PRIMARY PRODUCTIVITY IN WATER RECLAMATION LAKES AT MICHIGAN STATE UNIVERSITY

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DONALD WAYNE SCHLOESSER

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ABSTRACT

PRIMARY PRODUCTIVITY IN WATER RECLAMATION
LAKES AT MICHIGAN STATE UNIVERSITY

By

Donald Wayne Schloesser

Primary productivity in the first lake in a series of four in a water reclamation facility was dominated by phytoplankton. Macrophytes plus their epiphytes, dominated primary productivity in the fourth lake. Using the diurnal oxygen curve method for obtaining estimates of net productivity and respiration, the plankton of the first lake on the average accounted for 100% of the ecosystem primary productivity and 75% of the ecosystem respiration. The remaining respiration occurred in the benthic community. In the fourth lake, an *Elodea canadensis*-epiphyte complex was responsible on the average for 75% of the ecosystem primary productivity and a like percentage of the ecosystem respiration. The remaining primary productivity occurred in the plankton. Primary productivity and respiration in the benthic community of this lake were too low to measure.

Mean P/R ratios for the first and fourth lakes over the growing season were 0.99 and 1.07 respectively. The latter was obtained after correcting gross primary production and respiration in the macrophyte component for maximum internal lacunar oxygen changes that might have occurred. Repeated studies of the lakes are

necessary to show whether increased seasonal autotrophy through the system is a consistent trend.

Harvest of aquatic macrophytes from water reclamation lakes may be a desirable management strategy. A P/R for the macrophytes can be estimated by the diurnal oxygen curve method used here to indicate the time of maximum biomass accrual. Experiments with different harvesting times and methods are needed to indicate whether multiple cuttings at maximum P/R or single cutting at maximum seasonal standing crop would give the most desirable yield of macrophytes.

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By

Donald Wayne Schloesser

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INTRODUCTION

Over the last two decades ecological theory, emanating from consideration of energy flow (Odum, 1956, 1957), has been concerned with metabolic patterns rather than structural composition. As one progresses up the organizational hierarchy of populations, ecosystem subunits, and ecosystems, certain metabolic patterns become increasingly evident. This is because a large system is more apt to reflect homeostatic mechanisms than a smaller unit (Odum, 1953). The results of measurements become more consistent due to checks and balances that dampen biological oscillations along the hierarchical line. By monitoring the highest hierarchical level, the ecosystem, one should be able to classify systems by function, while considerable variability can exist in structural composition. Such an approach was described by Odum (1956) and expanded by Margalef (1968). A P/R ratio, where P = gross primary production and R = community respiration was used in their scheme. System types have been defined by their deviation of P/R from unity. An autotrophic system would exhibit a $P/R > 1$; a heterotrophic system would exhibit a $P/R < 1$. A third type, the mature undisturbed system, has been considered to be in steady-state having a $P/R = 1$.

Odum (1956) has shown P/R ratios to be an effective ecosystem indicator in studies of the White River, exhibiting heterotrophy in an area highly polluted with organic material, autotrophy in a nutrient rich recovery area, and steady-state in an unenriched area. From this comes a theory that the more organically polluted a system, the lower the expected P/R ratio. This scheme appears ideal for classifying aquatic environments that have been exposed to man's activities. One purpose of this study was to determine whether the *in situ* oxygen measurement methods of Odum could be used to detect differences in the P/R ratios of lakes in the Michigan State University water reclamation facility.

A second purpose of this study was to partition ecosystems of the wastewater lakes into compartments by type of primary producer and to determine their influences on the total ecosystem P/R ratio. In this way ecological dominance by primary producer types could be determined. Where submersed vascular plants are a dominant type and their harvest is considered a desirable management strategy, Odum (1971) suggests that their P/R ratio measured over the growing season can be used to set the best time for harvest.

A third purpose of this study was to determine P/R for *Elodea canadensis* growing in a lake of the Michigan State University system over the season so that recommendations regarding the time of harvest might be made.

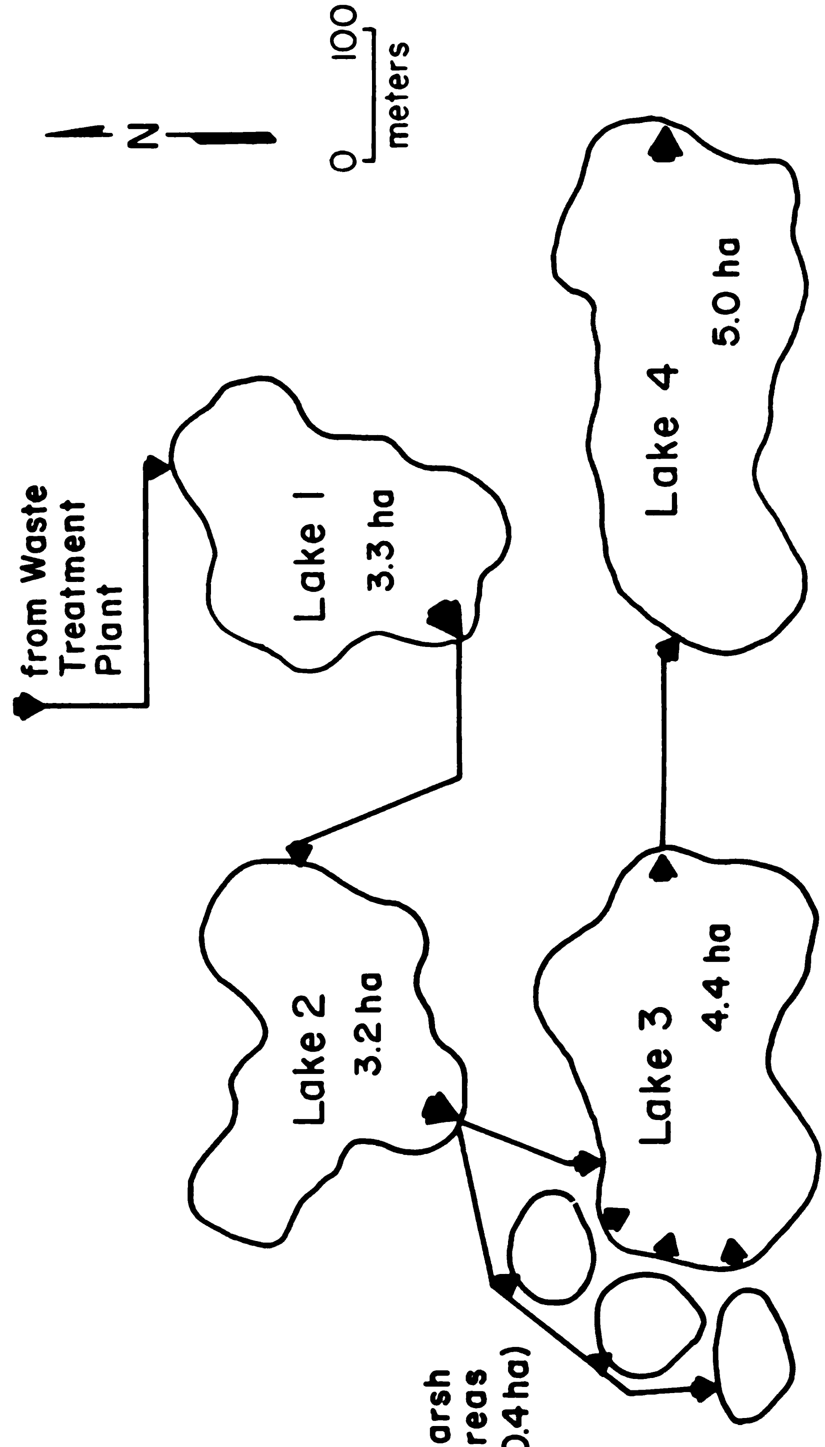
DESCRIPTION OF STUDY SITE

This study was carried out on Lakes 1 and 4 of the Michigan State University Water Quality Management facility (Figure 1). Built in 1973, this lake system receives effluent water from an East Lansing sewage treatment plant. The plant performs primary screening, activated sludge and partial tertiary treatment of domestic sewage. During this study approximately 45.6 million liters per day (ML/d) were processed at the plant with 43.5 ML/d discharged into the Red Cedar River. The remaining 1.9 ML/d were pumped 7.25 kilometers and discharged into Lake 1. Of the 1.9 ML/d entering Lake 1, 0.4 ML/d were taken for spray irrigation at a nearby site. Under gravitational flow, the remaining 1.5 ML/d were channeled through the lakes successively, with the effluent from Lake 4 going into Herron Creek.

The four lakes of the MSU system make up a total surface area of 16 hectares; they have a working depth of two meters. There are an additional 58 hectares equipped for spray irrigation. Three 0.4 hectare marshes are interconnected between Lakes 2 and 3. Lakes in the system are sealed with clay to prevent water loss. Relatively little detritus was present on the bottoms of the basins during this study.

The water in Lakes 1 and 4 differed noticeably in appearance over the study interval. It was very turbid in Lake 1. Algae

Figure 1.--Lakes of the water reclamation facility located on the Michigan State University campus. Arrows indicate direction of flow.



N
0 100
meters
from Waste
Treatment
Plant
Lake 1
3.3 ha
Lake 2
3.2 ha
Lake 3
4.4 ha
Lake 4
5.0 ha
Marsh
Areas
(0.4 ha)

scum and an associated odor were noted for brief periods in hot weather. The water of Lake 4 was clear and had none of the unpleasant aesthetic properties found in Lake 1. Water analysis showed that Lake 4 had lower concentrations of important nutrients than Lake 1 (Table 1).

Measurements made in this study showed oxygen was uniform in open water down to the water-sediment interface. Occasional low values were obtained at the water-sediment interface, but total depletion was not observed. Such lowering of oxygen concentrations at the interface is typically due to bacterial activity (Alsterberg, 1922; Edwards and Rolley, 1965). Percent oxygen saturation in the water columns of Lakes 1 and 4 ranged from 25% to 210% and 71% to 143% respectively. Over this study both lakes were aerobic.

Water temperatures found in these lakes were typical of shallow systems in the temperate zone (Macan, 1958; Butler, 1963). Temperatures rose to approximately 10°C early in May, gradually reaching highs of 25 to 30°C by mid-summer. By mid-October water temperatures were again about 10°C. Maximum changes of 3°C in the entire mass of a lake over a ten-hour period were recorded. Solar and atmospheric heat influx and wind were related to temperature shifts that occurred.

Average Secchi disk visibility in Lakes 1 and 4 were 1.3 and 2.0 meters respectively. Visibility in Lake 1 was divided into two distinct periods. During the 27 April to 15 July interval, mean Secchi transparency was 0.8 meters; in mid-summer visibility increased. In the interval 15 July to 17 October, the mean Secchi

TABLE 1.--Selected characteristics of influent and effluent water in Lakes 1 and 4 expressed as means taken on survey dates during the interval 27 April to 17 October, 1975.

Parameter	Lake 1	Lake 4
Hardness mg/l-$CaCO_3$[a]		
Influent	320	186
Effluent	313	145
Alkalinity mg/l-$CaCO_3$[a]		
Influent	149	82
Effluent	158	61
Nitrate mg/l-N[a]		
Influent	8.30	0.33
Effluent	6.50	0.17
Total Phosphorus mg/l-P[a]		
Influent	1.04	0.80
Effluent	0.68	0.07
Kjeldahl Nitrogen mg/l-N[a]		
Influent	1.17	1.14
Effluent	3.39	0.64
Surface pH	8.6	9.9
Mean Surface Dissolved Oxygen mg/l	9.1	9.8

[a]Hourly composite sample on survey dates analyzed by Technicon Solid Prep 111 Autoanalyzer.

disk determination was 1.5 meters. Lake 4 visibility extended to the bottom of the basin throughout the season.

Macrophytic vegetation was composed of species that had been seeded into Lakes 2, 3 and 4 during the fall of 1973 (McNabb *et al*., 1975). *Potamogeton foliosus* Raf., *Elodea canadensis* Michx. and *Cladophora fracta* (Dillw.) Keutzing were the abundant macrophytes during this study. In unseeded Lake 1, macrophyte growth was negligible until mid-August; patches of *P. foliosus* (44 g/m^2 ash-free dry weight) and *C. fracta* (13 g/m^2 ash free dry weight) were present thereafter. Lake 4 produced the largest macrophyte crop in 1975. *E. canadensis* formed dense monotypic stands of vegetation (157 g/m^2 ash-free dry weight). *P. foliosus* formed thin patches of growth (10 g/m^2 ash-free dry weight) around the outer margins of the *E. canadensis* stands. *C. fracta* occurred in sparse amounts in Lake 4.

Phytoplankton quantity and quality fluctuated dramatically over the summer of 1975 (McNabb *et al*., 1975). In Lake 1, the total number of algal cells ranged from 1,500 to 70,000/ml with a summer mean of 15,300 cells/ml. In Lake 4, total numbers ranged from 100 to 74,000/ml with a summer mean of 12,400 cells/ml. Lake 1 was dominated by species of green algae and diatoms while Lake 4 was dominated by species of green and blue-green algae. Table A-1 gives a list of major species which were enumerated in water samples.

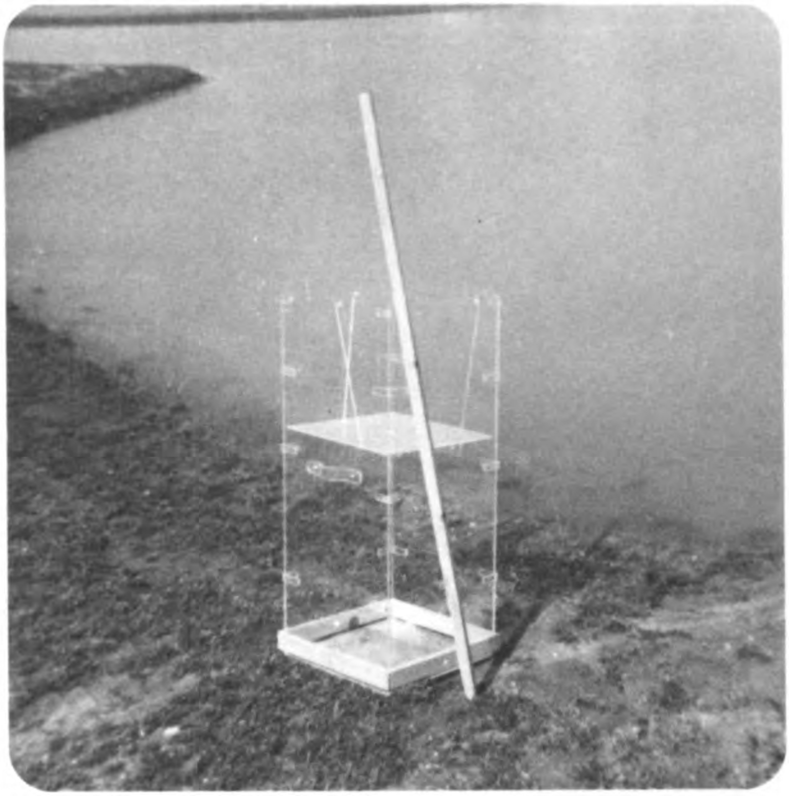
METHODS

This study took place during the first growing season in which the MSU water reclamation facility was operating. Combinations of plexiglass enclosures were used to partition the ecosystem so that benthic, planktonic and macrophytic production and respiration could be estimated. The nature of the enclosures is shown in Figure 2. They were made of 0.64 cm plexiglass and were 0.57 m by 0.57 m by 1.5 m in dimensions. For a set of measurements on primary production and community respiration, one enclosure was pushed into the sediments in an area free of aquatic vascular plants. In Lake 4, where _Elodea canadensis_ existed over the entire study area, 3 m by 3 m sections were randomly cleared 6 weeks in advance of measurements. This time interval proved satisfactory in that _E. canadensis_ recolonization did not occur and Waters (1961) had shown it to be adequate for epipelic algal development. In Lake 4 where the submersed vascular plants were an important component of the ecosystem, a second enclosure was pushed into the sediments to surround a stand. A third enclosure, with one end sealed using plexiglass, was filled with water to pond-depth and placed upright in the water column with the sealed end down.

The diurnal oxygen curve method of Odum and Hoskins (1957) and McConnell (1962) was used to measure rates of primary production and respiration within enclosures. The need to make corrections for

Figure 2.--Plexiglass enclosure (A) used for _in situ_ productivity and respiration measurements (B).

A



B

surface gas exchanges was eliminated by covering the enclosed water with adjustable plexiglass lids. The particular technique was based on the light-dark bottle concept of Gaarder and Gran (1927). By measuring oxygen changes between dawn and dusk, it was possible to estimate net primary production (NP); the differences between oxygen concentrations at dusk and the following dawn were taken as estimates of respiration (R).

A Yellow Springs Instrument Model 54 oxygen and temperature probes and meter were used in the measurements. Frequent membrane changes and Winkler standardizations (azide modification of APHA, AWWA and WPCF, 1971) assured accurate dissolved oxygen determinations; $\pm$ 1% full scale deflection, the maximum being $\pm$ 0.2 mg/l. Measurements were taken at the surface, at depths of 0.5 m and 1.0 m, and at the water-sediment interface at depth 1.1 m. Oxygen concentrations were plotted against depth for each series of measurements. Dawn-dusk and dusk-dawn differences in oxygen concentrations for enclosed water columns as a whole were obtained from these graphs using a polar compensating planimeter. Mean hourly net productivity and respiration rate were obtained by dividing the change in oxygen concentration for a light or dark interval by the number of hours in that interval. Hourly net productivity and respiration rates were added to obtain an estimate of gross primary productivity. Daily productivity was made equal to the hourly rates multiplied by the number of daylight hours. Daily respiration was made equal to the hourly respiration rate multiplied by 24. Knowing the volume (390 liters) and areal dimensions of the enclosures, the results were expressed as g O_2/m^2/day. For reference and in the interest of uniformity suggested by Vollenweider (1969), gross primary productivity was calculated as g C/m^2/day and the results presented in the Appendix (Table A-2). These data were obtained by assuming a mean photosynthetic quotient of 1.2 (Westlake, 1963) and multiplying g O_2/m^2/day by 0.312 (Vollenweider, 1969).

With the combination of enclosures and the methods employed, primary productivity and community respiration estimates of the ecosystem were partitioned into planktonic, benthic and vascular plant-epiphyte components. Rates of the planktonic component were measured directly in enclosures containing only the plankton. Rates in the benthic component were obtained by subtracting planktonic rates from rates measured in enclosures open to the bottom, but lacking macrophytes. Rates for the vascular plant-epiphyte component were obtained by subtracting planktonic and benthic rates from measurements in enclosures open to the bottom and containing macrophytes.

Sampling in these enclosures took place at regularly spaced intervals between 27 April and 17 October, 1975. Studies spanning 36-hour cycles were conducted 13 times in Lake 1 and 15 times in Lake 4. Only one of the lakes was surveyed on any particular date. Dates were not selected for particular conditions of weather. On each occasion a position was selected along the lake perimeter and the enclosures were set from a boat in 1.1 m of water. Wooden stakes were used to hold them steady in the water. Two replicates of each type of enclosure were used at any given time of measurement.

The units were positioned approximately 10 hours before water analyses were begun. All construction materials were non-growth inhibiting as described by Dyer and Richardson (1961).

Percent transmittance of incident light was determined at each sampling with a submarine photometer connected to a low resistance galvometer (Fred Schueler, Waltham, Massachusetts). Transmittance, as compared to surface measurements, was determined at the 0.5 to 1.0 m depths. The quantity of incident solar radiation was determined by planimetry of curves from a recording Epply pyrheliometer. Michigan State University's South Farm climatological station, approximately one kilometer north of the study area, maintained this pyrheliometer.

Chlorophyll-a was selected as the quantitative measure for phytoplankton abundance. Equal volumes of water were taken from the two plankton stations, combined and immediately transported to the laboratory. After major zooplankters were screened (250 micron mesh), volumes of water were filtered through 0.45 $\pm$ .02 micron glass filters (Gilman Instrument Company, Metricel G.A.-6) at a pressure of 20 to 30 cm Hg. A 0.45 micron pore size has been shown to remove all significant phytoplankton (Lasker and Holmes, 1957). Samples were dark-stored at 4°C for 2 to 3 weeks before extraction was performed (Collins _et al._, 1975). Extraction was carried out under reduced light by manual grinding in an aqueous solution of reagent grade 90% acetone rendered basic with magnesium carbonate. After centrifugation, spectrophotometric procedures were carried out on a Bausch and Lomb Spectronic 20 to obtain an estimate of chlorophyll-a. Calculations followed those of Talling and Driver (1963). Corrections for phaeophytins followed those of Lorenzen (1967). Knowing the volume and areal dimensions of the enclosures, mean values of three replicates were expressed as mg/m^2 chlorophyll-a.

E. canadensis was harvested from enclosures at the end of a period of measurement. While in the field, plants were handwashed trying not to brush off silt-like deposits found on the leaves and stems. Dry and ash weights were determined in the laboratory under desiccation at 105° and 550°C respectively. Ash-free dry weights (organic weights) were computed. Biomass was expressed as g/m^2 ash-free dry weight.

RESULTS

Abundance of Primary Producers

A one-way analysis of variance was performed on phytoplankton chlorophyll-a concentrations found in Lakes 1 and 4 (Table 2). Means were positively correlated with variances; the values were coded by adding one and making a logarithmic transformation (Snedecor and Cochran, 1967). Homogeneity of variances was then varified by F_{max} tests.

Lake 1 had significantly greater phytoplankton chlorophyll-a concentrations than Lake 4 (99.5% probability level). Concentrations in Lake 1 ranged from 2.7 to 52.1 mg/m^2 with a seasonal mean of 17.4 mg/m^2 chlorophyll-a. Phytoplankton chlorophyll-a in Lake 4 ranged from 0.0 to 5.9 mg/m^2 with a seasonal mean of 2.5 mg/m^2. In Lake 1 it was consistently high early in the season (up to 25 June), and then varied widely. In Lake 4, concentrations were relatively high in early spring, then gradually decreased as the study progressed.

E. canadensis vegetation in Lake 4 was sufficient in early spring to quickly shade the sediments upon which it was growing. Biomass within the enclosures ranged from 2.8 to 408.5 g/m^2 ash-free dry weight with a mean of 220.6 g/m^2 (Table 3). Percent ash of dry weight increased over the season; carbonate deposits were observed to increase concurrently on the adaxial plant surfaces.

TABLE 2.--Mean phytoplankton chlorophyll-a concentrations in mg/m^2 in 1.1 m of water.

Date	Lake 1	Date	Lake 4
5/6/75	52.1	4/27	5.9
6/3	12.9	5/16	5.0
6/17	20.7	6/10	3.2
6/25	34.5	6/19	1.8
7/6	7.8	7/1	4.4
7/15	14.4	7/10	5.8
7/29	7.1	7/22	3.4
8/7	21.8	8/2	0.3
8/16	9.0	8/12	0.8
8/27	3.2	8/21	3.3
9/9	34.3	9/14	0
9/19	6.3	9/24	0.8
10/1	2.7	10/8	1.6
		10/17	0.5
Seasonal mean	17.4		2.5

TABLE 3.--Weight determinations (g/m^2) for the biomass of *Elodea canadensis* taken from enclosures within Lake 4.

Date	Percent Ash of Dry Weight	Ash-free Dry Weight
4/27/75	-	108.1 8.2
5/16	-	64.9 165.5
6/10	27.6	243.3 313.7
6/19	24.3	226.1 320.3
7/1	29.0	282.6 226.3
7/10	30.4	273.5 71.6
7/22	38.0	305.9 297.6
8/2	36.3	173.8 108.7
8/12	38.1	269.2 338.5
8/21	40.1	375.7 232.0
9/2	35.6	363.4 137.6
9/14	40.0	408.8 102.8
9/24	36.8	124.0 227.5
10/8	49.9	272.6 222.3
10/17	43.4	199.3 195.9

Conditions of Light

The input of energy for study dates on Lake 1 varied less than for dates of measurement on Lake 4; seasonal coefficients of variation were 35% and 55% respectively (Table 4). Over the period of the study, enclosures in Lake 4 received less solar energy than those of Lake 1; means were 3401 kcal/m^2/day and 4398 kcal/m^2/day respectively.

In Lake 1, light attenuation was related to the amount of chlorophyll-a found in the water; the product moment correlation coefficient (PMCC) was 0.72. There was an approximately linear relationship when the extinction coefficient (Vollenweider, 1955) was related to the logarithmic function of the chlorophyll-a concentrations (Figure 3). A relationship such as this was not found in Lake 4; there the PMCC was 0.20. The percent transmittance of incident light in Lake 4 (cf. Table A-3) was greatly reduced by canopies of *E. canadensis* (Figure 4). Light transmittance into a canopy was regularly reduced to 1% of incident within the first 15 cm of vegetation. No differences in extinction occurred between the water above a canopy and the same stratum of water in areas that had been cleared of vegetation.

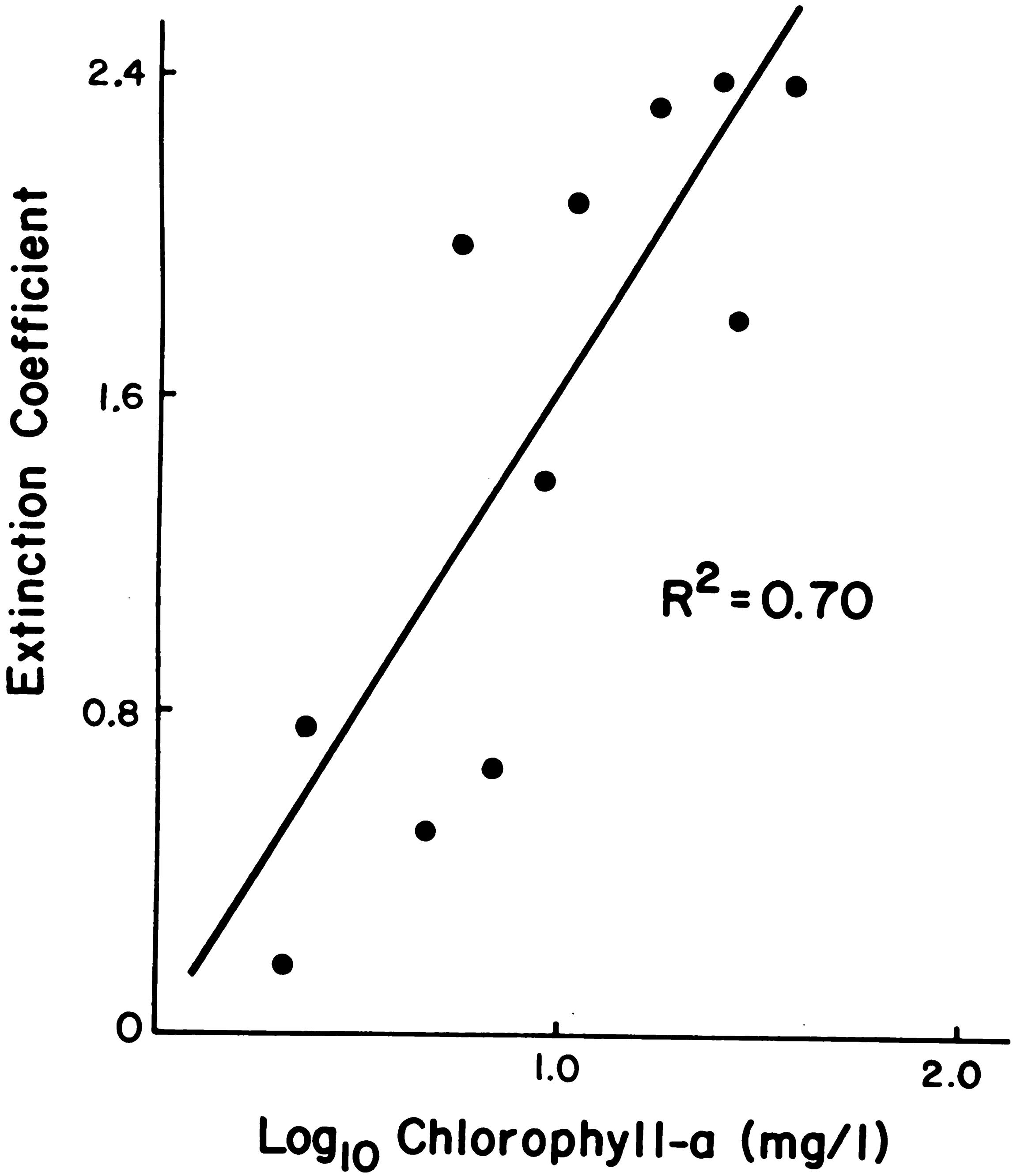
Primary Productivity and Respiration

A two-way analysis of variance with replicates was performed on changes in the dissolved oxygen content of the water columns in enclosure types within Lakes 1 and 4 for daylight and darkness periods after the methods of Snedecor and Cochran (1967). Tukey's

TABLE 4.--Daily surface radiation (kcal/m^2/day) on dates of study in Lakes 1 and 4.

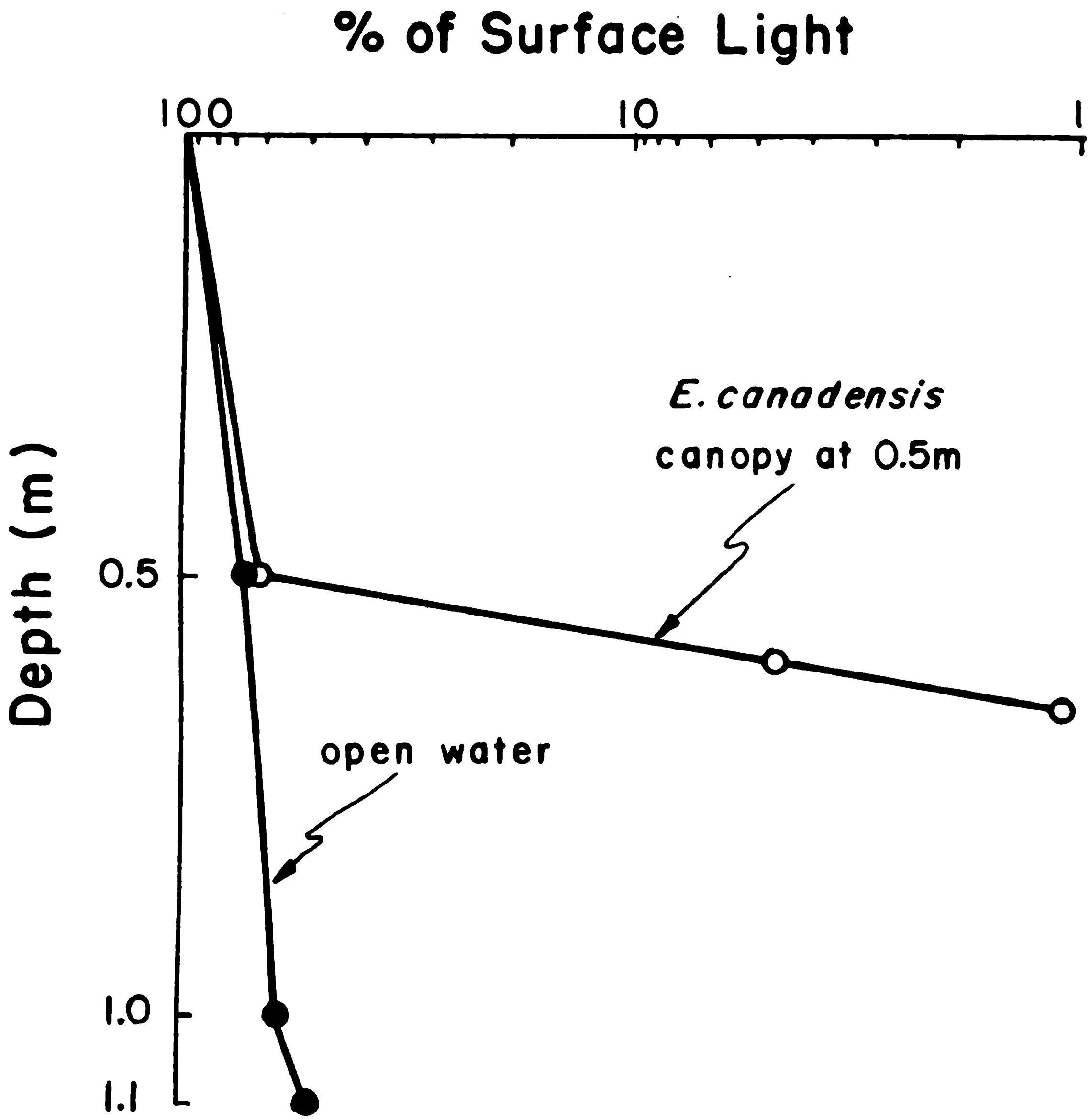
Date	Lake 1	Date	Lake 4
5/6/75	3558	4/27/75	846
6/3	5166	5/16	4686
6/17	4023	6/10	6192
6/25	3920	6/19	4324
7/6	4648	7/1	5240
7/15	4806	7/10	3948
7/29	6659	7/22	5766
8/7	5713	8/2	1211
8/16	5205	8/12	4051
8/27	5341	8/21	611
9/9	5272	9/2	3883
9/19	1344	9/14	4328
10/1	1518	9/24	3179
		10/8	1549
		10/17	1094
Seasonal Means	4398		3401
Coefficient of Variation	35%		55%

Figure 3.--The relationship between the extinction coefficient of light and the chlorophyll-a concentrations found in Lake 1.



2.4
1.6
0.8
0
1.0
2.0
Extinction Coefficient
$R^2 = 0.70$
Log10 Chlorophyll-a (mg/l)

Figure 4.--Light transmittance occurring in the open water and in a canopy of Elodea canadensis in Lake 4.


% of Surface Light
100
10
1
Depth (m)
0.5
1.0
1.1
E. canadensis
canopy at 0.5m
open water

test for additivity was used to check block-treatment interaction of all analyses. In Lake 1, daylight oxygen changes within planktonic and benthic enclosures were significantly different (95% probability level). The planktonic enclosures gained more oxygen in the daytime than the benthic enclosures. In Lake 4, these oxygen changes were not significantly different; however, E. canadensis enclosures had significantly greater oxygen gains during the day and greater oxygen loss at night than the planktonic and benthic enclosures (99% probability level). These results point to functionally different relationships between oxygen metabolizing components of the ecosystems of these lakes.

Gross primary productivities in the planktonic and benthic enclosures of Lake 1 were not significantly different at the 95% level of confidence. This result was taken to mean that productivity of benthic algae, if it occurred at all, was negligible relative to that of the phytoplankton. The procedure employed in this study to estimate productivity of the benthic algal community was to subtract daily gross production in the planktonic enclosures from daily gross production in the benthic enclosure. When this was done, values for the benthic estimate were positive 35% of the times, zero 4% of the times, and negative for the remaining percentage of times. The mean for this value over the study period was -0.66 g O_2/m^2/day. The chi-square goodness of fit test (Snedecor and Cochran, 1967) showed that individual benthic estimates were normally distributed around a mean not significantly different from zero (95% probability level). If gross primary productivity occurred in the benthos, these results suggest that on the average it was small and that the experimental technique used was not sufficiently precise to measure it. The benthic community of Lake 1 was taken to be essentially non-photosynthetic, consuming oxygen produced by the plankton at a measurable rate both day and night.

Since daytime gains and nighttime losses in dissolved oxygen in the water columns of planktonic and benthic enclosures in Lake 4 were not different for the study dates, as cited above, the benthic component of the lake was taken to have a negligible impact on both gross primary production and respiration of the ecosystem. When gross primary productivity of the benthos was calculated by the method of this study, the mean for the sampling dates was 0.23 g O_2/m^2/day. The chi-square goodness of fit test as presented above for Lake 1 benthic productivity was applied to the daily benthic estimates from Lake 4 with the same result as for Lake 1. The benthic community of Lake 4 was taken to be essentially non-photosynthetic for the study interval. The rate of respiratory oxygen use by the benthic community was also too small to measure.

With these considerations in mind, a modified two-way analysis of variance was performed on the estimates of gross primary productivity within and between lakes (Table A-4). Negative estimates for the benthic components were included for purposes of this analysis. The procedure involved a classification with unequal numbers having proportional subclasses (Snedecor and Cochran, 1967). After logistic transformations, variances were found to be homogeneous by Tukey's test. Between lake comparisons were performed even though measurements were taken on the lakes on different dates. Observed differences between lakes (e.g. radiation influx), as well as unobserved differences, introduced an error not incorporated into the pooled residual used to test between lake differences. Pooled data showed significant differences existing between Lakes 1 and 4. Several LSD tests were conducted to determine where differences between lakes existed. Results of all tests (LDS having the lowest significance level of 95%) indicated a hierarchy of primary productivity as:

Lake 1 Phytoplankton = Lake 4 Macrophyte-Epiphyte Complex

v

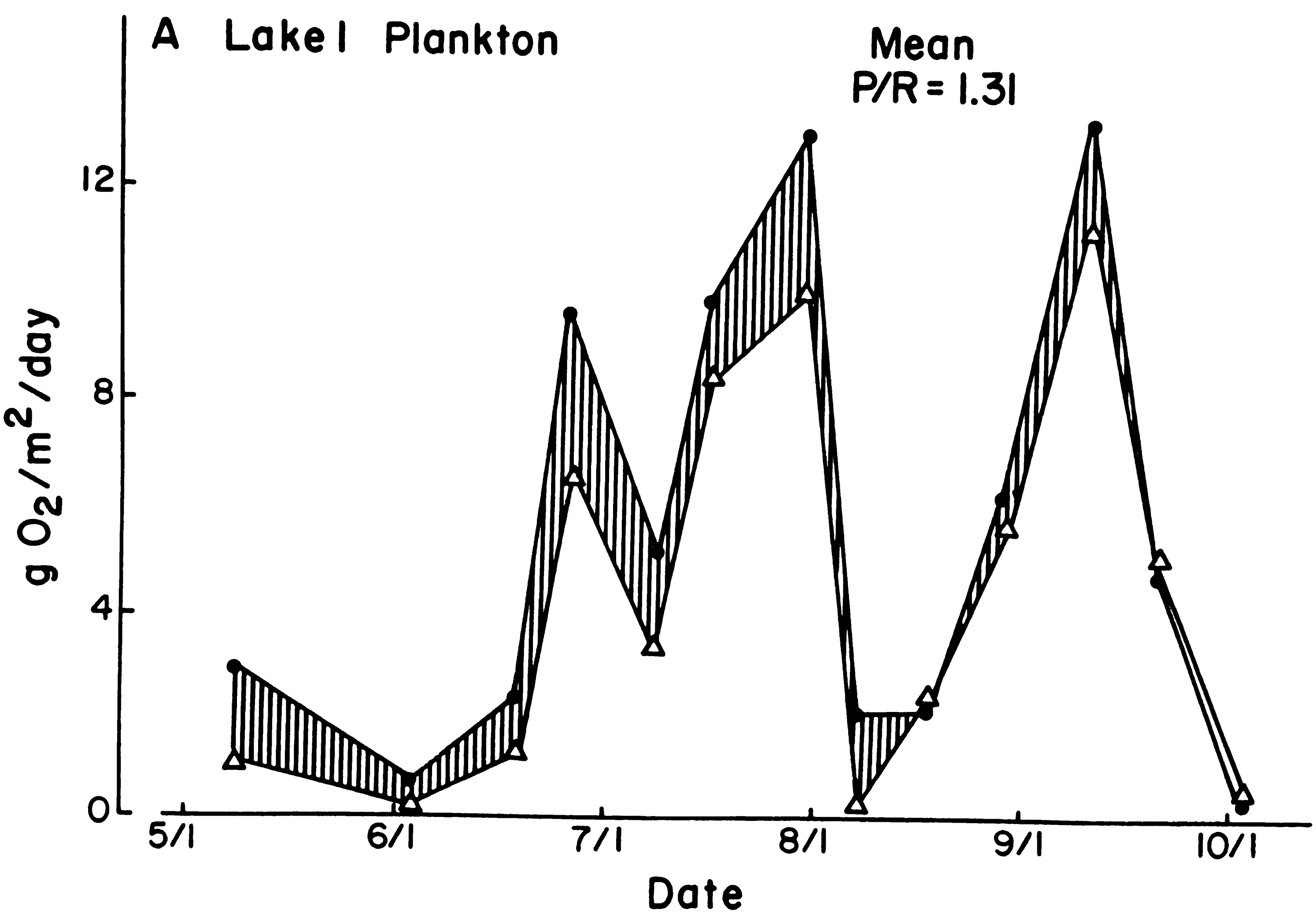
Lake 4 Phytoplankton

v

Lake 1 Benthos = Lake 4 Benthos

Estimates of gross primary production, community respiration, and net primary production for the days of study are shown in Figures 5 and 6. In Lake 1, phytoplanktonic oxygen production exceeded daily planktonic respiration except for three dates, on these latter occasions, P/R was very close to 1 (Figure 5A). Gross productivity was relatively high from mid-June to early August, and again on dates in September. In general, respiration in the planktonic community was high when gross primary productivity was high, and was low when algal productivity was low. The mean P/R ratio in the plankton for the dates of study was 1.31.

Figure 5.--Plankton (A) and whole ecosystem (B) productivity and respiration in Lake 1 in 1975. Differences between gross productivity (●) and respiration (△) are darkened to show net productivity.


A Lake I Plankton
Mean
P/R = 1.31
g O_2/m^2/day
0
4
8
12
5/1
6/1
7/1
8/1
9/1
10/1
Date

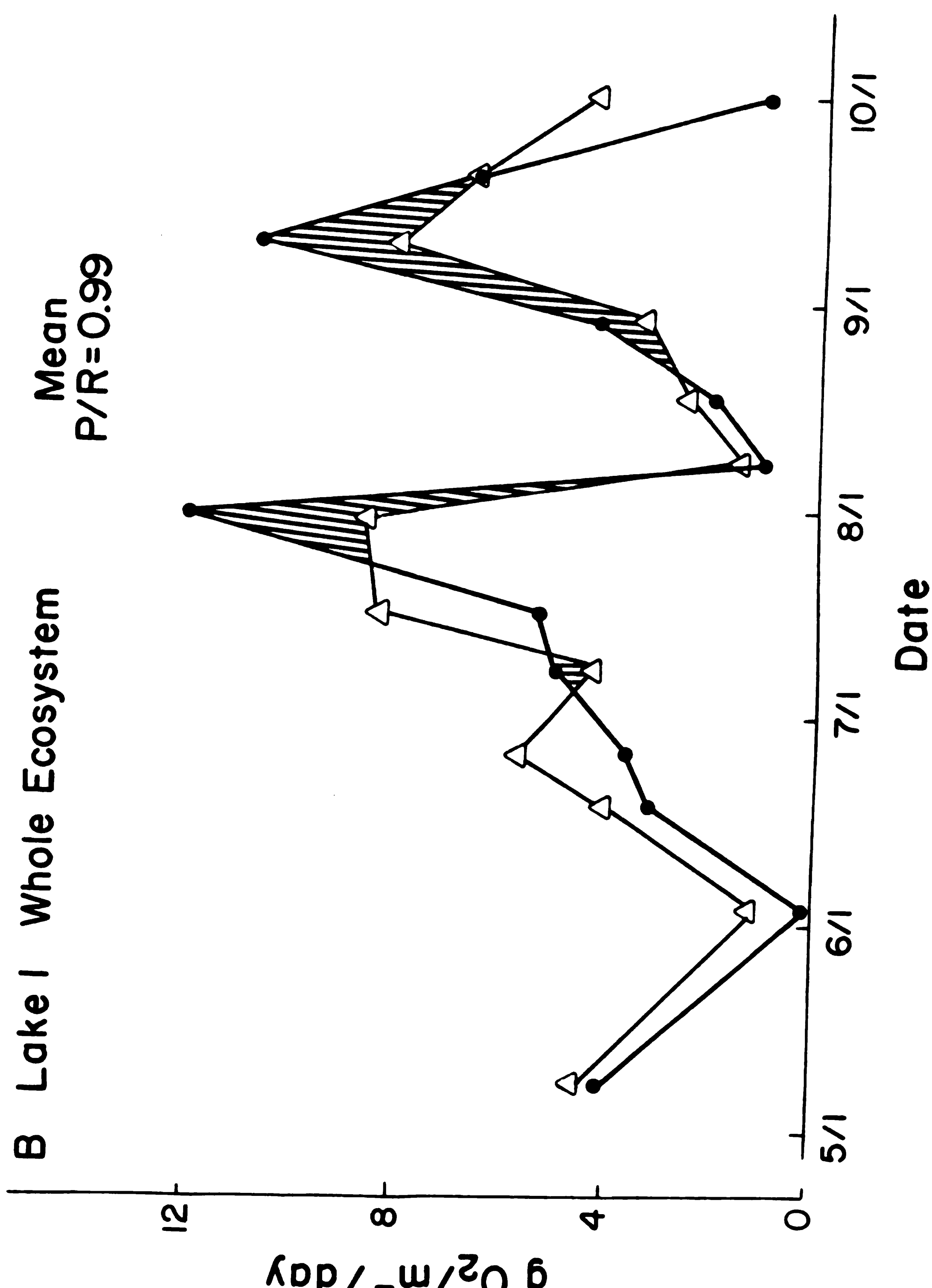
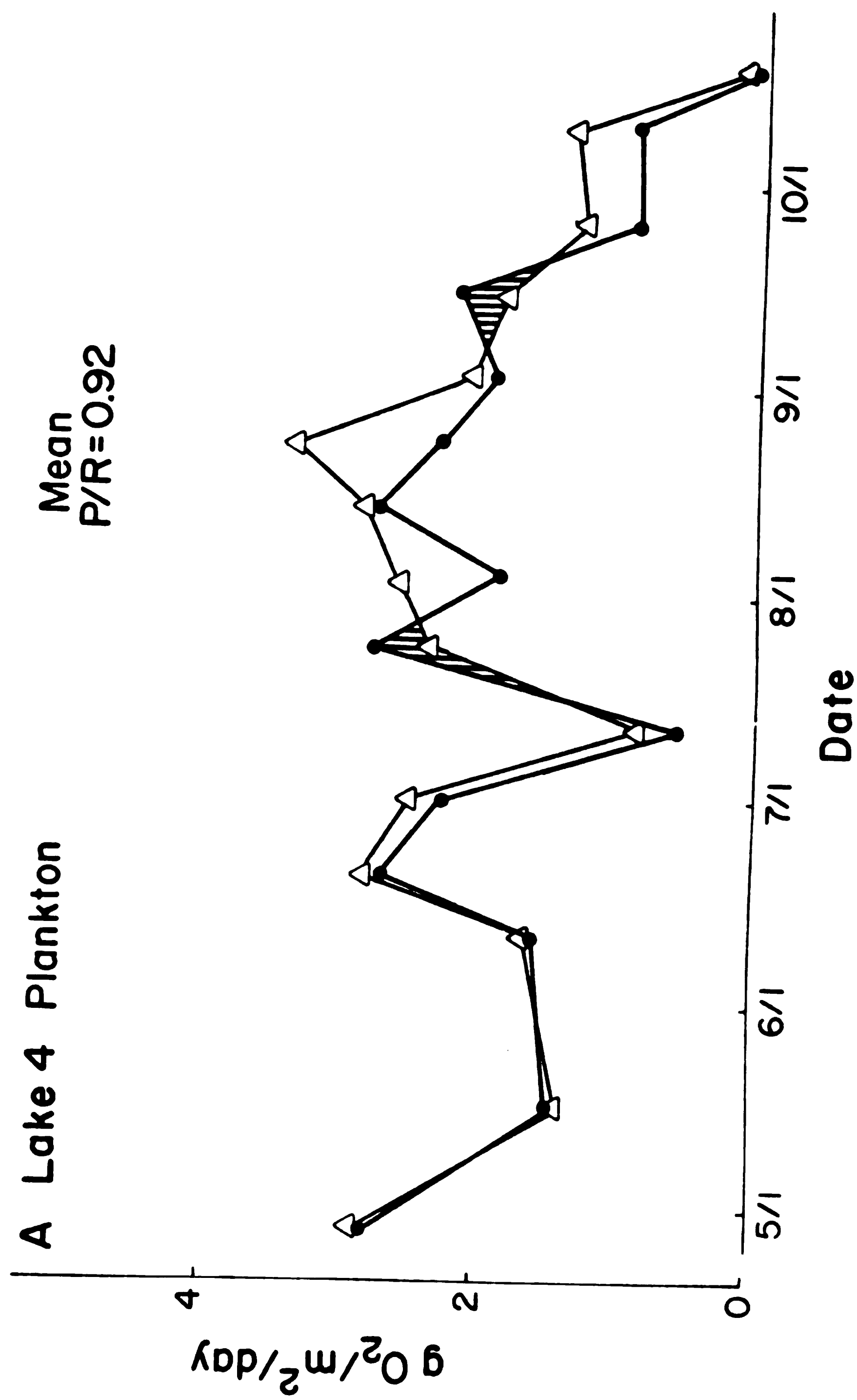
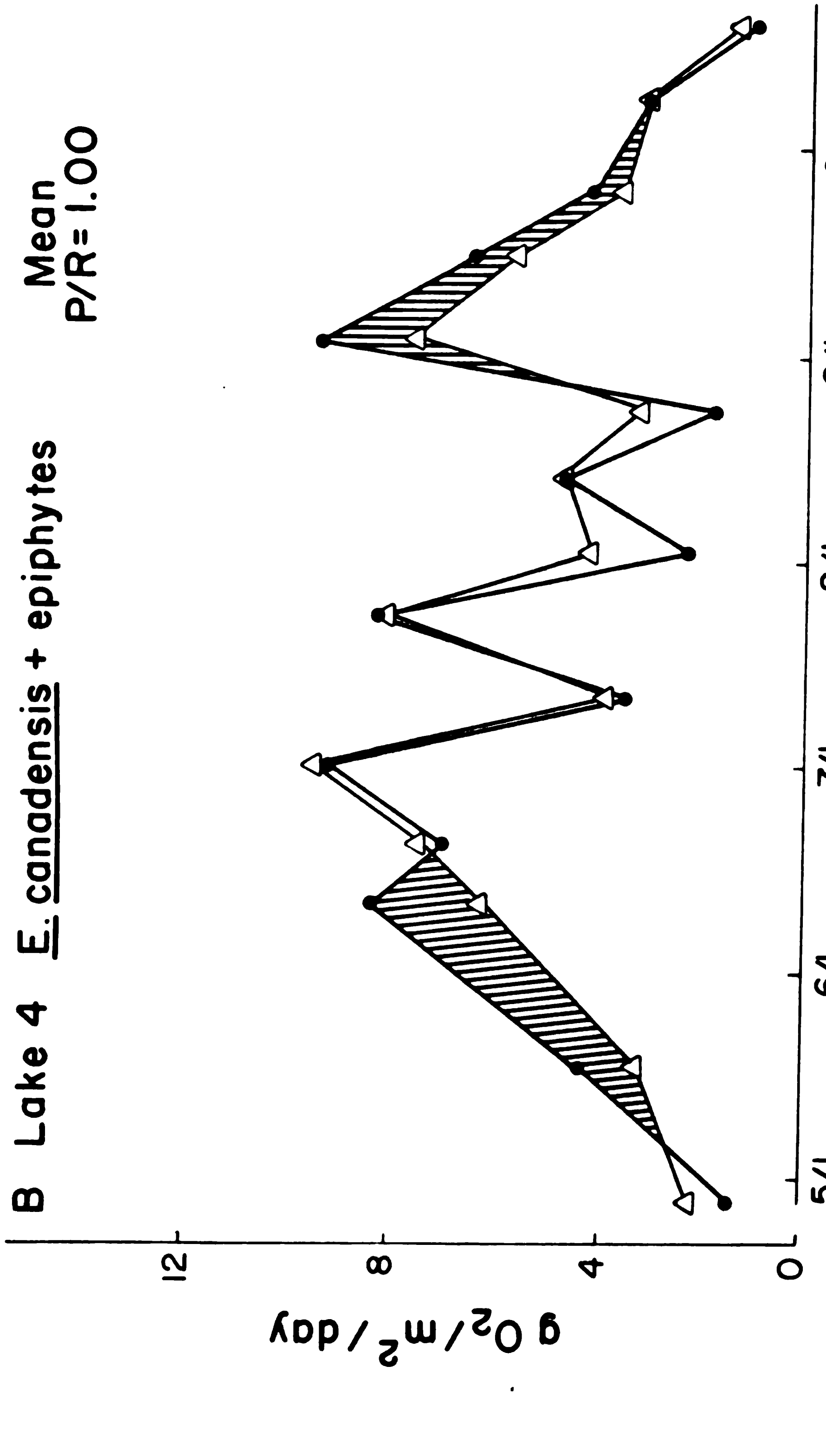
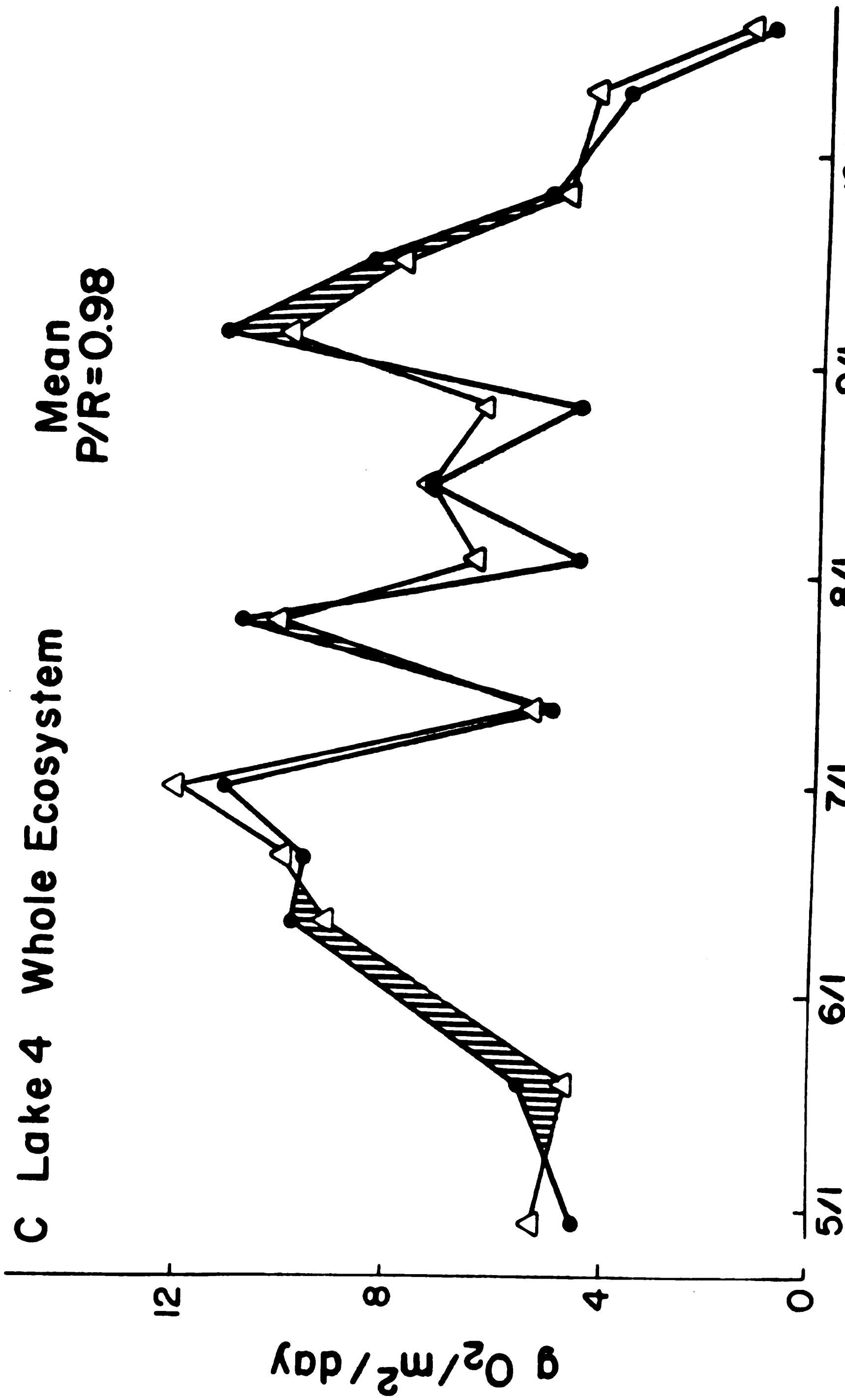

B Lake I Whole Ecosystem
Mean
P/R=0.99
g O_2/m^2/day
0
4
8
12
5/1
6/1
7/1
8/1
9/1
10/1
Date

Figure 6.--Plankton (A), _Elodea canadensis_ plus its epiphytes (B), and whole ecosystem (C) productivity and respiration in Lake 4 in 1975. Differences between gross productivity (●) and respiration (△) are darkened to show net productivity.


A Lake 4 Plankton
Mean
P/R=0.92
g O2/m2/day
0
2
4
5/1
6/1
7/1
8/1
9/1
10/1
Date


B Lake 4 E. canadensis + epiphytes
Mean
P/R= 1.00
g O2 / m2 / day
0
4
8
12
5/1
6/1
7/1
8/1
9/1
10/1
Date


C Lake 4 Whole Ecosystem
Mean
P/R=0.98
g O_2/m^2/day
0
4
8
12
5/1
6/1
7/1
8/1
9/1
10/1
Date

From the discussion of benthic oxygen metabolism given above, where gross productivity was taken to be zero, the seasonal P/R ratio for that community was zero. Figure 5B, considering the ecosystem as a whole, shows that daily oxygen consumption regularly exceeded gross production on dates early in the growing season. From early August to late September, whole ecosystem enclosures tended to have P/R ratios close to, or greater than 1. Measured respiration rates for the benthos can be obtained from Figure 5 by subtracting the planktonic respiration rate from the respiration rate given for whole ecosystem enclosures. Instances of heterotrophy and autotrophy balanced out over the study interval so that the mean P/R ratio for the ecosystem was very close to 1 (0.99).

Figure 6 presents data in a similar manner for Lake 4. The P/R ratio of the benthic community was taken to be zero because of lack of gross primary productivity. Since respiration in the benthos was too small to measure, that effect is not included in the data of Figure 6. The plankton community surrounding the vascular plants of the lake tended to be heterotrophic; plankton respiration exceeded phytoplanktonic gross O_2 productivity on 12 of 15 study dates (Figure 6A). A mean P/R ratio of 0.92 was observed for the plankton over the study interval as a whole. Figure 6B shows that the Elodea canadensis-epiphyte component of the ecosystem switched from an autotrophic to a heterotrophic, then back to an autotrophic mode during the study. Comparison of Figures 6A and 6B reveals that rates of gross production and respiration in the vascular plant complex were regularly 2 to 3 times greater than the same rates in the plankton. Because of this, parallel pulses and recessions are evident when comparisons of oxygen metabolisms for the vascular plant-epiphyte component and the ecosystem as a whole are made with Figures 6B and 6C. This dominance by the E. canadensis-epiphyte component is further demonstrated by no substantial differences of P/R ratios, these being 0.98 for E. canadensis and 1.00 for the whole ecosystem.

Estimates for seasonal means of productivity and respiration for the dates of study are given in Table 5. One hundred percent of gross primary productivity and an estimated 75% of respiration in the Lake 1 ecosystem were accounted for by the plankton community. Mean gross primary production and respiration for the ecosystem of Lake 4 were found to be substantially higher than for Lake 1. On the average, 26% of the gross primary production in Lake 4 was attributable to the phytoplankton; 74% was attributable to the E. canadensis-eiphyyte complex. Respiration in these two components of the system was in the same ratio as gross production.

TABLE 5.--Seasonal means of productivity and respiration in g $O_2/m^2/day$ for community types and ecosystems in Lakes 1 and 4 during 1975.

	Lake 1			Lake 4			
	Plankton	Benthos	Ecosystem	Plankton[c]	Benthos	Elodea-Epiphyte Complex	Ecosystem
Net Production	1.25	-1.30	-0.05	-0.16	0	0.02	-0.16
Respiration	3.99	(1.30)[b]	5.29	1.99	0	5.29	7.28
Gross Primary Production	5.25	(0)[a]	5.25	1.83	0	5.30	7.12

[a]Best estimate for reasons discussed in text.

[b]Actual mean value of 0.65 was obtained by subtraction of calculated daily oxygen loss of planktonic enclosure from benthic enclosure. This estimate corrected to 1.30 on assumption that gross production in benthos was 0, and the measured observation that net benthic production was -1.30. Total ecosystem values adjusted accordingly.

[c]Because significant differences did not exist between changes in daytime and night-time oxygen content of planktonic and benthic enclosures in Lake 4 (no effect by the benthos), values from planktonic and benthic enclosures were used to obtain these means.

DISCUSSION

Phytoplankton standing crops have been shown to be directly related to the nutrient status of the water (Lund, 1957; Moss, 1969). Algae concentrations in Lakes 1 and 4 were consistent with this observation. Nutrient rich Lake 1 had significantly greater concentrations of chlorophyll-a than Lake 4. Additionally, the antagonistic effect of vascular aquatic plants upon algal growth (Fitzgerald, 1969; Goulder, 1969; and others) may have been important in causing this difference. Early season phytoplankton chlorophyll-a concentrations in Lake 4 were relatively high, gradually decreasing as canopies of *E. canadensis* formed.

Seasonal mean phytoplankton chlorophyll-a concentrations in Lakes 1 and 4 were within the range of values typically found in natural waters (Vollenweider, 1969; Wetzel, 1975). However, Lake 1 showed sporadic concentrations, often 1.5 to 2.0 times the maximum concentrations normally found in natural systems. Lake 4 concentrations were always in the lower portions of the normal range.

The ecological dominants of primary producers in Lakes 1 and 4 were the phytoplankton and the *E. canadensis*-epiphyte complex respectively. The plankton in Lake 1 was responsible for 100% of the productivity and 75% of the ecosystem respiration over the season. In nutrient rich systems, phytoplankton dominance over other community types is not unusual (Wetzel, 1975). In Lake 4, the E. canadensis-epiphyte complex made up an average of 74% of the total productivity and a like percentage of ecosystem respiration. This dominance of the macrophyte component of the total primary productivity was similar to that observed by Wetzel et al. (1972) for net primary production in a relatively deep, hard water lake. Findings such as these have indicated the importance of littoral production to total ecosystem production.

In Lake 1, phytoplankton net oxygen production exceeded daily planktonic respiration over a large share of the growing season. The benthic community in Lake 1 was non-photosynthetic and oxygen consuming over the study period like the communities analyzed by Edwards and Rolley (1965) and Rich et al. (1970). Early summer respiration estimates were higher than those observed after August 1. Warm spring temperatures would have allowed increased microbial utilization of organics (Hargrave, 1969) that could have accumulated in the sediments during the pre-study period. These changes in benthic respiration resulted in the switch of total ecosystem metabolism from a heterotrophic to an autotrophic mode at mid-summer. The aerobic condition of the lake was partially maintained by the oxygen liberated from the autotrophic plankton community which had a mean P/R greater than one for the growing season as a whole.

The plankton community of Lake 4 was found to be largely heterotrophic. Light penetration data suggest that self-shading of basal portions of plants by the canopy of E. canadensis was occurring. Ikeda and Ueda (1964) showed that shaded biomass would degenerate within 5 days under such conditions. This process along with continual dissolved organic matter secretions from the macrophytes (Wetzel, 1969; Wetzel and Manny, 1972) apparently made organic substrates available for bacterial use. As a result, bacterial oxygen consumption exceeded gross photosynthesis in the water surrounding the macrophytes.

Major sources of error in gross production measurements with E. canadensis stem from the occurrence of photorespiration and gas storage within the plant. Photorespiration has been shown by Hough and Wetzel (1972) to be present in submerged vascular plants. This increase in oxygen consumption in daylight was not accounted for in measurements of gross primary productivity of E. canadensis since respiration estimates were derived from dusk to dawn measurements in enclosures. Photorespiration thus could have caused an underestimate in computing gross primary production of the plants. The extent of underestimation in this study was unknown.

Internal gas storage is a potential source of error when the productivity of aquatic vascular plants is being measured by the oxygen exchange method (Hough, 1974; Wetzel and Hough, 1973; Hartman and Brown, 1967). Potential errors as great as 200% have been found to occur in production estimates (Davies, 1970). Basic to this is the fact that oxygen evolved during photosynthesis is stored within internal lacunae and used in respiration without appearing in the external environment. Accurate monitoring of internal gas concentrations during photosynthesis is not technically feasible due to the distribution and varied geometric sizes of the spaces; there are as many as 31 distinct types in E. canadensis (Hulbary, 1944). Internal oxygen storage by day and use by night would result in underestimates of net community production and community respiration by the methods of this study, causing a double underestimate of gross primary productivity.

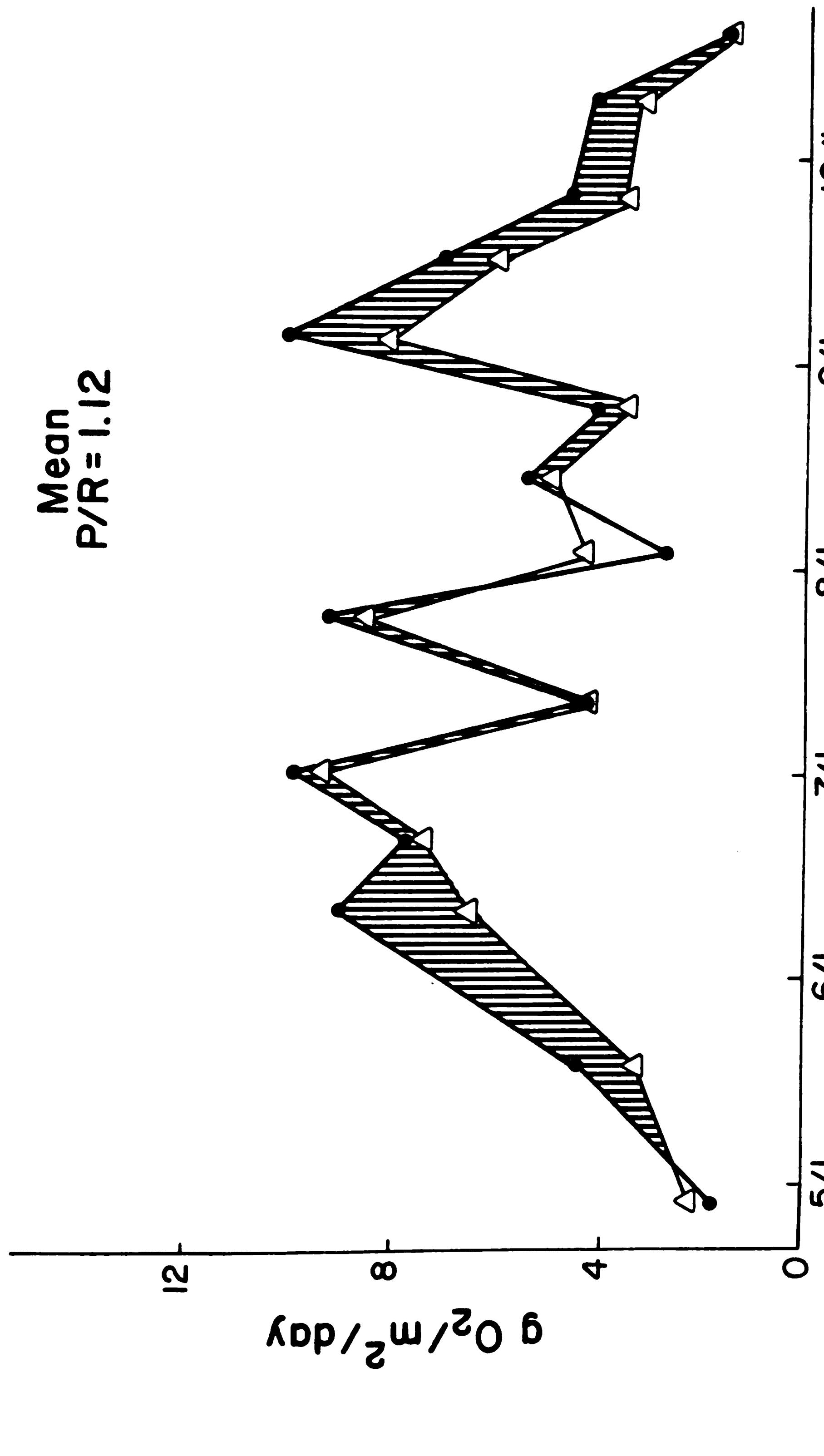
Maximum potential errors due to oxygen storage within E. canadensis were estimated using factors derived from Hartman and Brown (1967). They found that the maximum internal gas storage may be 40% of the total plant volume, while 20% of the internal gas storage may be due to oxygen. By combining these two factors with the volume of macrophytes that occurred, the volume of water in which oxygen changes occurred in enclosures, the density of oxygen (adjusted for physical effects), and the measured gross primary productivity of E. canadensis and its epiphytes, it was possible to obtain the maximum potential error to net primary production and plant respiration that may have occurred due to internal oxygen metabolism.

The largest single calculated gross primary productivity error was an underestimate of 207%. As might be expected, this occurred with large biomass (376 g/m^2 ash-free dry weight) and concurrent low gross primary productivity (0.49 g O_2/m^2/day). Greater than 80% of the calculated gross primary productivity underestimates were less than 20%. The mean maximum calculated error was 24%; the median maximum underestimate was 12%. Daily corrected gross primary productivity and respiration for the E. canadensis-epiphyte complex of Lake 4 is shown in Figure 7 with the corrected seasonal P/R ratio of 1.12.

This correction does not substantially change the bimodal character of net productivity shown for the macrophyte complex in Figure 6B; net productivity occurred principally in May and June, was near zero in July and early August, then increased through September. Penfound (1956) and Jervis (1969) suggested that the highest aquatic macrophyte net productivity occurs in spring and fall because of elevated respiratory demand in the plants over the warm summer months. The growing season P/R ratio corrected from 1.00 to 1.12 is more indicative of a system accumulating biomass as Lake 4 did during the study. When the corrections for gross productivity and respiration in the E. canadensis-epiphyte complex are applied to the whole water column estimates for Lake 4, a seasonal P/R of 1.07 results. This suggests increased seasonal autotrophy in Lake 4 as compared to Lake 1 (P/R = 0.99). Repeated studies of the MSU lakes would show whether increased autotrophy through the lake system is a trend consistent with that observed by Odum (1956) in communities downstream from outfalls of organic pollutants.

Odum (1971) has pointed out that the time of greatest biomass accrual in a plant community corresponds to the time of largest P/R ratio. If the harvest of plants at this time simulated continued net productivity at the same rate, P/R could be used to set the time of harvest in wastewater systems where plant removal was considered to be desirable. The data of Figure 7 show that given

Figure 7.--Gross primary productivity (●) and respiration (△) for the _Elodea canadensis_-epiphyte components in Lake 4 corrected for internal gas storage.


Mean
P/R = 1.12
g O_2/m^2/day
12
8
4
0
5/1
6/1
7/1
8/1
9/1
10/1
Date

the assumption of regrowth without adverse effect from the harvesting process, _E_. _canadensis_ should have been harvested from Lake 4 during early June. The maximum biomass of _E_. _canadensis_ in the lake in 1975 according to McNabb _et al_. (1975) occurred in mid-August. Experiments with different harvesting times and methods are necessary to demonstrate whether a single cutting at the time of maximum crop or multiple cuttings at maximum P/R would give the most desirable yield of _E_. _canadensis_.

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APPENDIX

TABLE A-1.--Phytoplankton organisms found in Lakes 1 and 4.[a]

	Lake 1	Lake 4
Division Euglenophyta		
Euglenoid	X	
Division Cryptophyta		
Crytomonas sp.	X	X
Rhodomonas sp.	X	X
Unknown Rhodomonad		X
Division Cyanophyta		
Anabaena sp.		X
Anabaenopsis sp.		X
Coelosphaerium sp.		X
Gomphosphaeria sp.		X
Merismopedia sp.		X
Division Chrysophyta		
Achnanthes sp.	X	
Cocconeis sp.	X	
Cyclotella sp.	X	X
Melosira spp.	X	
Navicula sp.	X	
Nitzschia palea	X	X
Nitzschia sp.	X	
Division Chlorophyta		
Actinastrum sp.	X	
Ankistrodesmus sp.	X	
Chlamydomonas sp.	X	
Chlorella sp.	X	X
Cosmarium sp.		X
Franceia sp.	X	
Kirchneriella sp.		X
Micractinium sp.	X	
Pediastrum sp.	X	
Scenedesmus incrassatulus	X	
Scenedesmus quadricauda	X	X
Schroederia sp.	X	
Sphaerocystis sp.		X
Unknown Coccoid Green		X
Unknown Colonial Green		X
Unknown Unicellular Green	X	
Number of types numerous enough to count on membrane filters	21	17
Number of types identified from living material	46	45

[a]Weekly samples from July to October 1975 (McNabb *et al.*, 1975).

TABLE A-2.--Gross primary production in g C/m^2/day for ecosystem components in Lakes 1 and 4.

	Date	Plankton	Benthos
Lake 1			
	5/6/75	0.67	0.28
		1.03	0.57
	6/3	0.35	-0.22
		0.17	-0.02
	6/17	0.83	-0.06
		0.51	0.84
	6/25	3.08	-1.38
		3.10	-2.40
	7/6	2.04	0.17
		1.41	-0.29
	7/15	3.61	-2.88
		2.50	0.23
	7/29	4.81	-1.11
		3.77	0.06
	8/7	0.72	-0.30
		0.58	-0.06
	8/16	0.86	0.18
		0.42	-0.12
	8/27	1.49	-0.51
		2.29	-0.63
	9/9	3.55	-1.23
		4.79	-0.30
	9/19	1.29	0.89
		1.82	0.00
	10/1	0.14	0.48
		0.13	-0.07
Mean		1.77	-0.30
Range		0.13 - 4.81	-2.88 - 0.89

TABLE A-2.--Continued.

	Date	*E. canadensis*-epiphytes	Plankton	Benthos[a]
Lake 4	4/27/75	0.81	0.92	1.21
		0.24	0.66	0.91
	5/16	0.89	0.71	0.39
		1.70	0.31	0.37
	6/10	1.92	0.17	0.02
		3.24	0.98	0.82
	6/19	1.47	0.82	0.87
		2.94	0.58	1.19
	7/1	3.21	0.55	0.93
		2.77	0.87	0.63
	7/10	1.90	0.19	0.16
		0.40	0.03	0.40
	7/22	2.11	0.87	1.24
		3.31	0.78	0.72
	8/2	0.39	0.78	0.53
		1.19	0.48	0.62
	8/12	1.29	0.50	1.39
		1.75	0.64	0.96
	8/21	0.16	0.44	0.62
		1.07	1.06	0.78
	9/2	4.10	0.57	0.75
		1.86	0.55	0.61
	9/14	2.64	1.03	0.57
		1.35	0.65	0.59
	9/24	1.23	0.39	0.35
		1.45	0.27	0.11
	10/8	0.69	0.24	
		1.22	0.32	
	10/17	0.22	0.00	
		0.42	0.01	
Mean		1.60	0.55	0.68
Range		0.16 - 4.10	0.00 - 1.06	0.02 - 1.39

[a]Column is Lake 4 benthic enclosure that was determined to be insignificantly different from Lake 4 plankton enclosure at the 95% probability level.

TABLE A-3.--Percent transmittance of surface radiation at the 0.5 m and 1.0 m depths in Lakes 1 and 4 on dates of study.

	Date	0.5m	1.0m
Lake 1:	5/6/75	40	4
	6/3	46	6
	6/17	27	0
	6/25	37	3
	7/6	23	0
	7/15	29	2
	7/29	26	6
	8/7	59	41
	8/16	56	47
	8/27	--	--
	9/9	70	60
	9/19	88	85
	10/1	--	--
Lake 4:	4/27	49	31
	5/16	64	44
	6/10	70	56
	6/19	66	49
	7/1	72	59
	7/10	67	35
	7/22	56	31
	8/2	63	45
	8/12	64	45
	8/21	82	61
	9/2	72	61
	9/14	70	65
	9/24	89	85
	10/8	--	--
	10/19	--	--

TABLE A-4.--Results of a modified two-way analysis of variance performed on gross primary production estimates within and between lakes.

Source	df	SS	MS	F	Sig. Level
Lake 1					
Days	12	0.0950			
P_1 vs B_1[a]	1	0.2050	0.2050	22.36	99.5%
Interaction	12	0.1100	0.0092		
Residual (P_1 vs B_1)	52	0.1114	0.0021		
Lake 4					
Days	12	2.2879			
P_4 vs E_4[b]	1	1.8217	1.8217	7.60	97.5%
Interaction	12	3.6628	0.3052		
Residual (P_4 vs E_4)	26	6.2281	0.2395		
Pooled Comparisons					
P_1 & B_1 vs P_4 & E_4	1	0.4740	0.4740	5.83	95.0%
Pooled Residual	78	6.3395	0.0813		

[a] P_1 = plankton Lake 1, B_1 = benthic Lake 1.

[b] P_4 = plankton Lake 4, E_4 = *E. canadensis* Lake 4.