UTILIZATION OF BENTHIC DETRITUS IN A MARL LAKE

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PETER HAMILTON RICH

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ABSTRACT

UTILIZATION OF BENTHIC DETRITUS IN A MARL LAKE

By

Peter Hamilton Rich

The importance of detritus has been demonstrated in estuaries and streams. Similarities between these two lotic situations and small, temperate lakes suggested that detritus may also be important in some lentic situations. In the absence of direct methods of measuring lacustrine detritus, an indirect method was postulated and examined.

Stoke's Law implies that the production of lacustrine detritus occurs in the benthos. A preliminary benthic carbon budget of a southern Michigan marl lake indicates that benthic community productivity is relatively high with respect to phytoplankton productivity and is dominated by submersed macrophytes. Benthic community respiration is also higher than expected, but not sufficient to account for all benthic carbon not lost to the permanent sediments. Thus, the utilization of benthic detritus is initially confirmed.

UTILIZATION OF BENTHIC DETRITUS IN A MARL LAKE

By

Peter Hamilton Rich

A THESIS

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My wife, Nancy, performed or checked many of the calculations, including the macrophyte planimetry. Nancy and my son, Jonathan, have been most patient and forgiving during three neglectful years.

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I. INTRODUCTION

A. Introduction

The detritus food chain formulated by Odum and de la Cruz (1963) is based on the balance of primary production not consumed by macro- or grazer-herbivores. The remaining material becomes the substrate for a complex microflora and -fauna which modifies frequently poor quality or otherwise unavailable material to produce detritus. Detritus, including both the microorganisms and the modified substrate, represents a relatively high quality food source for several terrestrial and aquatic communities. To date, knowledge of the origin and importance of detritus in aquatic situations has been limited to estuaries and streams.

The best documented estuarine example is the Duplin River behind Sapelo Island, Georgia. The estuary whose vegetation is dominated by an emergent macrophyte, the salt water cord- or marsh-grass (*Spartina alterniflora* Loisel.), is subjected to vigorous tidal circulation (Ragotskie and Bryson, 1955). The partially decomposed remains of *Spartina* are suspended and flow into the estuarine waters where they are utilized by the planktonic community (Starr, 1956; Starr, *et al.*, 1957; Ragotskie, 1959). The bacterial decomposition of *Spartina* produces significant amounts of amino acids and B_{12} vitamins, and has been postulated as a "transformer" which increases the protein levels of primary organic material for utilization by marine animals (Burkholder and Burkholder, 1956; Burkholder, 1956). The dominance of the detritus food chain in the marsh community is revealed by estimates that less than 1% of the annual net production of *Spartina* is consumed alive (Smalley, 1960), and that 11% is rapidly converted to bacterial biomass (Burkholder and Bornside, 1957).

Detritus is important in several types of temperate streams (Teal, 1957; Nelson and Scott, 1962; Hynes, 1963; Ross, 1963; Cummins, *et al.*, 1966; Minshall, 1967). Unlike the estuarine situation, allochthonous detrital material in streams originates largely as autumn-shed leaves of riparian trees. Detrital maturation in streams is also associated with protein production by fungi rather than bacteria (Kaushik and Hynes, 1968). Marine and estuarine detritivores may assimilate the carbohydrate substrate as well as the microorganisms of detritus (Darnell, 1964). Fox (1950) demonstrated that marine filter-feeders secrete abundant amylase and glycogenase enzymes but insignificant amounts of proteolytic and lipoclastic enzymes. On the other hand, stream insects seem to depend upon the microorganisms (Fredeen, 1960, 1964). In general, far fewer animal phyla are represented in the freshwater sessile community than in its marine counterpart, possibly as a consequence of osmotic stress in larval forms (Hutchinson, 1964).

By examining gut contents, Darnell (1964) established the importance of detritus for both invertebrates and vertebrates in a tropical headwater stream, an estuary (Lake Pontchartrain), and the Neuse River in North Carolina. Terrestrial or semiterrestrial plants supplied a major share of the detrital material in all cases.

The role of detritus in temperate lakes has not been studied directly, although lakes have several features which suggest the importance of detritus. Like streams, small lakes have high shoreline to surface area ratios, and are influenced by frequently bordering deciduous trees (Goldman, 1961; Szczepanski, 1965). Like salt-marsh estuaries, small lakes frequently have large annual crops of littoral macrophytes which are not significantly grazed (Westlake, 1965). Filter-feeders dominate the fauna of lakes; however, they are planktonic rather than sessile as in the sea, and consist of microcrustaceans rather than insect larvae found in streams.

Probably the only important influence upon detritus common to estuaries and streams which is not shared by lakes is vigorous movement, a feature that imposes several consequences. Because lakes generally do not have significant outflows, detrital production cannot be estimated directly by filtering techniques such as those used in estuaries (Odum and de la Cruz, 1967). Unfortunately, the small size of lake detritivores makes gut content analysis even more difficult than stream detritivores and the possibility of direct estimation of detrital production and utilization in lakes remote. Indirect methods of assaying the diet of zooplankton have suggested a significant detrital fraction but have been both laborious and subject to many assumptions (Nauwerck, 1963).

A physical consequence of the lack of circulation in lakes suggests that recently formed ("young") detritus may have a defined flow even if lake water does not. Stoke's Law states that a sphere of a given density falls through a static, viscous liquid at a rate directly related to the square of its radius. Thus, the decomposition of detritus from large, descrete objects which sink rapidly to small, bacterially modified and colonized fragments (Rodina, 1963) must occur mostly in the benthic community. As the radii of organic particles decrease with decomposition ("maturation") of the detritus, the possibility of resuspension occurs. While the small amount of turbulence associated with most lakes is not sufficient to prevent fine mineral particles from entering the sediments permanently, resuspended small particulate organic matter is abundant in the water column when it is completely mixed (Davis, 1968). However, many planktonic filter-feeders of lakes are known to spend daylight hours in or near the sediments and may utilize unsuspended benthic detritus.

B. Objectives

The initial goal of this investigation was an estimate of lacustrine detrital production. Secondarily, some techniques have been tested for further refinement of the initial estimate. This estimate of detrital production is based upon the potential inputs from submersed macrophytes, epiphytes, and phytoplankton, losses due to permanent sedimentation, and benthic respiration of CO_2. The secondary testing includes a preliminary search for factors correlated with respiration, sedimentation rates measured by sediment traps, and the organic content of the sediment surfaces.

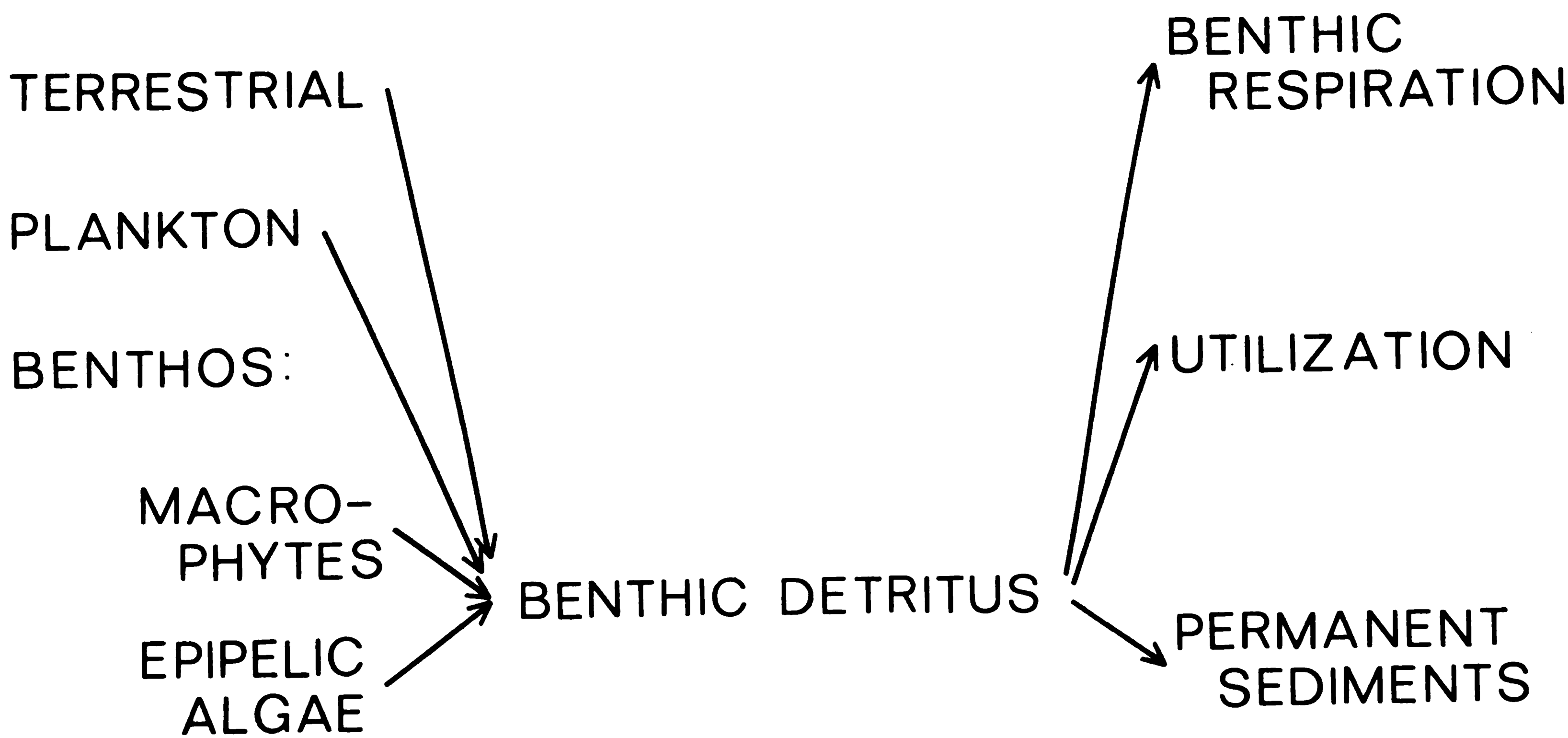
C. Methods

In the absence of direct methods of estimating the production and utilization of lacustrine detritus, the initial segregation of "young" detritus was accomplished by an indirect method which permitted the estimation of certain parameters of benthic metabolism as a basis for estimating facets of detrital metabolism. Assuming that benthic autotrophy and permanent loss of carbon to the sediments are known, rates of benthic respiration during decomposition ("maturation") of detritus determines the efficiency of detrital production and the ultimate amount of material available. Further, assuming that known inputs of carbon into the benthic community equal known outputs, rates of loss of benthic carbon by respiration and permanent sedimentation estimate the amount of organic carbon leaving the benthos and respired elsewhere by difference ("utilization") (Figure 1). The actual form in which the carbon leaves the lake bottom is unspecified and may be as the suspension of detritus into the water, detrital feeding by planktonic invertebrates and vertebrates, the emergence of detritus-feeding insects, or predation at any point in the benthic trophic structure derived from detritus.

The sources of error in the above equation are several. Theoretical problems revolve about the definition of organic carbon leaving the benthos as detrital production or utilization. Detritus suspended into the water column is subject to further respiration which suggests that it does not represent net production, and a large part of the detritus suspended may never be utilized except by the metabolism of its associated bacteria. On the other hand, predation upon benthic detritivores by planktonic animals is not detrital production but, rather, detritivore production. Also, the carbon respired by detritivores is not detrital respiration, but is included in the parameter benthic respiration. Consequently, the loss of organic carbon from the benthos must be defined as either a composite parameter or in terms of communities rather than individuals or populations. Thus, the parameter is defined as the utilization of the benthic detritus food chain at all levels by the open water community. The

Figure 1.--Diagrammatic representation of a benthic community carbon budget.

Figure 1


TERRESTRIAL
PLANKTON
BENTHOS:
MACRO-PHYTES
EPIPELIC ALGAE
BENTHIC DETRITUS
BENTHIC RESPIRATION
UTILIZATION
PERMANENT SEDIMENTS

respiration of detritus in the open water is interpreted as part of planktonic respiration. Detritus decomposed by its bacterial flora is interpreted as utilized by the planktonic community if the process occurs in the open water, and part of detrital maturation, i.e., benthic respiration, if it occurs in the benthic community. Predation upon the benthic community at any level by nonbenthic animals is considered to be utilization of benthic detritus because the process of detrital maturation dominates the benthic community. Similarly, the respiration of benthic animals is not part of detrital utilization in a community sense, but belongs to benthic community respiration.

The practical problems posed by the equation involve two steps. Firstly, all potential sources and fates of carbon entering the benthos must be accommodated by the experimental design. Secondly, of this material, the actual amount of carbon entering the benthos must be estimated. The latter problem is discussed with the appropriate parameter below.

Benthic inputs are derived from terrestrial, planktonic, and benthic sources, and may be in the particulate or dissolved phase. Terrestrial and planktonic production of dissolved organic matter (DOM) is assumed to be entirely utilized by planktonic respiration. Benthic DOM production occurs from macrophytes (Wetzel, 1969; Wetzel and McGregor, 1968) and epiphytic algae (Allen, 1969) and can not be discounted in epipelic algae.

Macrophytic and epiphytic DOM production is also interpreted as entirely utilized by planktonic respiration, but epipelic DOM production, both algal and bacterial, is considered to be part of benthic respiration. This assumption is made on the basis of the "Law of Microbial Infallibility" (Brock, 1966) which states that microbial communities are capable of degrading any natural organic substrate in their environment.

Particulate input from the terrestrial environment, the plankton, and the benthos each presented special problems. No direct, practical means of measuring terrestrial input were available, so terrestrial effects had to be estimated among the three transects (Figure 2). Transect B_1 originated in a highly organic Carex mat shoreline and was located between tributaries of the incoming stream. Transect B_3 originated in a more calcareous, less disturbed Carex mat and was located at the extreme leeward side of the lake. Both of these transects (B_1 and B_3) were considered to have large terrestrial inputs of organic matter. Transect B_2 was isolated from shore by a dredged zone which protects this transect from terrestrial input. An intermittent layer of tree leaves at the bottom of the dredged basin attests to this function. Thus, terrestrial effects may be detected among transects by means of the null hypothesis $B_2 = \frac{B_1 + B_3}{2}$.

Primary production in the plankton community was measured over an annual cycle by ^{14}C uptake (Wetzel, et al., in prep.), and estimates of sedimentation rates were attempted by means of sediment traps. The sediment trap results suggested that estimates of actual plankton sedimentation based upon trapping techniques are highly inferential and such estimates were not made from the sediment trap data presented here. However, the sediment trap results were useful as a relative measure of detrital circulation and abundance among transects.

In situ benthic production was partitioned into macrophytes, epiphytes, and epipelic algae. Macrophytic production was estimated from biomass data (Rich, *et al.*, in prep.) and epiphytic production by ^{14}C methodology (Allen, 1969). Epipelic production was detected by ^{14}C uptake; however, the net production of the sediment surface community was negative and epipelic carbon fixation ignored in the carbon cycle (although this might not be warranted in an energy budget).

Core samples of the sediments were assayed for ash-free dry (organic) weight for correlation with the measurements of sediment respiration and to detect any fluctuations in organic content which might ultimately provide a direct means of measuring benthic detrital productivity.

The fates of carbon in the benthos were partitioned into loss to the permanent sediments, loss as respiration of CO_2, and utilization. Loss to the permanent sediments was estimated from the amount of sediments under the lake, their organic content, and the age of the lake. Losses as CO_2 evolution were estimated from pH changes directly over the sediment surface (see Chapter III). At this time respiration rates are simply being tested for significance. Correlations of this with other factors will be made elsewhere (Rich, et al., in prep.).

D. Lawrence Lake

Lawrence Lake is located in southwestern lower Michigan, near the southern boundary of Barry County. The lake is at approximately 42° 26! north latitude, 85° 21' west longitude (Tier 1 North; Range 9 West; Section 27). The lake landing, on private property, is 2.1 km east of the Hickory Corners Post Office. The elevation of the lake surface is 275.3 m above sea level.

Lawrence Lake is located in the Southern Upland topographic province of Michigan, an area of smooth, undulating plains with arcs of morainic headlands (Veatch, 1953). Lawrence Lake, Little Lawrence Lake, and the marsh associated with them are contained in a basin lying along the southern outwash apron of the Kalamazoo morainic system (Leverett and Taylor, 1915). The morphometry of the lake basin suggests that Lawrence is an ice-block lake. Glacial over-burden is gray drift with medium to strong influence from limestone and, locally, sandstone and shale. Soils on uplands surrounding the marsh containing Lawrence Lake are sandy loams of moderate fertility and good to excessive drainage (Deeter and Trull, 1928). The marsh itself contains marl overlain by muck and peat.

The first settler arrived at Lawrence Lake in 1834, and his descendants presently live nearby. Records of this family and others, the history of the nearby community, and detailed information concerning the cultural history of the lake are discussed elsewhere (Rich, 1970). Major human activities associated with the lake have included intensive agriculture, land reclamation, and marl removal.

The watershed of Lawrence Lake is approximately 10 times the surface area of the lake and consists of fallow fields and woodlots. The lake receives water from two small inlets and several vernal springs. A single outflow drains through a large marsh to Augusta Creek. Water levels have remained stable throughout the post-settlement period with the exception of a brief drop during the drought years around 1930 (Rich, 1970).

The most striking physical feature of the lake is a broad underwater marl bench which extends from the shoreline 10-20 m to the 1 m depth contour (Figure 2). The thick deposits of marl underlying this bench have been commercially dredged at several points on the circumference of the lake since about 1918 (Rich, 1970). The dredged

Figure 2.--Morphometric map of Lawrence Lake, Barry County, Michigan, showing Transects B_1 (organic mat shoreline), B_2 (isolated from shoreline by dredged zone), and B_3 (typical wave-swept shoreline).

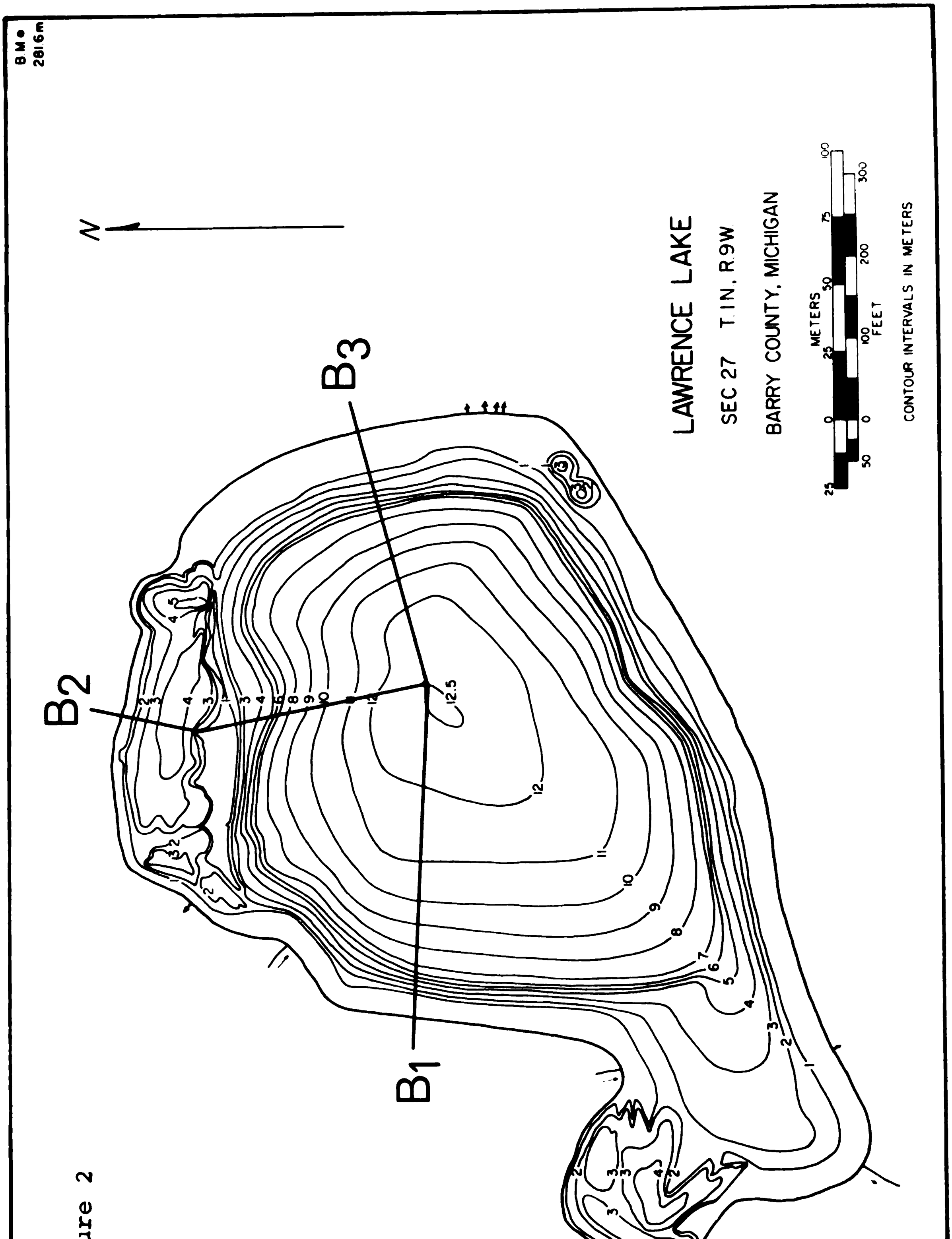

BM
281.6m
N
B1
B2
B3
12.5
LAWRENCE LAKE
SEC 27 T.1N, R.9W.
BARRY COUNTY, MICHIGAN
METERS
FEET
CONTOUR INTERVALS IN METERS

Figure 2

areas are discernible on the morphometric map by the departure from simple concentric contour lines on the north side, west end, and a small area in the southeast corner of the lake. Except for the dredged zones, the marl bench extends around the entire circumference of the lake. Altogether, marl removal has added 5,250 m^2, representing 10.6%, to the lake area, and 16,445 m^3, or 5.6%, to the volume.

The excavations have shown that marl underlies not only the exposed marl bench beneath the shallows of Lawrence Lake, but much of the surrounding marsh. For instance, marl occurs and is reputed to be 11 m deep at the extreme western end of the lake which is now 50 m back from the original shoreline. Recent cores to glacial till at the central depression indicate that marl is greater than 8 m thick (R. O. Kapp, personal communication).

The bathymetric map was constructed for Lawrence Lake from depth data derived from several sonar transects (200 Ks/c, Model F-850-A, Furuno Electric Co., Ltd., Japan). Morphometric data calculated from this map include:

Surface area:	49,600 m^2 (4.96 ha)
Maximum depth:	12.6 m
Mean depth:	5.89 m
Volume:	292,000 m^3
Shore development:	1.29
Relative depth (Z_r):	5.01%

It is apparent from these data that Lawrence Lake is very deep for its size. Relative depth, the maximum depth as a percentage of the mean diameter, is quite high in spite of the shallow dredged areas. Shoreline development is low, indicating that the lake has a shoreline to surface area ratio similar to that of a perfect circle.

II. THE DISTRIBUTION AND PRODUCTIVITY OF SUBMERSED MACROPHYTES

A. Introduction

The macrophytic flora of Lawrence Lake is restricted to species commonly associated with calcareous, alkaline waters, and marl substrates. The assemblage has only one important emergent (*Scirpus acutus* Muhl.), floating leaved form (*Nuphar variegatum* Engelm.), and submersed angiosperm (*Scirpus subterminalis* Torr.). The latter species dominates the entire lake between 1 and 6 m. Macrophytic algae (*Chara vulgaris* L. and *C. Globularis* Thuill.) are important only in the shallow littoral (0-1 m) of protected shores. Wetzel (1969) and Wetzel and McGregor (1968) have suggested that the low macrophyte diversity of marl lakes is caused by detrimental nutritional and physiological effects related to the concentrations of available carbon and of major cations, e.g., Ca^{++}, Mg^{++}, and Na^{+}, in the water. A detailed survey of the species of macrophytes found in Lawrence Lake with further discussion is presented elsewhere (Rich, Wetzel, and Thuy, 1970; q.v. attached). An exhaustive limnological investigation of the lake, involving both field and laboratory evidence, will make special reference to the effects of cations (Wetzel, *et al.*, in prep.).

The spatial distribution of aquatic macrophytes is sharply limited by the morphometry of Lawrence Lake. The wide, shallow, marl bench has a very poorly developed macrophytic flora even in protected areas. Wave-swept shores are virtually barren of macrophytes. From the outer edge of the marl bench (approximately the 1 m contour) the bottom slopes precipitously to the central depression and supports macrophytes to a depth of 7 m. The colonized zone (1-7 m) represents only 42% of the total lake surface area.

Submersed macrophytes were estimated to enter the benthic detritus pool intact. Floating-leaved and emergent species in Lawrence Lake were not quantitatively important, and their litter was observed to drift into windrows along with terrestrial debris. Upon death, losses of cellulose and other resistant materials in aquatic plants proceed slowly (Burkholder and Bornside, 1957; Felföldy and Zsuzsu, 1958; Kormondy, 1968). Losses of soluble protoplasmic materials upon death are probably similar to losses of volatile substances incurred in the oven drying (105°C) of macrophyte samples in the laboratory. Predation upon living plants was probably negligible (Westlake, 1965).

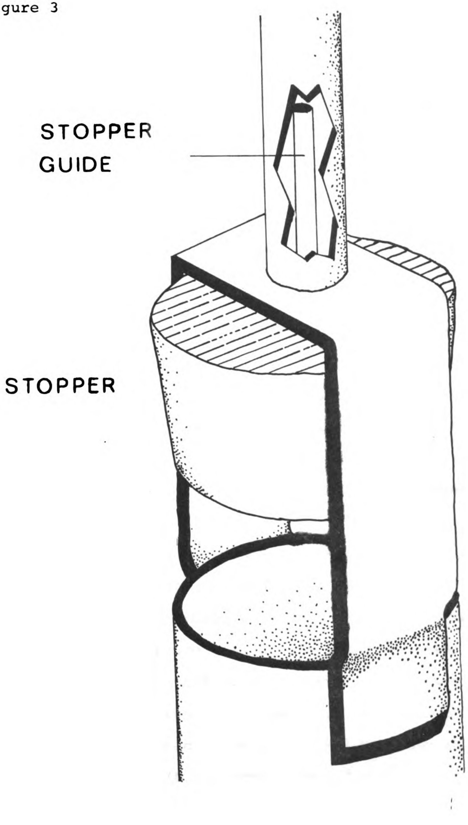
B. Methods

Quantitative macrophyte samples were taken at one-meter depth intervals along three transects (B_1, B_2, and B_3; Figure 2). Samples were also taken at a depth of 1/2 m on the marl bench of each transect. A sample consisted of four 40.72 cm^2 replicates, each of which was washed and sorted separately. The material was air dried, dried at 105°C, combusted at 550°C, and re-weighed; all results are given as g m^{-2} ash-free dry weight (organic weight). Fifty-six sets of samples along the transects were made between 1968 and 1970 with some concentration of dates in the spring and summer to follow the life-cycle of annuals more closely. Each transect was usually sampled at least once in every month of the year.

Samples were taken by means of a specially constructed free-fall core sampler (Figure 3). The body of the sampler consisted of a 60 cm length of 7.2 cm diameter steel tubing with sharp, triangular teeth along the lower, cutting edge. The upper orifice was fitted with a free-working rubber stopper which functioned as a one-way valve. In use, about one-half of the length of the tube penetrated the sediments and took a very clean-cut sample of the generally close lying benthic vegetation. In a few areas where the macrophytes (*Potamogeton*) were much elongated, the sampler was less efficient, as evidenced by larger variance in the samples. Frequently in these areas, the sampler would strike the base of a plant and

Figure 3.--Macrophyte sampler, detail of closing mechanism.

Figure 3



exclude the stem. Stems severed in this manner floated to the surface where they were collected and added to the sample.

Identification and nomenclature for angiosperms follows Fassett (1957) and Fernald (1950), and for the Characeae, Wood and Imahori (1964, 1965).

C. Results

1. Biomass

Biomass cycles for each species at each depth of each transect were plotted from pooled data for 1968-1970, and the areas over each month of the annual plots were planimetered to provide monthly biomass values. The landward end of transect B_2 (B_2-dredged) crosses an atypical, dredged zone which is only 4 m deep and these data were not used in the summary annual mean presentations (Figures 4, 5, and 6).

The monthly organic biomass values have been summarized in three ways: (1) annual biomass pattern for the important macrophyte groups as a mean transect summed with respect to depth (Figure 4); (2) the annual biomass pattern of a mean transect including depth distribution (Figure 5); and (3) the distribution of mean annual biomass over depth for each transect, including the atypical area of transect B_2 (B_2-dredged) separately (Figure 6).

TABLE 1.--Mean annual biomass of each submersed macrophyte group by transect. Biomass is given as g m^{-2} ash-free dry (organic) weight.

Transect	*S. subterminalis*	Characeae	Annuals	Total
B_1	533.1 (67.7%)	179.3 (22.8%)	75.5 (9.6%)	787.9 (100.0%)
B_2	704.0 (86.5%)	39.5 (4.9%)	70.7 (8.7%)	814.1 (100.0%)
B_3	594.4 (84.2%)	46.4 (6.6%)	65.4 (9.3%)	706.3 (100.0%)
B_2-dredged*	277.5 (58.6%)	188.5 (39.8%)	7.3 (1.5%)	473.3 (100.0%)
	2109.0 (75.8%)	453.7 (16.3%)	218.9 (7.9%)	2781.6 (100.0%)

*Transect B_2-dredged is only 4 m deep.

TABLE 2.--Variance estimates for the mean annual biomass of *Scirpus subterminalis* at important depths for each transect. Biomass is given as g m^{-2} ash-free dry (organic) weight.

Transect	Depth	Mean	Standard Error	90% Confidence Interval
B_1	2 m	196.9	43.9	78.7
	3	117.3	34.6	69.5
	4	151.2	27.1	68.6
B_2	2 m	206.3	51.5	84.0
	3	184.9	44.1	85.6
	4	185.5	29.5	73.9
B_3	2 m	172.3	30.2	76.9
	3	61.1	28.6	69.9
	4	124.1	23.6	64.9
B_2 dredged	3	178.6	34.5	77.7

Figure 4.--Annual biomass [g m^{-2} ash-free dry (organic) weight] pattern for the important macrophytic groups as a mean transect summed with respect to depth. Annuals include *Potamogeton* spp., *Najas flexilis*, and trace amounts of several other species.

Figure 4

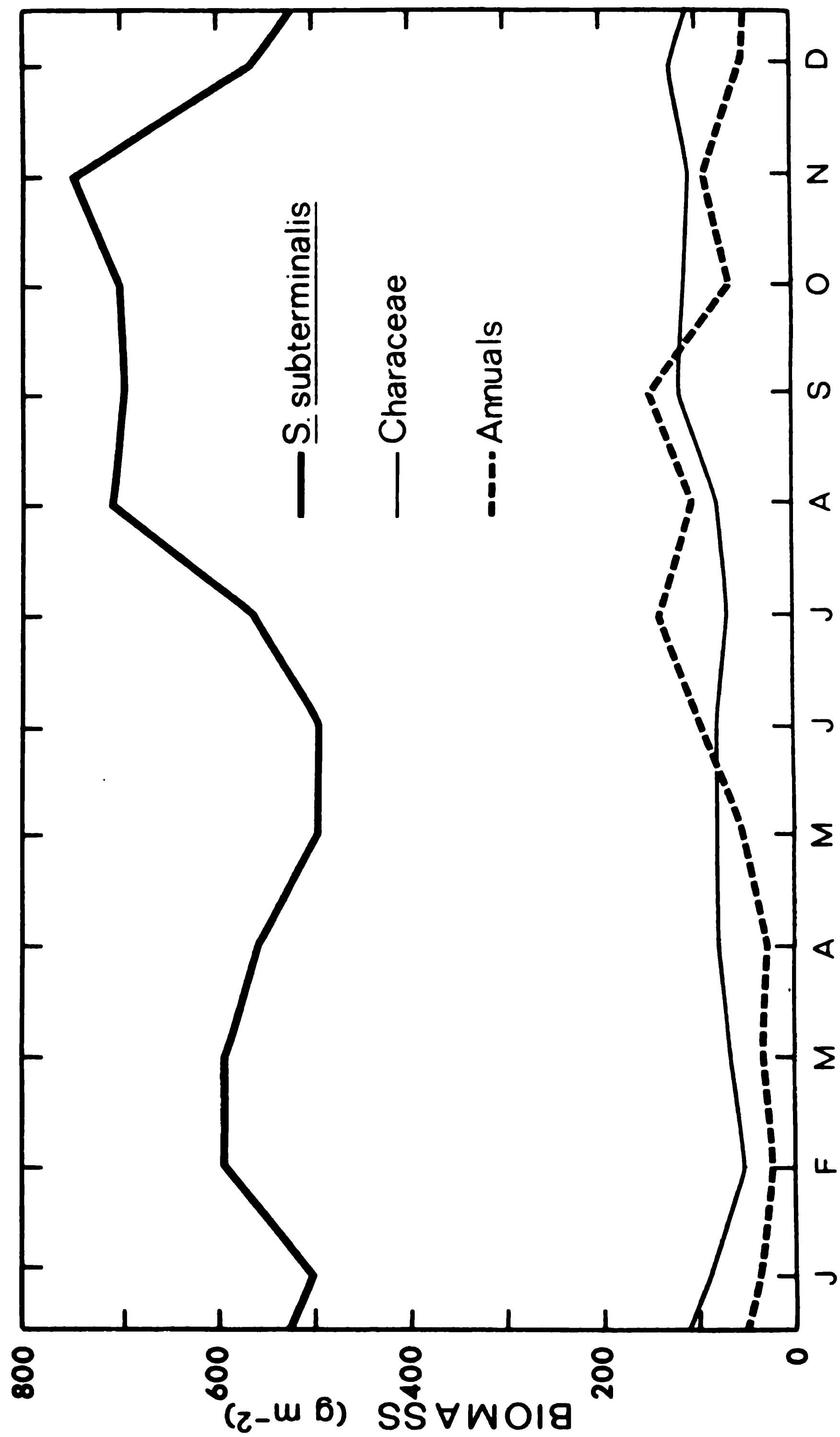

S. subterminalis
Characeae
Annuals
BIOMASS (g m-2)
0
200
400
600
800
J
F
M
A
M
J
J
A
S
O
N
D

Figure 5.--Annual biomass [g m^{-2} ash-free dry (organic) weight] pattern of a mean transect including depth distribution for *Scirpus subterminalis*.

Figure 5

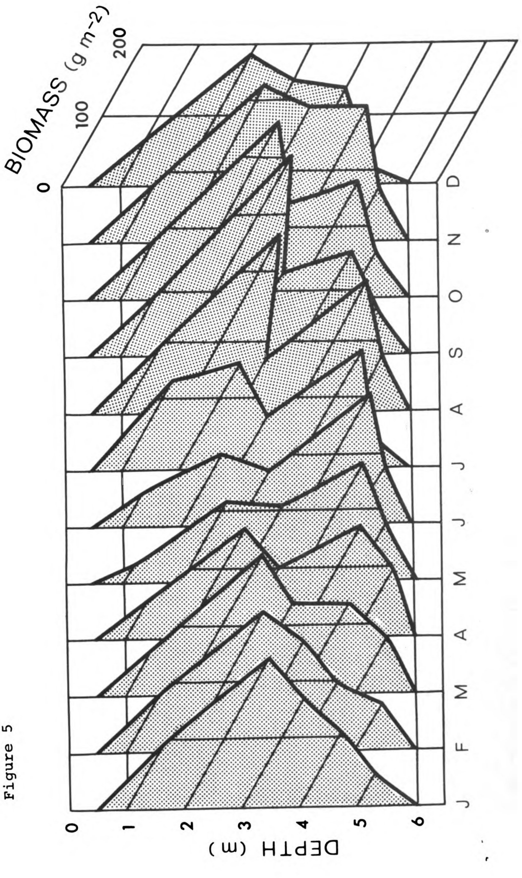
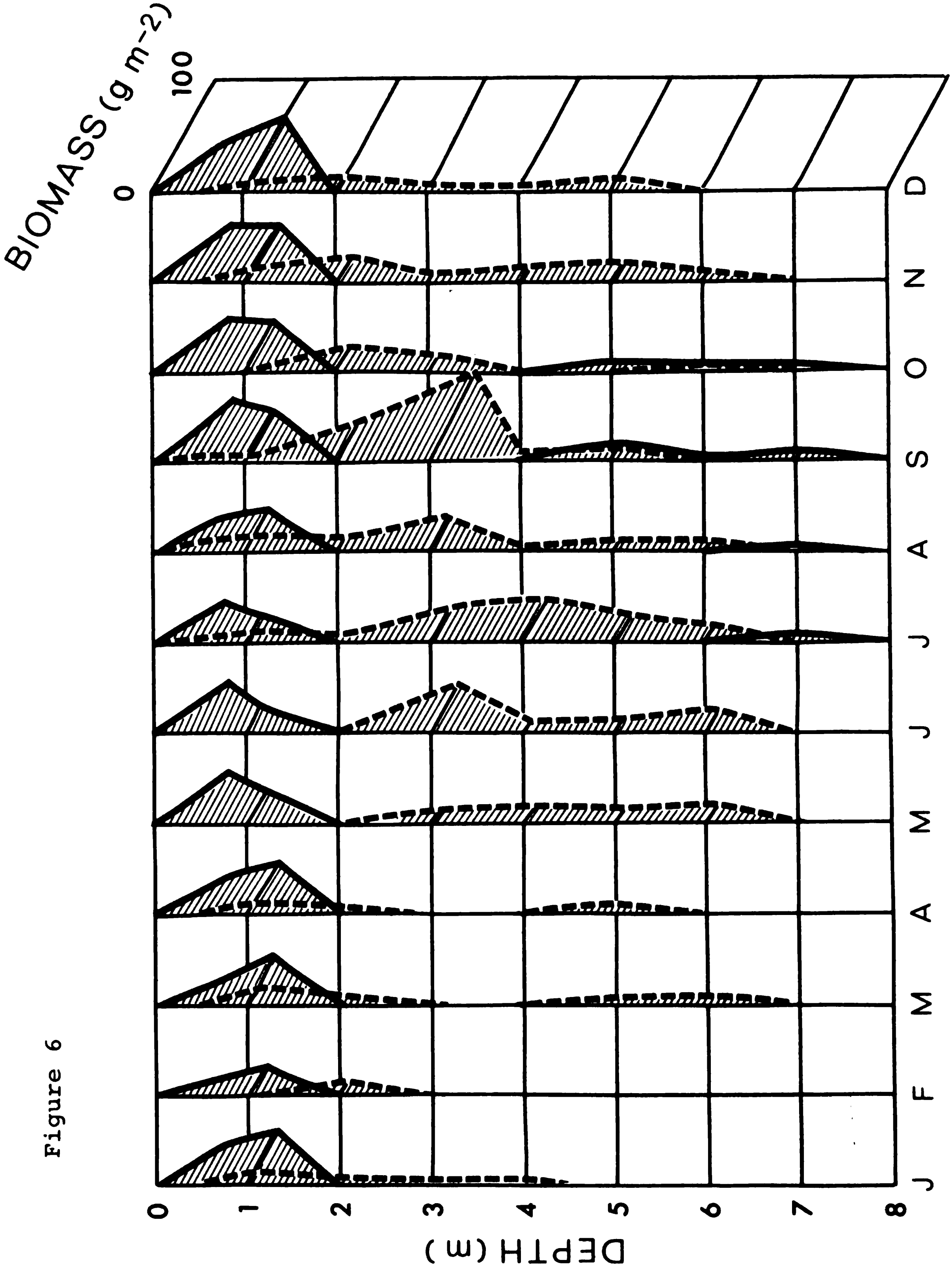


Figure 6.--Annual biomass [g m^{-2} ash-free dry (organic) weight] pattern of a mean transect including depth distribution for *Chara* (solid line) and annuals (dashed line).

Figure 6



Biomass is measured as g m^{-2} ash-free dry (organic) weight in all cases.

Water bulrush (<u>Scirpus</u> <u>subterminalis</u>) was the dominant component (76% of all sampled material) of the submersed macrophytic flora at all times of year. Fall and late winter biomass maxima are evident (Figure 4); however, the species is best described as perennial or, more accurately, an "evergreen" population. The two annual maxima resulted from dissonant peaks at different depths (Figure 5). The larger fall maximum consisted of a major October peak at 2 m and the terminal stages of a June-August peak at 4 m. The late winter maximum was compounded from minor peaks at 3 and 5 m, the beginning of the summer 4 m peak, and a subsequent minimum created by a marked decrease in the 2 m population in June.

A fall peak in the Characeae (16% of all sampled material) was evident within a relatively constant seasonal biomass distribution. Again, this group is best described as an "evergreen" population Figures 4 and 6). The appearance of <u>Nitella</u> <u>flexilis</u> at 7 m (transect B_3 only) in July-October and <u>Chara</u> at 5 m in September-October was interpreted as an interaction between light, thermal, and carbon stratification. Another species of <u>Nitella</u> is known to be limited by dissolved CO_2 availability above pH 7.3 (Smith, 1967). During the month of July, the hydrogen ion concentration at 7 m in the deep water column shifted from about pH 8.3 to pH 8.1 as summer stagnation progressed.

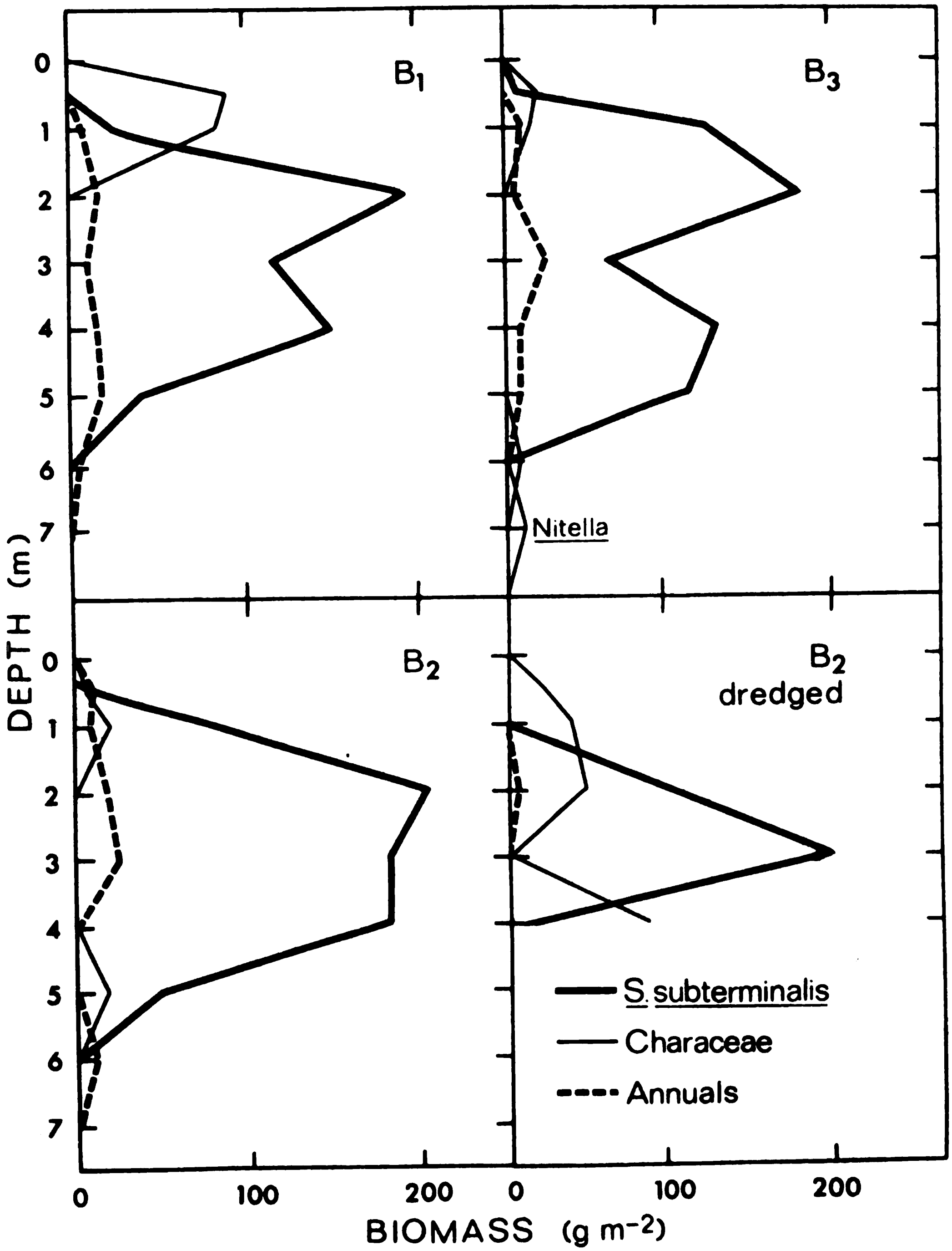
The shift may be even greater at the 7 m contour where the lake sediments were in contact with the 7 m water stratum. The disappearance of *Nitella* and *Chara* at the end of October coincided with fall overturn.

The other species of macrophytes, collectively termed annuals (8% of all sampled material), were not sufficiently abundant in the samples to provide reliable estimates of biomass. As a whole, these species (mostly *Potamogeton*) died in the fall, and their maximum biomass occurred during the commonly accepted growing season, June through September. Two maxima are apparent in Figure 4 and may also be discerned in Figure 6. The early, deeper peak (4-6 m) was largely of *Potamogeton praelongus* Wulfen, and the later, shallower peak (3 m) was largely of *P. illinoensis* Morong.

Differences among transects, excluding the dredged zone of transect B_2, were not great. Qualitatively, transect B_3 differs from the others in the presence of *Nitella* at 7 m. Only traces of Nitella were found at B_2 and no Characeae were ever found below 2 m at transect B_1. *Chara* was more important in the shallow littoral of transect B_1 and the dredged portion of B_2 which are protected from wave action, than at transects B_2 and B_3 which are exposed. *Chara* thrived in the presence of *Nuphar variegatum* at 0.5 m along transect B_1. (The amount of *Nuphar* was minor and was not included in the biomass or productivity figures; it only appeared at transect B_1.)

Figure 7.--Distribution of mean annual biomass over depth for each transect, including the atypical area of transect B_2 (B_2-dredged) separately. Biomass is given as g m^{-2} ash-free dry (organic) weight.

Figure 7



B1
B3
Nitella
B2
B2
dredged
DEPTH (m)
0
1
2
3
4
5
6
7
S. subterminalis
Characeae
Annuals
0
100
200
BIOMASS (g m-2)

In all cases, the biomass of *Scirpus subterminalis* at 1 m was inversely correlated with the amount of *Chara* present. With the exception of transect B_2-dredged, the mean annual biomass of *Scirpus subterminalis* was highest and consistently close to 200 g m^{-2} at 2 m. Biomass for this species was also consistently greater at 4 m than at 3 m. Field observations suggest that a springy, fibrous peat stratum at 3 m may have caused the apparent decrease in biomass by either reducing actual colonization by macrophytes or possibly by reducing the efficiency of the sampler.

Some quantitative differences existed between transects with respect to *Scirpus subterminalis* and *Chara*. Transect B_1 had more *Chara* than the other two transects. The total mean annual biomass for transect B_2, which had the least *Chara* and the most *Scirpus subterminalis*, was similar to that of transect B_1. Transect B_3 had low amounts of *Chara* and *Scirpus subterminalis*, and the lowest total annual biomass. Transect B_3 with the wave-swept shallow littoral also had the most pronounced 3 m low.

The biomass proportions of transect B_2-dredged were very different from those of the undisturbed transects. *Chara* replaced *Scirpus subterminalis* at 4 m, and represented a much higher proportion of the mean annual biomass. Annuals were poorly represented in the transect.

2. Productivity

Estimating the productivity of the perennial or "evergreen" species, whose biomass levels remained relatively constant throughout the year, was problematical. Generally, estimates of productivity of aquatic macrophytes in the temperate zone have been based upon measurements of biomass increments of emergent and submergent annuals between seed germination and maximum biomass. The simple increment method may be modified to account for the low mortality and losses during the growth period by a turnover rate of 2-20%. The method is confounded in the case of perennials by the lack of clearly defined increments uncomplicated by losses of material persisting from prior growth and by an indeterminate growth period.

Borutskii (1950) observed _Elodea canadensis_ to be a perennial in Lake Beloie. A similar observation was made for this species in a marsh of western Lake Erie (Rich, 1966). Based upon estimated losses throughout the year, Borutskii concluded that productivity could be as high as 5 times maximum biomass for this species. Much of the turnover in this case was attributed to damage caused by human interference; a condition not true of Lawrence Lake. Summarizing several other instances where biomass persisted from one growing season to the initiation of the next, Westlake (1965) suggests that annual net production is only 50-80% of maximum biomass in such cases. Thus, productivity given in the literature for submersed perennials in the temperate zone range from 0.5 to 5.0 times maximum biomass.

While grazing, damage, and mortality may be negligible or low in the brief period prior to the biomass peak of fast-growing annuals, this assumption is not realistic for perennials maintaining populations throughout a year. Further, a turnover factor established for the observed growth of the "evergreen" group would not account for the annual maintenance of the significant annual minimum biomass. In the absence of large storage structures as perennating organs for either *Scirpus subterminalis* or *Chara*, maintenance metabolism must be significant at all times of year. *Scirpus subterminalis*, particularly, is a very fragile plant consisting of a rosette of long (3-5 dm), narrow (1-2 mm), delicate leaves. *Chara* replaced *Scirpus subterminalis* in the shallow littoral probably because it is more resistant to wave action. However, *Chara* is subject to rapid marl incrustation which makes the plant very brittle. Ice movements have been observed which must inflict much damage to the *Chara* at 0.5 m in winter as well.

On the basis of the above observations, the biomass increment method was discarded in favor of two newer concepts of turnover estimation. The better documented method, and probably most applicable to the Lawrence Lake flora, is the Allen curve technique (Allen, 1951) as modified for Glyceria maxima and other plants by Mathews and Westlake (1969). The method follows from the observation that Glyceria continuously produces cohorts of leaves and stems which go through annual life cycles. Those cohorts whose growth periods coincide with spring and summer dominate the annual biomass and productivity, but growth and mortality are experienced by all cohorts at all times of year. The most conservative turnover factor of 1.5 for overall annual net production as a function of maximum biomass was selected and applied to the biomass maximum (summer or winter) within each depth population of Scirpus subterminalis and Chara of each transect (Table 3).

Both summer and winter peaks were selected and entered into the calculations as two distinct cohorts as an extreme case of this method. The calculation is not warranted in that winter biomass peaks occur at less than 1/10 summer light levels (as measured at 2 m; Rich and Wetzel, 1969). Winter accumulation of biomass is interpreted as resulting from a decrease in the proportion of respiration to photosynthesis.

A second calculation method was based on an estimate that aquatic macrophyte productivity based on oxygen production is approximately twice the net accumulation of the growth period (Westlake, 1965, 1966). Assuming a normal growing period of 4 months, the "evergreen" populations in Lawrence Lake must turnover 3 times to maintain

TABLE 3.--Production rates for the aquatic macrophytes of Lawrence Lake as ash-free dry weight. Maximum site figures equal the mean of maximum sites of the 3 transects.

	Maximum Site (g $m^{-2}yr^{-1}$)			Total Lake	
	S. subt.	*Chara*	Annuals	kg $lake^{-1}yr^{-1}$	g $m^{-2}yr^{-1}$
Allen Curve Method (x 1.5)					
1 Cohort (max. biomass)	507	165	199	9,403	189
2 Cohorts (summer and winter)	838	273	199	13,989	281
Mean Annual Biomass Method (x 3)	565	155	199	8,893	178
Observed Mean Biomass (g m^{-2})					
Maximum	338	110	133		
Maximum mean annual	188	52	12		

themselves during the year. Consequently, the mean annual biomass of each species at each depth of each transect was multiplied by a turnover factor of 3. When a constant winter biomass was not apparent for a particular species and sample depth, a factor of 2 was applied to the mean annual biomass to account for the missing turnover period. Although the calculation was expected to seriously underestimate productivity as a consequence of using mean annual instead of maximum biomass, the results are quite close to the 1 cohort Allen curve method (Table 3). In all cases the production of annuals was calculated as maximum observed biomass times a turnover factor of 1.5.

3. Marl Removal

As previously mentioned, only 42% of the present surface area of Lawrence Lake supports submersed macrophytes. Of the total lake area, 12% has resulted from marl removal. Excavation has been largely confined to the marl bench area and landward (Figure 1). The resulting basins are 3-4 m deep and are completely colonized by macrophytes. Thus little of the original macrophyte zone of the lake was disturbed by dredging, and 21% of the present macrophyte zone is artificial.

Based on the B_2-dredged transect data and the 189 g $m^{-2}yr^{-1}$ ash-free dry weight estimate of productivity, the dredged areas of the lake support 29,200 kg or 31% of the total productivity. Consequently, a 12% increase in lake area (6% volume) has caused very significant quantitative changes in submersed macrophyte distribution and production. Estimation of biomass composition of disturbed areas on the basis of the B_2 dredged transect is not warranted, however the atypical biomass composition and distribution of that transect suggest changes are to be expected.

III. THE SEDIMENTS

A. Sediment Traps

Sediment traps were placed at the 5 m contour of transects B_1, B_2, B_3, and at the deepest point (4.5 m) along transect B_2-dredged. The orifices of the traps were at 4 m, one meter above the sediments (3.5 m along transect B_2-dredged). The traps consisted of 65 cm lengths of extruded acrylic tubing (4.44 cm inside diameter, wall thickness 2-3 mm). Duplicate traps were placed upright, 50 cm apart at each sampling station. The tubes were held in racks which kept the orifices 25 cm away from the marker line to prevent encrusting material sloughed from the line from entering the traps. The tubes were made opaque to discourage algal colonization. The traps were collected and reset at approximately 40-day intervals. The material from the traps was filtered (glass fiber), dried at 105°C, combusted at 550°C, and reweighed. Results are given as ash-free dry (organic) weight. An additivity experiment demonstrated no significant losses during the sampling interval.

The annual pattern shows sedimentation maxima in April and October which correspond to ice-melt and the last stages of summer stratification, respectively (Figure 8). Total annual organic sedimentation was highest at transect B_3 on the lee side of the lake (251 g $m^{-2}yr^{-1}$), intermediate at transects B_1 and B_2 dredged (199 and 183 g $m^{-2}yr^{-1}$, respectively), and lowest at transect B_2 which was isolated from terrestrial input (169 g $m^{-2}yr^{-1}$). A two-way analysis of variance with replication, fixed model, was performed to test the significance of transect and annual differences. The assumption of variance homogeneity was verified by the nonparametric Corner Test (Steel and Torrie, 1960). Both factors were significantly different at the 99% level. Interaction was significant at the 95% level (Table 4).

As discussed in the introduction, the sediment trap results were not used to estimate sedimentation from the planktonic community. The bimodal periodicity corresponding to periods of turnover and the impossibly high (approximately twice phytoplanktonic production) and variable rates of accumulation in the traps strongly support the contention of Davis (1968) that much of the material captured in sediment traps has been resuspended from the sediments. Sediment traps placed in the hypolimnion of Lawrence Lake produced more reasonable annual patterns and sedimentation rates approximating 10% of phytoplankton production (Miller, 1970).

Figure 8.--Annual sedimentation rate [g $m^{-2}day^{-1}$ ash-free dry (organic) weight] pattern at 4 m for each transect including the atypical area of transect B_2 (B_2-dredged) where trap depth was 3.5 m.

Figure 8

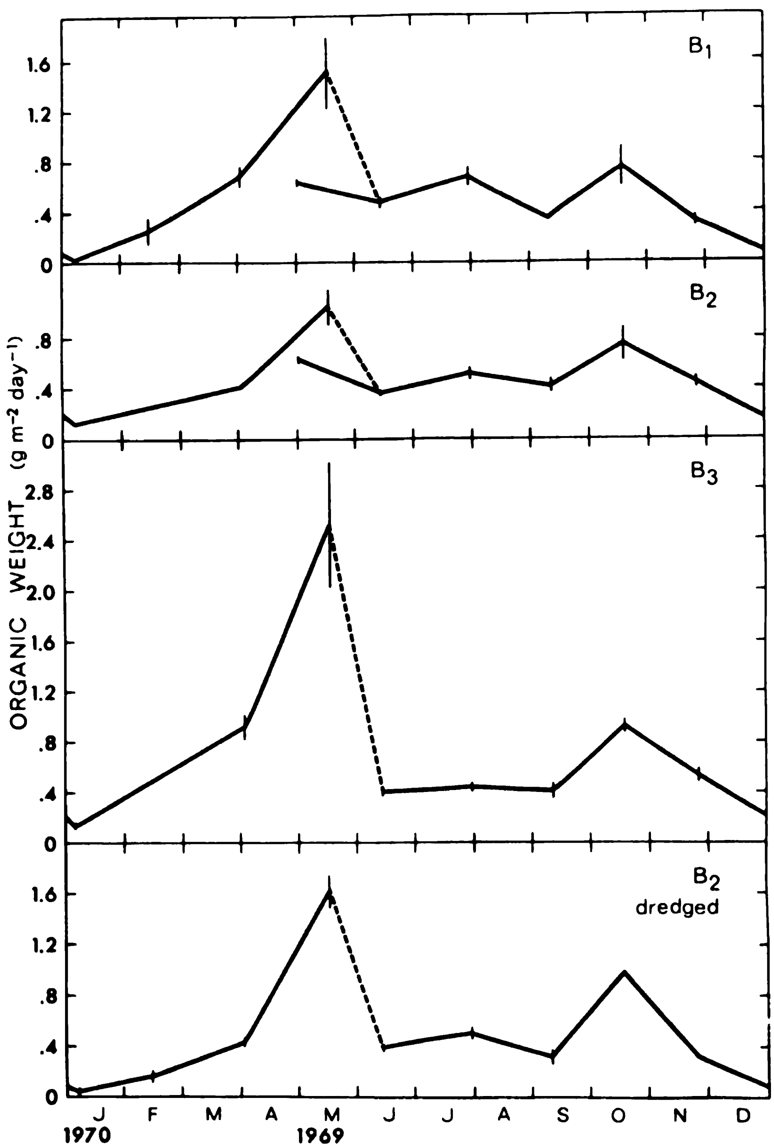

B1
B2
B3
B2
dredged
ORGANIC WEIGHT (g m-2 day-1)
1.6
1.2
.8
.4
0
2.8
2.4
2.0
J
F
M
A
M
J
J
A
S
O
N
D
1970
1969

TABLE 4.--Analysis of variance of the sediment trap data (ash-free dry weight), 2-way with replication, fixed model. (x = significant at 95% level; xx = significant at 99% level.)

Source of Variance	Degrees of Freedom	Mean Square	F Statistic
A (transect)	3	771.200	5.3607^{xx}
B (sampling dates)	8	5,413.950	37.6333^{xx}
AB	24	323.692	2.2500^{xo}
Error	36	143.861	
Total	71	824.969	

B. Sediment Core Samples

Sediment core samples were taken by means of a small piston corer from the material collected for measurement of benthic respiration. The cores were frozen then sawed into four 2 cm segments (horizons) which included 0-2, 2-4, 4-6, and 6-8 cm strata of the surface sediments. The material was dried at 105°C, weighed, combusted at 550°C, saturated with distilled water to rehydrate clay materials, dried at 105°C, and weighed to determine ash-free dry (organic) weight.

Transect B_3 on the lee side of the lake had the highest percentage organic weight, and Transect B_2, protected from terrestrial input, had the lowest (Figure 9). Transect B_1 was intermediate except for an extreme maximum at 7 m (transect-depth interaction is significant at the 99% level). A mean transect plotted over depth and season shows a complex relationship (Figure 10). The percentage organic weight was high at 7 m in summer and fall while that at all other depths is high in fall and winter. This indicates an accumulation of organic material at 7 m during summer stratification, and a redistribution of organic matter associated with fall overturn.

A 4-way analysis of variance with replication, fixed model, was performed on the sediment core data (% organic weight) which classified transects, depth, horizons, and seasons as factors (Table 5). Transect, depth, and their interaction terms (Figure 9) contributed most of the

Figure 9.--Mean annual percentage organic weight in the surface sediments (0-8 cm) over depth for each transect.

Figure 9

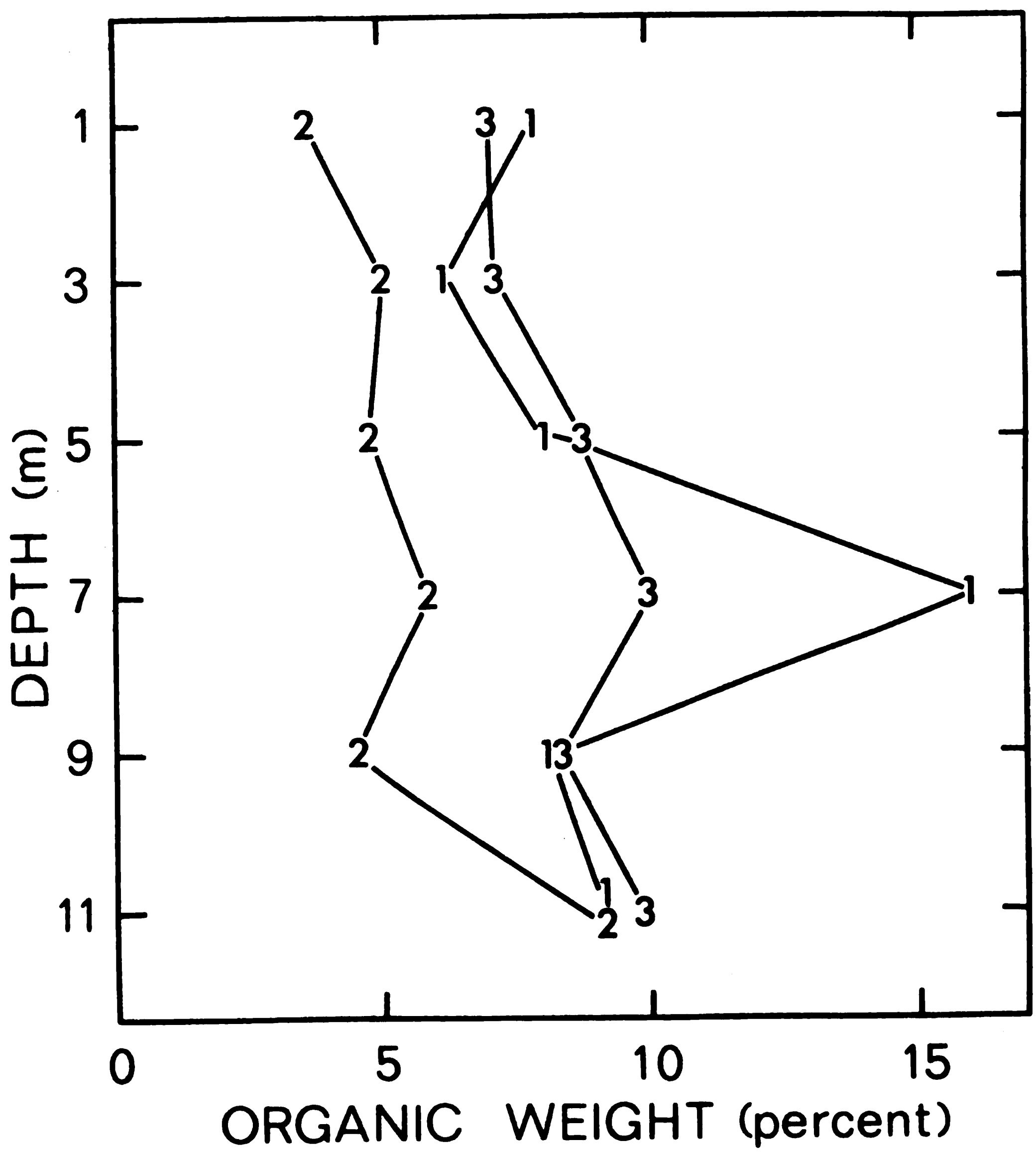


Figure 10.--Seasonal patterns of percentage organic weight of the surface sediments of a mean transect over depth, and showing horizon (not significant) fluctuations.

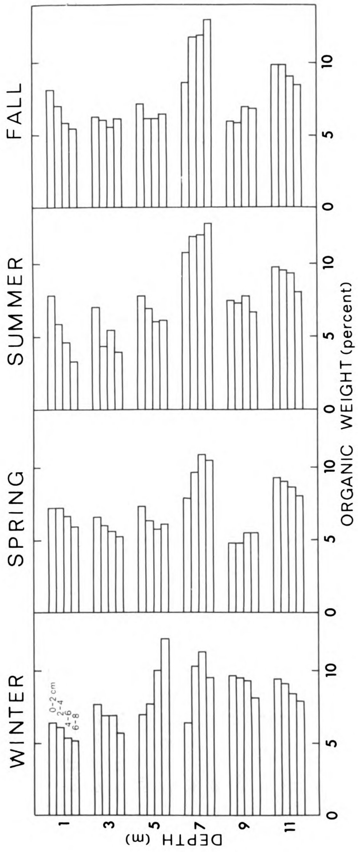

WINTER
SPRING
SUMMER
FALL
0-2 cm
2-4
4-6
6-8
DEPTH (m)
1
3
5
7
9
11
ORGANIC WEIGHT (percent)
0
5
10

Figure 10

TABLE 5.--Analysis of variance of the sediment core data (% ash-free dry weight); 4-way with replication, fixed model. Remaining error = sum of interactions between replications and all other effects: Mean square = 3.41069.

Source of Variance	Degrees of Freedom	Mean Square	F Statistic
E (Replication)	3	4.02458	1.17999^{oo}
A (Transect)	2	1483.79745	435.04361^{xx}
B (Depth)	5	618.96014	181.47669^{xx}
AB	10	250.02778	73.30717^{xx}
C (Horizon)	3	7.01188	2.05585^{oo}
AC	6	9.02742	2.64680^{xo}
BC	15	32.00051	9.38243^{xx}
ABC	30	8.07088	2.36635^{xx}
D (Season)	3	56.86363	16.67220^{xx}
AD	6	26.33505	7.72133^{xx}
BD	15	55.30708	16.21582^{xx}
ABD	30	70.76894	20.74918^{xx}
CD	9	8.34907	2.44792^{xx}
ACD	18	3.74830	1.09899^{oo}
BCD	45	6.82012	1.99963^{xx}
ABCD	90	4.25080	1.24632^{oo}

variance and were highly significant. Season and season interactions were also significantly heterogeneous. Horizons were not significantly different at the 90% level, although some horizon interaction terms were significant at 99%. These results suggest that the surface sediments of Lawrence Lake differ with respect to location in the lake and change during the year. The quantitative importance of these phenomena is suggested by the homogeneity of the horizons which indicates that as much change occurs at 8 cm in the sediments as at the surface of the sediments. Thus, about 4000 m^3 of sediments appear to be involved in the detritus cycle of the lake.

C. Permanent Sedimentation

Loss of organic carbon to the permanent sediments was calculated from estimates of the amount of organic carbon in the surface sediments, the thickness of the sediments under the lake, and the age of the lake. An estimate of the water content of the sediments of 80% was derived from Wetzel (1970). The sediment core data showed that the average ash-free dry (organic) weight of the surface sediments was approximately 10%. Approximately one-half of this was estimated to be carbon, i.e., 5% of the dry weight. The density of $CaCO_3$ is 2.2 (Hodgman, 1959), and 9.4 m of sediments exist under the deepest point in the lake (R. O. Kapp, personal communication). The age of Lawrence Lake is probably similar to that of Pretty

Lake in northern Indiana which has been radiocarbon dated at approximately 14,000 years before present (Wetzel, 1970).

$$9.4\ m^3 \times 10^6\ cc \times 20\% \times 2.2 = 4.14 \times 10^6\ g\ CaCO_3/m^2/14{,}000\ yrs.$$

$$5\%\ \text{organic carbon} = 0.207 \times 10^6\ g\ \text{organic}\ C/m^2/14{,}000\ yrs.$$

$$\frac{207 \times 10^{\circ}}{14} = 14.8\ g\ \text{organic}\ C/m^2/\text{year}.$$

IV. BENTHIC RESPIRATION

A. Introduction

Benthic respiration has been traditionally measured by O_2 uptake Pamatmat, 1965, 1968; Pamatmat and Banse, 1969; Pamatmat and Fenton, 1968; Carey, 1967; Edwards and Rolley, 1965; Hargrave, 1969a,b; Hayes and MacAulay, 1959; Kanwisher, 1962; Odum, 1957a,b; Odum and Hoskin, 1958; Wieser and Kanwisher, 1961). Several workers (Copeland and Jones, 1965; Park, Hood, and Odum, 1958; Verduin, 1960) using both the CO_2-pH change technique which assays CO_2 as a function of pH (Beyers and Odum, 1959; Beyers, Larimer, Odum, Parker, and Armstrong, 1963) and the O_2 uptake technique in plankton production studies have observed respiratory quotients ($RQ = CO_2/O_2$) greater than one. Preliminary measurements of CO_2 release and O_2 uptake by the sediments of Lawrence Lake produced respiratory quotients of 1-3. Consequently, the CO_2-pH change method was used exclusively in this study to estimate the loss of respiratory carbon from the benthic community. Carbon dioxide was assumed to be the only carbonaceous respiratory product of the benthic community and the only factor influencing the pH changes observed at the sediment-water interface.

B. Methods

Shallow sediment cores were obtained with a free-fall sampler designed by Dr. G. H. Lauff (unpublished). The sampler consisted of a steel tube threaded to a one-way water valve above and a cutting head below. A clear acrylic tube was held within the steel tube by shoulders below the one-way valve and within the cutting head, and could be removed, containing an intact sample, from either end of the sampler. Upon retrieval of a sediment core, an initial sample was removed from the water overlying the sediments for pH determination and titration. The level of the sediments within the insert was adjusted so that a known volume of water (usually 200 ml) was held between the surface of the sediments and the top of the acrylic insert. The tube was then sealed with either clear acrylic caps or Saran Wrap (Dow Chemical Co., Midland, Michigan), placed in a rack to hold the sediments in place inside the inserts, and returned to the original depth of the sample for incubation. The initial water sample was returned to the laboratory and allowed to reach room temperature (1-2 hours) before electrometric determination of pH was made (Beckman Expandomatic pH meter, Corning combination electrode).

After incubation, a second sample was removed from the water trapped over the sediments for pH determination and calculation of the pH change during the incubation period. A smaller core of sediments was taken from the material in the insert by means of a small piston sampler for organic weight analysis (see Chapter III), and the insert was washed in preparation for the next sample. In the laboratory, the initial water sample (100 ml) was titrated with CO_2-saturated distilled water prepared in a tonometer (Beyers, et al., 1963), and the pH change observed in the incubated sample was converted to CO_2 accumulation (see Appendix I).

Four replicates were taken at each depth (1, 3, 5, 7, 9, and 11 m), two as light "bottles" and two having black cloth hoods as black "bottles." The acrylic (cast) inserts had an inside diameter of 4.49 cm, a wall thickness of 2-3 mm, and light transmission of 92% (Cadillac Plastics & Chemical Co.). Four complete sets of samples were taken along each transect, corresponding to summer (stratified), fall (overturn), winter (stratified), and spring (overturn and early stratification), over the study period.

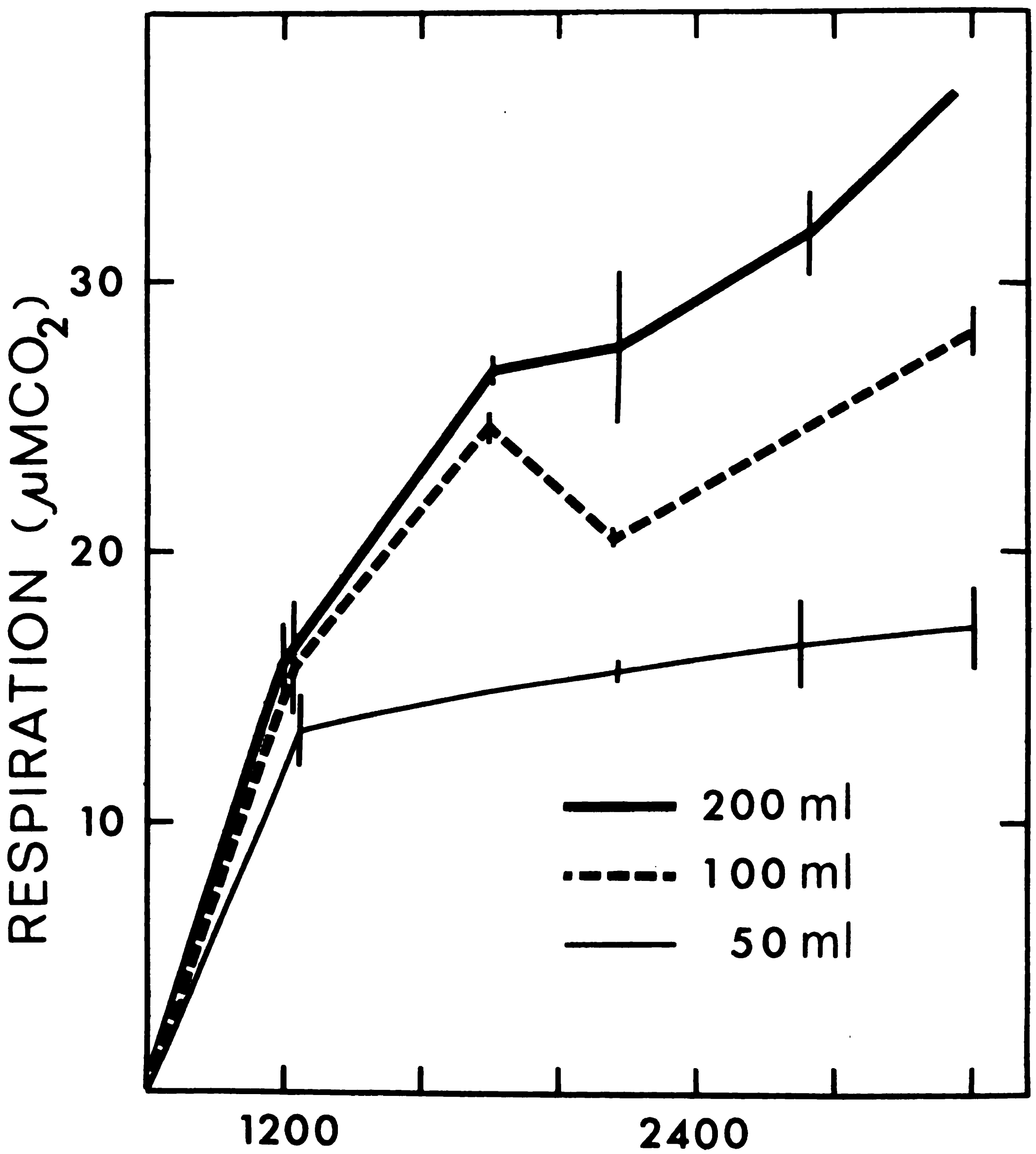
Shortly after starting the sampling regime reported here, the means of sealing the acrylic inserts was changed from hand-lapped acrylic caps to Saran Wrap held with rubber bands. Despite great care in the construction and fitting of the acrylic caps, erratically low results suggested that CO_2 was escaping from the incubated samples. Consequently the caps were tested against Saran Wrap and were found to be less dependable. Further, good results using capped inserts were not significantly different from unselected results obtained with Saran Wrap.

Observations for a particular date and depth consisted of a complete 24-hour diurnal cycle. Depending upon the rate of CO_2 evolution expected, one to four separate samples were incubated for four to 24 hours and summed to obtain a 24-hour duration. A saturation effect was detected (Figure 10) which caused the rate of CO_2 evolution to decrease above a certain level of accumulation. An exact determination of the critical accumulation was complicated by normal diurnal changes during the experiment. No samples (200 ml) were used for preparation of the annual CO_2 budget which had accumulated more than 25 μM CO_2.

The possible effects of bacterial overgrowth stimulated by container surface (Zobell, 1943; Zobell and Anderson, 1936) upon respiration were tested in several additivity experiments performed both day and night and using both light and dark bottles. Except during the first one-half hour, storage effects were consistently inhibitory, though not significantly so until accumulation exceeded 30 μM CO_2 200 ml^{-1}.

Figure 11.--CO_2 accumulation *vs*. time for three incubation volumes. Variations in 200 ml volume interpreted as diurnal effects up to approximately 30 μM CO_2. Vertical lines represent range of two samples.

Figure 11



Titration errors were examined (Figure 12) and found to be negligible with respect to the pH ranges observed in the incubated samples. Only one addition was made in titrating the field samples as they were timed to approach 20 μM CO_2 and 0.5 ml of CO_2-saturated distilled water approximated 30 μM CO_2. The final point in Figure 12 represents a 0.5 ml addition, but was accomplished by two 0.25 ml additions to obtain the middle (0.9 mgC) point. Thus the 90% confidence interval is probably larger than average.

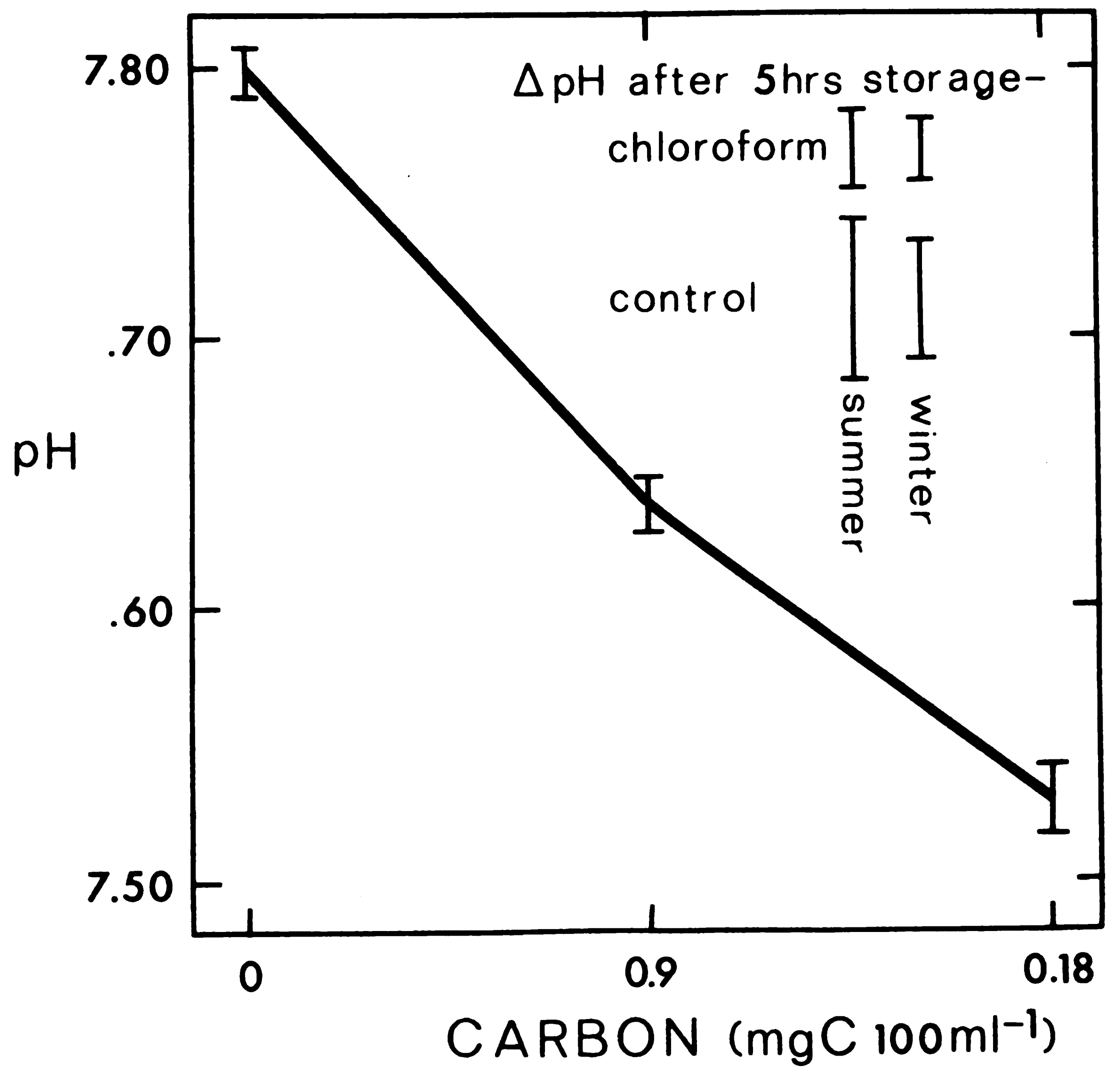
Sample drift during transportation from the field and warming to room temperature was negligible during the 1-2 hour period involved, and was further reduced by adding a few drops of chloroform to the sample in the field. The drift at the end of 5 hours with chloroform (Figure 11) was less than 0.03 pH units in both summer and winter. Further, the drift was in the same direction, consistently downward, for both initial and final samples.

C. Results

The annual estimate for benthic respiration of the entire lake, calculated on the basis of the four complete samples (Figure 13), was 117.5 g C $m^{-2}yr^{-1}$ or 5,861.2 kg C $lake^{-1}yr^{-1}$. The estimate may be improved by the application of correlative factors determined by the analysis of other data. The annual benthic respiration per unit area for Lawrence Lake is twice that determined for Marion

Figure 12.--Titration error and pH sample drift during transportation and warming. Vertical lines on titration curve represent 90% confidence intervals (n=6).

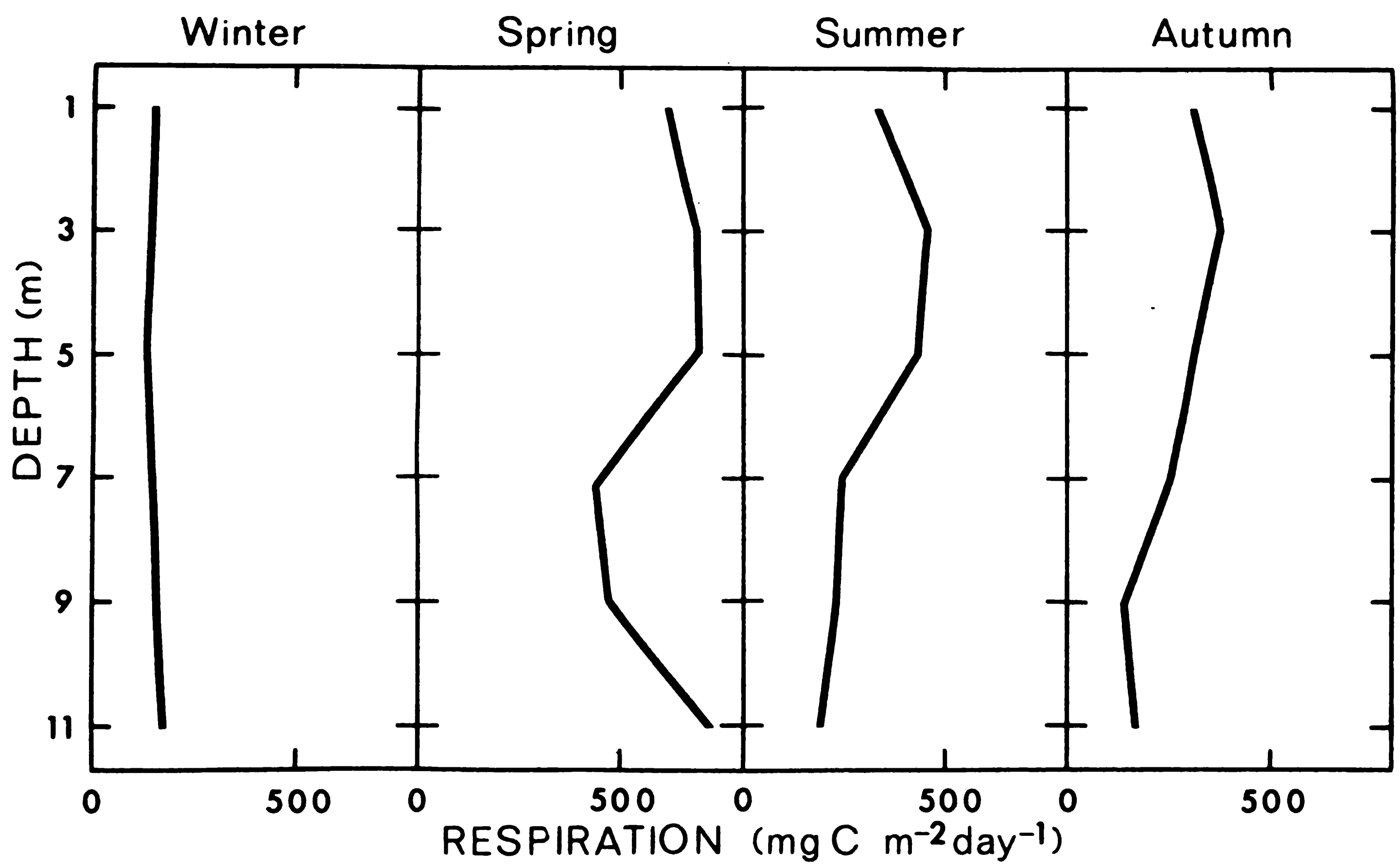
Figure 12



7.80
.70
.60
7.50
pH
ΔpH after 5hrs storage-
chloroform
control
summer
winter
0
0.9
0.18
CARBON (mgC 100ml⁻¹)

Figure 13.--Seasonal patterns of benthic respiration as a mean transect over depth.

Figure 13


Winter
Spring
Summer
Autumn
DEPTH (m)
1
3
5
7
9
11
0
500
RESPIRATION (mg C m-2 day-1)

Lake, British Columbia, by the 0_2 uptake technique and a questionable respiratory quotient of 0.85 (Hargrave, 1969a). The discrepancy could be adequately explained by the larger respiratory quotients empirically determined for the benthos of Lawrence Lake.

A 5-way analysis of variance with replication, fixed model, was performed on the benthic respiration results as a preliminary search for significant factors. The factors classified included transect, depth, season, light (light and dark bottles), and diurnal period (time of day). Light was the only single factor which was not significantly heterogeneous at the 99% level, which suggests that epipelic photosynthesis is not important to the carbon budget of Lawrence Lake, Diurnal variation was highly significant, however, and suggests that light may still be an important factor with respect to some other biological parameter, e.g., an energy budget. Many factors were jointly important, particularly season-time of day (diurnal period). Thus, benthic respiration has a complex distribution in the lake, and is strongly influenced by season (Table 6).

TABLE 6.--Analysis of variance of the benthic respiration data; 5-way with replication, fixed model. Remaining error = sum of interactions between replications and all other effects: Mean square = 1834.81481. (x = significant at 95% level; xx = significant at 99% level.)

Source of Variance	Degrees of Freedom	Mean Square	F Statistic
F (Replication)	1	7964.59566	4.34082^{xo}
A (Transect)	2	13047.45002	7.11104^{xx}
B (Depth)	5	91434.33672	49.83301^{xx}
AB	10	12272.65674	6.68877^{xx}
C (Light-Dark Bottles)	1	1541.96928	0.84040^{oo}
AC	2	241.07544	0.13139^{oo}
BC	5	10872.17202	5.92549^{xx}
ABC	10	2914.01963	1.58818^{oo}
D (Season)	3	2192872.84399	1195.14669^{xx}
AD	6	173639.95163	94.63623^{xx}
BD	15	120438.09486	65.64046^{xx}
ABD	30	14454.70669	7.87802^{xx}
CD	3	3206.25893	1.74746^{oo}
ACD	6	1706.30817	0.92996^{oo}
BCD	15	5959.94878	3.24826^{xx}
ABCD	30	2556.05508	1.39145^{oo}

TABLE 6.--(continued)

Source of Variance	Degrees of Freedom	Mean Square	F Statistic
E (Diurnal Period)	1	574817.32626	313.28357^{xx}
AE	2	15733.81519	8.57515^{xx}
BE	5	43151.61721	23.51824^{xx}
ABE	10	2253.93935	1.22843^{oo}
CE	1	5638.32038	3.07296^{oo}
ACE	2	1331.19776	0.72552^{oo}
BCE	5	2412.33166	1.31475^{oo}
ABCE	10	2121.36074	1.15617^{oo}
DE	3	575040.28705	313.40508^{xx}
ADE	6	66387.658707	36.18221^{xx}
BDE	15	39911.203744	21.75217^{xx}
ABDE	30	7570.64179	4.18061^{xx}
CDE	3	538.01918	0.29323^{oo}
ACDE	6	1213.42217	0.66133^{oo}
BCDE	15	6689.20540	3.64571^{xx}
ABCDE	30	1101.45296	0.60031^{oo}

V. CONCLUSIONS

An Annual Benthic Carbon Budget for Lawrence Lake

Inputs:	
Submersed macrophytes:[1]	$+87.9\ g\ C\ m^{-2}yr^{-1}$
Epiphytes:[2]	+39.9
Sedimentation:[3]	+10.2
Terrestrial:[4]	+ 5.2
Outputs:	
Benthic respiration:	-117.5
Permanent sedimentation:	- 14.8
Balance:	$+\ 8.9\ g\ C\ m^{-2}yr^{-1}$

1. Calculated from ash-free dry (organic) weight by a factor of 46.5% (Westlake, 1965).

2. From Allen (1969).

3. Calculated as 20% phytoplankton production (Miller, 1970).

4. Estimated as 200 g C m^{-1} shoreline (Szczepański, 1965).

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APPENDIX

APPENDIX I

RESPIRATION CALCULATIONS

$M = \text{mM } CO_2 \text{ ml}^{-1}$ titrant (obtained from Table 3, Beyers, *et al.*, 1963).

M' = M corrected for volume of titrant used = $\text{volume}_{tit.} \times M$.

$$\frac{M'}{\Delta ph_{ton.}} = \frac{X}{\Delta pH_{incub.}}; \quad \frac{\Delta pH_{incub.} \times M'}{\Delta pH_{ton.}} = X$$

Correction for 200 ml incubation = $2 \times X_{100ml}$ (titration)

$= X_{sample}$

$X/m^2 = X_{sample} \times 631.56$

$$X/m^2/hr. = \frac{X/m^2}{hrs._{incub.}}$$

Errors:

1. Dilution effect upon pH of titration:

   Error for 0.5 ml distilled H_2O when $pH_{initial}$ is above 7.00 = $0.005 \times 7.00 - pH_{initial}$ = $0.005 \times -1.00 = -0.005$ at pH 8.00.

   Net effect: increases ΔpH tonometer and decreases ΔCO_2 sample estimate.

2. Volume change of titration:

   Factor for $\text{volume}_{\text{incub.}} = \frac{100.5 \text{ ml}}{200.0 \text{ ml}} = 0.025$ for 0.5 ml titrant.

   Net effect: increases ΔCO_2 estimate.

Net effect: errors tend to cancel, resulting in a small under-estimate of ΔCO_2.