.56	9.86	16.40	32.52	40.90	52.03
6-16	2.00	16.79	16.80	13.36	32.32	26.86	51.71
						$\bar{X}=11.07$	$\bar{X}=23.44$

* Irregular corrected oxygen rate-of-change curve which could not be manually analyzed.

** Computer calculated.

*** Manually calculated.

dome at Station B alleviated the need for consideration of diffusion because there was no contact between the enclosed water and the atmosphere.

Insolation and Productivity

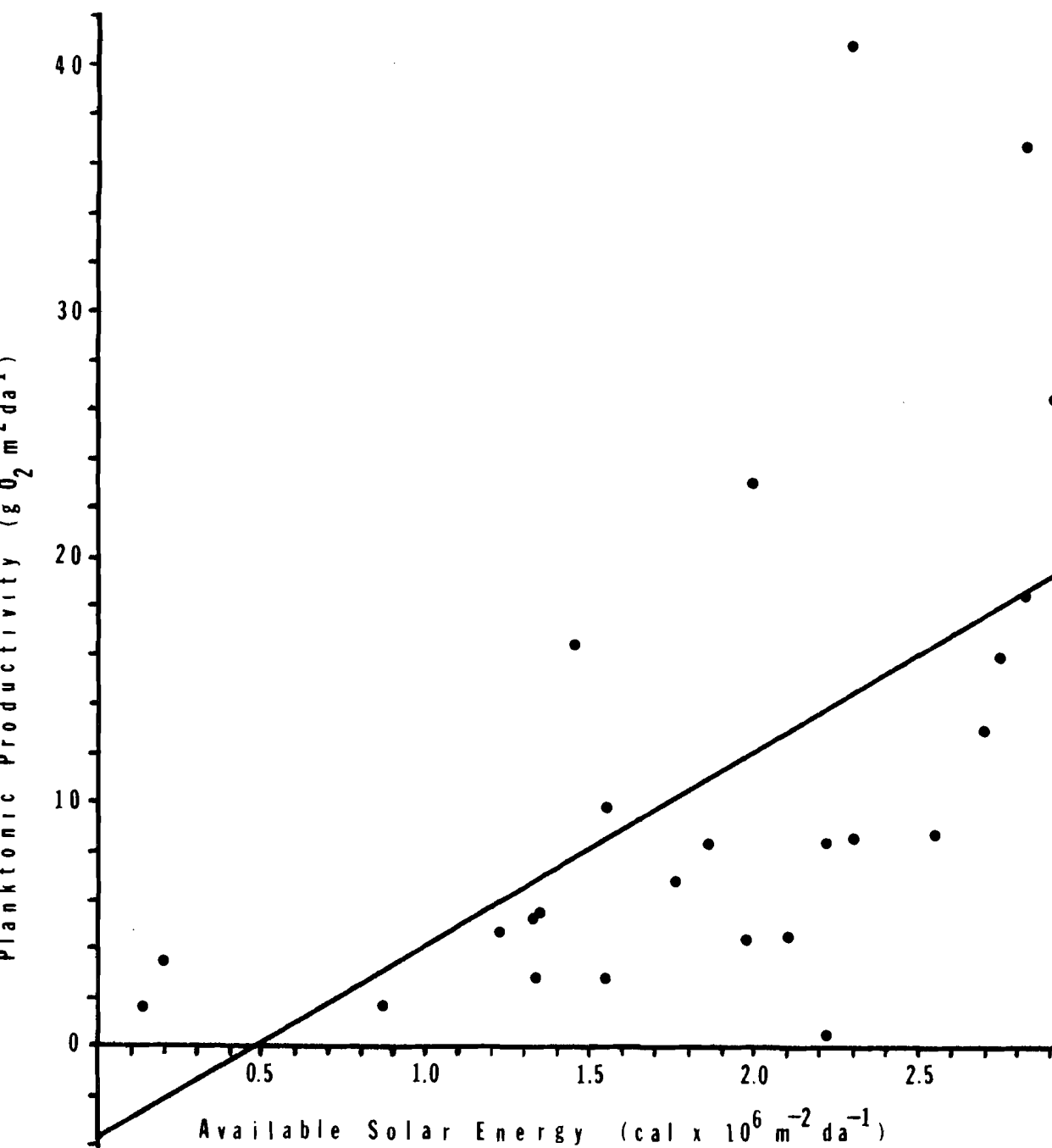
The growth of algae and rate of photosynthesis are directly related to quantitative light intensity (Wetzel, 1975). In a turbid system such as Gladfelter Pond, where turbidity is largely humic dissolved compounds and abiogenic particulate seston, the maximum possible productivity is decreased due to light attenuation. Pomeroy (1959) reported that the optimal intensity for photosynthesis is between 1.2 and 13.6 cal cm⁻² hr⁻¹ and that within this range of intensity other environmental factors become increasingly consequential. At light intensities greater than 13.6 cal cm⁻² hr⁻¹, which would be within a few centimeters of the surface in Gladfelter Pond, photoinhibition causes a decrease in solar energy utilization and an overall decrease in productivity as well as photosynthetic efficiency.

In temperate lentic systems the seasonal variability of incident solar energy is the controlling mechanism for annual cycles in aquatic primary productivity. This relationship is particularly apparent in less productive lakes which are located at higher latitudes in the temperate zone (Wetzel, 1975).

Planktonic Productivity

Figure 5 is a linear regression (slope=8.03, y-intercept=-3.87) showing the relationship between photosynthetically

Figure 5. Linear regression showing the relationship between planktonic productivity and available insolation



active insolation available and planktonic productivity. Observed daily planktonic gross primary production (Station A) ranged from 0.48 to 40.9 g O_2 m^{-2} da^{-1} with a mean of 11.07 g O_2 m^{-2} da^{-1} (Table I). Simultaneously recorded insolation corrected for photosynthetic wavelength and loss due to surface reflection ranged from 2.0×10^5 to 2.92×10^6 cal m^{-2} da^{-1} and averaged 1.86×10^6 cal m^{-2} da^{-1} .

The regression indicates that planktonic gross primary production for Gladfelter Pond ranged from zero at 2.0×10^5 cal m^{-2} da^{-1} to 19.58 g O_2 m^{-2} da^{-1} at 2.92×10^6 cal m^{-2} da^{-1} . This equates to 110.66 kg O_2 $pond^{-1}$ da^{-1} average daily planktonic production within the entire trophogenic zone.

From the regression an annual daily mean for planktonic productivity was estimated at 10.01 g O_2 m^{-2} da^{-1} . This was accomplished by applying the regression equation to latitude-dependent average daily insolation rates for the various months of the year as reported by Hutchinson (1957).

Gross primary production for Gladfelter Pond has been previously estimated by Osborne (1968) at from zero to 6.60 g O_2 m^{-3} da^{-1} using the light-dark bottle method of measurement. Weedon (1970), in a comparison of methods of estimating gross primary production, recorded ranges in Gladfelter Pond of 0.24 to 1.42 g O_2 m^{-3} da^{-1} for the light/dark bottle method, 0.23 to 12.9 g O_2 m^{-3} da^{-1} for the pH variation method, and 0.09 to 9.95 g O_2 m^{-3} da^{-1} for the daily oxygen variation method.

It is a general consensus that the light/dark bottle method of estimating primary production yields figures that are below actual rates. The limitations and problems encoun-

tered with enclosed communities and specifically with the light/dark bottle method were discussed by Talling and Fogg (1969). Eley (1970), in his study of Keystone Reservoir, Oklahoma, and Weedon (1970), in her study of Gladfelter Pond, both performed comparisons of methods and concurred that estimates of productivity derived from the daily oxygen variation method were higher than those calculated by the light/dark bottle method. Both of these studies also revealed, however, that yet higher estimates were obtained from the daily pH variation method. Obviously, there is some debate as to which of these methods, not to mention carbon-14 methodologies, yields productivity data which most closely approximate actual rates. It is difficult to compare productivity studies because of the variability in methodologies and scope of various investigations.

Benthic Productivity

The majority of lakes throughout the world are relatively small and shallow with the ratio of colonizable substratum to pelagic water being very high (Wetzel, 1975). Therefore, littoral regions, which have been largely ignored, frequently constitute a major site of energy fixation.

In Gladfelter Pond depth frequently fluctuates with seasonal weather cycles causing the littoral substratum to change accordingly. Colonization of newly inundated or newly irradiated substratum by periphyton occurs quite rapidly (Wetzel, 1975). With the decrease in volume of pelagic waters the ratio of littoral area to pelagic volume is increased, thus

increasing the significance of benthic primary production.

The majority of the littoral zone in Gladfelter Pond has a preponderance of the macroalga, Chara spp., which is the dominant submersed macrophyte. Along with their contribution to littoral productivity, macrophytes also provide a large surface area for colonization by epiphytic algae. Probably the most abundant of the periphyton in Gladfelter Pond are the epipellic algae which are sessile on the sediments. It was observed that at times when solar radiation was intense, dislodged sections of the mat of epipellic algae were buoyed to the surface by oxygen bubbles entrapped among the algal filaments. Another group of algae which is aggregated on the bottom, the metaphyton, are those organisms, both planktonic and periphytic in origin, which are neither attached nor truly planktonic (Wetzel, 1975). There was no attempt to differentiate between macrophytic, periphytic, or metaphytic productivity which, collectively, was termed benthic littoral productivity.

Because of the uniformity of the sediments in the majority of Gladfelter Pond it was assumed that the distribution of littoral flora had a high degree of homogeneity.

Observed daily benthic littoral productivity at Station B ranged from 333.71 to 2379.16 mg O_2 m^{-2} of substratum da^{-1} and had a mean of 1067.59 mg O_2 m^{-2} of substratum da^{-1} (Table II). Utilizing the depth/productivity constant (4241) previously described, it was determined that benthic littoral gross primary production for Gladfelter Pond ranged from 1.42 to 10.09 kg O_2 $pond^{-1}$ da^{-1} and averaged 4.53 kg O_2 $pond^{-1}$ da^{-1} .

Table II. Computer calculated and corrected areal gross primary production (GPP) and community respiration (RESP) for the benthic littoral community.

	COMPUTER CALCULATED		AREAL BENTHIC METABOLISM	
	(g O ₂ m ⁻³ da ⁻¹)		(mg O ₂ m ⁻² da ⁻¹)*	
	GPP	RESP	GPP	RESP
5-28	7.72	7.05	1515.44	1383.92
5-29	3.67	7.47	720.42	1466.36
5-30	3.70	7.00	726.31	726.31
5-31	6.45	3.30	1266.14	647.79
6-1	12.12	11.53	2379.16	2263.34
6-2	5.74	6.34	1126.76	1244.54
6-3	2.10	2.80	412.23	549.64
6-4	4.29	3.90	842.13	765.57
6-5	1.70	4.10	333.71	804.83
6-6	2.70	5.90	530.01	1158.17
6-11	5.70	6.15	1118.91	1207.25
6-12	2.87	4.22	563.38	828.39
6-14	11.79	12.60	2314.38	2473.38
6-15	5.59	7.50	1097.32	1472.25
			$\bar{X}=1067.59$	$\bar{X}=1213.70$

* of substratum

The relationship between productivity of the benthic littoral producers and photosynthetically active solar radiation is shown in the regression (slope=0.685, y-intercept=-0.334) in Figure 6. From the regression, estimates of productivity were from 330 mg O_2 m^{-2} of substratum da^{-1} at 9.7×10^5 cal m^{-2} da^{-1} to 1590 mg O_2 m^{-2} of substratum da^{-1} at 2.81×10^6 cal m^{-2} da^{-1} . The annual daily mean was estimated at 850.60 mg O_2 m^{-2} of substratum da^{-1} from the regression in the same manner as for the planktonic community.

Based on annual daily mean values, the contribution of the benthic littoral community was 3.48 % of total gross primary production for the pond. Table III shows a comparison of component productivity for Gladfelter Pond and other aquatic systems. A conversion of 0.375 (Westlake, 1969), assuming a photosynthetic quotient of 1.0, was used to convert oxygen production to carbon for the sake of comparability of data.

As discussed previously, there is much variability in productivity estimates derived from different methodologies. However, even though the carbon-14 method, which is predominant in Table III, yields productivity values which are believed to be something less than gross productivity, the percentage contribution of each of the components of the producer community is indicative of relative importance.

Photosynthetic Efficiency

Forti (1965) stated that 118 kcal of solar energy is required to produce one mole of oxygen through photosynthesis.

Figure 6. Linear regression showing the relationship between benthic littoral productivity and available insolation

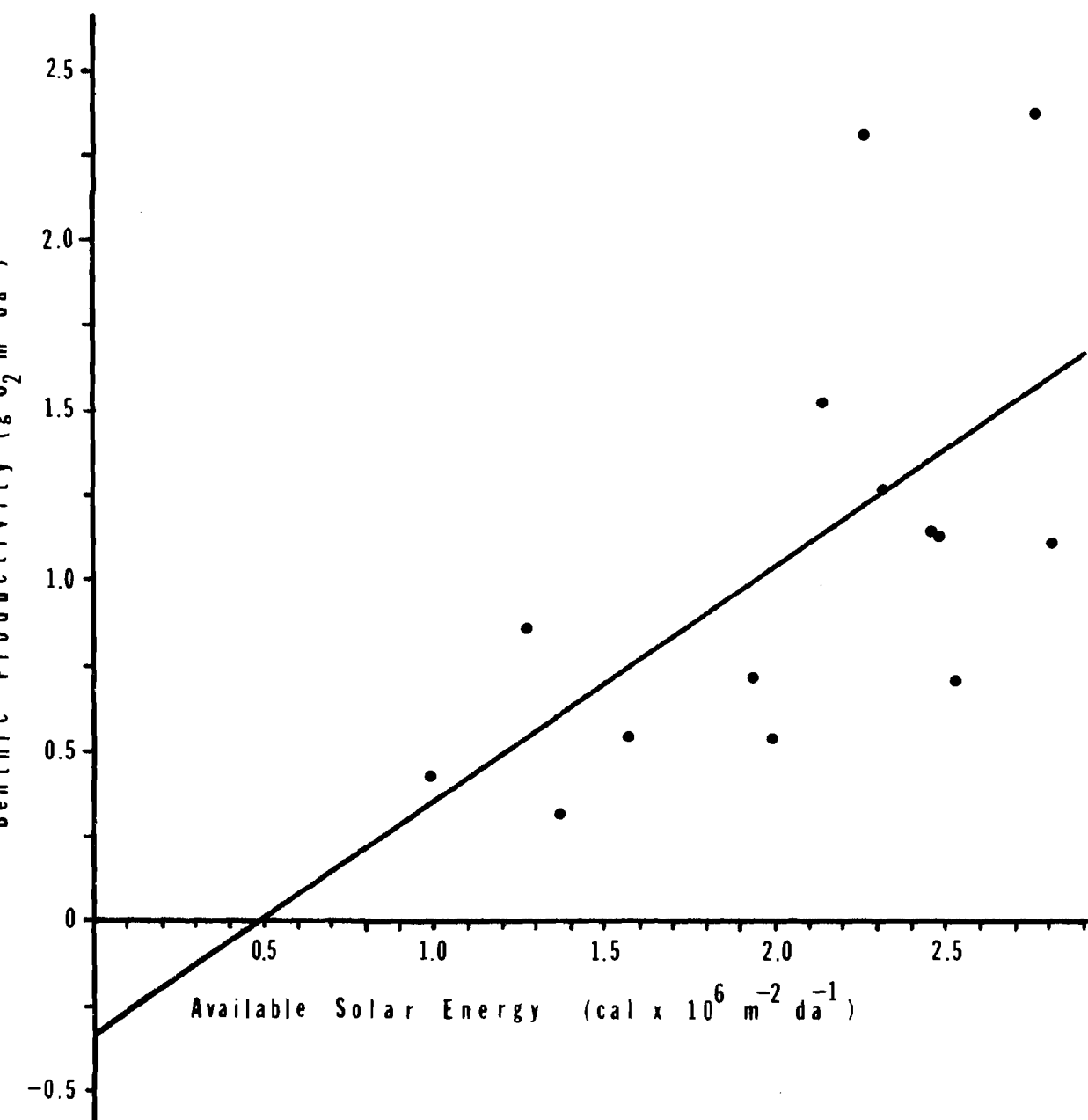


Table III. A comparison of primary productivity by different communities in various aquatic systems.

COMMUNITY	REFERENCE	METHOD OF MEASUREMENT	ANNUAL DAILY MEAN (mg C m ⁻² da ⁻¹)	PERCENTAGE
Gladfelter Pond				
Phytoplankton	Present Study	O ₂ Curve	3753.75	96.52
Benthic Littoral			318.98	3.48
Marion Lake, B.C.				
Phytoplankton	Efford (1967)*	Carbon-14	21.90	1.60
Epibenthic	Hargrave (1969)	L & D Bottle	109.60	62.20
Macrophyton	Davies (1968)*	Carbon-14	49.30	36.10
Borax Lake, Calif.				
Phytoplankton	Wetzel (1964)	Carbon-14	249.30	56.80
Littoral Algae			731.50	42.50
Macrophyton			76.50	0.70
Lawrence, Mich.				
Phytoplankton	Wetzel, et al.	Carbon-14	118.90	25.40
Littoral Algae	(1972)**		2003.00	23.30
			240.80	51.30
Keystone Res., Oklahoma	Eley (1970)	O ₂ Curve	11850.00	
Tuttle Creek Res., Kansas	Osborne (1972)	Carbon-14	66.00	
Gladfelter Pond	Osborne (1968)	L & D Bottle	588.00	

* from Hargrave (1969)

** from Wetzel (1975)

In Gladfelter Pond, at mean available insolation (1.86×10^6 cal m^{-2} da^{-1}), the combined total of planktonic and benthic littoral gross primary production was 114.69 kg O_2 pond $^{-1}$ da^{-1} . Based on the total solar energy available for photosynthesis (1.86×10^{10} cal pond $^{-1}$ da^{-1}) and the photosynthetic energy conversion described above, photosynthetic efficiency was calculated to be 2.27 %.

Wetzel (1975) stated that in aquatic systems phytoplankton efficiency is usually less than 1 % but may be as high as 3 % in tropical lakes. Hargrave (1969) in his study of epibenthic productivity of Marion Lake, British Columbia, reported efficiencies of from 0.4 % to 3.1 %. In his study of Keystone Reservoir, Oklahoma, Eley (1970) reported that photosynthetic efficiency ranged from 0.52 % to 32.68 %, which is probably somewhat high.

The efficiency of an aquatic system generally varies inversely with suspended solids as a result of light attenuation, especially at lower wavelengths (Wetzel, 1975). Therefore, in turbid systems such as Gladfelter Pond decreased efficiency may be anticipated.

Metabolic Ratio and Community Respiration

During this study Gladfelter Pond appeared to be a heterotrophic system. Production/respiration ratios for the planktonic community averaged 0.55 while benthic-littoral ratios averaged 0.90. This indicates that the system was not self-sustaining and was dependent upon imported detritus from the surrounding terrestrial environment to augment autochthonous

energy fixation.

Community respiration is a measure of oxygen diminution caused by a variety of aerobic micro- and macroorganisms within the community. In his study of epibenthic metabolism in Marion Lake, Hargrave (1969) established the relative rates of respiration for each of the major groups of organisms as a percentage of community respiration. He found that the macrofauna were the greatest oxygen consumers at 33 %, while algae consumed the least at 15 %, with protozoans and bacteria consuming 22 % and 30 %, respectively. This relationship is, of course, not applicable to Gladfelter Pond but, nevertheless, offers insight as to the possible relative significance of each group.

Planktonic community respiration (Station A) varied between 5.71 and 58.88 g O₂ m⁻² da⁻¹ and had a mean value of 23.44 g O₂ m⁻² da⁻¹ (Table I). With average gross primary production at 11.07 g O₂ m⁻² da⁻¹ the average deficit in primary production was 12.37 g O₂ m⁻² da⁻¹. Utilizing Westlake's (1969) 0.375 oxygen production to carbon conversion and extrapolating to the total volume of the trophogenic zone this equated to 46.39 kg of allochthonous carbon which was utilized daily.

Community respiration for the benthic littoral community (Station B) ranged from 549.64 to 2473.38 mg O₂ m⁻² of substratum da⁻¹ and had a mean value of 1213.70 mg O₂ m⁻² of substratum da⁻¹. This equates to an average of 6.68 kg O₂ pond⁻¹ da⁻¹ which fell short of total littoral gross productivity which was 4.53 kg O₂ pond⁻¹ da⁻¹ by 2.15 kg O₂ pond⁻¹

da^{-1} or $806.25 \text{ g C pond}^{-1} \text{ da}^{-1}$. The difference was, presumably made up of chemosynthetic and allochthonous organic material.

SUMMARY

In situ estimates of benthic and planktonic community metabolism in Gladfelter Pond were made by means of the daily oxygen variation method of analysis. Calculation of a corrected oxygen rate-of-change curve and community metabolism values was done by a computer program devised by Eley (1970).

Annual daily means for gross primary production were estimated at $10.01 \text{ g O}_2 \text{ m}^{-2} \text{ da}^{-1}$ for the plankton and $850.60 \text{ mg O}_2 \text{ m}^{-2}$ of substratum da^{-1} for the littoral benthos. The contribution of the benthic littoral community was calculated to be 3.48 % of total pond production.

The total daily gross productivity during the study averaged $114.69 \text{ kg O}_2 \text{ pond}^{-1} \text{ da}^{-1}$ while average insolation corrected for photosynthetic spectrum and reflection averaged $1.86 \times 10^{10} \text{ cal pond}^{-1} \text{ da}^{-1}$. Photosynthetic efficiency was calculated to be 2.27 %.

Metabolic ratios of 0.55 and 0.90 for the planktonic and benthic littoral communities indicated that Gladfelter Pond was heterotrophic. With community respiration values that averaged $23.44 \text{ g O}_2 \text{ m}^{-2} \text{ da}^{-1}$ and $1213.70 \text{ mg O}_2 \text{ m}^{-2}$ of substratum da^{-1} for the planktonic and benthic littoral communities, respectively, it was determined that the system largely depended upon allochthonous organic material as a source of energy.

LITERATURE CITED

- Copeland, B.J., and W.R. Duffer. 1964. Use of a clear plastic dome to measure gaseous diffusion rates in natural waters. *Limnol. Oceanogr.*, 9:494-499.
- Davies, G.S. 1968. The productivity of the macrophytes of Marion Lake, B.C. Master of Science Thesis, The University of British Columbia, Vancouver, B.C. 28 p.
- Efford, I.E. 1967. Temporal and spatial differences in phytoplankton productivity in Marion Lake, British Columbia. *J. Fish. Bd. Canada*, 24:2283-2307.
- Eley, R.L. 1970. Physicochemical limnology and community metabolism of Keystone Reservoir, Oklahoma. Doctor of Philosophy Dissertation, Oklahoma State University, Stillwater, Oklahoma.
- Fogg, G.E. 1965. *Algal Cultures and Phytoplankton Ecology*. University of Wisconsin Press, Madison. 126 p.
- Forti, G. 1965. Light energy utilization in photosynthesis. *Mem. 1st Ital. Idrobiol.*, 18(Suppl.):17-35.
- Griffith, S. 1961. The physical and chemical characteristics and occurrence of fauna in a new impoundment. Master of Science Thesis, Kansas State Teachers College, Emporia, Kansas.
- Hargrave, B.T. 1969. Epibenthic algal production and community respiration in the sediments of Marion Lake. *J. Fish. Bd. Canada*, 26:2002-2026.
- Hartman, E.L. 1960. The F.B. and Rena G. Ross Natural History Reservation. Emporia State Research Study, 8(4): 5-39.
- Hutchinson, G.E. 1957. *A Treatise on Limnology. I. Geography, Physics, and Chemistry*. John Wiley & Sons, Inc., New York. 1015 p.
- Odum, H.T. 1956. Primary production in flowing waters. *Limnol. Oceanogr.*, 1:103-117.
- _____, and C.M. Hoskins. 1958. Comparative studies on the metabolism of marine waters. *Inst. Mar. Sci.*, Texas, 5:16-46.
- Osborne, J.A. 1968. Some limnological features of Gladfelter Pond, June, 1965 - May, 1966. Master of Science Thesis, Kansas State Teachers College, Emporia, Kansas. 52 p.
- _____. 1972. The application of a photosynthesis model for turbid reservoirs - a field investigation. Doctor of Philosophy Dissertation, Kansas State University, Manhattan, Kansas. 125 p.

- Penfound, W.T. 1956. Primary production of vascular plants. *Limnol. Oceanogr.*, 1:92-101.
- Perez, G.R. 1970. A comparative study of some physicochemical and biological characteristics of Gladfelter Pond, 1969 - 70. Unpublished Research Paper, Kansas State Teachers College, Emporia, Kansas.
- Pomeroy, L.R. 1959. Algal productivity in salt marshes in Georgia. *Limnol. Oceanogr.*, 4:386-398.
- Prophet, C.W. 1966. Limnology of John Redmond Reservoir, Kansas. Emporia State Research Study, 15(2):1-27.
- Sladachova, A. 1962. Limnological investigation methods for the periphyton ("Aufuchs") community. *Bot. Rev.*, 28: 286-350.
- Talling, J.F. 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New. Phytol.*, 56:29-50.
- _____, and G.E. Fogg. 1969. Methods for measuring production rates. *In* Vollenweider, R.A. (ed.), *A Manual on Methods for Measuring Primary Production in Aquatic Environments*. Int. Biol. Program Handbook 12. Blackwell Scientific Publications, Oxford, p. 41-125.
- Thomas, G.D. 1964. Primary production and its relation to variations in chlorophyll *a* in John Redmond Reservoir, June to August, 1964. Unpublished Research Paper, Kansas State Teachers College, Emporia, Kansas.
- Vollenweider, R.A. 1969. Environmental factors linked with primary production. *In* Vollenweider, R.A. (ed.), *A Manual on Methods for Measuring Primary Production in Aquatic Environments*. Int. Biol. Program Handbook 12. Blackwell Scientific Publications, Oxford, p. 152-171.
- Waite, S.W. 1975. Filter-feeding dynamics of two Kansas cladocerans. Master of Science Thesis, Emporia Kansas State College, Emporia, Kansas. 40 p.
- Weedon, C. 1970. Comparison of three methods of primary production measurement in Gladfelter Pond. Unpublished Report, Kansas State Teachers College, Emporia, Kansas.
- Westlake, D.F. 1969. Units and comparability. *In* Vollenweider, R.A. (ed.), *A Manual on Methods for Measuring Primary Production in Aquatic Environments*. Int. Biol. Program Handbook 12. Blackwell Scientific Publications, Oxford, p. 113-117.
- Wetzel, R.G. 1963. Primary productivity of periphyton. *Nature*, 197(2):1026-1027.

- _____. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large shallow lake. Intern. Rev. Ges. Hydrobiol., 49:1-61.
- _____. 1965. Techniques and problems of primary productivity of higher aquatic plants and periphyton. Mem. 1st Ital. Idrobiol., 18 (Suppl.):249-267.
- _____. 1970. Recent and post glacial production rates of a marl lake. Limnol. Oceanogr., 15:491-503.
- _____. 1975. Limnology. W.B. Saunders Co., Philadelphia. 743 p.
- _____, P.H. Rich, M.C. Miller, and H.L. Allen. 1972. Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. Mem. 1st Ital. Idrobiol., 29 (Suppl.):185-243.
- Wilson, J.S. 1963. Flowering plants of the Ross Natural History Reservation, Lyon and Chase Counties, Kansas. Emporia State Research Study, 11(4):5-91.