A COMPARISON OF TWO IN-SITU METHODS FOR DETERMINING COMMUNITY METABOLISM OF LAKES AND HORIZONTAL VARIATION OF PRIMARY PRODUCTION IN LAKE CARL BLACKWELL, OKLAHOMA

By

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PREFACE

The objectives of the present study were to: (1) compare the method of Odum and Hoskin with that of McConnell for determining community metabolism data from diurnal cycles in oxygen concentration in an in-situ study, and (2) investigate causes of horizontal variation in community metabolism among areas of Lake Carl Blackwell.

Dr. Troy C. Dorris served as major adviser. Dr. Jerry Wilhm and Dr. Don F. Kincannon served on the advisory committee and criticized the manuscript. Dr. Ronald McNew assisted with statistical analyses and computer programming, and Steve Miller was very helpful with the field work. I am grateful for the assistance of all these people.

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CHAPTER I

INTRODUCTION

Statement of the Problem and Objectives

Diurnal changes in in-situ oxygen concentration can be used to calculate gross primary production, community respiration, and net community production in aquatic systems. The method of Odum and Hoskin (1958) is based on diurnal changes in rate of change of oxygen concentration measured at regular intervals. A method developed by McConnell (1962) based on the oxygen concentration requires only three data points over a 24-hr period.

Both methods assume a constant rate of diffusion for the 24-hr period. Changes in concentration by diffusion are corrected by applying a diffusion constant to the average oxygen saturation deficit at the surface. Diffusion will have little effect on either method if the dissolved oxygen concentration of the surface water is close to saturation.

Both methods rely on indirect estimates of daytime community respiration. The three-point method assumes community respiration to be constant throughout the 24-hr period. In the oxygen rate of change method a constant rate of community respiration is assumed (Odum and Hoskin 1958), or a daytime community respiration rate is interpolated between pre-sunrise and post-sunset rates (Odum and Wilson 1962, Eley 1970). It has been hypothesized that the average

daytime rate of community respiration is greater than the nighttime rate, and if such is the case, a method which assumes a constant rate throughout day and night would underestimate gross primary production and community respiration. There is considerable evidence to indicate that the rate of respiration is not constant throughout a 24-hr period (Jackson and McFadden 1954; Ryther 1954; Verduin 1957, 1960; Odum and Wilson 1962; Odum, Beyers, and Armstrong 1963; Beyers 1965; and Eley 1970). A maximum rate of respiration often occurs immediately after sunset with a decline in rate through the night to a minimum before sunrise. Respiration decreases exponentially during the night (Odum, Beyers, and Armstrong 1963; Beyers 1963, 1965). It is assumed that the rate of respiration increases during the day, but the mathematical function describing this increase is not known.

The three-point method seems most applicable in situations requiring extensive data collection with limited time and resources. Comparisons between these methods are needed to determine their relative value for in-situ estimations of community metabolism parameters.

Investigations have shown that primary production measurements obtained at a single station in a lake cannot be extrapolated to the whole body of water. Goldman and Wetzel (1963) correlated differences in primary production with water transparency among four stations in Clear Lake, California. Production was greater in less turbid waters, and differences among stations were smaller during periods of low turbidity in the entire lake. Eley (1970) attributed downstream increases in area-based rates of primary production and community respiration to increases in the euphotic zone depth in Keystone Reservoir, Oklahoma. Efford (1967) attributed reduction in production to

exhaustion of nutrients from inlet to outlet in Marion Lake, British Columbia, Canada. Productivity per unit volume and per unit surface area increased with nearness to the major tributaries providing nutrients in Brooks Lake, Alaska (Goldman 1968). No clear pattern in areal variation of primary production was found in Lake Tahoe, California (Goldman and Armstrong 1969). A single index station provided a good average production value for the lake, but considerable variation was exhibited among areas. Gerletti (1968) demonstrated a significant difference in production between two groups of stations in Lake Maggiore, Italy, which he attributed to uneven distribution of phytoplankton. These studies show a need for the investigation of causes of horizontal variation of primary production within reservoirs.

The proposed study was designed to investigate photosynthetic activity of phytoplankton populations in different areas of Lake Carl Blackwell, Oklahoma, a municipal water supply reservoir.

Objectives of the study are:

(1) To compare the most commonly used method of Odum and Hoskin with that of McConnell for determining community metabolism data from diurnal cycles in oxygen concentration in an in-situ study.

(2) To investigate causes of horizontal variation in community metabolism among areas of the lake.

Indirect Methods of Measuring Production by Phytoplankton

Early investigations were based on direct gravimetric or volumetric measurement of the standing crop of phytoplankton. According to Steeman-Nielsen (1952), Atkins (1923) first attempted indirect

measurements of organic production by estimating loss of carbon dioxide and phosphates from the water as they were taken up by photoplankton.

Productive natural waters show appreciable diurnal variations in dissolved oxygen. The analysis of such diurnal variations in-situ can be used to obtain estimates of primary production and community respiration on the assumption that for every gram of oxygen produced, approximately a gram of organic matter is fixed (Odum 1956, Odum and Hoskin 1958, Talling 1957, Eley 1970, McConnell 1962, and Welch 1968).

Changes in oxygen concentration of water can result from photosynthetic oxygen production, community respiration, diffusion, import by inflowing water, and export by water discharges. If import and export are negligible, changes brought about by photosynthesis, respiration, and diffusion can be calculated from the diurnal oxygen change. If the rates of diffusion and community respiration can be determined, primary production can be estimated. The rate of net production during the day and the rate of community respiration during the night can be estimated by integrating the rate of change curve for oxygen concentration, corrected for diffusion, over time (Odum and Hoskin 1958) or directly from the oxygen concentration curve (McConnell 1962).

Odum and Hoskin (1958) proposed the following basic requirements of diurnal oxygen change analysis:

(1) The measurements must be made in water representative of the designated community area or body of water.

(2) The metabolic history of the water entering and leaving the area must be similar.

(3) Circulation must be gentle as created with slowly drifting currents and gentle wave action.

(4) Samples must be taken at several levels if the water is vertically stratified.

(5) Several stations must be sampled to determine if a single station is representative of the water mass.

Eley (1970) attempted to correct for errors due to horizontal water movements in Keystone Reservoir, Oklahoma, by averaging observations at as many as six substations within each sampling area.

Corrections for diffusion are made by estimating a diffusion constant for the water body by the formula of Odum and Hoskin (1958), or by the use of a clear plastic dome and gas analysis (Copeland and Duffer 1964, Scholander 1942). Variations in factors which affect diffusion constants such as current velocity and wave action introduce error into diurnal oxygen change analysis since a uniform constant must be assumed day and night. Talling (1957) suggested that values of the diffusion constant in known situations indicate that oxygen exchange with the atmosphere is small in comparison with oxygen production by photosynthesis.

The three-point method of analysis of oxygen concentration changes used by McConnell (1962) in carboy microcosms and by Welch (1968) in Lago Pond, Florida, requires data points only at sunset on the first day and at sunrise and sunset the following day. Assumption that respiration is constant over a 24-hr period probably is the major shortcoming of this method. Kemmerer and Neuhold (1969) used the three-point method to estimate gross primary production in polyethylene enclosures in sewage stabilization ponds and found a possible lack of precision at low production levels. Eley (1970) concluded that the three-point method underestimates gross production and respiration if

minimum oxygen concentrations do not occur at sunrise and if the rate of community respirations is not constant throughout the 24-hr period.

Most other methods of measuring the rate of primary production and community respiration are based on changes in the concentration of a product or raw material of photosynthesis and respiration. The light and dark bottle method of Gaardner and Gran (1927) measures changes in oxygen concentration of water samples which are incubated in opaque and transparent bottles. Steeman-Nielsen (1952) developed a method based on the rate of ^{14}C uptake by the phytoplankton. The free-water pH-CO_2 change technique used by Verduin (1956, 1960) and Beyers and Odum (1969) is similar to the oxygen rate of change method (Odum and Hoskin 1958) except that changes in the carbon dioxide concentration are determined. Other methods include measurement of chlorophyll content and available energy (Ryther and Yentsch 1957) and harvest methods determining the rate of accumulation of plant biomass.

Controlling Factors of Aquatic Photosynthesis

Only about 5 percent of the total radiant energy can be fixed in gross photosynthesis under the most favorable conditions (Odum 1971). In most cases the maximal use of solar energy in a body of water does not exceed 1 percent (Pyrina 1967). Linear relationships exist between low light intensities and photosynthetic rates (Edmondson 1956, Strickland 1958, Ryther 1956, Sakmoto and Hogetsu 1963, and Steeman-Nielsen 1962). Inhibition or inactivation of the photosynthetic process may take place in extremely bright light.

The process of light adaptation is important in photosynthetic organisms (Menzel 1959, Steeman-Nielsen, Hansen, and Jorgensen 1962).

Algae protect cell constituents against high light energy by the inactivation of a part of the photochemical process (Steeman-Nielsen 1962). At high light intensities, photosynthesis apparently is reduced because of photo-oxidation of enzymes (Odum 1971).

The wavelength of light is also an important factor in regulating photosynthetic rates. At low intensities the photosynthetic rate for red light is higher than for blue and green lights (Sakmoto and Hogetsu 1963). It is generally assumed that only radiant energy between the wavelengths of approximately 400 and 700 mμ (visible light) is effective for photosynthetic production (Strickland 1958, Edmondson 1956). The vertical variations in potential photosynthetic rate are determined largely by the transparency or turbidity of the water (Edmondson 1956).

Daily fluctuations of chlorophyll a content of natural phytoplankton populations have been observed by Yentsch and Ryther (1957) and in unicellular algae under laboratory conditions by Gibor and Meehan (1961). These diurnal fluctuations influence the capacity of photosynthesis at optimal light intensity and probably are the basis for the photosynthetic daily periodicity (Yentsch and Ryther 1957). Ryther and Yentsch (1957) determined a mean value of 3.7 g of carbon assimilated per hour per gram chlorophyll at light saturation in natural populations and in cultures of marine phytoplankton.

The ratio of carotenoids to chlorophylls may serve as an index to the ratio of heterotrophic to autotrophic metabolism in the community as a whole (Odum 1971). The ratio of the absorbance of acetone extracts of pigments at 430 and 665 mμ (D430/D665) positively correlates with species diversity according to Margalef (1968). Aging of phytoplankton populations has been related to such pigment ratios. Margalef

found that young, growing populations tend to have lower ratios than older, stable populations. However, Wilhm and Long (1969) found no such relationship during succession of algal mat communities. Cooper (1972) could not correlate aging in stream periphyton communities with change in pigment diversity over time or distance downstream. Margalef (1965, 1967) found a high inorganic carbon uptake/unit biomass and productivity/respiration ratio associated with a low biotic diversity or with a low pigment ratio.

Carbon dioxide can limit production of aquatic communities, but because of its high solubility in water, carbon dioxide is less limiting than other factors (Odum 1971). However, Wright (1960) suggested that the decline of carbon dioxide concentration as standing crop increased was the most probable cause of the inverse photosynthesis-standing crop relationship observed in Canyon Ferry Reservoir, Montana.

Horizontal Variation of Primary Production in Lakes

Irregularities in the spatial distribution of zooplankton and phytoplankton can lead to serious difficulties in the exact evaluation of the standing crop of a body of water. Horizontal irregularities or patchiness of phytoplankton have been ascribed to the varying relations between the availability of nutrients and the grazing intensity (Tonolli and Tonolli 1958). Margalef (1958) attributed heterogeneous patterns in phytoplankton communities to succession factors such as grazing, convergence, and seral stages.

Goldman and Wetzel (1963) found that if an inflow of nutrients were accompanied by high turbidity, the productivity was higher in more

transparent areas of Clear Lake, California, at some distance from the inflow. Considerable variation in primary production occurred in different parts of Clear Lake during the winter and spring periods of high turbidities. During summer months transparency increased and there was more uniform production at the different stations in the lake. No clear pattern of areal variation was found in Lake Tahoe, California, by Goldman and Armstrong (1969). Production data from several stations indicated that a single index station provided a good average production value for the lake.

In Keystone Reservoir, Oklahoma, turbidity decreased and depth of euphotic zone increased downstream (Eley 1970, Spangler 1969). Eley found that depth-weighted annual means of primary production and community respiration showed different spatial variation than area-based estimates. Production in the euphotic zone was highest upstream but increased downstream from a minimum at an intermediate station. Eley attributed the increases in area-based rates of primary production and community respiration downstream to increases in depth of the euphotic zone.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

Lake Carl Blackwell is located 12 km west of Stillwater, Oklahoma, on Stillwater Creek in the Cimarron River Basin. Construction of the reservoir was completed in 1938.

Maximum surface area is approximately 1500 ha and capacity is 80 million m^3 at spillway elevation of 287.8 m above mean sea level (MSL). The lake level was 283.1 m above MSL on March 20, 1972, and had fallen to 282.0 m above MSL by August 20, 1972. The shoreline length was approximately 40 km in March, 1972.

The drainage basin of 172.7 km^2 consists of grazing land, farmland, and scrub oak forest. Most of the nutrient influx to the reservoir is from agricultural runoff.

Lake Carl Blackwell lies in an east-west direction with the deepest part in the east end near the dam. Mean depth was approximately 3 m during the study period. Vertical stratification occurs only for short periods during June, July, and August because of the shallow water depth and winds which are unhampered by the low shoreline. Turbidity is high because of wind-induced currents and shoreline erosion (Norton 1968). Because of low transparency, primary production is almost entirely limited to the phytoplankton. The euphotic zone of the lake seldom extends below 2 m.

Station I (Figure 1) is located in cove A, which was similar to

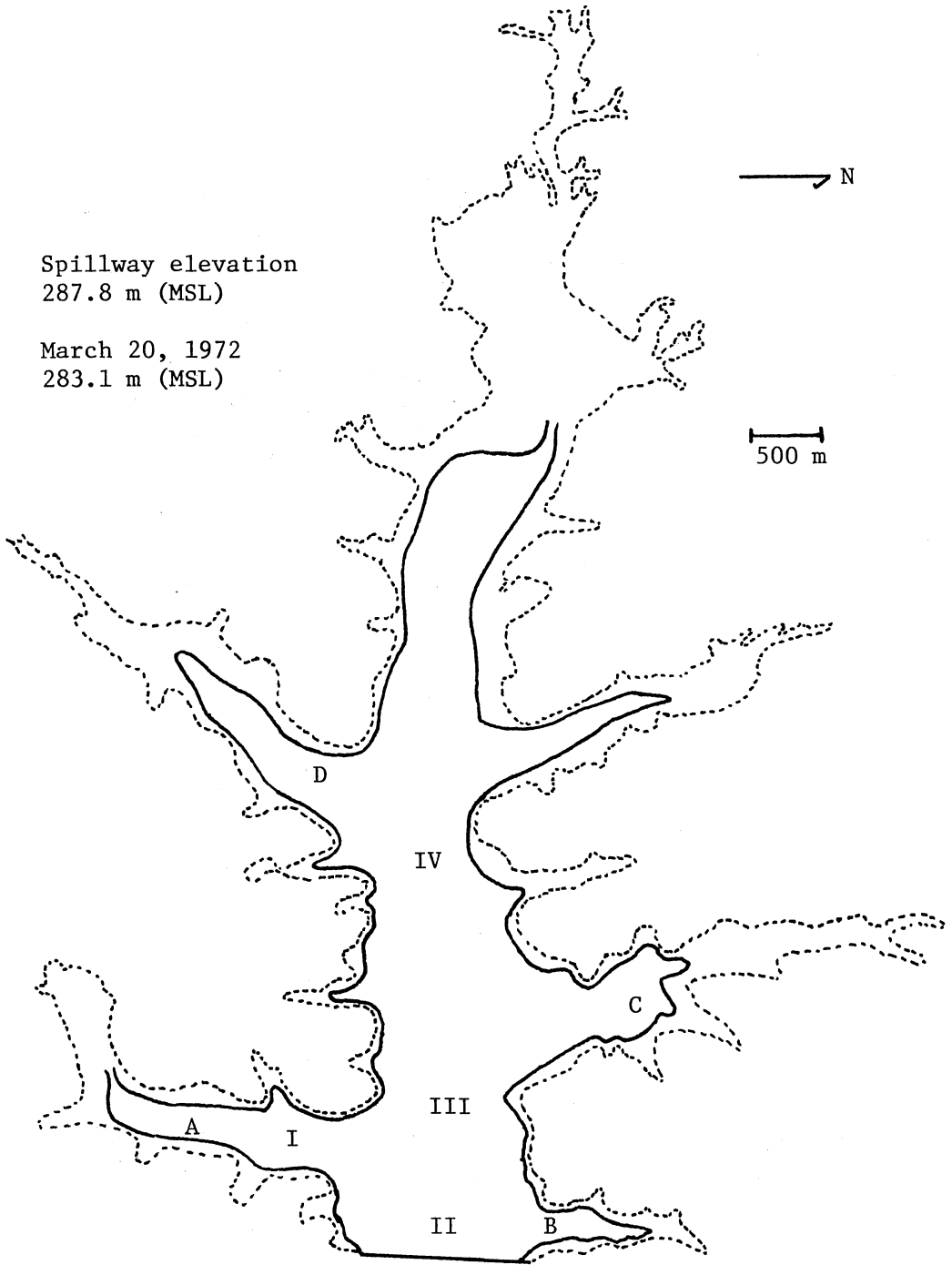

Figure 1. Map of Lake Carl Blackwell Showing Sampling Stations with Roman Numerals and Coves Used in Pilot Study with English Letters

the other three coves sampled in respect to maximum depth, euphotic zone depth, dissolved oxygen, and turbidity (Table I). Stations II, III, and IV are located approximately 200, 1500, and 2750 m west of the dam, respectively, and were approximately 9, 5, and 3 m deep on November 20, 1971. The continuously falling water level made it necessary to select areas of the lake which were accessible throughout the study period.

TABLE I

PHYSICAL PARAMETERS OF COVE AREAS OF LAKE CARL BLACKWELL, NOVEMBER 20, 1971

Cove	Depth (m)	Euphotic Zone (m)	Dissolved Oxygen (g/m^3)	Turbidity (JTU)
A	3	1.50	10.6	31.5
B	3	1.50	10.7	35.0
C	3	1.45	10.7	38.0
D	2	1.40	10.7	37.5

CHAPTER III

EXPERIMENTAL DESIGN

Samples were collected on eight occasions at each of the four stations during spring and summer, 1972. Two substations were established approximately 100 m apart at each sampling station.

Dissolved oxygen and temperature were measured at each meter of depth at each substation. Chlorophyll a concentration, pigment diversity, and turbidity were determined for composite samples taken from the euphotic zone at one substation in each sampling area. Duplicate observations were made of the five parameters. The euphotic zone depth was determined at each sampling area. Gross production, community respiration, net production, and gross production/respiration ratios were calculated for all substations on all sampling dates by the methods of Odum and Hoskin (1958) and McConnell (1962).

The null hypothesis that there is no difference between the two techniques of analyzing diurnal oxygen curves was tested with t-tests for matched pairs at the 5 percent level. The statistical layout for the t-test was:

Method 1 X_1	Method 2 X_2	Difference $D = X_1 - X_2$	Deviation $d = D - \bar{D}$	Squared Deviation d^2

Ho: $\bar{D}=0$, $\alpha=.05$

$$S_{\bar{D}}^2 = \frac{(D-\bar{D})^2}{n-1}$$

$$t(cal) = \bar{D}/S_{\bar{D}}$$

$t(tab)$ for $n-1$ df

Rejection Criteria

if $t(cal) < t(tab)$ do not reject Ho

if $t(cal) \geq t(tab)$ reject Ho

The null hypothesis that there is no difference among areas of the lake in community metabolism was tested with a split plot design analysis of variance:

Sources of Variation	Degrees of Freedom	
Stations	a-1	3
Substations/Stations	(r-1)a	4
Time	b-1	7
Stations x Time	(a-1)(b-1)	21
Substations x Time/Stations	(r-1)(b-1)a	28
Total	(abr)-1	63

where a = number of stations (4)

b = number of times (8)

r = number of substations (2)

Procedures for the statistical analysis were taken from Snedecor and Cochran (1967) and Steel and Torrie (1960).

CHAPTER IV

METHODS

Dissolved oxygen concentrations were determined with a galvanic cell oxygen probe calibrated against the azide modification of the Winkler method (APHA et al. 1971). Temperature profiles were measured with a thermister, euphotic zone depth with a submarine photometer, and daily solar radiation with a pyreheliometer. Duplicate water samples were taken from the euphotic zone at each station and returned to the laboratory for chlorophyll a and turbidity analyses. Turbidity was measured with a Bausch and Lomb Spectronic 20.

The methods described by Richards with Thompson (1952), Creitz and Richards (1955), and Strickland and Parsons (1965) were used for extraction of phytoplankton pigments. Water samples were filtered with type HA Millipore filter, pore size 0.45 μ. Ninety percent aqueous acetone was used for extraction of pigments. Extraction was carried out in darkness at 5 C for approximately 24 hr. The extracts were centrifuged for 8 to 10 min at 2,000-3,000 rpm before determination of absorbancies at 430, 665, and 750 mμ with a Bausch and Lomb Spectronic 20. Absorbance of acetone extracts was corrected for turbidity by subtracting the 750-mμ reading from the 665-mμ reading.

Chlorophyll a concentrations were computed by the formula (APHA et al. 1971):

$$\text{Ch. } \underline{a} \text{ (mg/m}^3\text{)} = \frac{C_a \times {}^{d}665 \times v}{V}$$

where ${}^{d}665$ = the absorbance at 665 mμ

v = the volume of acetone used for extraction, in milliliters

V = the volume of water filtered, in liters

C_a = (6.4), the absorption coefficient for chlorophyll *a* at 665 mμ for Lake Carl Blackwell plankton samples determined with the procedure described by Odum, McConnell, and Abbott (1958)

The ratio of absorbance at 430 and 665 mμ was determined for an estimate of pigment diversity (Margalef 1965).

Community metabolism parameters were estimated by the method of Odum and Hoskin (1958) as modified by Eley (1970). The amount of oxygen per square meter was determined at 3-hr intervals during a 24-hr period by summing the concentration of dissolved oxygen at each meter of depth. The average rate of change was calculated for each 3-hr interval. A diffusion constant (k) was multiplied by the oxygen saturation deficit of the surface waters during each 3-hr interval to correct for atmospheric diffusion. Values for k were calculated for each nighttime sampling interval by the formula:

$$k = \frac{q_n - q_{n+1}}{S_n - S_{n+1}}$$

where k = g $O_2/m^2/hr$ at 0% saturation

q_n = the rate of change of the surface g O_2/m^3 at nighttime n

q_{n+1} = the rate of change of the surface g O_2/m^3 at nighttime n+1

S_n = the oxygen saturation deficit of the surface waters at nighttime n

S_{n+1} = the oxygen saturation deficit of the surface water at nighttime n+1

The corrected oxygen rate of change per hour for each interval was plotted against time, and a daytime respiration line was drawn between pre-sunrise and post-sunset negative rate of change points. Community respiration was represented by the area above the nighttime negative rate of change line and daytime respiration line and below the zero rate of change line. Gross production was represented by the area above the daytime respiration line and below the daytime rate of change line.

The three-point method (McConnell 1962) was used in estimating community metabolism. The amount of oxygen per square meter was determined at sunset and at sunrise and sunset on the following day. The observed concentrations were plotted against time (Figure 2). A line was drawn from the first sunset point (A) to the sunrise point (B) and extended through the daylight period to the time of the second sunset point (D). The oxygen concentration at D ought to have resulted if no oxygen production had occurred and if diffusion of oxygen at the air-water interface were disregarded. The difference between point D and the final sunset oxygen concentration, point C, was the amount of gross production (Pg) for the 24-hr period. A diffusion correction (dc) was computed as the product: diffusion constant (k) x experiment duration in hours x average surface saturation deficit as a decimal fraction. This value was then added to the concentration at point D. The difference between the resulting concentration (D') and the initial sunset oxygen concentration is the amount of community respiration (Rt) for the 24-hr period.

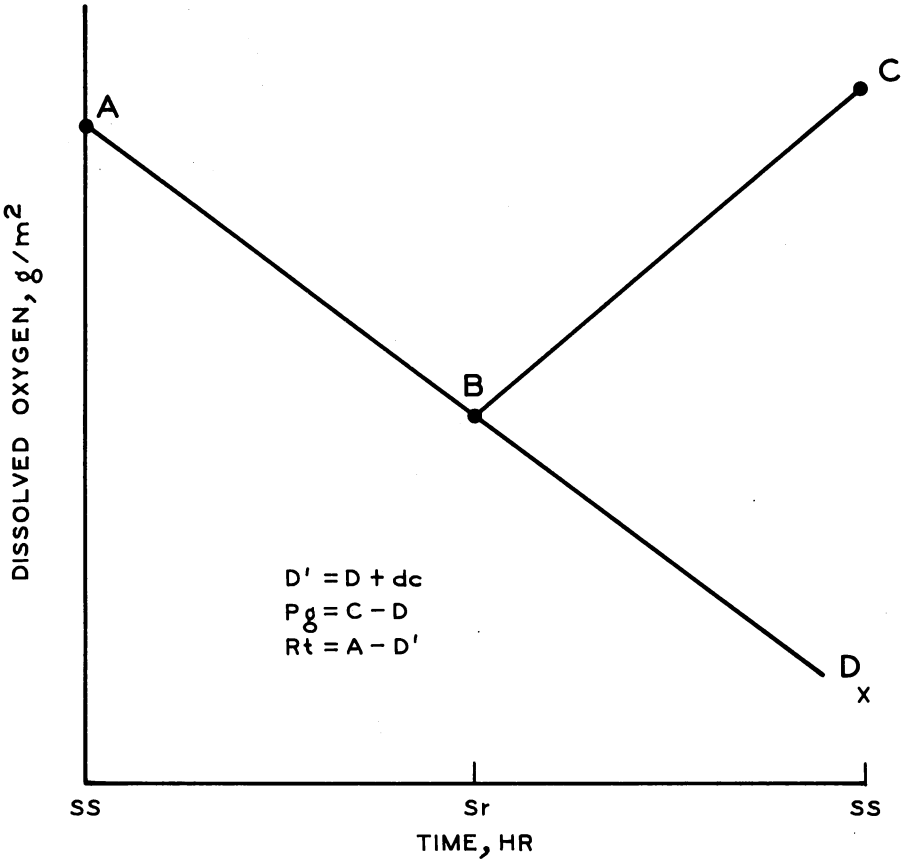

Figure 2. Diagram of Calculations of Pg and Rt Using the Three-Point Method

CHAPTER V

RESULTS AND DISCUSSION

Comparison of Methods Used in Calculating Community Metabolism

Sixty-two paired sets of data were used to compare the rate of change method with the three-point method for eight dates at four stations with two substations each. Gross production (Pg) and community respiration (Rt) values calculated with the three-point method usually were lower than those calculated by the rate of change method (Figures 3 and 4). Pg and Rt values for the two methods were different at the 99 percent confidence level (Table II). The mean of the Pg values calculated with the three-point method was 5.00 g O_2/m^2/day with a maximum of 15.71 and a minimum of 0.41. The mean Pg calculated with the rate of change method was 5.86 g O_2/m^2/day with a maximum of 19.10 and a minimum of 0.79. The three-point estimate of Pg was highest in only nine pairs of data. A mean of 0.82 was calculated for the ratio of Pg values calculated with the three-point method to Pg values calculated with the rate of change method.

The mean of the Rt values for the three-point method was 7.17 g O_2/m^2/day with a range from 17.09 to 2.41. The average Rt calculated with the rate of change method was 7.93 g O_2/m^2/day with a maximum of 20.50 and a minimum of 2.72. The three-point estimates of Rt were higher in nine pairs of data. The mean ratio of Rt values for the two

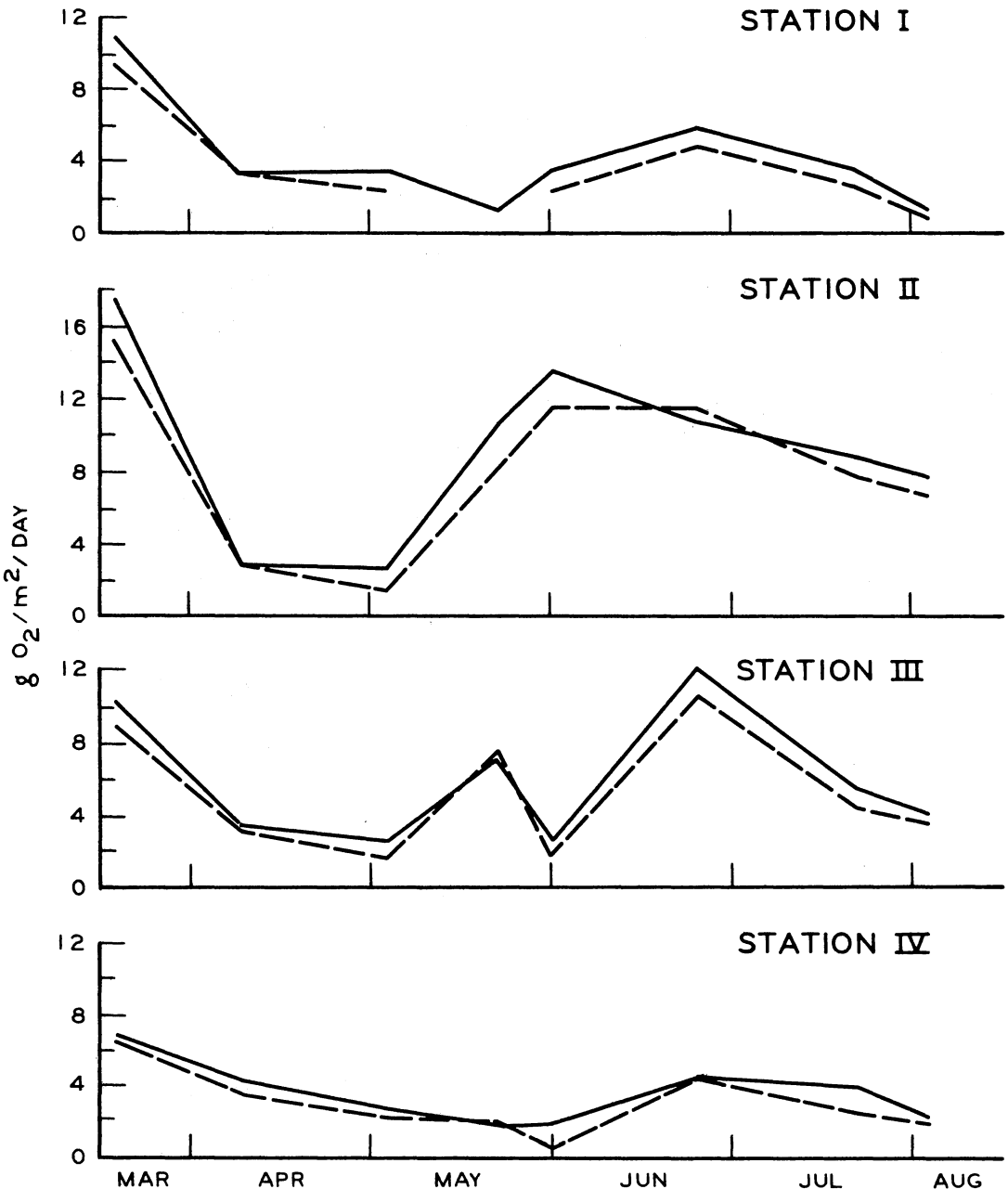

Figure 3. Daily Station Means of Pg for Three-Point (— —) and Rate of Change (———) Methods

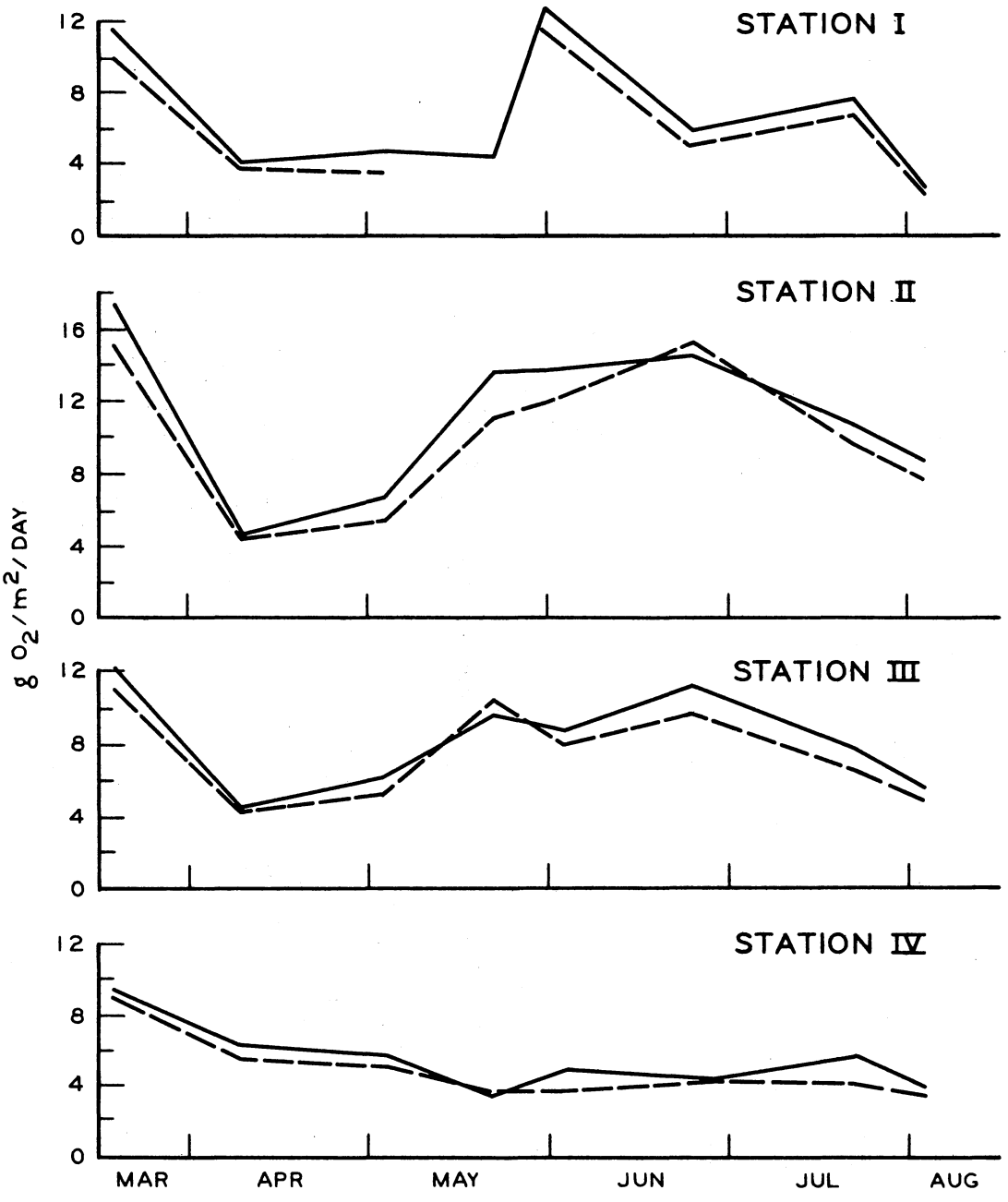

Figure 4. Daily Station Means of Rt for Three-Point (— —) and Rate of Change (——) Methods

methods was 0.89. Net production (Pn) values calculated with the two methods were nearly identical with an average of 2.17 g $O_2/m^2/day$ for each method (Table II). There was a significant difference between Pg/Rt ratios, but the average difference was only about 0.03 (Table II).

TABLE II

MEANS OF COMMUNITY METABOLISM (g $O_2/m^2/day$) USING THREE-POINT AND RATE OF CHANGE METHODS

Parameter	Three-Point		Rate of Change
Gross Production	5.00	*	5.82
Community Respiration	7.17	*	7.93
Net Production	-2.17		-2.17
Production/Respiration	0.65	*	0.68

* Asterisk indicates a difference between means at the 99% confidence level.

Negative gross production values were obtained from the two substations at station I on May 21 using the three-point method. Negative productivity estimates obtained from water enclosed in polyethylene columns floating in sewage stabilization ponds by Kemmerer and Neuhold (1969) using the three-point method were attributed to changes in the rate of diffusion between the air-water interface during a 24-hr period. The negative production values obtained during this study were

disregarded in comparing the methods.

The differences between the community metabolism parameters result from methods of estimation of daytime community respiration. In the rate of change analysis, a hypothetical daytime respiration rate was interpolated from the pre-sunrise and post-sunset rates of change, but daytime community respiration was assumed to proceed at the same rate as nighttime community respiration with the three-point method. When daytime community respiration was estimated in the same way, there was no difference in Pg or Rt values between the two methods (Table III).

According to Odum and Hoskin (1958) and Eley (1970) interval length for the rate of change method should be no longer than 3 hr. Faust (1972) concluded that more frequent sampling permits a more precise interpretation of rates of change and corresponding Pg and Rt estimates. However, the addition of pre-sunrise and post-sunset observations to the three-point procedure permits the interpolation of daytime respiration rates and will give the same estimates of community metabolism parameters as short-interval rate of change measurements.

The long-interval technique was applied to data taken from Keystone Reservoir, Oklahoma, by Faust in 1968, at 1-hr intervals for a 24-hr period (Table IV). Values calculated with the five-point technique are in close agreement with those calculated by Faust. Pg values for all dates and Rt values for 8/7/68 are nearly identical. There is about a 2 percent difference in Rt values between the two techniques for 8/4/68, and about a 4 percent difference in Rt values for 9/17/68. On these two dates there were positive rates of change in oxygen concentration at night which were disregarded by Faust in his calculations.

TABLE III

Pg AND Rt (g O_2/m^2/day) ASSUMING A CONSTANT RATE OF Rt FOR THE 24-HR PERIOD WITH BOTH THE THREE-POINT AND RATE OF CHANGE METHODS

Date	Station	Substation	Three-Point		Rate of Change	
			Pg	Rt	Pg	Rt
3/18	I	1	10.23	10.21	10.27	10.19
		2	8.23	9.69	8.27	9.68
	II	1	15.71	17.09	15.72	17.12
		2	14.69	12.96	14.66	12.94
	III	1	9.33	11.83	9.23	11.67
		2	8.60	10.27	8.54	10.27
	IV	1	6.61	9.52	6.45	9.32
		2	6.62	9.32	6.54	9.23
4/8	I	1	2.98	3.82	2.98	3.85
		2	3.35	4.13	3.35	4.11
	II	1	4.59	6.17	4.60	6.18
		2	1.13	3.13	1.14	3.22
	III	1	2.73	4.26	2.80	4.37
		2	3.56	4.22	3.62	4.25
	IV	1	3.56	5.40	3.56	5.43
		2	3.89	5.77	3.87	5.76
5/3	I	1	2.47	3.58	2.41	3.53
		2	2.31	3.81	2.28	3.76
	II	1	0.63	4.33	0.54	4.33
		2	2.08	6.61	2.12	6.67
	III	1	1.75	5.30	1.73	5.34
		2	1.40	5.02	1.43	5.11
	IV	1	2.07	5.32	2.06	5.35
		2	2.26	5.11	2.22	5.08
5/22	I	1				
		2				
	II	1	7.47	10.48	7.66	10.69
		2	8.63	11.66	8.59	11.66
	III	1	7.11	9.39	7.10	9.39
		2	7.72	11.47	7.66	11.39
	IV	1	1.51	3.20	1.61	3.17
		2	2.38	3.77	2.41	3.78

TABLE III (Continued)

Date	Station	Substation	Three-Point Pg	Three-Point Rt	Rate of Change Pg	Rate of Change Rt
6/1	I	1	2.38	11.27	2.38	11.29
		2	2.17	11.51	2.16	11.48
	II	1	10.84	12.29	10.82	12.12
		2	12.26	11.80	12.22	11.77
	III	1	1.84	8.00	1.85	8.01
		2	1.79	7.79	1.72	7.84
	IV	1	1.02	4.05	1.03	3.99
		2	0.91	4.10	0.92	4.04
6/25	I	1	4.38	4.57	4.40	4.56
		2	5.46	5.34	5.49	5.35
	II	1	12.62	16.39	12.63	16.37
		2	10.26	13.99	10.26	14.00
	III	1	11.07	10.32	11.02	10.27
		2	9.86	9.11	9.87	9.02
	IV	1	4.36	4.24	4.35	4.12
		2	4.54	3.94	4.54	3.95
7/20	I	1	2.34	6.56	2.36	6.60
		2	2.50	6.73	2.50	6.72
	II	1	8.53	10.57	8.59	10.59
		2	7.16	8.63	7.15	8.67
	III	1	4.34	6.71	4.34	6.71
		2	4.09	6.15	4.09	6.18
	IV	1	2.39	3.92	2.38	3.96
		2	2.29	3.85	2.28	3.85
8/3	I	1	0.89	2.48	0.89	2.48
		2	1.00	2.41	1.00	2.52
	II	1	6.64	7.42	6.64	7.44
		2	7.24	8.24	7.23	8.24
	III	1	3.43	4.96	3.42	4.98
		2	3.30	4.51	3.39	4.46
	IV	1	1.61	3.53	1.61	3.51
		2	2.20	3.54	2.21	3.55
MEAN			5.00	7.17	5.01	7.18

This anomaly cannot be detected with the longer interval five-point method and results in lower nighttime respiration estimates.

TABLE IV

Pg AND Rt VALUES (g O_2/m^2/day) CALCULATED WITH 25-POINT AND 5-POINT DIURNAL OXYGEN CURVE ANALYSES

Date	25-Point Diurnal*		5-Point Diurnal	
	Pg	Rt	Pg	Rt
8/4/68	103.47	104.98	103.46	102.86
8/7/68	125.75	144.56	125.75	144.58
9/17/68	57.35	58.80	57.31	56.47

* From Faust (1972).

A problem of both techniques is that of estimating atmospheric exchange of oxygen at the air-water interface. Diffusion constants must be assumed for use with the three-point method, whereas nighttime rates of change make it possible to calculate a diffusion constant with the rate of change method. If the dissolved oxygen content of the surface water is close to saturation, diffusion will have little effect on the Pg and Rt values calculated by either method. It is not necessary to correct Pg values for diffusion with the three-point method unless the average saturation deficit of oxygen concentration at night is not

similar to the average daytime saturation deficit. Error in the extrapolated daytime respiration estimate due to diffusion usually compensates for this underestimate or overestimate of the daytime increase in oxygen concentration caused by diffusion.

The three-point calculations for this study were made using diffusion constants calculated for each sampling date ranging from -1.81 to -0.80 g $O_2/m^2/hr$ at 100 percent saturation deficit. The three-point calculations of Rt were also made using a diffusion constant of -1.44 which was the average of the calculated diffusion constants. The Rt estimates were similar on most dates (Figure 5). No difference was found at the 95 percent confidence level using a paired t-test between the Rt values determined with calculated and assumed diffusion constants (Table V).

It would seem to be quite reasonable to assume a diffusion constant for small calm bodies of water or reservoirs which have previously been studied and for which diffusion constants have been calculated for a range of conditions.

Horizontal Variation of Community Metabolism

Sixty-four oxygen curves were analyzed by the rate of change method during the spring and summer of 1972. Concurrent measurements were made at four stations with two substations each in Lake Carl Blackwell on eight occasions. Solar radiation ranged from 497 ly/day to 635 with an average of 556. Average euphotic zone depth ranged from 1.25 m at station I to 1.71 m at station II. Euphotic zone depth rarely exceeded 2 m with a maximum of 3 m at station II. Gross primary production (Pg) and community respiration (Rt) were higher at the deeper stations II

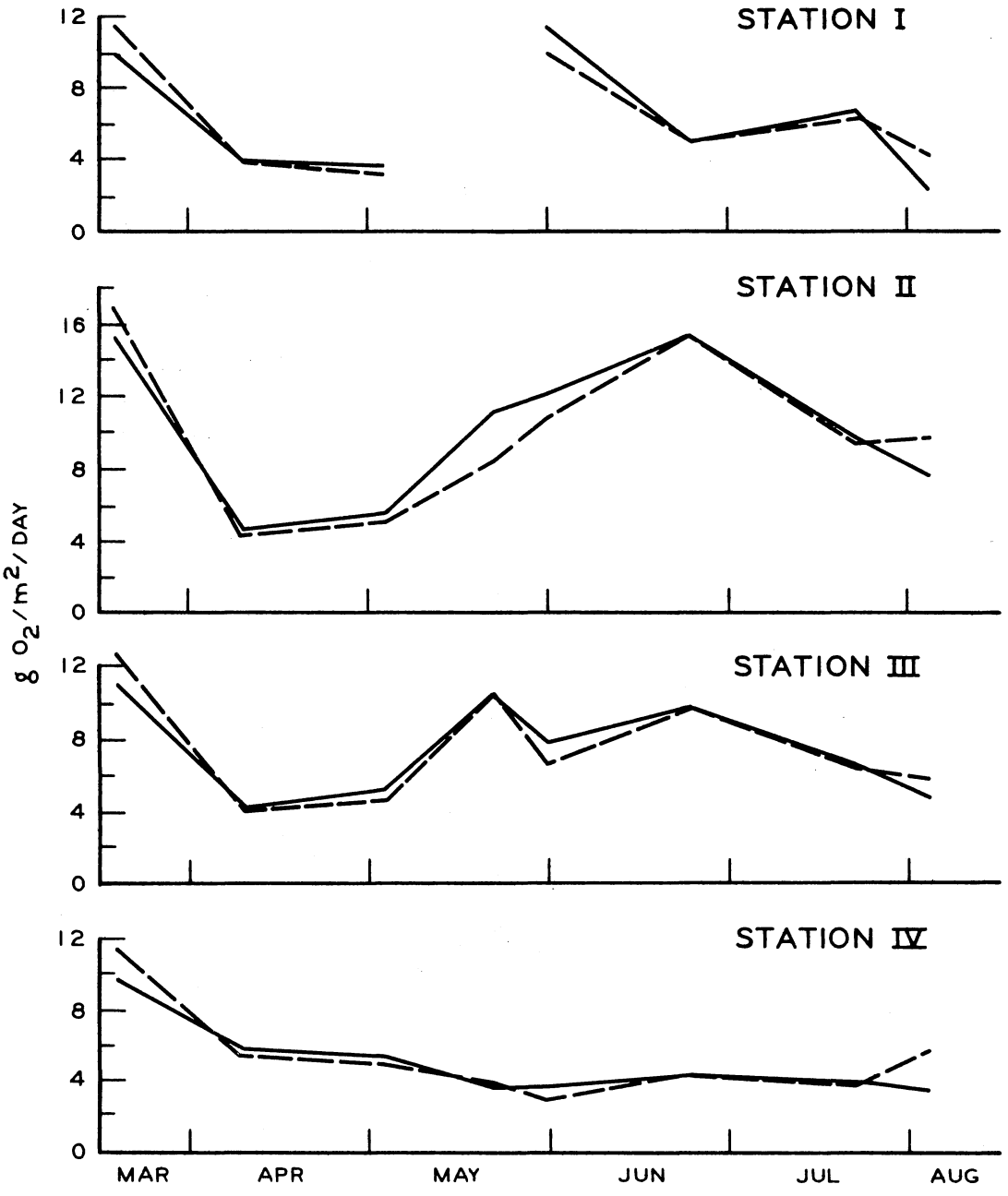

Figure 5. Daily Station Means of Rt Calculated with the Three-Point Method Using Calculated (——) and Assumed (— —) Diffusion Constants

TABLE V

Rt (g O_2/m^2/day) CALCULATED WITH THE THREE-POINT METHOD USING CALCULATED AND ASSUMED DIFFUSION CONSTANTS (K)

Date	Station	Substation	Calculated K	Rt	Assumed K	Rt
3/18	I	1	-1.00	10.21	-1.44	11.87
		2		9.69		11.40
	II	1		17.09		19.03
		2		12.96		14.80
	III	1		11.83		13.78
		2		10.27		12.09
	IV	1		9.52		11.50
		2		9.32		11.18
4/8	I	1	-1.50	3.82	-1.44	3.76
		2		4.13		4.07
	II	1		6.17		6.08
		2		3.13		3.04
	III	1		4.26		4.17
		2		4.22		4.14
	IV	1		5.40		5.24
		2		5.77		5.61
5/3	I	1	-1.64	3.58	-1.44	3.36
		2		3.81		3.60
	II	1		4.33		3.94
		2		6.61		6.31
	III	1		5.30		4.87
		2		5.02		4.59
	IV	1		5.32		4.96
		2		5.11		4.71
5/22	I	1	-0.91		-1.44	
		2				
	II	1		10.48		10.10
		2		8.63		8.25
	III	1		9.39		9.46
		2		11.47		11.52
	IV	1		3.20		3.42
		2		3.77		4.01

TABLE V (Continued)

Date	Station	Substation	Calculated K	Rt	Assumed K	Rt
6/1	I	1	-1.81	11.27	-1.44	9.73
		2		11.51		9.88
	II	1		12.20		11.02
		2		11.80		10.75
	III	1		8.00		6.87
		2		7.79		6.62
	IV	1		3.55		2.97
		2		3.60		2.96
6/25	I	1	-1.44	4.57	-1.44	4.57
		2		5.34		5.34
	II	1		16.39		16.39
		2		13.99		13.99
	III	1		10.32		10.32
		2		9.11		9.11
	IV	1		4.24		4.24
		2		3.94		3.94
7/20	I	1	-1.47	6.56	-1.44	6.47
		2		6.73		6.64
	II	1		10.57		10.50
		2		8.63		8.56
	III	1		6.71		6.64
		2		6.15		6.08
	IV	1		3.92		3.86
		2		3.85		3.79
8/3	I	1	-0.80	2.48	-1.44	4.33
		2		2.41		4.29
	II	1		7.42		9.30
		2		8.24		10.07
	III	1		4.96		7.09
		2		4.51		6.59
	IV	1		3.53		5.73
		2		3.54		5.57
MEAN			-1.44	7.17	-1.44	7.40

and III (Table VI). Mean Rt exceeded mean Pg values at all stations. Net production ranged from -2.64 g O_2/m^2/day at station I to -1.88 at station IV. Average Pg/Rt ratios indicated that all four stations were heterotrophic (Table VI).

Horizontal variation of Pg was similar to that of Rt with a maximum at station II and a minimum at station IV for both area-based and euphotic zone depth-weighted estimates (Figure 6). However, the variation among stations I, III, and IV was considerably less for depth-weighted estimates. Differences in Pg and Rt among stations were readily apparent for all sampling dates except April 8 and May 3 (Figures 7 and 8).

The relationship of community metabolism to turbidity, euphotic zone depth, chlorophyll a concentration, and pigment diversity was investigated in an effort to explain horizontal variations in metabolic rates. The restriction of the euphotic zone by turbidity was a major factor governing variation among area-based estimates of Pg. Direct relationships existed among Pg, Rt, euphotic zone depth, and column depth for all stations, and an inverse relationship existed between turbidity and Pg, Rt, euphotic zone depth, and column depth (Figure 9). Turbidity ranged from 45.2 JTU at stations I and IV to 30.4 JTU at station II. Mean turbidity values were significantly different among all stations except I and IV (Table VI). In general, turbidity was greatest and euphotic zone depth was least at the shallower stations I and IV (Figure 9). Station I had a mean depth during the study period of 2.5 m and was located in a fairly large cove. Station IV had a mean depth of 2.5 m and was located in the western end of the lake.

Horizontal variations of area-based estimates of Pg were caused by

TABLE VI

GROSS STATION MEANS OF COMMUNITY METABOLISM, TURBIDITY, CHLOROPHYLL A, PIGMENT DIVERSITY, AND COLUMN DEPTH RANKED FROM HIGHEST TO LOWEST

Parameter	Station $\bar{X}$			
Pg (g O_2/m^2/day)	II 9.34***	III 5.90***	I 4.10*	IV 3.53
Rt (g O_2/m^2/day)	II 11.31***	III 8.24***	I 6.73**	IV 5.42
Pn (g O_2/m^2/day)	I -2.64	III -2.34	II -1.97	IV -1.88
Pg/Rt	II 0.77**	III 0.69	IV 0.65	I 0.61
Pg (g O_2/m^3/day)	II 6.00***	III 3.88	I 3.52	IV 2.97
Turbidity (JTU)	I 45.2	IV 45.2***	III 35.2***	II 30.4
Chlorophyll *a* (mg/m^3)	IV 9.66***	I 8.70	III 8.68	II 8.61
Pigment Diversity	III 3.60	IV 3.58	I 3.54	II 3.54
Column Depth (m)	II 8.5	III 4.5	I 2.5	IV 2.5

Asterisks indicate significant differences between means.

*** (α = 0.01)
** (α = 0.05)
* (α = 0.10)

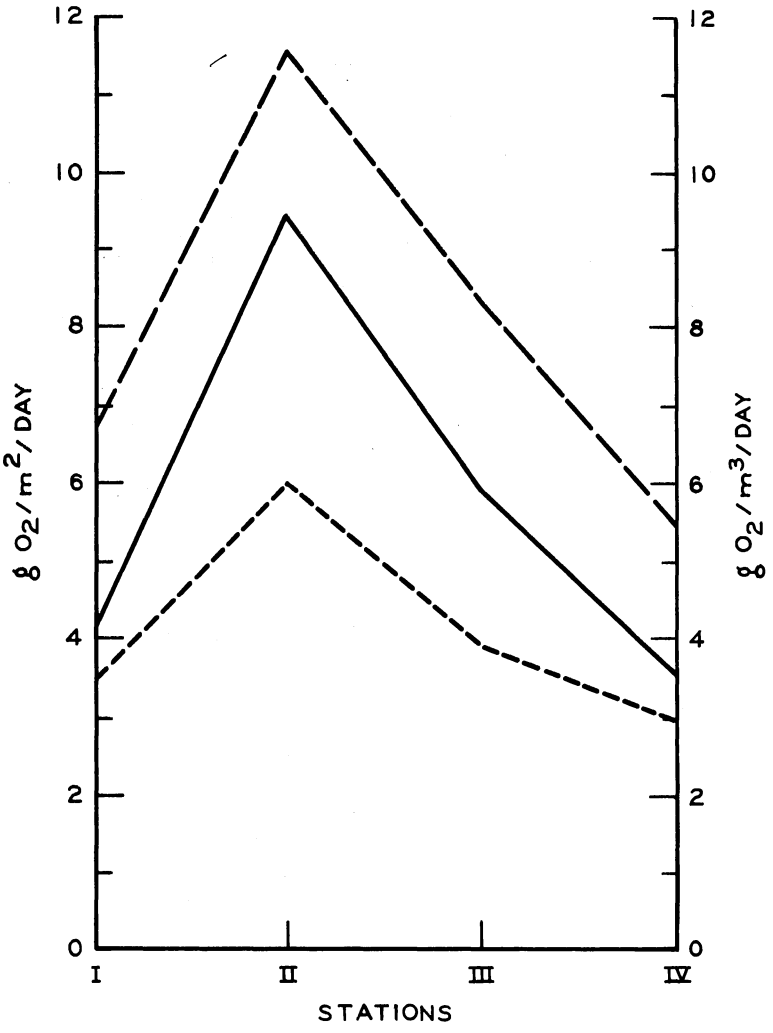

Figure 6. Gross Station Means of Area Based Pg (——) and Rt (— —), and Euphotic Zone Depth-Weighted Pg (– – –)

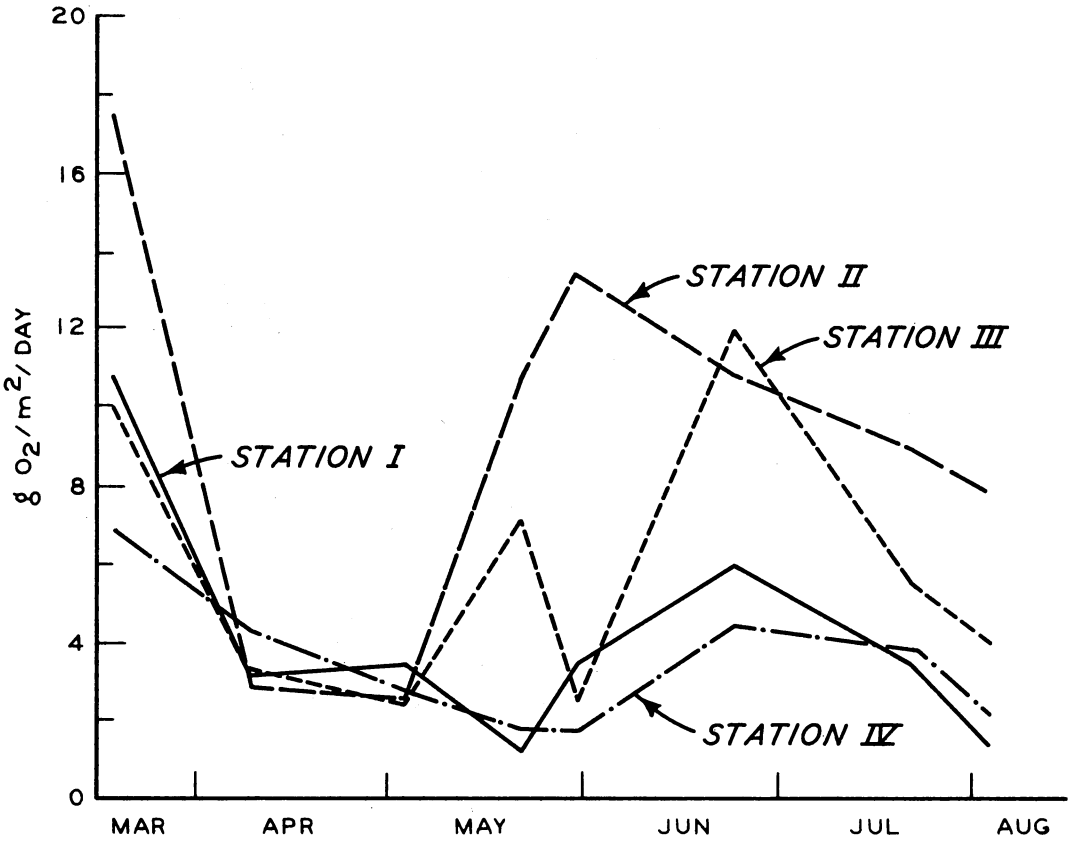

Figure 7. Daily Station Means of Pg

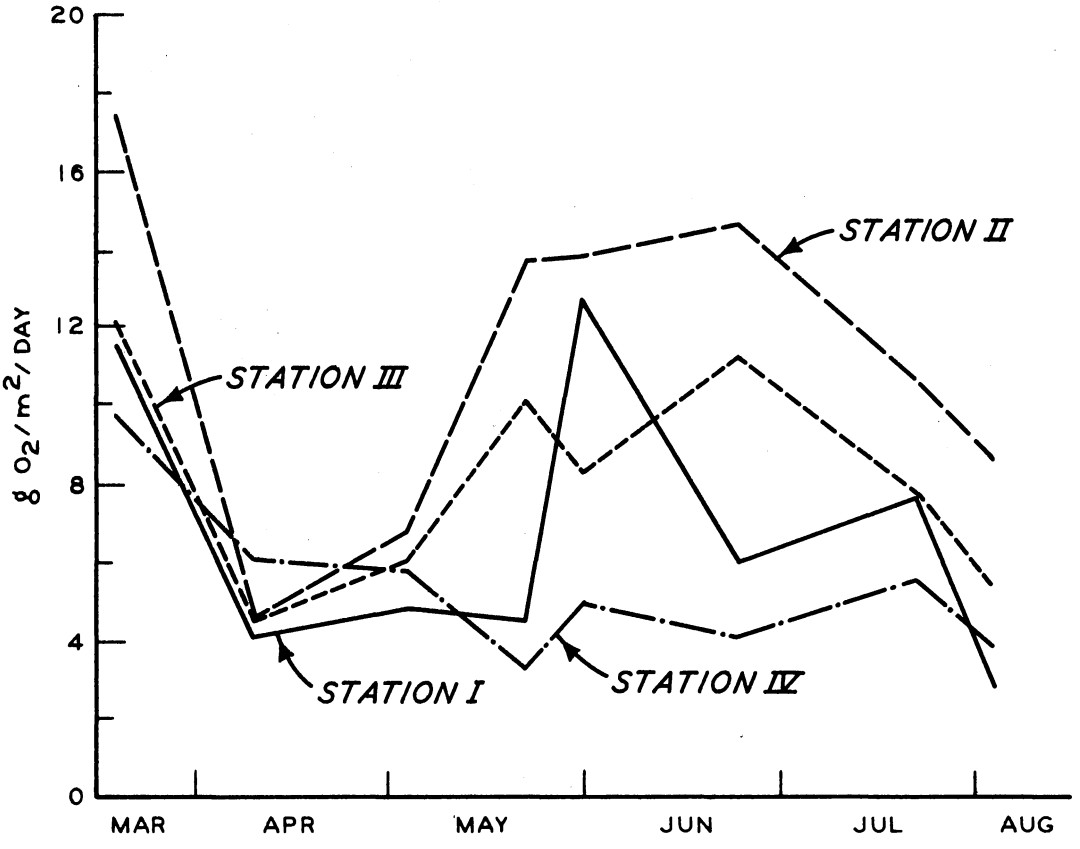

Figure 8. Daily Station Means of Rt

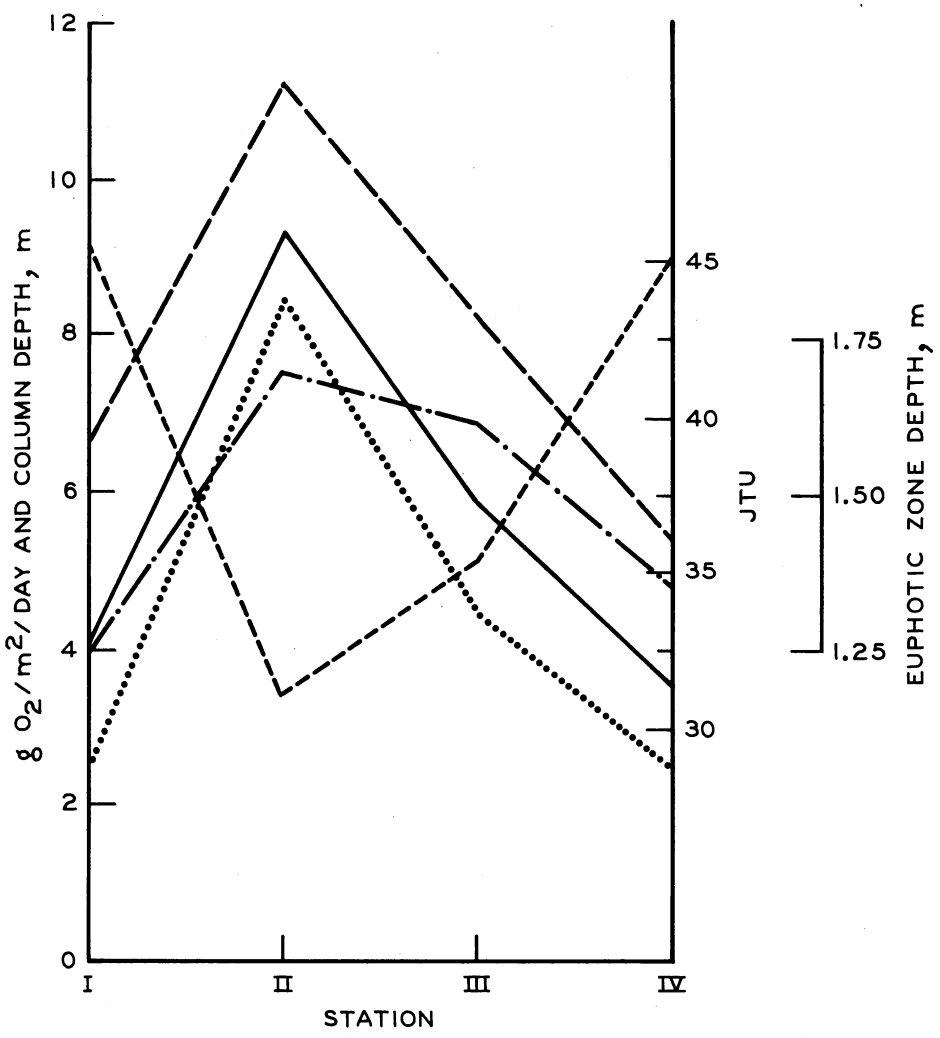

Figure 9. Gross Station Means of Pg (———), Rt (— —), Turbidity (– – –), Euphotic Zone Depth (—·—), and Column Depth (·····)

differences in euphotic zone depth, but horizontal variation in depth-weighted means of Pg indicates that other factors also influenced metabolic rates. Correlations between Pg and chlorophyll a concentration were apparent on some dates, but at other times no relationship existed (Figure 10). There was no relationship between gross means of chlorophyll a and Pg (Figure 11). The maximum chlorophyll a mean of 9.66 mg/m^3 for station IV was significantly higher than all other stations, but there was significant differences among the other stations (Table VI). Chlorophyll a varied from 14.6 mg/m^3 to 4.3 mg/m^3.

The method of analysis for chlorophyll a concentration used during this study gives a total chlorophyll a value which, according to some investigators, may not represent the active pigment present, but may include inactive phaeo-pigments. The interference of inactive phaeophyton might explain the poor correlation between community metabolism parameters and chlorophyll a.

Pigment diversity seemed not to be related to community metabolism. Gross means of pigment diversity were uniform over all stations (Table VI). No apparent relationship existed between pigment diversity and Pg/Rt ratios for Lake Carl Blackwell communities (Figure 12). Pigment diversity ranged from a high of about 4.1 for all stations to a low of about 3.0 for all stations.

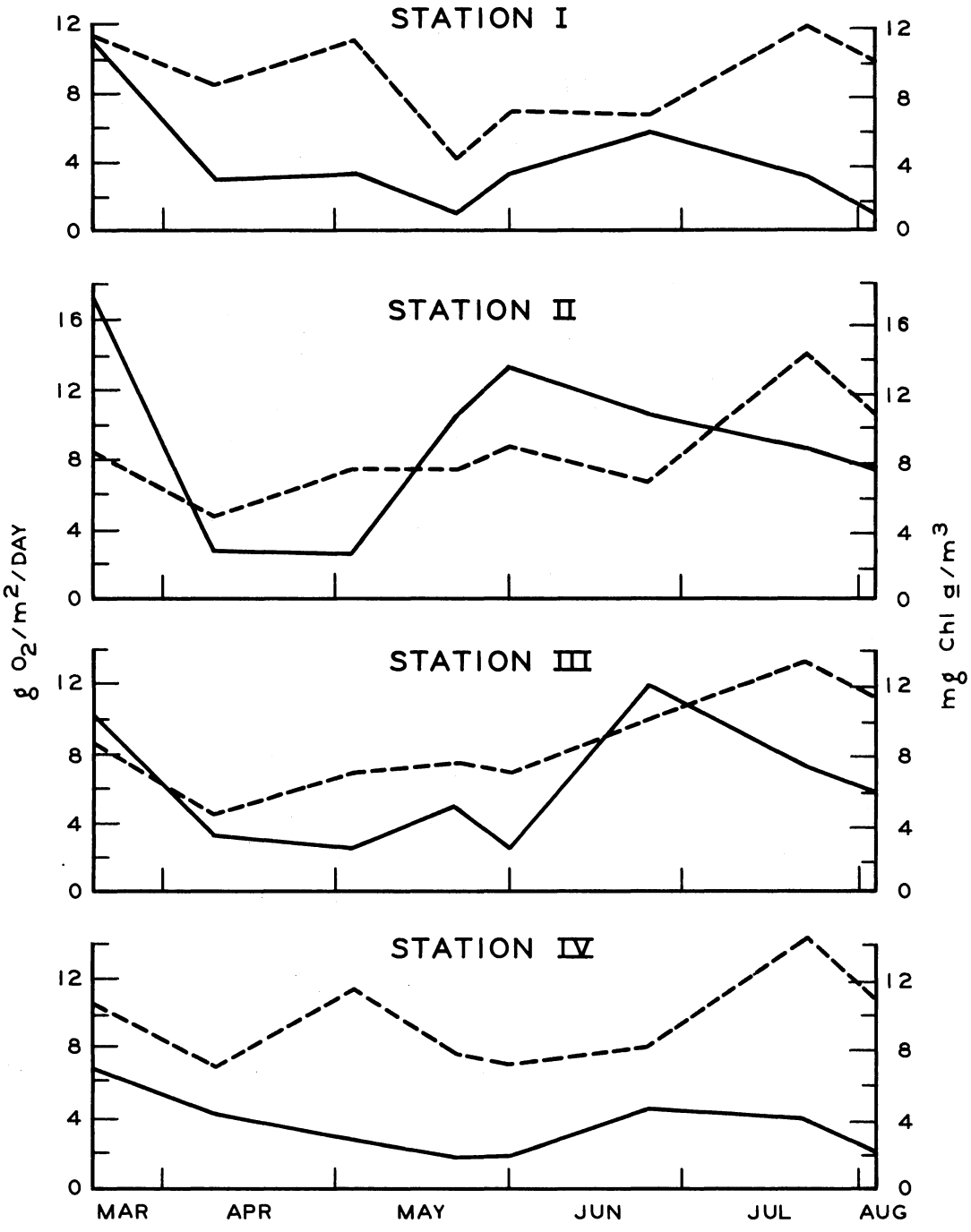

Figure 10. Daily Station Means of Pg (——) and Chlorophyll a (– – –)

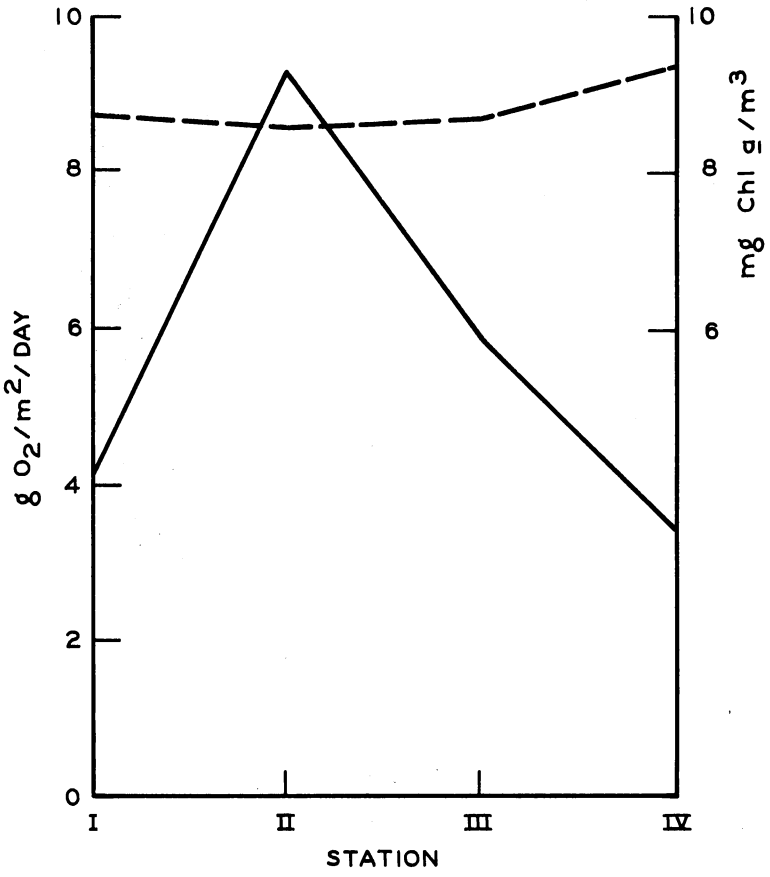

Figure 11. Gross Station Means of Pg (——) and Chlorophyll a (— —)

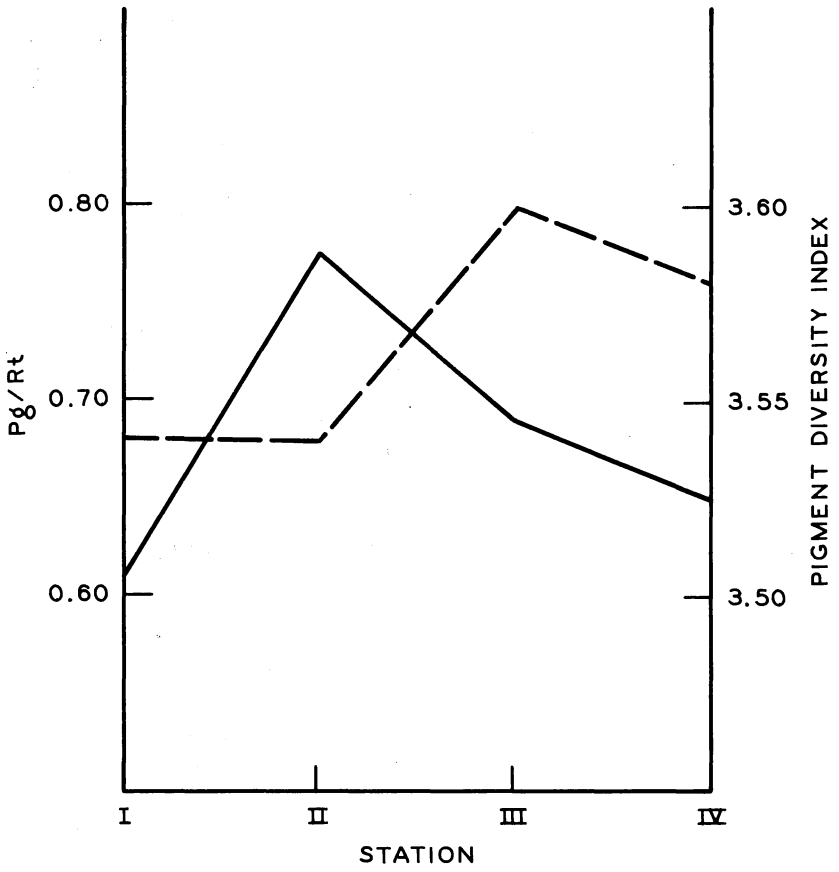

Figure 12. Gross Station Means of Pg/Rt Ratios (——) and Pigment Diversity Index (— —)

CHAPTER VI

CONCLUSIONS

Comparison of Methods Used in Calculating Community Metabolism

The three-point method requires much less time in collecting and analyzing data than the rate of change method. Data for the three-point method can be collected daily by using a small inexpensive, portable oxygen probe for an extended period of time. Three to five observations of dissolved oxygen concentration over a 24-hr period are sufficient for determining community metabolism parameters in many aquatic systems.

Investigators using the rate of change method often have to rely on few data over long periods of time. It is impossible to detect trends when day to day fluctuations are as great as seasonal fluctuations. Continuous or semi-continuous monitoring of dissolved oxygen over a period of several days often requires expensive, complicated, and frequently unreliable monitoring equipment.

The three-point method normally produces lower estimates of Pg and Rt when a constant rate of respiration is assumed over a 24-hr period. These estimates may be as precise as any other, however, since the true relationship of daytime to nighttime respiration is not known.

Horizontal Variation of Community Metabolism

Water transparency influenced variation in area-based estimates of Pg. Variation in euphotic zone depth-weighted Pg estimates followed the same pattern as area-based estimates. Direct relationships existed among Pg, Rt, euphotic zone depth, and column depth, and an inverse relationship existed between turbidity and Pg and Rt. No relationship was found between chlorophyll _a_ and Pg or Rt, possibly because the method does not give an estimate of active chlorophyll _a_. Pigment diversity had little relationship to community metabolism.

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