THE UNIVERSITY OF MANITOBA

THE PRIMARY PRODUCTION OF SUBMERGED MACROPHYTES IN WEST BLUE LAKE, MANITOBA

by

Robert Love

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

MASTERS OF SCIENCE

October 1974

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ABSTRACT

The primary productivity of 5 species of submerged macrophytes was determined by continuous cropping of plant biomass, and in situ by uptake of ^{14}C. Both methods were studied by summed transect and random sampling procedures. Areas of the littoral zone colonized by macrophytes were marked off with floats and total area determined by planimetry. The carbon content of plant material per unit of organic weight was analyzed and found to be lower than previously published values. An "in-vial" combustion procedure was devised to allow the combustion of wet and dry samples and quantitatively determine the amount of $^{14}CO_2$ fixed. The maximum difference between the activity of wet and dry samples was found to be 4.1% and not significant in order that a correction factor need by employed. When distribution and carbon content were applied to ^{14}C experiments, only 2 species contributed significantly to the total macrophyte energy input. These 2 species, Potamogeton Richardsonii (Benn.) Rydb. and Myriophyllum alterniflorum DC., along with Chara vulgaris L., also contributed to the majority of production determined from biomass changes. Maximum production from biomass changes for the summed transect method was 13.6 mgC m^{-2} day^{-1} and for the random method was 11.0 mgC m^{-2} day^{-1}. Maximum production from

^{14}C uptake for the summed transect method was 93.7 mgC m^{-2} day^{-1} and for the random method was 102.0 mgC m^{-2} day^{-1}. Cumulative net productivities for the random and summed transect methods were 8.0 mgC m^{-2} day^{-1} and 9.4 mgC m^{-2} day^{-1} respectively. These figures are lower than previous studies, although those studies were conducted on much shallower lakes in which the macrophytes occuppied a relatively larger area.

Turnover times were calculated for 4 of the 5 macrophyte species and times ranged from 1.45 to 142.01 days. The turnover times were shown to be rather abstract numbers, the difference between any two being magnified by exponential growth.

ACKNOWLEDGEMENTS

The author is deeply indebted to Dr. G.G.C. Robinson for his guidance and encouragement throughout this investigation. Helpful advice was also provided by Dr. F.J. Ward.

This thesis work was financed by the National Research Council of Canada, the Fisheries Research Board of Canada and the Manitoba Provincial Government through Dr. Robinson, and by the University of Manitoba.

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INTRODUCTION

Research commenced in May, 1973 to determine the productivity of the submerged macrophytes in West Blue Lake, Manitoba. The study was part of a larger program concentrating upon the definition of energy routes and transfers within this ecosystem.

The predominant submerged macrophyte species in West Blue Lake are Potamogeton Richardsonii, Potamogeton pectinatus, Myriophyllum alterniflorum, Megalodonta Beckii, and Chara vulgaris. These species are important not only in the sense of production, but also in supplying niches for the growth of aquatic invertebrates (Biette 1969) and an epiphytic community.

It was the purpose of this study to employ ^{14}C and biomass production techniques and utilize different sampling procedures. Summed transect and random samples along transects were the two procedures chosen. Previous investigators (Davies 1968, Rich, Wetzel and Van Thuy 1971) have utilized one or the other of the above procedures. Summed and random transect sampling results are compared by analysis of variance to determine significant differences. In addition to determining weaknesses in methodology, macrophyte and phytoplankton productivity were compared over the experimental period to indicate relative energy inputs to the West Blue Lake ecosystem.

LITERATURE REVIEW

In recent years, studies of the limnological role of the primary producer have dealt mainly with phytoplankton. Wetzel (1964a) indicated that in shallow situations the importance of benthic regions is often underestimated.

Biomass has long been used as a means of estimating macrophyte productivity. A number of mechanical devices have aided in removing the plants while allowing the investigator to work at the water surface. Initially samplers were modifications of dredges originally designed for sampling benthos (Potzger and Van Engel 1942, Juday 1942, Walker 1947). Forsberg (1959, 1960) created a shearing-clamp apparatus to cut a known area of hydrophytes below the substrate surface. Grøntved (1957, 1958) found a sampler constructed on the principal of a large corer yielded reliable results. Similarly, Rich, Wetzel, and Van Thuy (1971) obtained rapid and excellent results with a modified free-fall core sampler. Nygaard (1958) employed a corer with the aid of self-contained underwater breathing apparatus to sample hydrophytes. Direct removal of plants from the substratum has generally been accomplished by placing a quadrat randomly along transects and clearing the area within the frame by hand (Rickett 1922, 1924, Pearsall and Gorham

1956, Wetzel 1964a, 1964b, Davies 1968, Ikusima 1966, Goulder 1969, Boyd and Vickers 1971). Other investigators have employed strip cutting along transects (Edwards and Owens 1960, Westlake 1961, Owens and Edwards 1961, 1962). Edwards and Brown (1960) have attempted to relate macrophyte distribution derived from aerial photographs to actual distribution recorded from strip cutting. This technique however was limited to shallow water and with varying sucess. Westlake (1964) and Owens, Learner, and Maris (1968) determined biomass from light attenuation through a weed bed. This technique has only shown applicability in certain situations. For some waterfowl food studies the distribution of macrophytes may be determined by visual census techniques (Siegler 1941, Bird 1959).

Wetzel (1965) and Westlake (1963, 1965) stress the importance of defining productivity in terms of some quantifying parameter. The wet weight of macrophytes per unit area has been used by a number of investigators (Rickett 1922, 1924, Juday 1942, Potzger and Van Engel 1942, Walker 1947, Edwards and Owens 1960, Owens and Edwards 1961, 1962, Westlake 1961, Wetzel 1964a, Goulder 1969). Although spin drying is considered more precise than air drying, Westlake (1963) and Wetzel (1964a) state that data obtained in this way should be used with reservation due to variability in water content between

individual plants and at different times during the growing season. Dry weight is generally considered superior to wet weight when quantitative measures of biomass are required but ash-free dry weight is more useful (Westlake 1963). Dry weight is usually obtained by heating samples at 105°C to constant weight. For macrophytes, the amount of drying time varies but twenty four hours is considered adequate (Westlake 1969). Ash-free dry or organic weight is the difference in weight following drying at 105°C and ignition at 550°C, followed by cooling in a dessicator. Without dessicant the reabsorption of water upon cooling may introduce errors ranging from 4 to 20% of oven dry weight (Westlake 1963). Westlake (1963, 1965) and Wetzel (1964a) discuss the problems associated with ash determinations. The main obstacle in any ash estimate is the presence of calcium carbonate deposits on the plant material. Calcium carbonate decomposes at temperatures exceeding 550°C and therefore care must be taken to insure ignition temperatures do not exceed this value. Wetzel (1960) has found marl encrustations as high as 0.80 grams soluble carbonate per gram plant material. The percentage carbon of ash-free dry weight is considered less variable than dry weight (Westlake 1963). Wetzel (1964a) and Westlake (1965) suggest dry combustion as opposed to wet combustion methods for the determination of percent carbon. The usual method proposed

is that of Belcher and Ingram (1950). Westlake (1965) reviews the percentage carbon in ash-free weights published from many sources. The ash content of submerged aquatics ranged between 15-25% of dry weight. Carbon values fitted a nuch more restricted range (43-48%).

Very little information has been obtained on the losses of plant material through the growing season by faunal or mechanical damage. Wetzel (1965) indicates that losses in biomass due to faunal destruction are small in comparison to phytoplankton. Exclosure studies in Erie Marsh by Rich (1966) lend support to this assumption. Any losses of plant material throughout the growing season would tend to depress productivity estimates. If one neglects seasonal losses then theoretically the maximum biomass divided by the number of growing season days gives an estimate of maximum cummulative net productivity.

Production estimates based on biomass changes have been determined for freshwater hydrophytes in a number of diverse habitats (Rickett 1922, 1924, Potzger and Van Engel 1942, Penfound 1956, Forsberg 1960, Edwards and Owens 1960, Owens and Edwards 1961, 1962, Westlake 1961, 1966, Rich 1966, Davies 1968, Bernatowicz, Pieczyńska and Radziej 1968, Boyd and Vickers 1971, Rich, Wetzel and Van Thuy 1971). Sculthorpe (1967) summarized the biomass data published by authors previous to that date.

Forsberg (1960) recorded the largest maximum crop of submerged angiosperms as 680 gm dry wt m^{-2}. In contrast, Davies (1968) found extremely low values, 8.9 gm dry wt m^{-2} in Marion Lake. Edwards and Owens (1960) and Owens and Edwards (1961, 1962) have determined crop values for temperate rivers. Their studies indicate that yield is no greater in polluted rivers than in unpolluted rivers. Maximum crops for two shaded areas, one polluted and one not polluted, were similar. Due to the greater standing crop in an unshaded area they concluded that macrophyte growth was limited by the amount of incoming solar radiation.

Determinations of photosynthetic rate have dealt with measurement of dissolved oxygen or carbon dioxide. The changes in dissolved oxygen concentrations in a given volume of water are the result of three processes (Sculthorpe 1967): a) exchange of oxygen between water and the atmosphere; b) consumption by chemical oxidations, bacteria, plants, and animals within the water or sediments; c) oxygen production as a result of photosynthesis. Measurement of oxygen production has been performed by Owens and Edwards (1962) and Goulder (1969). In flowing waters the rate of change of dissolved oxygen is measured between two stations (Owens and Edwards 1962). The exchange coefficient between the stations was measured by the passage of a volume of water which

had been deoxygenated by the addition of sodium sulphite and a cobalt catalyst. These measurements were taken between the hours of sunset and sunrise. Respiration rates have usually been taken as the mean nocturnal value of oxygen decline corrected for exchange (Goulder 1971). Oxygen levels were recorded at one or two hour intervals from sunrise to sunset to determine photosynthetic production. Goulder (1969), working on Sangwin pond, utilized a Mackareth probe to obtain the mass of oxygen per unit area. The data was used to construct a mass-time curve. The change in mass for daylight hours was found from the curve and the production calculated by the equation:

$$P = \Delta O_2 + R \pm E$$

ΔO_2 ($g\ m^{-2}\ h^{-1}$) = change in oxygen mass

R ($g\ m^{-2}\ h^{-1}$) = respiration rate

E ($g\ m^{-2}\ h^{-1}$) = surface exchange

Both these methods necessitated an estimation of community respiration other than by macrophytes. Owens and Edwards (1962) acquired values for respiration by cropping the macrophytes in one section of the river. Goulder however, neglected community respiration assuming it was negligible when compared to that of the macrophytes. Owens and Edwards (1962) found respiration of mud deposits of approximately 3 to 4 gm oxygen m^{-2} day^{-1} in late spring and summer, or about 30% of the total oxygen

demand of the habitat. The production values of the two communities demonstrated substantial agreement. Owens and Edwards (1962) found maximum gross photosynthesis was 17.55 gm oxygen m^{-2} day^{-1} while Goulder (1971) found maximum gross photsynthesis for Ceratophyllum demersum was 18.8 gm oxygen m^{-2} day^{-1}.

Changes in levels of dissolved oxygen produced by excised shoots of hydrophytes in light and dark bottles have been studied in relation to the effect of a number of environmental parameters on photosynthesis (Meyer and Heritage 1941, Meyer, Bell, Thompson and Clay 1943, Schomer 1934, Ikusima 1965, 1966, 1967, 1970, Hartman and Brown 1967, Goulder 1971). A study by Schomer (1934) showed optimal depths for photosynthesis by Ceratophyllum and Elodea tobe five meters. Temperature variations at different depths had little effect on respiration. Meyer and Heritage (1941) and Meyer, Bell, Thompson and Clay (1943) found apparent photosynthesis decreased with increasing depth. Water of decreased oxygen content was needed to reduce the formation of oxygen bubbles, and a period of equilibration with the media was essential for reproducible results. The first half hour of the experiment had to be disregarded due to gas bubbles diffusing into the medium. Ikusima has written a series of papers dealing with the influence of a number of environmental factors on photosynthesis. His first paper (Ikusima

1965) attempts to relate the light and dark bottle method to the vertical distribution of photosynthetic activity within the aquatic plant community. The bottle technique was less representative of community photosynthesis when more than 0.3 gm fresh weight of plant material were enclosed in containers. The photosynthetic rate of excised plants was higher in the terminal areas and decreased towards the basal regions. Incubation of terminal and basal portions under identical light conditions indicated the decrease was a physiological phenomenon. Ikusima (1966) found similar results in a submerged community of Vallisneria denseserrulata. The uppermost regions of the community contributed 2.8 to 5.6 times the photosynthetic production of the lower regions. Goulder (1971) recording oxygen production with a Mackareth probe found high production in the morning and decreased production in the afternoon. The major external factor controlling this situation was thought to be the availability of bicarbonate at the leaf surface. Initially the bicarbonate level was high, but depletion may have occurred as time progressed, causing a depression of photosynthesis in the afternoon.

Productivities obtained with the oxygen method must be viewed sceptically, especially in those experiments conducted by enclosure of plants. Removal of plants from the substratum and return to their original depth

exposes macrophytes to a number of abnormal conditions. Situations where various portions are enclosed may result in misleading values if the roots are not included. Controversy exists on the function of the roots. Some evidence suggests that the roots are solely organs of attachment while other evidence suggests that they are also nutrient absorbers. Most experiments on nutrient uptake with respect to roots and rhizomes consist of long incubations in the presence or absence of substrate. Experiments of this sort were performed by Denny (1972) on six macrophyte species. Plants grown on mud showed increased growth to those grown on sand. Although experiments of this sort are rather crude, they indicate that roots exert some control over nutrient uptake. Brown (1913 in Sculthorpe 1967) found the substrate effect could be overcome by increasing the CO_2 content of the water. He explained that dissolved carbon dioxide concentrations were probably higher over mud substrates, accounting for increased growth. Arber (1920) believed the roots had some nutrient absorptive properties but stated that in relation to land plants, "the function of anchorage has assumed a greater importance, while the function of absorption is less pre-eminent." Support for the roots as absorptive organs is presented by Frank and Hodgson (1964) who studied the uptake of ^{14}C labelled fenac in Potamogeton pectinatus. Autoradiograms confirm-

ed absorption by leaves and roots. Pearsall (1920), Butcher (1933), and Lind and Cottam (1969), have suggested a relationship between the nature of soil type and the vegetation growing on it. If in fact the roots are important nutritively, then a relationship would be expected.

Removal and incubation may seriously alter the metabolic rate of submerged macrophytes. Optimal photosynthesis of submerged communities occurs at light intensities lower than those of surface waters and it is possible that exposures to high light intensities could cause photo-oxidation of pigments, or alter the physiology of the plants in some way.

Productivity estimated by the oxygen technique measures respiration and photosynthesis of the entire community and not only the plant species under observation. Respiration from other sources (algal, faunal, bacterial) may be significant in experiments conducted over long incubation periods. Edwards and Owens (1962) found community respiration to be approximately 30% of total respiration for a chalk stream in England. If the photosynthetic rate is high, the medium in the container may become supersaturated and result in the emmission of oxygen bubbles. The problem of supersaturation has been overcome in a number of cases by incubation the plant material in a medium of reduced oxygen content. Removal

of the oxygen by boiling or chemical treatment may seriously affect the nutrient status of the medium (Wetzel 1964a). Perhaps the most important drawback to the use of oxygen is the presence of large lacunal systems. Wetzel (1964a) in his criticism of the oxygen method pointed to storage of oxygen in the lacunae as the major disadvantage. Support of this assumption has come from Hartman and Brown (1967). They showed a definite lag period existed between the increase of oxygen levels in the lacunae and in the medium. This process was most noticeable under conditions of low light intensity, near the compensation point. Oxygen levels increased in the internal atmosphere while remaining constant in the external medium. These results cast doubt on the validity of determining photosynthetic activity with the diurnal oxygen method. The lacunae of submerged hydrophytes appear to act as storage organs for internal gases. Oxygen accumulates rapidly in the lacunae and diffuses slowly into the surrounding medium but this does not seem to be the case for carbon dioxide.

Steeman-Neelsen (1952) first proposed the use of the ^{14}C method for measuring primary production in planktonic organisms. Wetzel (1964a, 1964b) modified the procedure for determining phytoplankton productivity in order to measure the in situ production of submerged macrophytes. The method was as follows: light and opaque

plexiglass containers were placed over individual plants and pressed into the sediment. $NaH^{14}CO_3$ was injected into each chamber with a syringe. The contents of the chambers were mixed by propellor blades to distribute the $NaH^{14}CO_3$ evenly. Following a four hour midday incubation period plants were removed from the substrate and taken to the laboratory for analysis. Quantitative estimates of $^{14}CO_2$ assimilated could not be determined directly by scintillation counting due to self-absorption by the plant tissues. Wetzel (1964a) overcame self-absorption problems with wet oxidation of a known quantity of plant material by Van Slyke chemical combustion (Van Slyke, Plazin, and Weisiger 1952) and analysis of evolved $^{14}CO_2$ in gas phase. Productivity was expressed as mg C mg dry weight^{-1} time^{-1} and converted to mg C m^{-2} time^{-1} from biomass data.

Very little quantitative information is available on in situ ^{14}C studies, and what studies have been done vary in incubation methods and analysis of fixed $^{14}CO_2$. Davies (1968) modified the experimental chambers designed by Wetzel (1964a) in order to measure in situ production of submerged and floating aquatics in Marion Lake, B.C. Methods of quantitative analysis of isotope fixed in photosynthesis have also varied. To date, combustion of plant tissues has been required to obtain quantitative estimates of radiocarbon fixed. Assay of the $^{14}CO_2$

was accomplished by Wetzel (1964a, 1964b) with a dynacon electrometer. Perhaps the major draw-back in this procedure was the time required to obtain the necessary clean glassware for each combustion. A modified oxygen combustion flask was proved effective in the more recent study by Davies (1968), although efficiency of recovery was calibrated at only 38%. Recovery was accomplished by drawing a mixture of toluene-POPOP-ethanolamine into the flask to absorb the CO_2. Following addition of the mixture to a scintillation vial, the contents were counted in a liquid scintillation counter. Gupta (1966) developed an "in-vial" combustion procedure for recapture of $^{14}CO_2$ from samples. This procedure was modified by Bell and Ward (1968) for determining secondary productivity in aquatic invertebrates. Love and Robinson (1974) further modified the procedure to determine macrophyte productivity. A high relative efficiency 84±3% was obtained with this procedure. Productivity without plant removal has been studied in marine environments by Towle and Pearse (1972). Polyethelene bags covered individual blades of Macrocystis pyrifera and following incubation in the presence of $^{14}CO_2$ subsamples were removed from the tip, midsection and base of each blade. Discs were digested in 2N KOH and H_2O_2 before counting in a scintillation counter. Only counts from midsection discs were used to calculate production rates.

The author found that combustion of discs from various parts of fronds gave a wide variation in counts, and therefore, extrapolation to total production from mid-section discs would give results that may be completely misleading.

Since large depositions of $CaCO_3$ are common to vascular aquatic plants, errors in production estimates through precipitation of monocarbonates may be significant. Wetzel (1965) found that fuming filters in phytoplankton studies may substantially reduce errors due to external precipitation. Thus in macrophyte studies involving ^{14}C fuming with HCl has become an integral part of laboratory procedures. No quantitative evidence is available on the rate of extracellular $CaCO_3$ deposition but it must be assumed that deposition will vary depending on the physiological status of the plant.

Production values for submerged macrophytes previous to this date have been expressed as mg C dry biomass weight^{-1} time^{-1}. Little attention has been paid to losses of activity due to volatization of compounds upon drying. Recently the magnitude of such loss has been examined. In phytoplankton studies, dessication of filtered cells has been demonstrated as causing losses in activity as high as 50% of wet values (Wallen and Geen 1968). Love and Robinson (1974) determined losses upon drying of macrophyte material at 105°C and found them

to be negligible (maximum 4.1%) in four submerged macrophyte species. From this data it appears that conversions to dry biomass weight may be applicable in macrophyte studies.

Productivity determined by the ^{14}C method appears to be more sensitive than either biomass or oxygen procedures (Wetzel 1964a). Where plants were growing slowly, the oxygen method produced negative results while the radiocarbon method showed slight carbon fixation. Davies (1968) found sensitivities with the ^{14}C method ranged from 6-31 times that of biomass estimates.

Due to precedents set in phytoplankton research, a number of papers have been published recently concerning the physiology of hydrophytes. The rate of carbon fixation, as in phytoplankton, is affected by respiration and excretion of dissolved organic matter (Wetzel and Hough 1973). The diurnal oxygen technique assumes respiration in the light is equivalent to dark respiration. Photorespirational research indicates the former assumption is in all probability wrong (Wetzel and Hough 1973). Since high O_2 tension in terrestrial plants favours photorespiration, reduced photorespiration may be expected in submerged hydrophytes (Hough and Wetzel 1972). A ^{14}C technique developed by Hough and Wetzel (1972) showed photorespiration occurring in Najas flexilis. Photorespiration was enhanced by high oxygen

levels in the light, but dark respiration was not increased by high oxygen levels. Although more significant in terrestrial studies, photorespiration would no doubt serve to depress production rates obtained in hydrophyte studies, especially over long incubation times.

Excretion of soluble organic compounds in submerged macrophytes has been demonstrated by Wetzel (1969) and Hough and Wetzel (1972). Due to rapid bacterial utilization of the excreted compounds, plants were grown axenically by methods outlined by Wetzel and McGregor (1968). Excretion of soluble organics in relation to nutrient levels present in marl lakes (Wetzel 1966) was low, and probably related to the presence of a high concentration of $CaCO_3$, which reduced cell wall permeability, and may have acted as a "sump" to reduce the availability of organic compounds for metabolic processes. Excretion of organics brings to light, relationships noted between epiphytes and the macrophytes upon which they exist (Prowse 1959). Allen (1971) found dissolved organic compounds excreted by macrophytes may subsequently be used by epiphytes. Interaction between macrophyte and epiphyte are viewed by Wetzel and Hough (1973) as "a symbiotic interaction between community components."

The fate of macrophyte productivity in lakes has been summarized by Pieczyńska (1973) in which five general

observations were made. The fate of macrophyte production may then be summarized briefly as:

1) consumption by grazing
2) decomposition
3) mechanical or faunal destruction
4) excretion of dissolved organic compounds
5) exportation by animals and man.

In reviewing methods for determining the primary productivity of submerged vascular aquatics emphasis has been placed on the three standard techniques employed, and the errors involved with each. Biomass estimates were seen to underestimate production, and frequently to be in direct opposition to results by both oxygen and carbon^{-14}. The carbon^{-14} method was acknowledged to be superior to oxygen in both sensitivity and replication, although corrections should be made for respiration and excretion.

MATERIALS AND METHODS

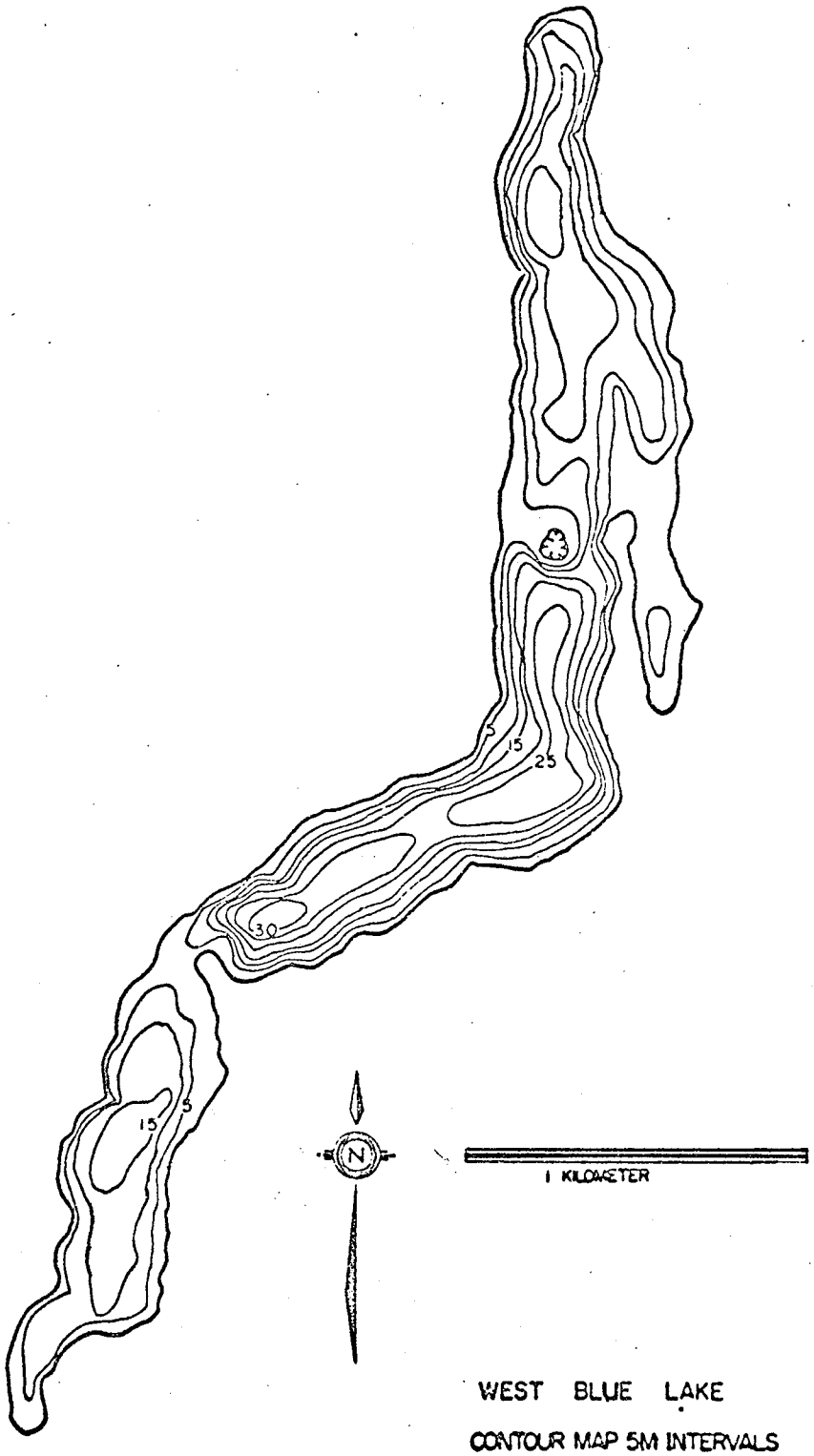
1. Description of West Blue Lake

West Blue Lake (Figure 1) is located in the Duck Mountain Provincial Park, Manitoba, approximately 480 kilometers north-west of Winnipeg, at an altitude of 670 meters. The lake is composed of three main basins, the remnants of a meltwater channel which was reoccupied by ice and drift (Ward and Robinson 1974). Reoccupation and subsequent melting resulted in the formation of a multibasin "channel lake", a variant kettle type.

The northern basin has a maximum depth of 20 meters, the central basin a maximum depth of 31 meters, and the southern basin a maximum depth of 18 meters. The mean depth is 11.3 meters and the total area 160 hectares (Bell and Ward 1970). The lake is 4.8 kilometers long, 0.52 kilometers at its widest point, and has a shoreline developement of 2.87. The lake is ideal for the study of trophic interactions because for all intents and purposes it represents a closed ecosystem. There are no outlet streams and two temporary inlet streams carry only spring runoff to the lake.

The littoral of West Blue Lake is populated by five macrophyte species of numerical significance, namely: Chara vulgaris L. (Wood 1967), Potamogeton Richardsonii (Benn.) Rydb., Potamogeton pectinatus L.,

Figure 1: Bathymetric map of West Blue Lake, Manitoba.



WEST BLUE LAKE

CONTOUR MAP 5M INTERVALS

Myriophyllum alterniflorum DC. and Megalodonta Beckii (Torr.) (Fassett 1940). Few emersed species are present and emergents limited to a small marsh at the north end of the lake.

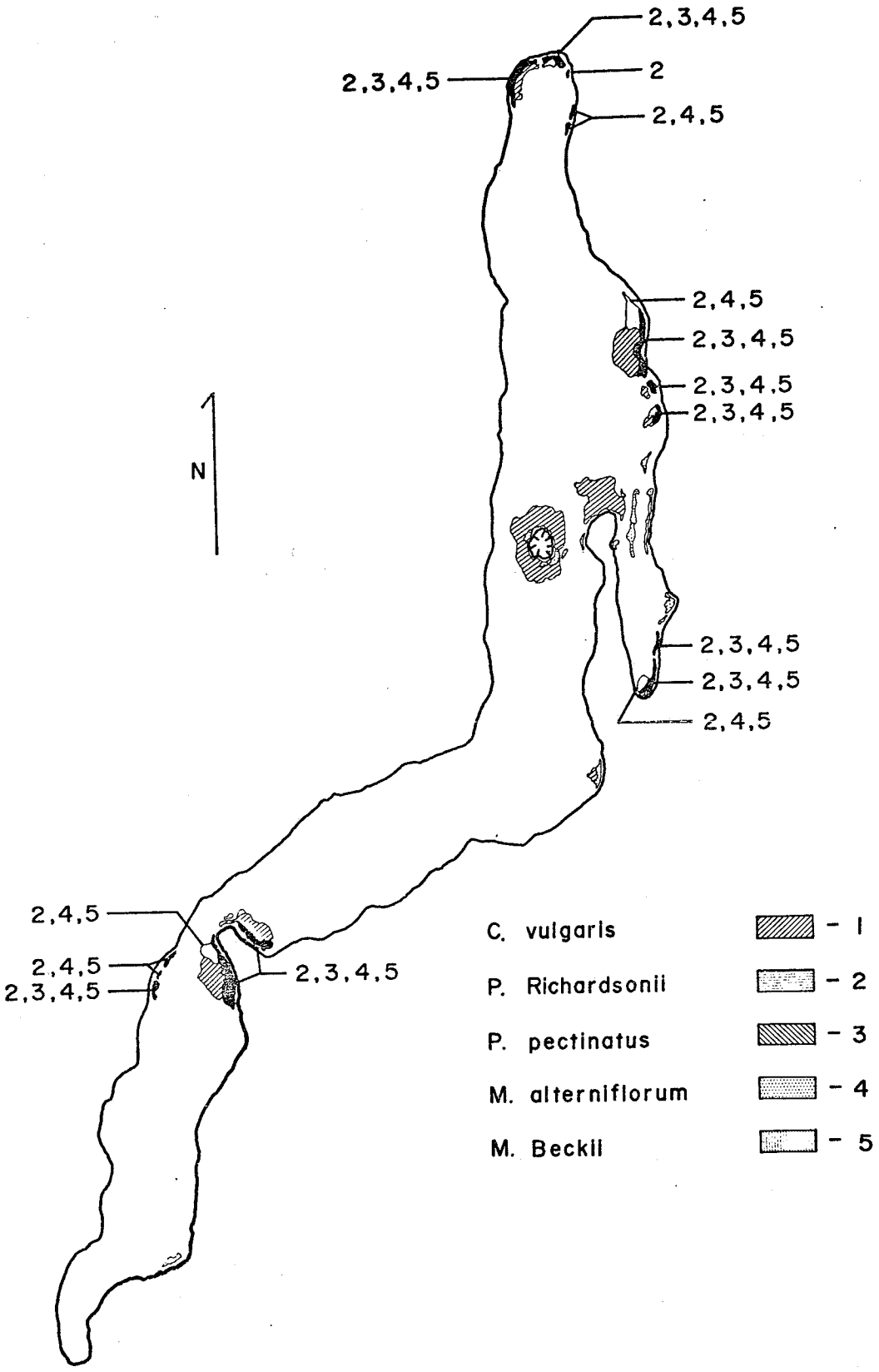
2. Mapping Procedure

Mapping of macrophyte beds was conducted throughout the summer of 1973 and followed the patterm suggested by Westlake (1969). Outer and inner limits of the vegatation were marked with buoys. If the vegetation extended to shore, the shoreline was marked with stakes. Distances between buoys were recorded. Pure stands of individual macrophyte species were marked off seperately. The area of the beds was then determined by planimetry (Figure 2).

3. Biomass Determination

Two stations were subjectively selected for sampling. Samples were collected along transects through the littorial zone, perpendicular to the shoreline. During each sampling period replicate samples were collected both randomly and at one meter depth intervals over the extent of the beds. Knowing the length of the bed, random samples were obtained along a line marked at one meter intervals and held at the lake bottom with weights. Random numbers were selected from a table of

Figure 2: Distributional map of the 5 predominant macrophyte species in West Blue Lake, Manitoba.


2,3,4,5
2,3,4,5
2
2,4,5
2,4,5
2,3,4,5
2,3,4,5
2,3,4,5
N
2,3,4,5
2,3,4,5
2,4,5
2,4,5
2,4,5
2,3,4,5
C. vulgaris - 1
P. Richardsonii - 2
P. pectinatus - 3
M. alterniflorum - 4
M. Beckii - 5

random numbers (Snedecor and Cochran 1967). A 1/16 m^2 hinged wooden frame, weighted to greater than neutral density with strips of iron bolted to the sides, was lowered into the vegetation and assembled underwater. All plants occurring within the frame, including roots and rhizomes, were removed by hand. A wet-suit and snorkel facilitated sampling at all depths. Sampling at two stations was based on the assumption that the spatial distribution of macrophytes is non-random, being related to a number of environmental parameters. It was hoped that the areas sampled would minimize environmental effects and provide a better indication of actual distribution than would be afforded by one specific site. Quadrat samples were placed in previously labelled polyethelene bags and taken to the laboratory for analysis.

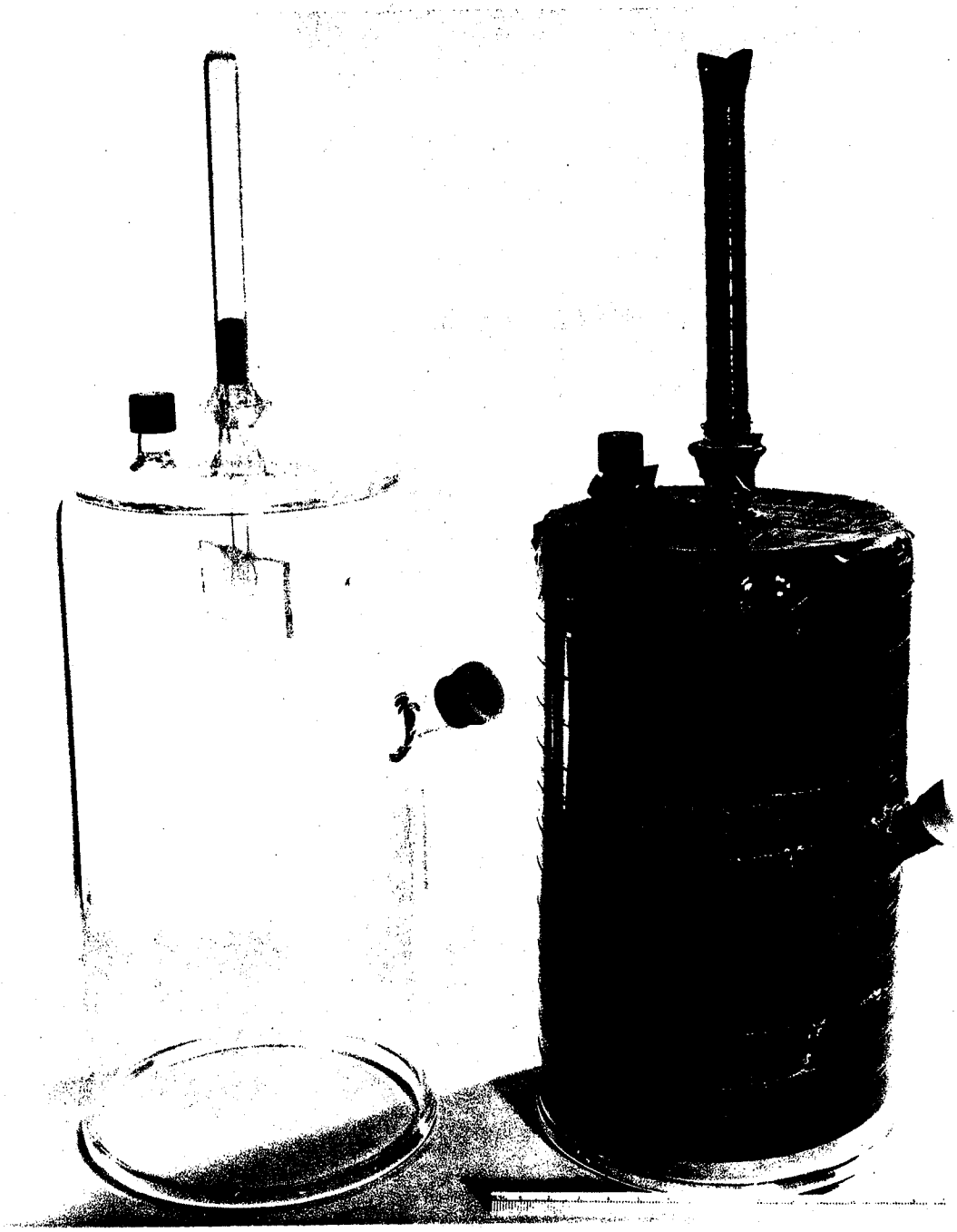
In the laboratory plants were sorted by species and washed under cold running water over a 0.5 mm mesh screen, to remove attached sediment and epiphytes. Plants were blotted for 10 seconds on absorbent paper and their fresh weight determined. All material was dried to constant weight in a drying oven at 105°C and weighed. Triplicate subsamples were ashed at 550°C in a muffle furnace, and a mean weight acquired. The differnce between dry and ash weights constituted the ash-free organic weight. The mean percentage organic weight was

used to calculate the total organic weight of each species in the sample.

4. ^{14}C uptake experiments

The uptake of ^{14}C as $NaH^{14}CO_3$ was studied in four of the five predominant macrophyte species in West Blue Lake. All species previously stated were examined with the exception of Chara vulgaris. Samples, as in biomass estimations, were taken randomly and at one meter depth intervals throughout the macrophyte bed. Glass chambers (Figure 3), a modification of those designed by Wetzel (1964a), were used for the incubation of plants. Chambers ranged in volume from 0.5 liters to 3.0 liters. A small bakelite screw cap situated at the top of each chamber allowed for expulsion of air while the chambers were being placed over the vegetation. In order to distribute the $NaH^{14}CO_3$ homogeneously within the chambers, a clear plexiglass stirring rod extended into each chamber from a glass ball and socket joint. A small lateral port capped with a serum bottle stopper was placed approximately 2/3rds of the way up the chamber and served for the introduction of ^{14}C. The lateral port was placed at an angle of approximately 20° to facilitate introduction of a hypodermic syringe, After gentle stirring with the plexiglass propellor the plants were incubated for a four hour midday period (10:00 - 14:00). Following incubation, the entire contents of the chamber were

Figure 3: Light and opaque glass incubation chambers.



removed from the substratum by cutting the sediment at the base of the flask with a galvanized steel plate. Sediment trapped in the bottom of the chamber acted as a plug while the apparatus was raised to the water surface. Sediment and labelled lake water were emptied into a plastic waste container for later disposal. Plants were placed in darkened plastic bags and returned to the laboratory where they were washed under cold running water to remove sediment and epiphytes. Individual plants were placed in plastic bags and frozen for later analysis.

Plants were later thawed, blotted, and exposed to the fumes of concentrated HCl for 10 minutes to remove any ^{14}C precipitated as monocarbonates (Wetzel 1965). Plants were dried at 105°C for 24 hours and cooled to room temperature over dessicant. The material was ground in a mortar and pestle to pass through the mesh of a #60 (250 μ diameter) sieve. ^{14}C uptake was determined from dry combustion of subsamples of the powder. Carbon uptake was calculated as productivity (Strickland and Parsons 1968). Initial results were expressed as mg C mg dry weight^{-1} 4 hours^{-1}, and subsequently converted to productivity per unit area (m^2) from biomass distributional data. Incoming solar radiation was measured with a recording pyrheliometer, and conversion to full-day photosynthesis calculated by multiplying results by a factor of the ratio of total incident radiation to radia-

tion received during the incubation period. The area of the macrophyte beds, distribution data, and total lake area were used to express final results as mg C m^{-2} lake surface.

The procedure used for the combustion of plant material was a modification of Gupta (1966). For each plant, 5 subsamples of 2-10 mg dry weight were placed into small silicon treated lens paper cups. Each cup was equipped with a blackened heat absorbing flag. Cups were supported on tungsten wire stands and placed into a 25 ml glass scintillation vial. Each vial was flushed with oxygen for 15 seconds then sealed with a serum bottle stopper. Cup and plant material in each vial were ignited by a beam of light from a 150 W, 120 V projection bulb, focussed by a concavo-convex lens onto the blackened flag. The vials were allowed to cool prior to the introduction of 1 ml of NCS (Nuclear Chicago) solubilizing agent through the serum cap. A 30 minute period was permitted for the absorption of CO_2 by the NCS, after which 10 ml of a toluene based fluor (Ward et al 1970) was introduced. Vials were allowed to stand one hour to exclude possible chemo-luminescence by the NCS. Specific activity of samples was determined in a scintillation counter (Picker Liquimat 220). All counts were adjusted to a preset statistic of $1.5 \pm 2\sigma$. Counting efficiency, determined by the channels ratio method

(Wang and Willis 1968), was approximately 75% for all samples.

Efficiency of recovery of ^{14}C by the above combustion procedure was calibrated by the addition of 5 aliquots of 0.5 μCi/ml ^{14}C glucose to 10 cellulose acetate discs. Five discs were combusted by the above procedure while 5 discs were added directly to a dioxane based fluor (Bray 1960). This procedure necessitated the preparation of two quench curves, one for the toluene based fluor and one for the dioxane-based fluor. Activity was determined in a scintillation counter, by methods stated previously. Counts from vials containing discs added directly to the dioxane-based fluor were taken as a theoretical 100% activity. Comparison of the activity recovered from combustion to the theoretically added activity, as determined by direct counts, provided a measure of efficiency. The efficiency was determined to be 84 ± 3%.

Since activity losses for phytoplankton can be extremely high upon drying (Wallen and Geen 1968), an experiment was designed to measure activity lost upon drying of the four macrophyte species, employing ^{14}C as a tracer. Individual plants were incubated in situ using the same experimental design stated previously. In all cases, experiments were conducted at a depth of 2 meters on July 31, 1973.

For each species, the plants were ground to a slurry in a mortar and pestle. Ten subsamples ranging from 2 - 10 mg fresh weight (blotted 10 seconds on absorbent paper) were removed for combustion. Half the subsamples were immediately combusted and one half oven dried at 105°C for 24 hours before combustion.

5. Carbon analysis

Analysis of carbon content per unit of ash-free organic weight was determined for all species. Plant material was removed from the substratum, washed, oven dried at 105°C for 24 hours, and stored over dessicant until cool. Individual plants were ground in a mortar and pestle to pass through a #60 (250 micron diameter) sieve. Replicate subsamples ranging from 0.5 to 1 mg were placed in small aluminum containers and weighed on a Cahn Gram Electrobalance. Aluminum boats and plant material were combusted at 700°C and carbon content analyzed in gas phase. Percent carbon per milligram dry weight was used to convert biomass data to gm carbon m^{-2}.

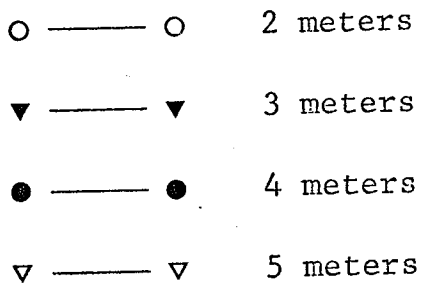
RESULTS

1. Biomass production

Productivity estimates from biomass increments were compared in the random and summed transect procedures. The summed transect method, as employed in this study, allowed for the comparison of productivities at different depths (Figures 4,5,6,7 and 8). The disparity between optimal and minimal depths for photosynthesis is apparent, and for all species studied there was a tendency towards decreasing productivity with increasing depth. Only P. Richardsonii and M. alterniflorum appeared at all depths examined, and for both species the optimal depth for photosynthesis was 2 meters. Productivity at 1 meter declined appreciably in both species to values approximating those at 3 and 4 meters. M. Beckii did not appear at 1 meter and C. vulgaris did not occur at depths less than 1.5 meters nor greater than 5.5 meters. P. pectinatus appeared to be the only species to adapt to the higher light intensities at a depth of 1 meter. This species grew sparsely at 2 meters and was not apparent at other depths.

With increased light attenuation at 3 and 4 meters, the initial productivity at these depths would be expected to be lower than at 2 meters, and perhaps the point of maximum productivity delayed. M. alterniflorum

Figure 4: Seasonal productivity of Chara vulgaris at 4 depths in West Blue Lake, Manitoba, as determined from changes in biomass.



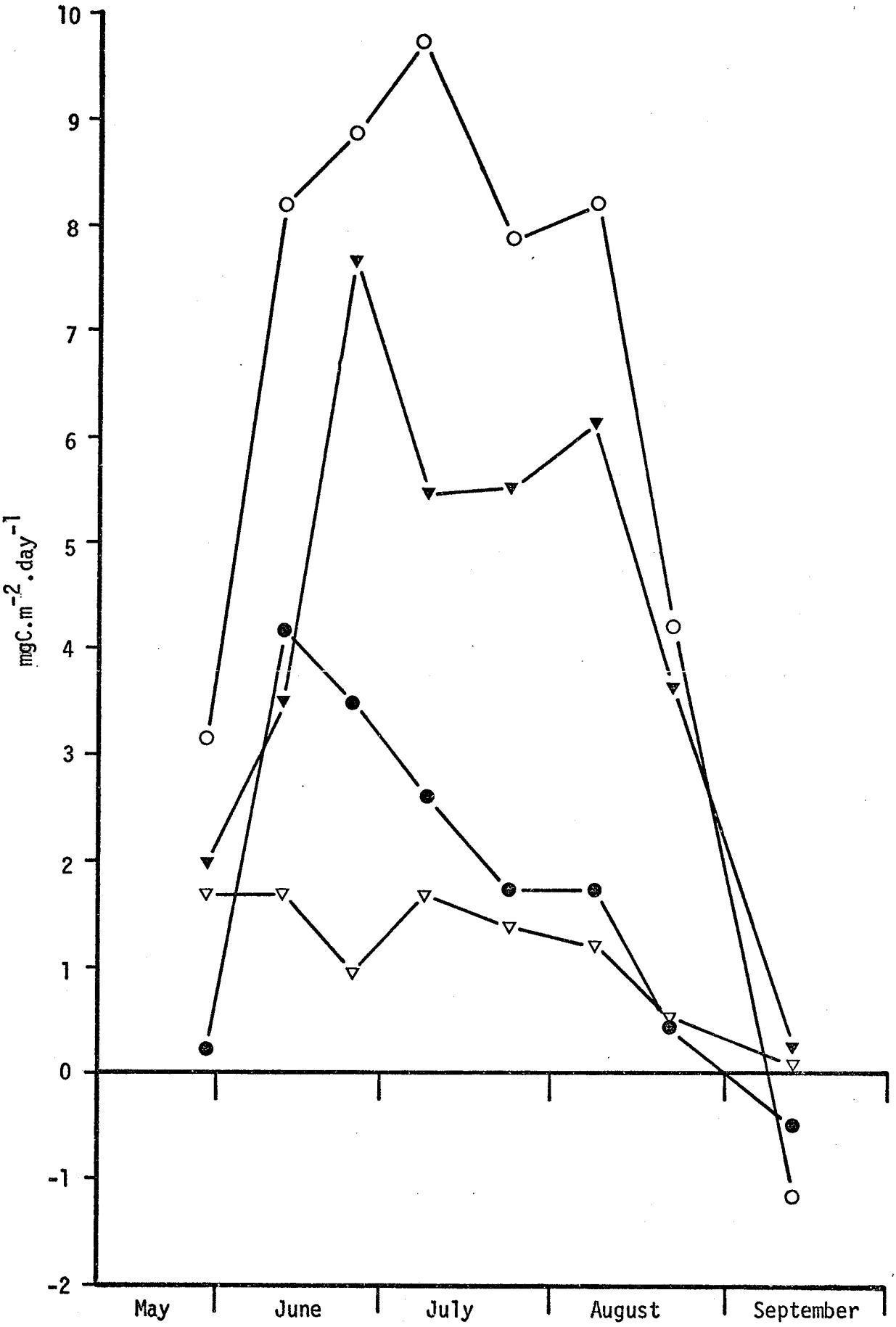
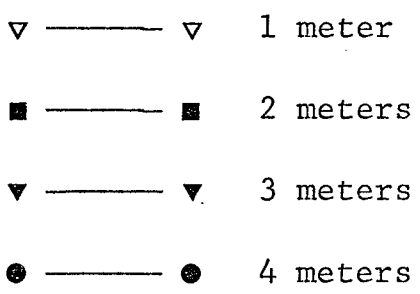

10
9
8
7
6
5
4
3
2
1
0
-1
-2
mgC.m-2.day-1
May
June
July
August
September

Figure 5: Seasonal productivity of Potamogeton Richardsonii at 4 depths in West Blue Lake, Manitoba, as determined from changes in biomass.



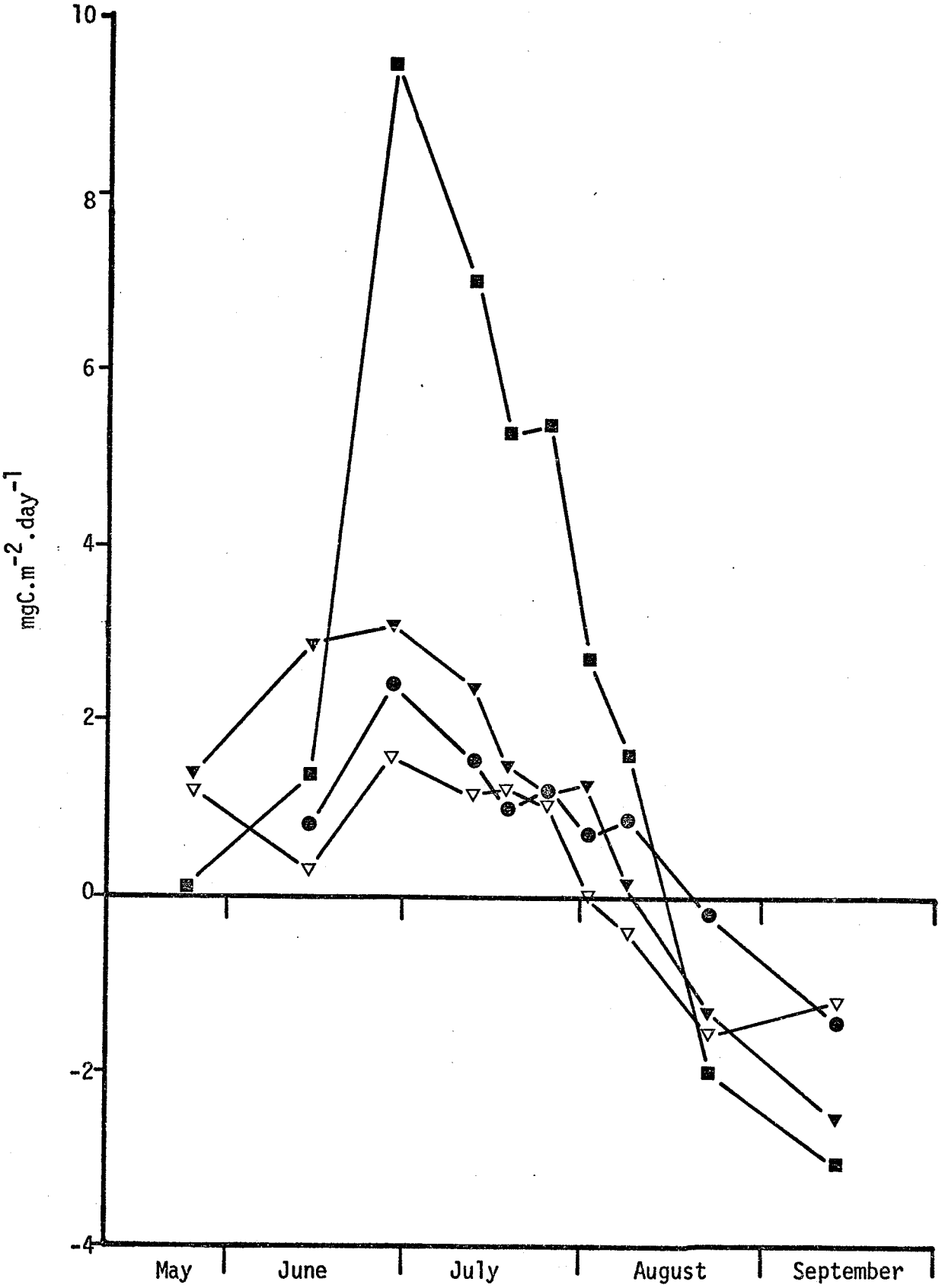

10
8
6
4
2
0
-2
-4
mgC.m-2.day-1
May
June
July
August
September

Figure 6: Seasonal productivity of Potamogeton pectinatus at 2 depths in West Blue Lake, Manitoba, as determined from changes in biomass.

▽ ——— ▽ 1 meter

▼ ——— ▼ 2 meters

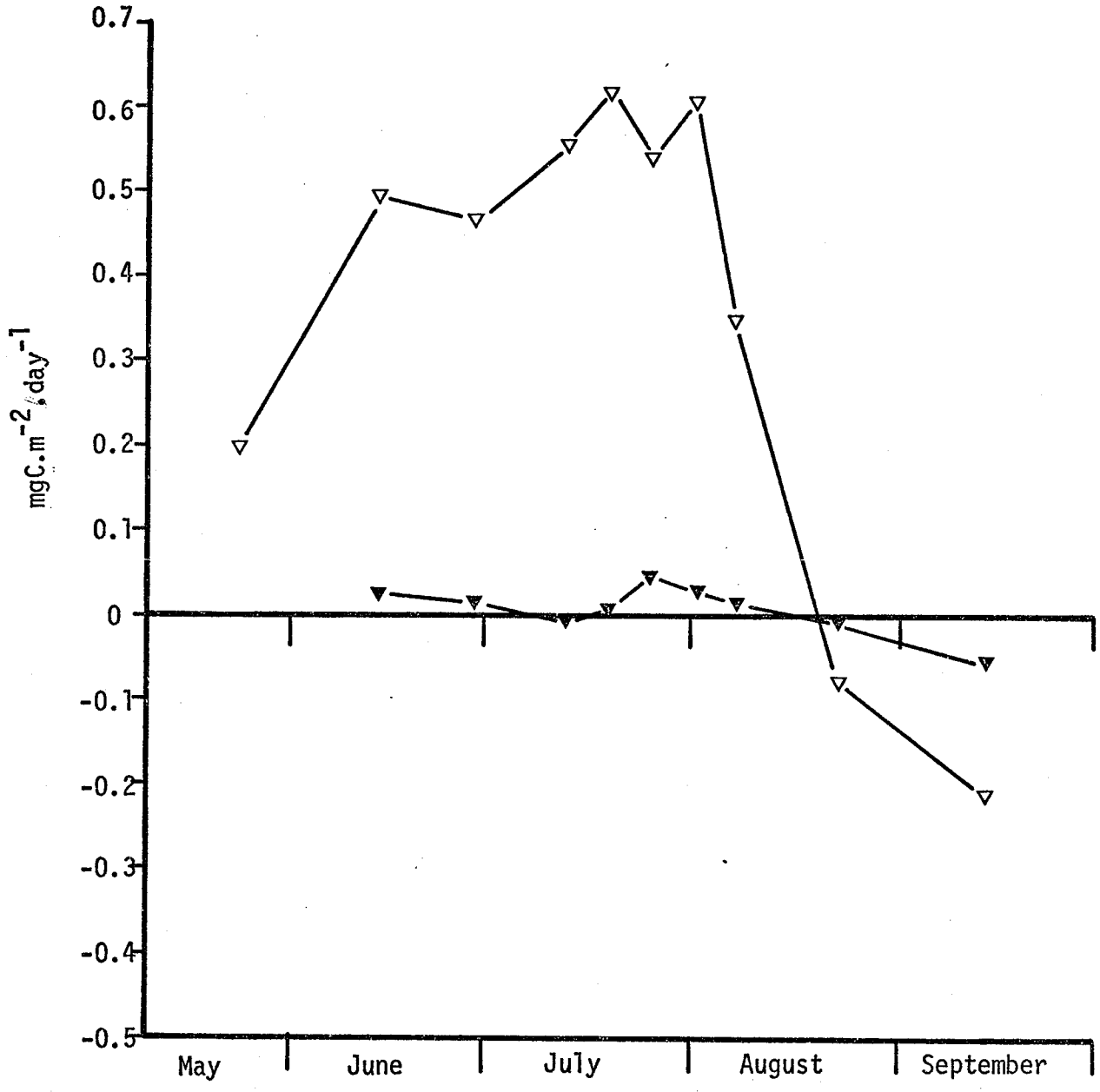

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
mgC.m-2.day-1
May
June
July
August
September

Figure 7: Seasonal productivity of Myriophyllum alterniflorum at 4 depths in West Blue Lake, Manitoba, as determined from changes in biomass.

■ ——— ■ 1 meter

○ ——— ○ 2 meters

▽ ——— ▽ 3 meters

□ ——— □ 4 meters

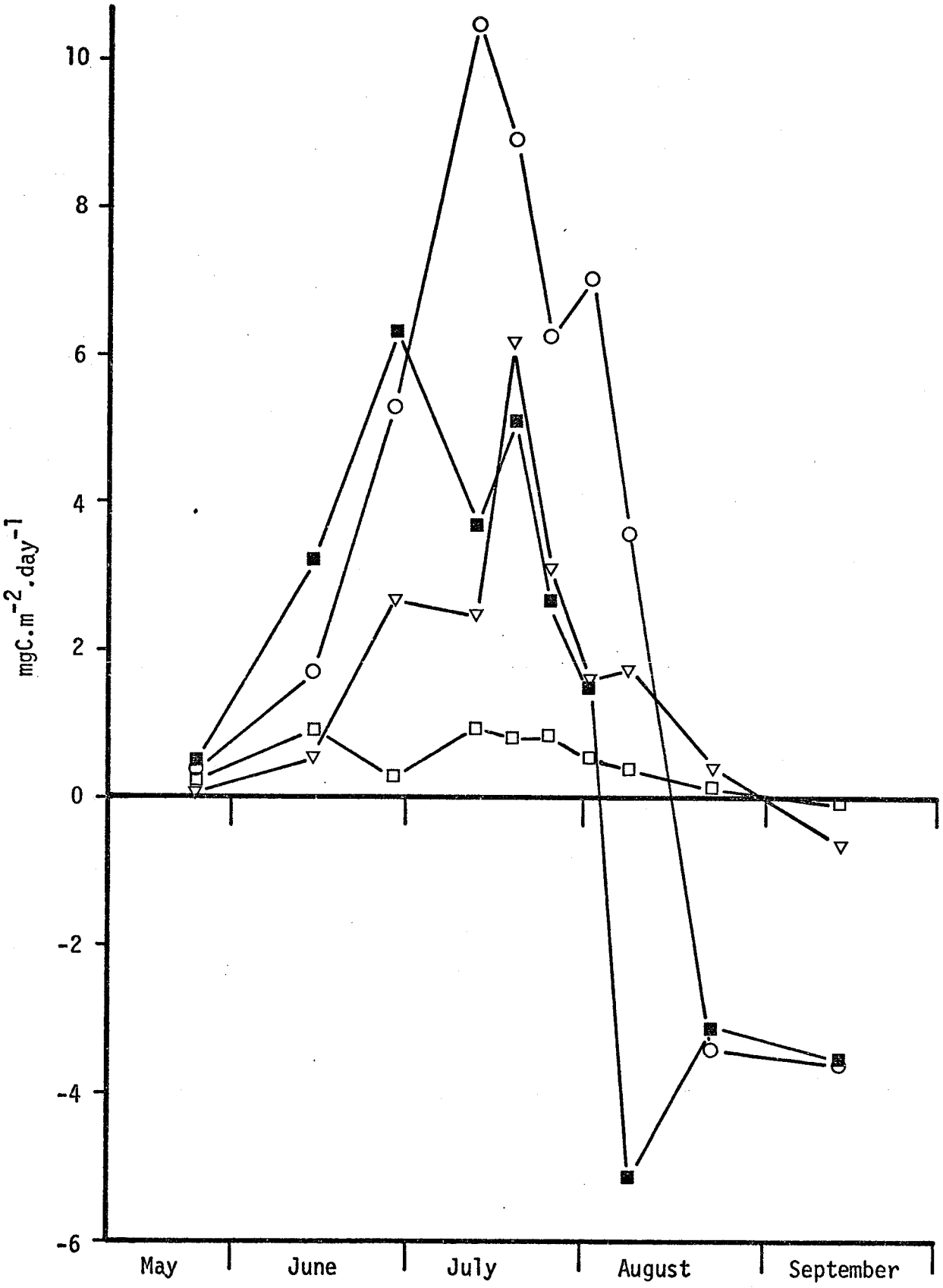
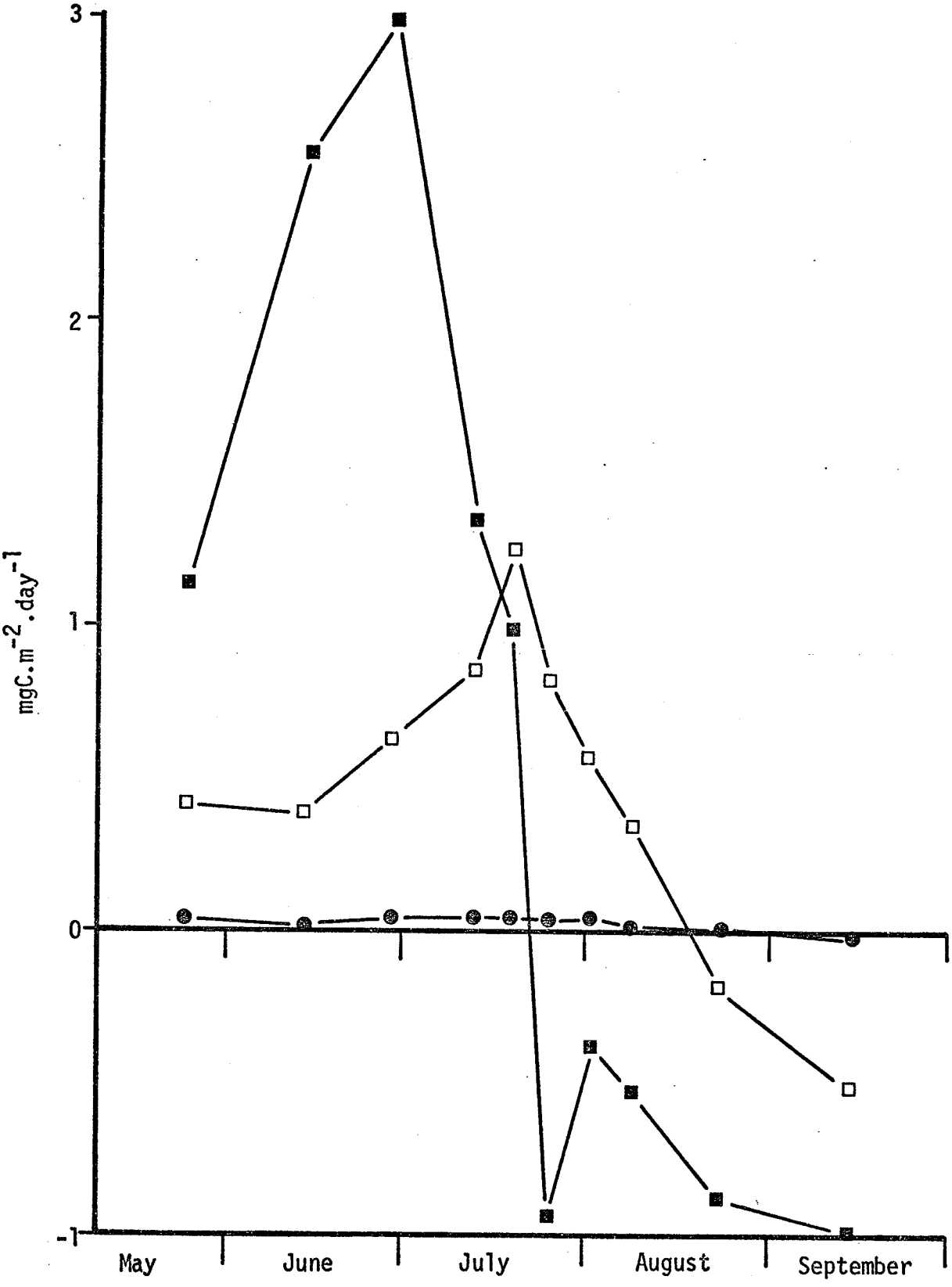

10
8
6
4
2
0
-2
-4
-6
mgC.m-2.day-1
May
June
July
August
September

Figure 8: Seasonal productivity of Megalodonta Beckii at 3 depths in West Blue Lake, Manitoba, as determined from changes in biomass.

■ ——— ■ 2 meters

□ ——— □ 3 meters

● ——— ● 4 meters


3
2
1
0
-1
mgC.m-2.day-1
May
June
July
August
September

and M. Beckii followed this pattern, but initial productivities were higher at greater depths for P. Richardsonii, and for both C. vulgaris and P. Richardsonii times of maximum production occurred earlier at 3 and 4 meters. If the times of peak production are derived from the mean of the summed transects, the following results are obtained; C. vulgaris, June 27; M. Beckii, June 28; P. Richardsonii, June 28; M. alterniflorum, July 25; P. pectinatus, August 1.

The productivity curves from random and summed transect samples are illustrated for all species in Figures 9, 10, 11, 12 and 13. Maximum productivities again occurred between June and August. Although random sample values for P. pectinatus are shown (Figure 11), these values are undoubtedly not indicative of its true growth pattern. The negative productivities that occurred at four seperate sampling dates are a reflection of the sampling process involved. The majority of P. pectinatus biomass was located at 1 meter. At any sampling period random numbers were generated over the entire length of the bed, irrespective of depth. When the number of samples from 1 meter was low on a given date, or when the number of samples taken at a sparsely populated depth was high, the resulting productivity was negative. Subsequently values from the following sampling period were overestimated. Although productivities were high at 2 meters

Figure 9: Comparison of the productivities of Chara vulgaris in West Blue Lake, Manitoba, as determined from changes in biomass by the summed transect and random sampling methods.

o ——— o Summed transect

● ——— ● Random

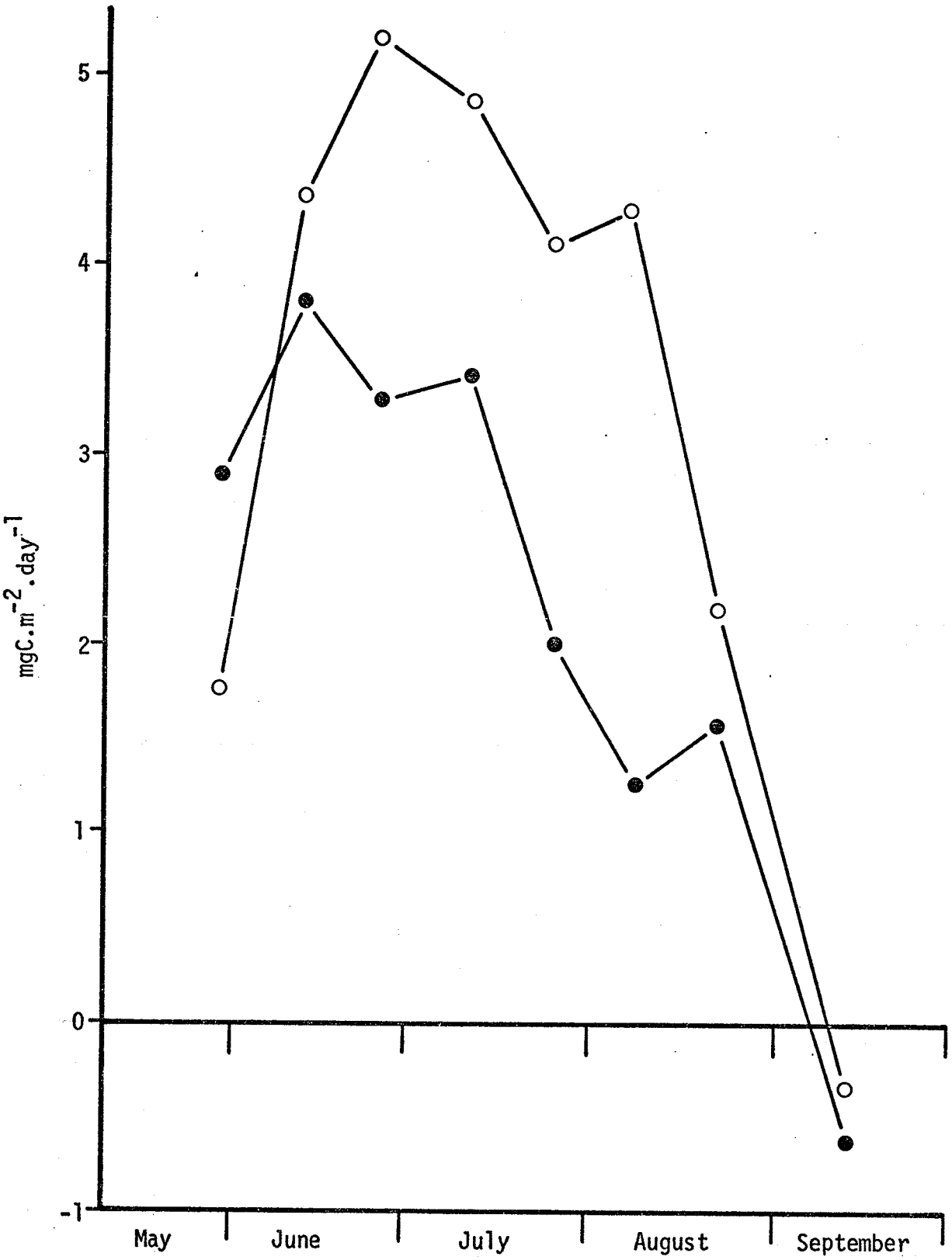

5
4
3
2
1
0
-1
mgC.m-2.day-1
May
June
July
August
September

Figure 10: Comparison of productivities of Potamogeton Richardsonii in West Blue Lake, Manitoba, as determined from changes in biomass by summed transect and random sampling methods.

■ ——— ■ Summed transect

□ ——— □ Random

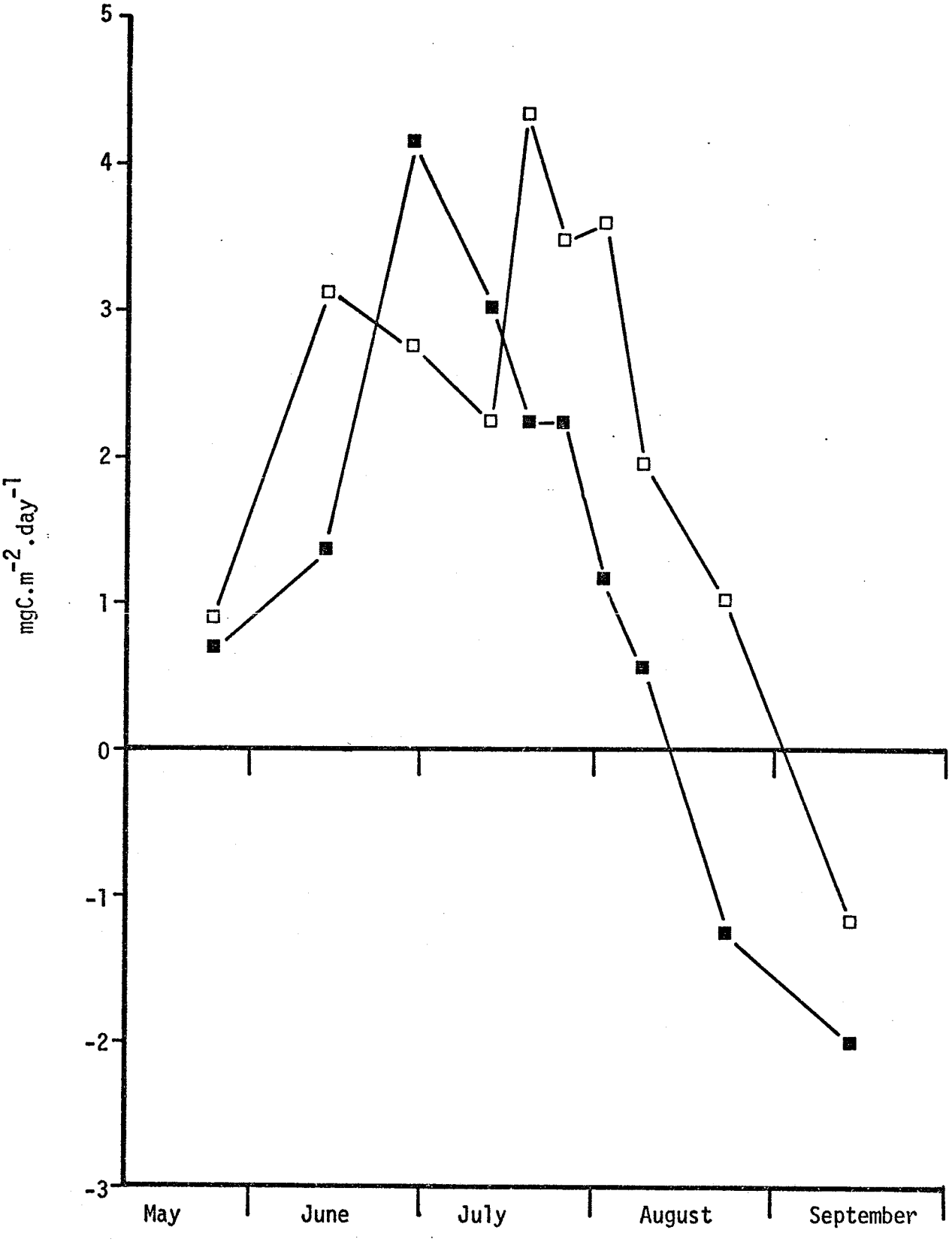

5
4
3
2
1
0
-1
-2
-3
mgC.m-2.day-1
May
June
July
August
September

Figure 11: Comparison of productivities of Potamogeton pectinatus in West Blue Lake, Manitoba, as determined from changes in biomass by summed transect and random sampling methods.

▼ ——— ▼ Summed transect

▽ ——— ▽ Random

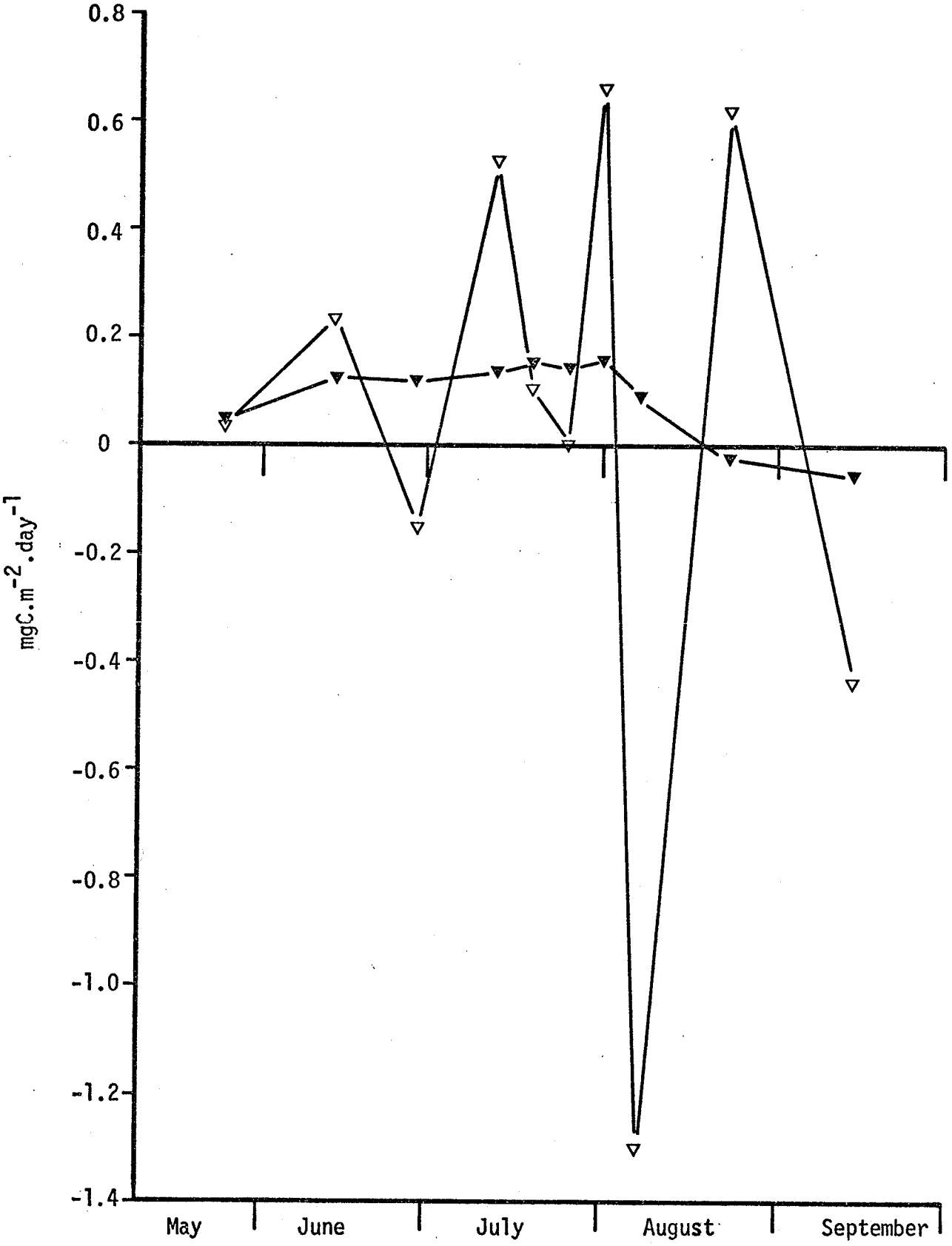

0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
mgC.m-2.day-1
May
June
July
August
September

Figure 12: Comparison of the productivities of Myiophyllum alterniflorum in West Blue Lake, Manitoba, as determined from changes in biomass by summed transect and ramdom sampling methods.

■ ——— ■ Summed transect

□ ——— □ Random

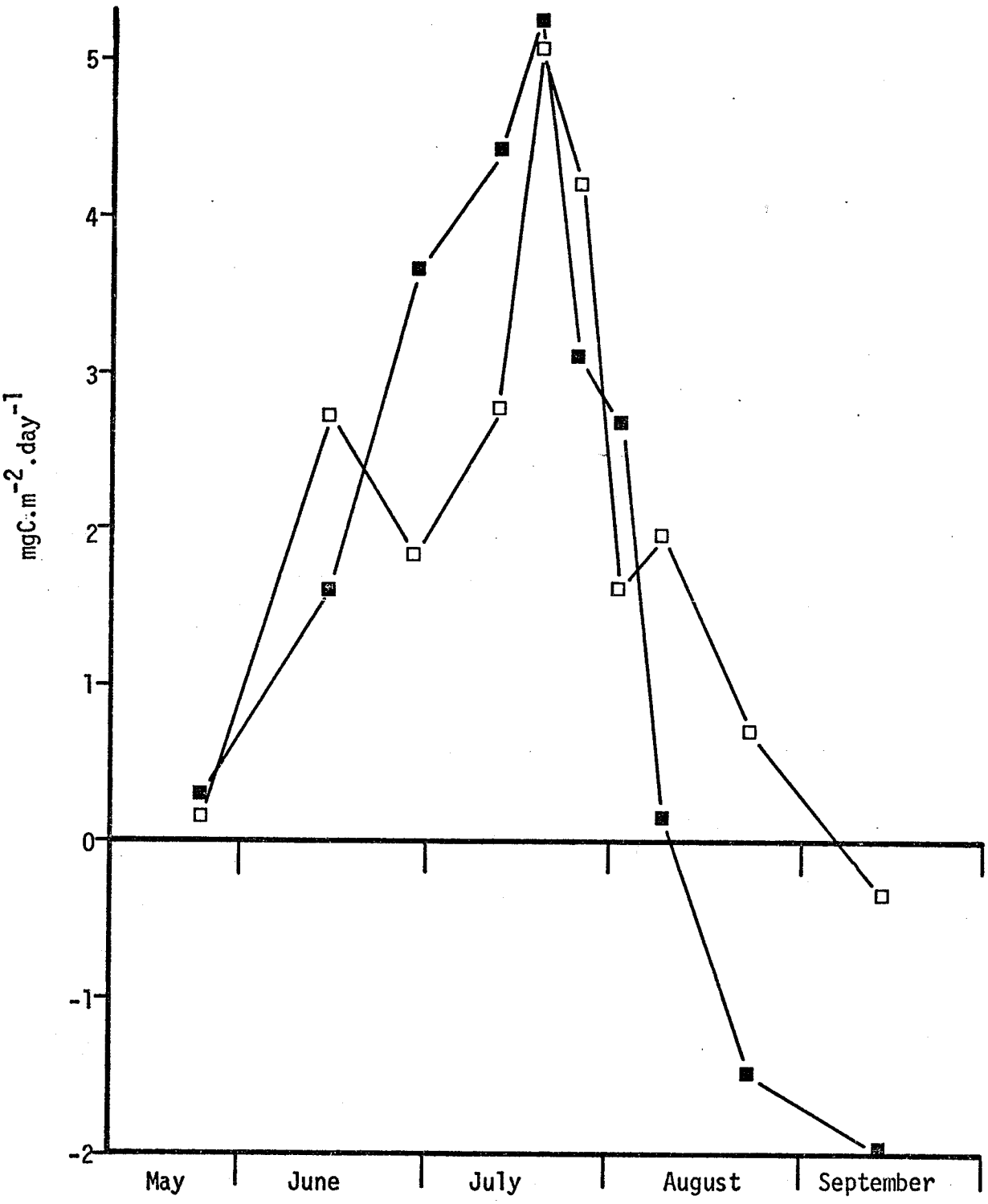
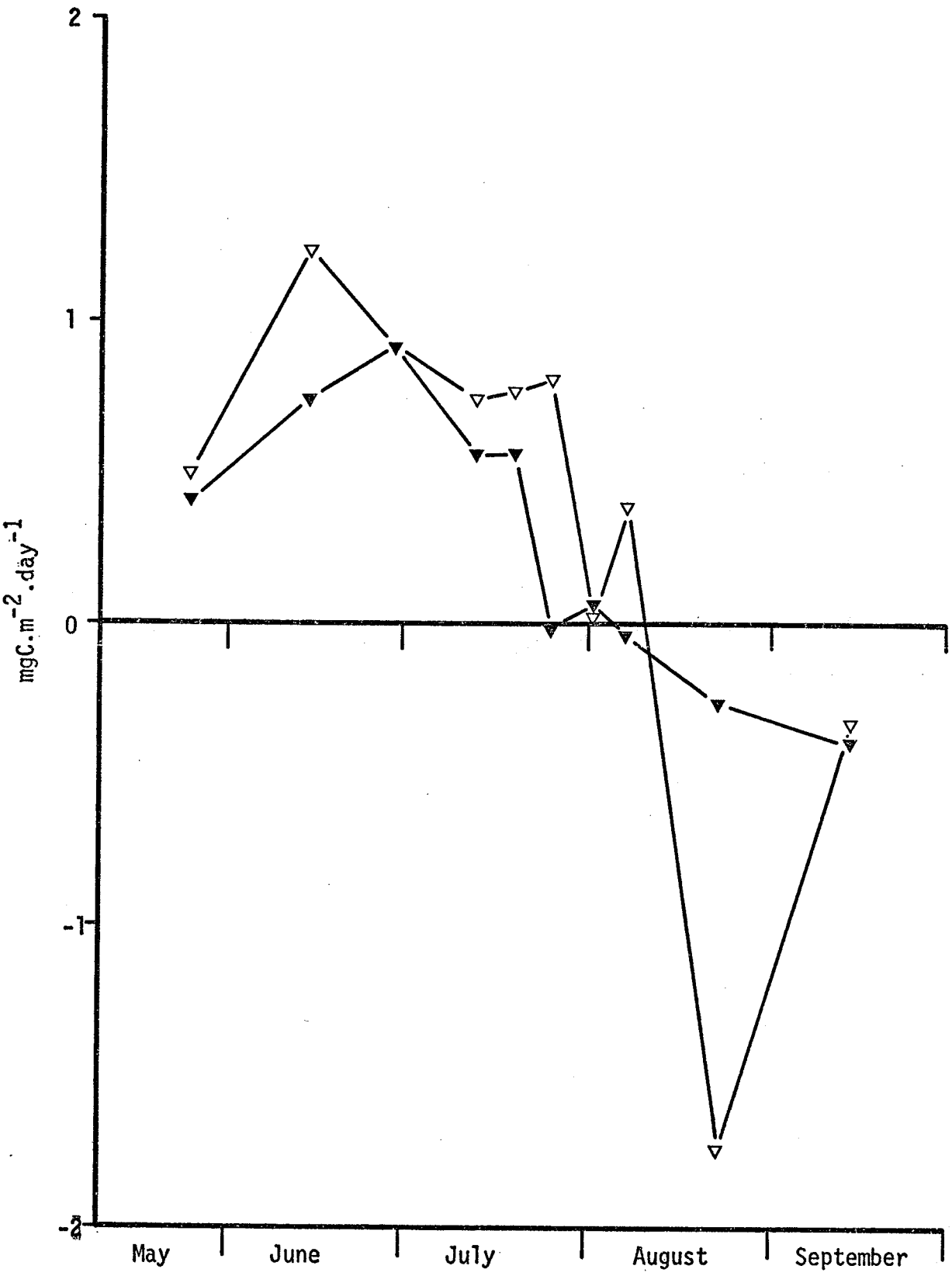

5
4
3
2
1
0
-1
-2
mgC.m-2.day-1
May
June
July
August
September

Figure 13: Comparison of the productivities of Megalodonta Beckii in West Blue Lake, Manitoba, as determined from changes in biomass by summed transect and random sampling methods.

▼ ——— ▼ Summed transect

▽ ——— ▽ Random


2
1
0
-1
-2
mgC.m^{-2}.day^{-1}
May
June
July
August
September

for all species except P. pectinatus (1 m), similar results were obtained for random and mean transect values. P. pectinatus was the exception, where random values oscillated from positive to negative (Figure 11).

A comparison of the means of summed transects (Figure 14) indicates the majority of macrophyte production in West Blue Lake was attributable to 3 species, C. vulgaris, P. Richardsonii, and M. alterniflorum. Similar results were detected from random sampling (Figure 15). Figure 15 also illustrates major and minor production peaks in four of the five species studied. When all species were taken into account (Figure 16), minor and major peaks were discernable in June and July respectively. A single maximum appeared on June 28th when employing the summed transect method.

The sum of the productivities of all species equals the total macrophyte carbon production for West Blue Lake at any given time. Since C. vulgaris was sampled separately from the angiosperms, interpolations were necessary to acquire total production at any specific date. After all species were totalled, the maximum macrophyte productivity employing the summed transect method was 14.2 mg C m^{-2} day^{-1} on June 28th. With random sampling methods maximum productivity was 12.9 mg C m^{-2} day^{-1} on July 18th, while a minor peak of 11.1 mg C m^{-2} day^{-1} occurred on June 14th.

Figure 14: Comparison of the productivities of 5 macrophyte species in West Blue Lake, Manitoba, as determined from changes in biomass by the summed transect method.

● ——— ● Chara vulgaris

□ ——— □ Potamogeton Richarsonii

■ ——— ■ Potamogeton pectinatus

▼ ——— ▼ Myriophyllum alterniflorum

▽ ——— ▽ Megalodonta Beckii

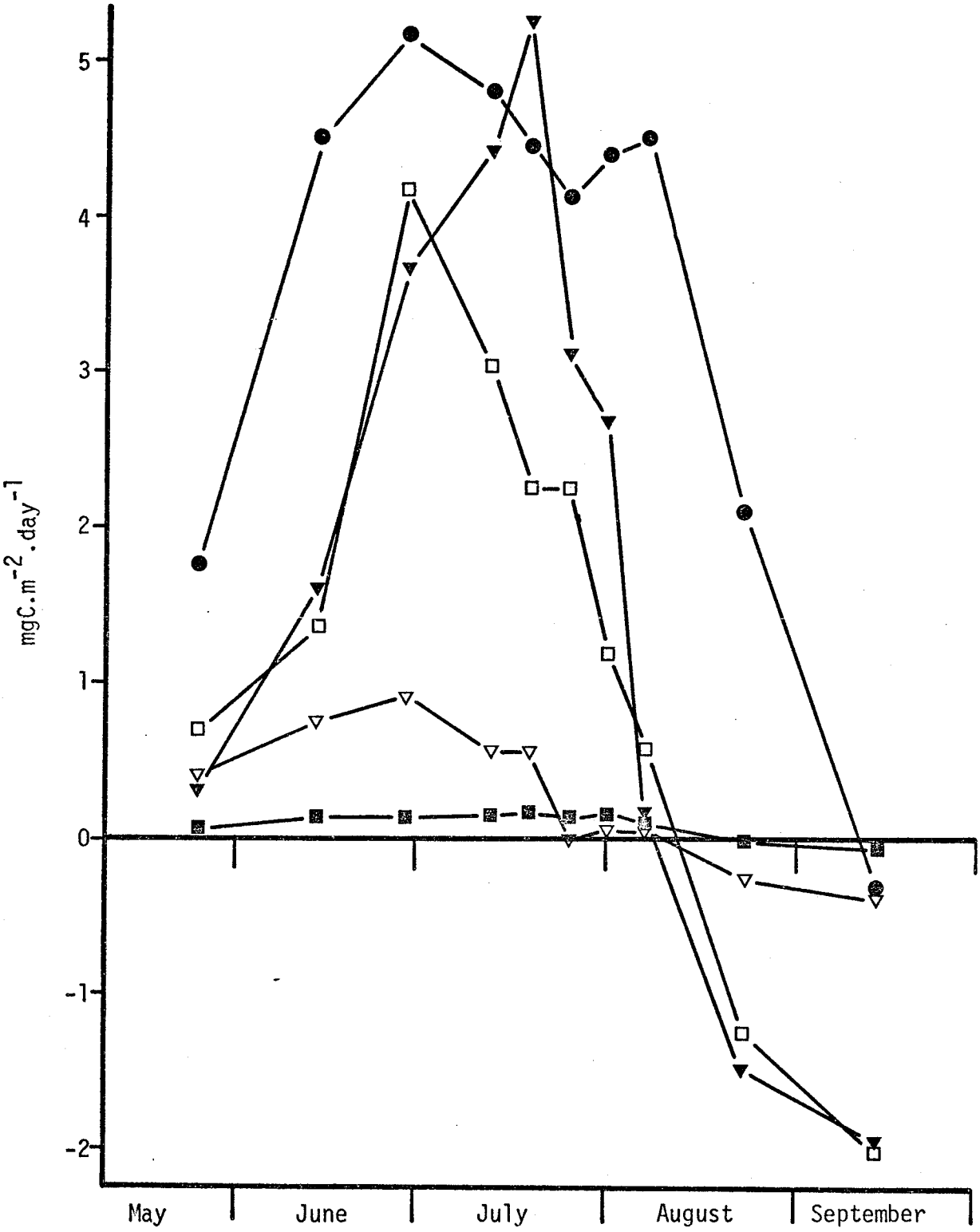

5
4
3
2
1
0
-1
-2
mgC.m-2.day-1
May
June
July
August
September

Figure 15: Comparison of the productivities of 5 macrophyte species in West Blue Lake, Manitoba, as determined from changes in biomass by random sampling methods.

▼ ——— ▼ Chara vulgaris

■ ——— ■ Potamogeton Richardsonii

□ ——— □ Potamogeton pectinatus

● ——— ● Myriophyllum alterniflorum

○ ——— ○ Megalodonta Beckii

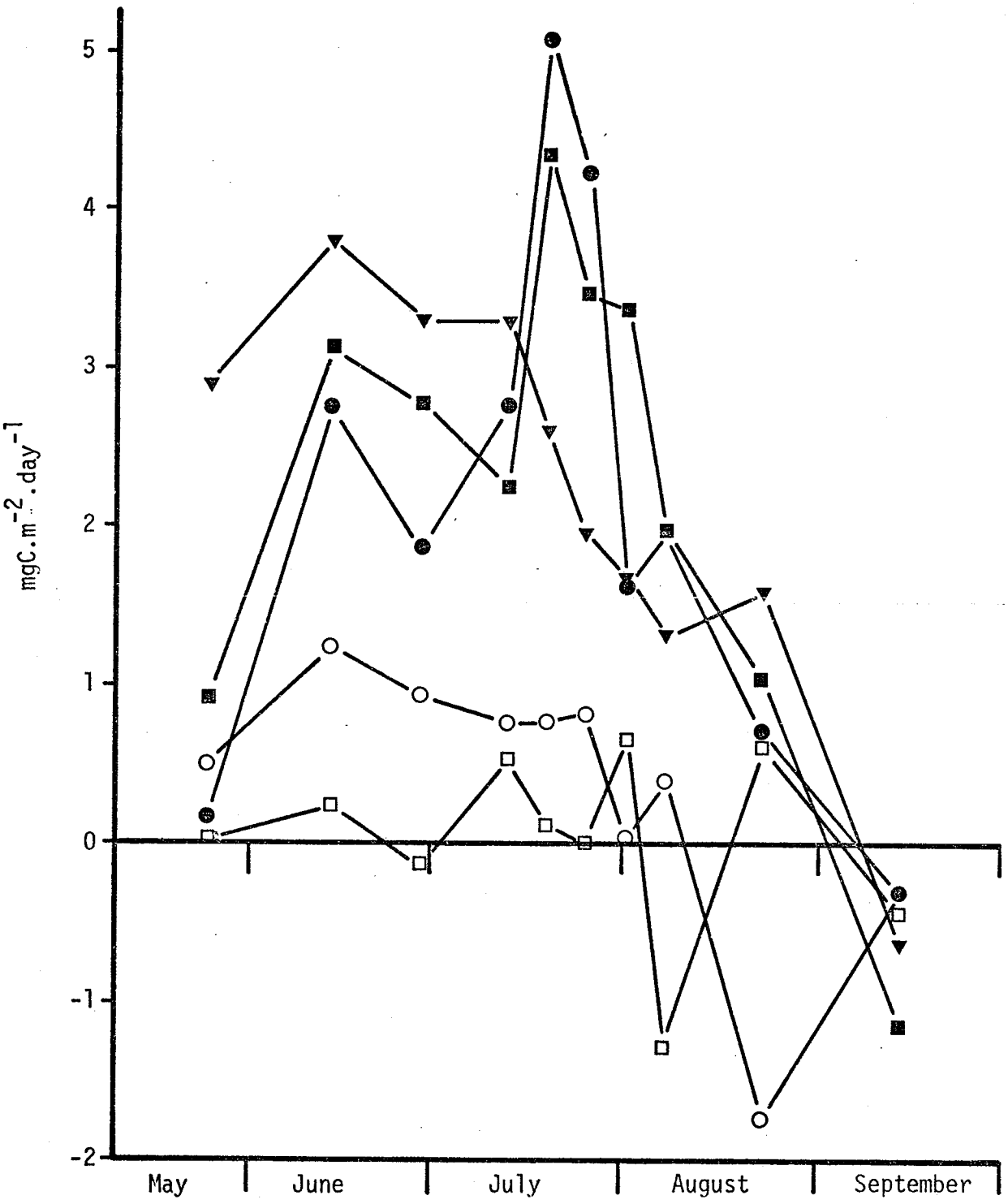
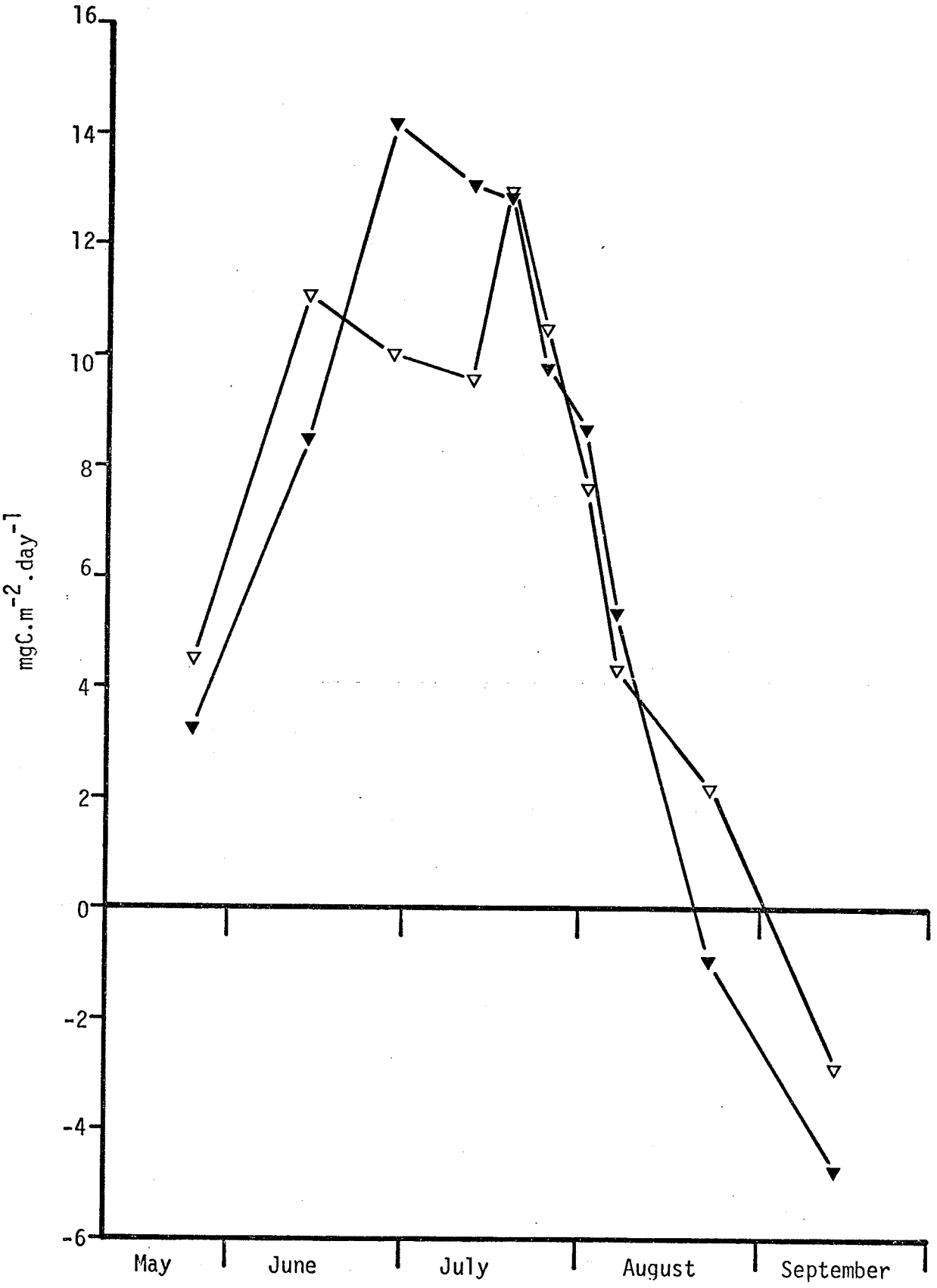

5
4
3
2
1
0
-1
-2
mgC.m^{-2}.day^{-1}
May
June
July
August
September

Figure 16: Comparison of the combined productivities of 5 macrophyte species in West Blue Lake, Manitoba, as determined from changes in biomass by summed transect and ramdom sampling methods.

▼ ——— ▼ Summed transect

▽ ——— ▽ Random


16
14
12
10
8
6
4
2
0
-2
-4
-6
mgC.m-2.day-1
May
June
July
August
September

2. ^{14}C production

The ^{14}C method provided instantaneous measures of photosynthetic carbon fixation. Experiments were conducted weekly, alternating with biomass sampling. C. vulgaris was not included in radiocarbon experiments. The depth distribution of production for all species (Figures 17, 18, 19 and 20) followed a pattern similar to biomass results. Production decreased with respect to depth. With the randomized design, determinations of productivity were reduced to 3 species. P. pectinatus was excluded for reasons previously stated. P. Richardsonii exhibited maximum production on June 20th and July 19th. These maxima were in good agreement with increases noted in biomass sampling although the minor peak in June was much more pronounced in ^{14}C uptake experiments. The production curve of M. alterniflorum (Figure 22) was also comparable in a number of respects to the biomass production curve (Figure 15), in that maximum production occurred in mid July, with 2 minor increases in June and August. Production rates for M. Beckii determined from biomass and ^{14}C techniques (Figures 15 and 22) manifested similar tendencies with maximum production in June followed by a secondary rise in July. However, the July rise occurred later and was less pronounced in biomass sampling.

A comparison of the means of summed transects

Figure 17: Seasonal productivity of Potamogeton Richardsonii at 4 depths in West Blue Lake, Manitoba, as determined from ^{14}C uptake.

▼ ——— ▼ 1 meter

○ ——— ○ 2 meters

■ ——— ■ 3 meters

● ——— ● 4 meters

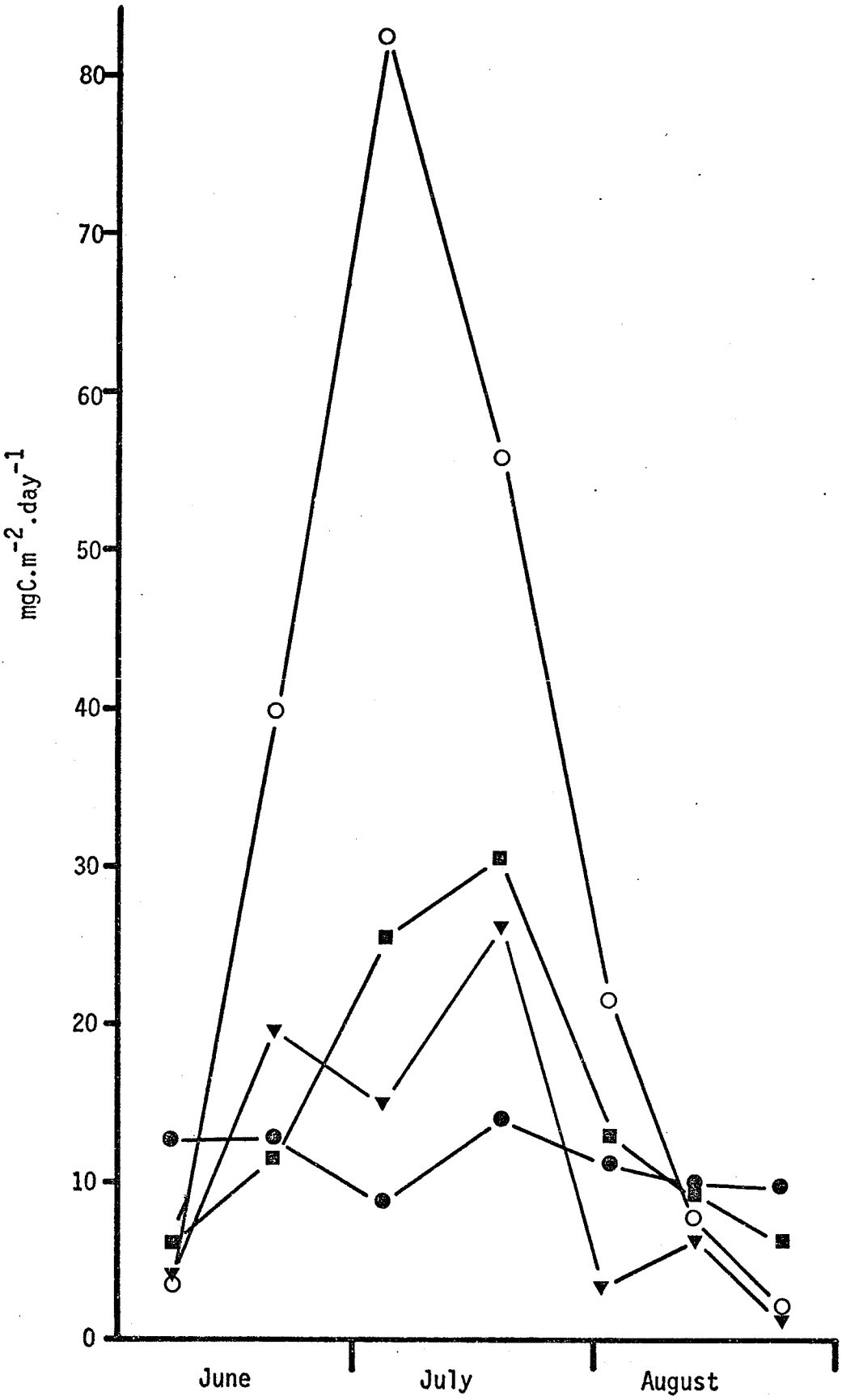

80
70
60
50
40
30
20
10
0
mgC.m^{-2}.day^{-1}
June
July
August

Figure 18: Seasonal productivity of Potamogeton pectinatus at 2 depths in West Blue Lake, Manitoba, as determined from ^{14}C uptake.

▼ ——— ▼ 1 meter

▽ ——— ▽ 2 meters

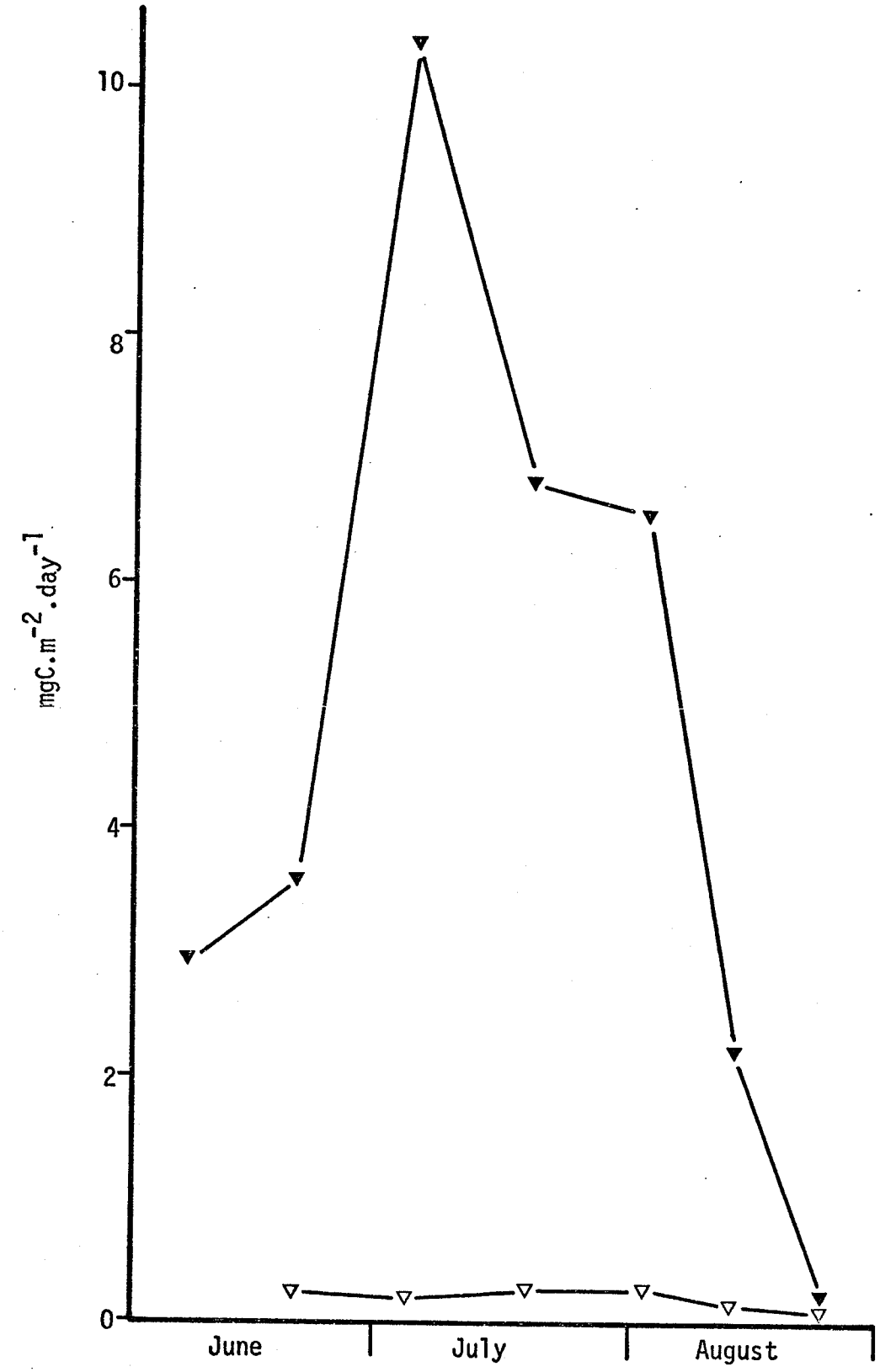

10
8
6
4
2
0
mgC.m^{-2}.day^{-1}
June
July
August

Figure 19: Seasonal productivity of Myriophyllum alterniflorum at 4 depths in West Blue Lake, Manitoba, as determined from ^{14}C uptake.

▼ ——— ▼ 1 meter

■ ——— ■ 2 meters

○ ——— ○ 3 meters

● ——— ● 4 meters

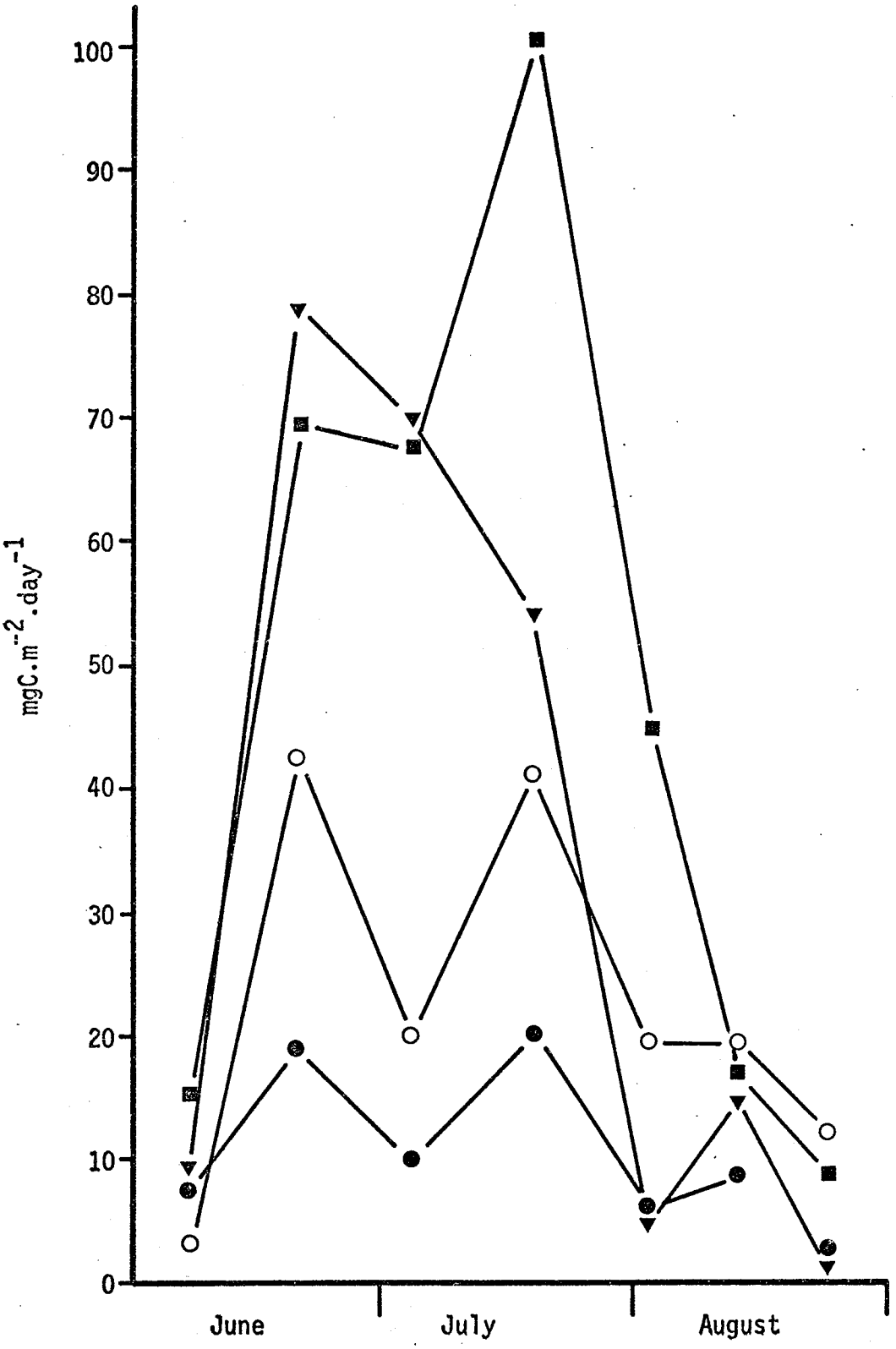

100
90
80
70
60
50
40
30
20
10
0
mgC.m^{-2}.day^{-1}
June
July
August

Figure 20: Seasonal productivity of Megalodonta Beckii at 3 depths in West Blue Lake, Manitoba, as determined from ^{14}C uptake.

○ ——— ○ 2 meters

● ——— ● 3 meter

■ ——— ■ 4 meters

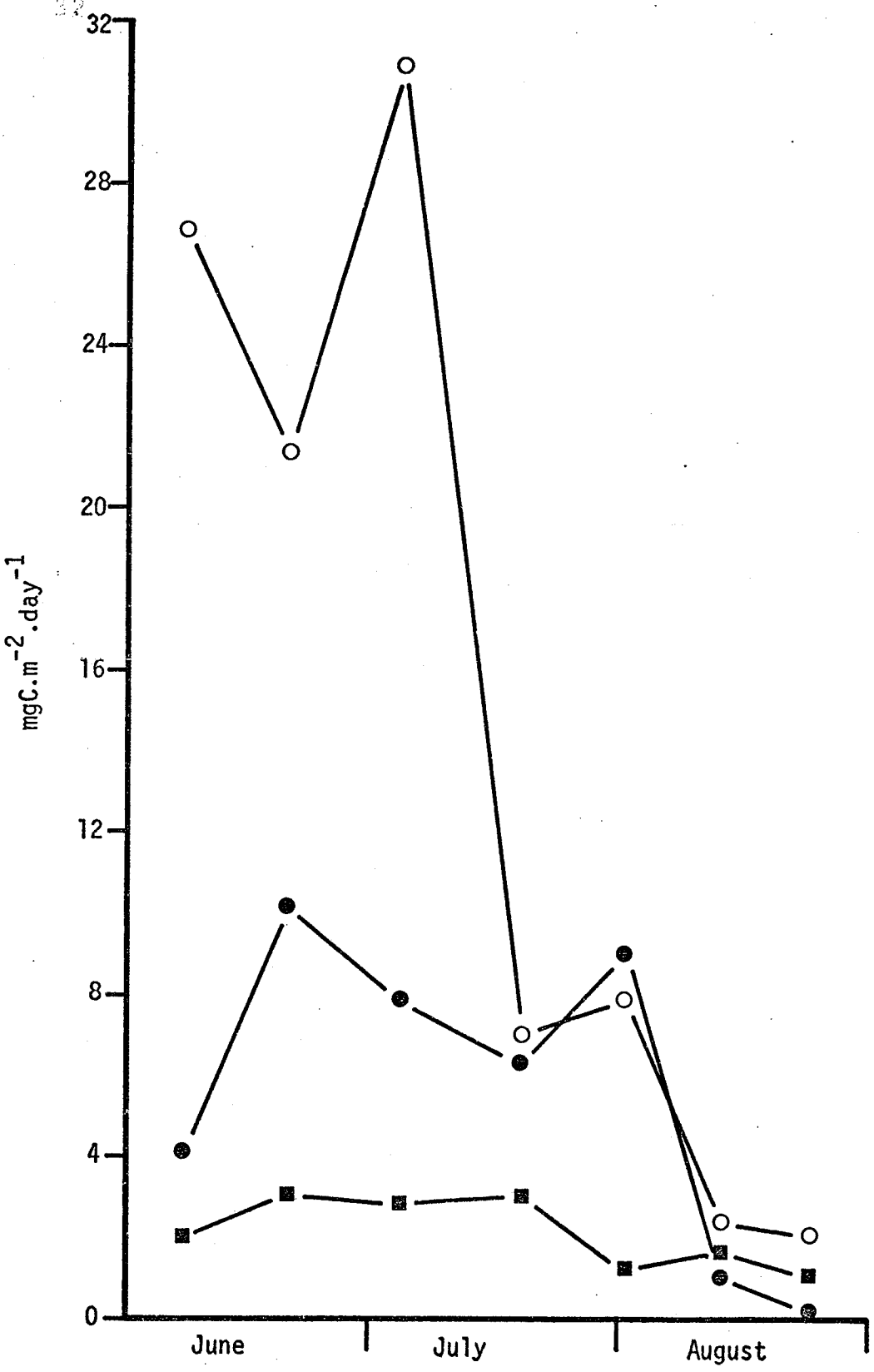

32
28
24
20
16
12
8
4
0
mgC.m-2.day-1
June
July
August

Figure 21: Comparison of the productivities of 4 macrophyte species in West Blue Lake, Manitoba, as determined from ^{14}C uptake by the summed transect method.

○ ——— ○ Potamogeton Richardsonii

▽ ——— ▽ Potamogeton pectinatus

● ——— ● Myriophyllum alterniflorum

■ ——— ■ Megalodonta Beckii

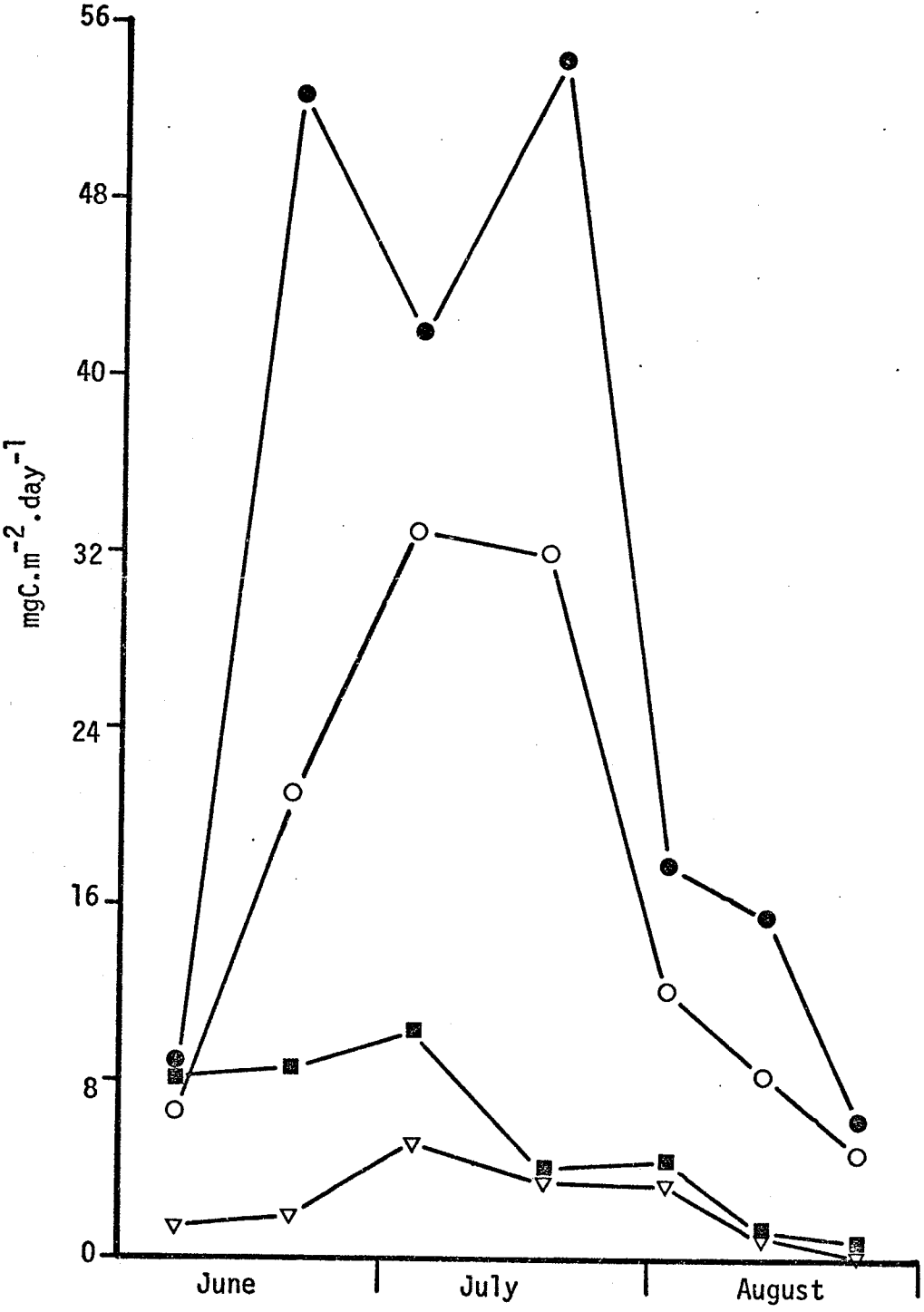
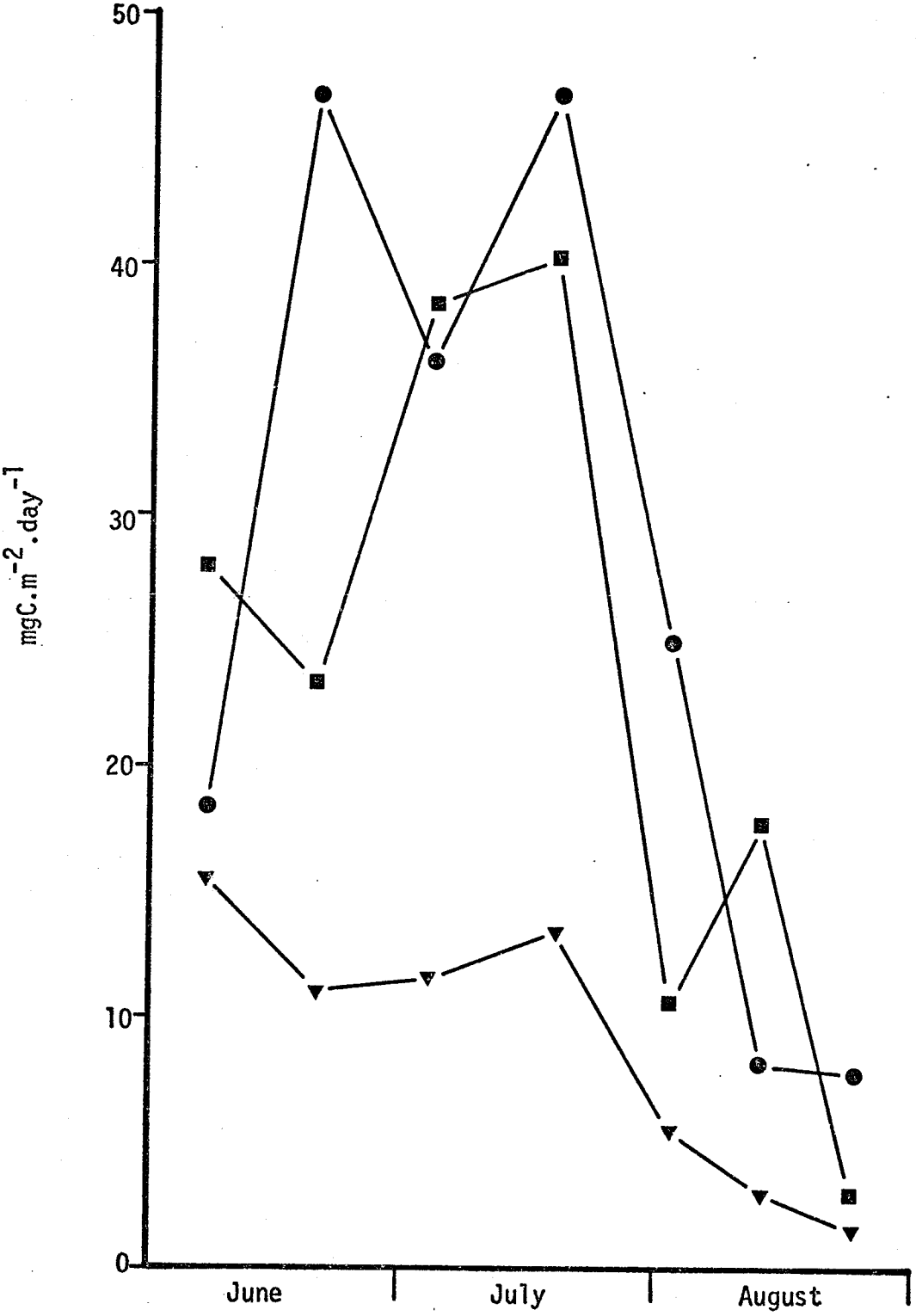

56
48
40
32
24
16
8
0
mgC.m^{-2}.day^{-1}
June
July
August

Figure 22: Comparison of the productivities of 3 macrophyte species in West Blue Lake, Manitoba, as determined from ^{14}C uptake by random sampling methods.

● ——— ● Potamogeton Richardsonii

■ ——— ■ Myriophyllum alterniflorum

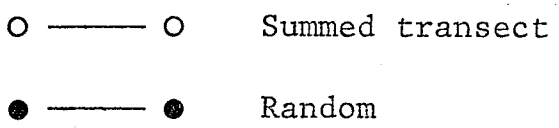
▼ ——— ▼ Megalodonta Beckii


50
40
30
20
10
0
mgC.m^{-2}.day^{-1}
June
July
August

(Figure 21) indicated that production was dominated by M. alterniflorum and P. Richardsonii. This pattern was duplicated in random samples (Figure 22). Comparisons of summed transect and random samples for each species (Figures 23, 24 and 25) demonstrate contrasting results. In all cases, periods of high productivity discernable by one method, were met by low productivities in the alternate method. However, when productivities were summed and compared (Figure 26), the resulting curves were extremely close. Figure 27 depicts the total production of the primary producers in West Blue Lake. Phytoplankton data was obtained from Ward and Robinson (1974). These experiments were conducted at weekly intervals during the summer at West Blue Lake. Except for a decline in mid June, phytoplankton dominated production throughout the year. The trend was especially prevalent in early spring and both mid and late summer. Although the data are not shown, phytoplankton production reached 320 mg C m^{-2} day^{-1} in May.

Percentages of dry and ash weights are presented in Table 1. The percentages fell within the values found by previous workers (Westlake 1963, Wetzel 1964a). The percentage carbon of the ash-free organic weight deviated considerably from the mean values given by Westlake (1963, 1965). No carbon analysis was performed on C. vulgaris because of large deposits of $CaCO_3$ encrusted

Figure 23: Comparison of the productivities of Potamogeton Richardsonii in West Blue Lake, Manitoba, as determined from ^{14}C uptake by summed transect and random sampling methods.



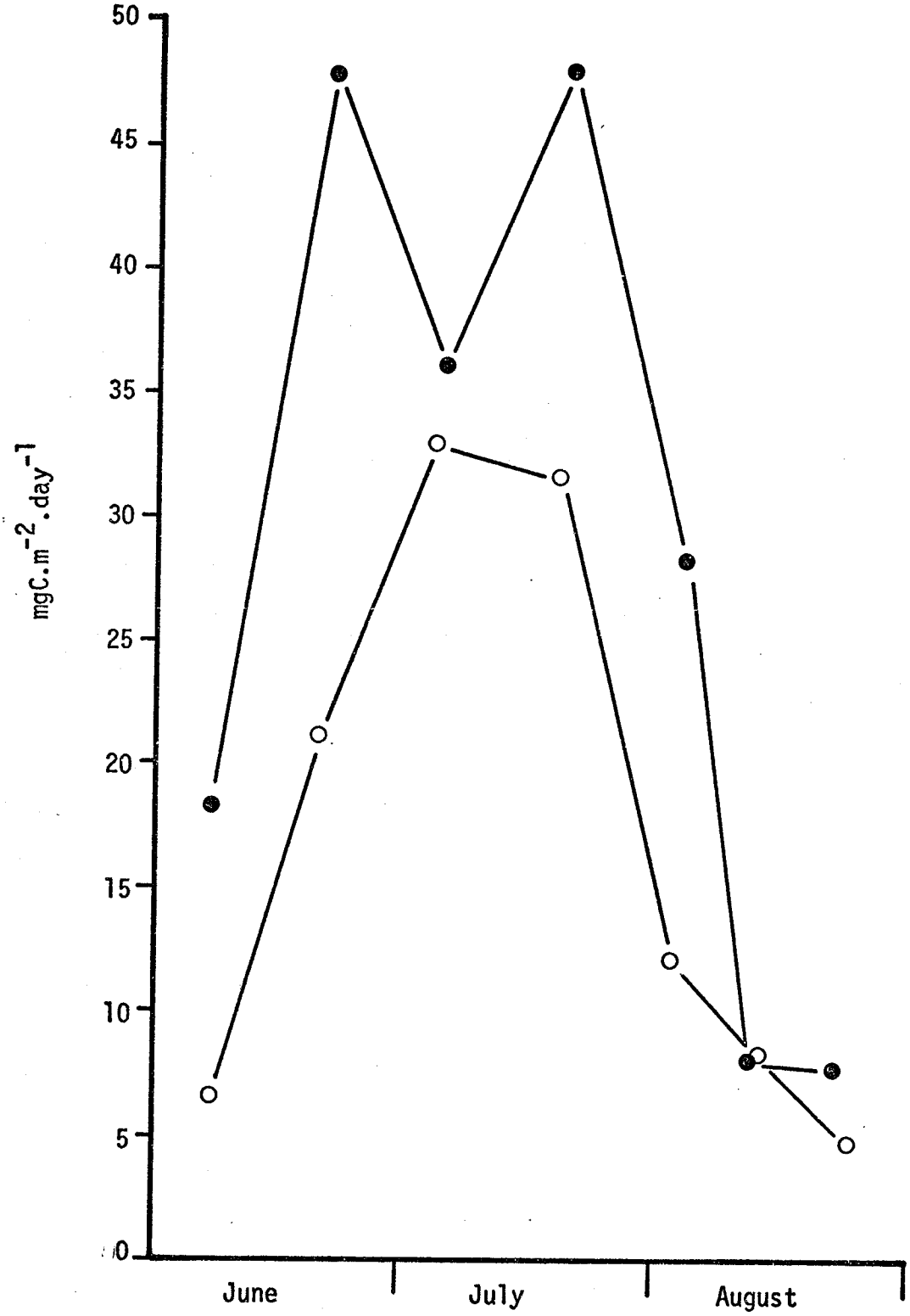

50
45
40
35
30
25
20
15
10
5
0
mgC.m-2.day-1
June
July
August

Figure 24: Comparison of the productivities of Myriophyllum alterniflorum in West Blue Lake, Manitoba, as determined from ^{14}C uptake by summed transect and random sampling methods.

● ——— ● Summed transect

○ ——— ○ Random

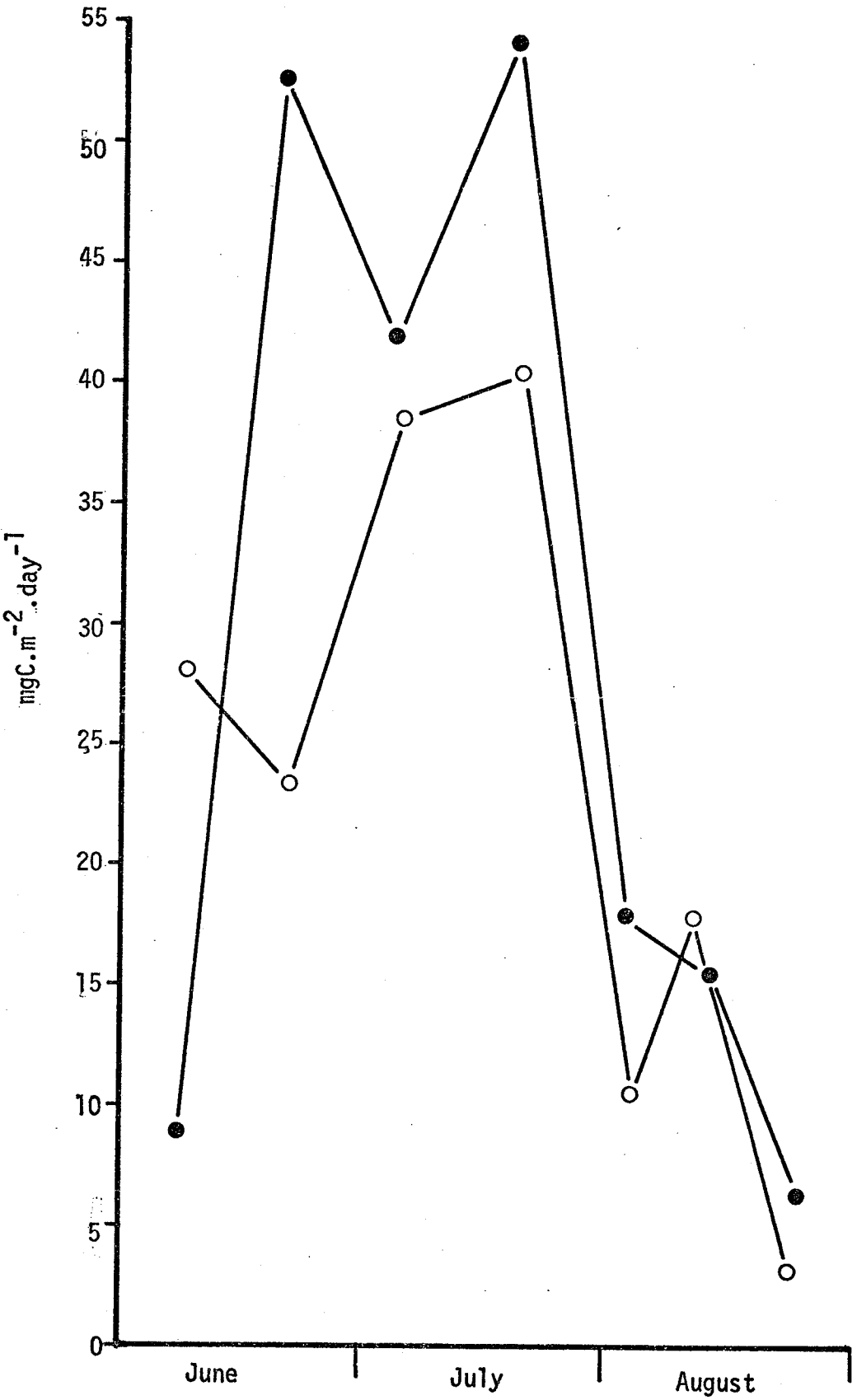

55
50
45
40
35
30
25
20
15
10
5
0
mgC.m^{-2}.day^{-1}
June
July
August

Figure 25: Comparison of the productivities of Megalodonta Beckii in West Blue Lake, Manitoba, as determined from ^{14}C uptake by summed transect and random sampling methods.

▼ ——— ▼ Summed transect

▽ ——— ▽ Random

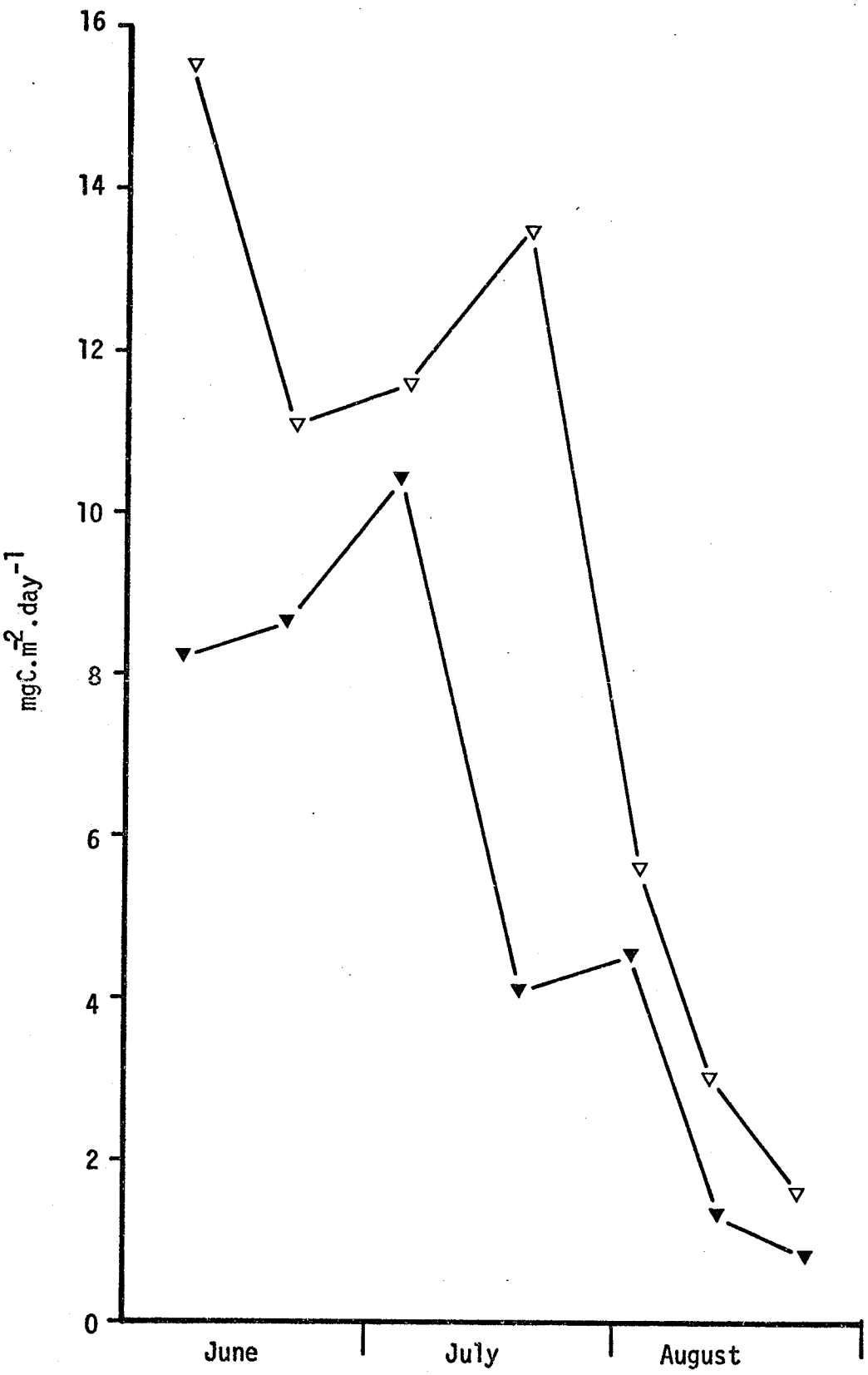

16
14
12
10
8
6
4
2
0
mgC.m^{-2}.day^{-1}
June
July
August

Figure 26: Comparison of the combined productivities of the submerged macrophytes in West Blue Lake, Manitoba, as determined from ^{14}C uptake by summed transect and random sampling methods.

● ——— ● Summed transect

○ ——— ○ Random

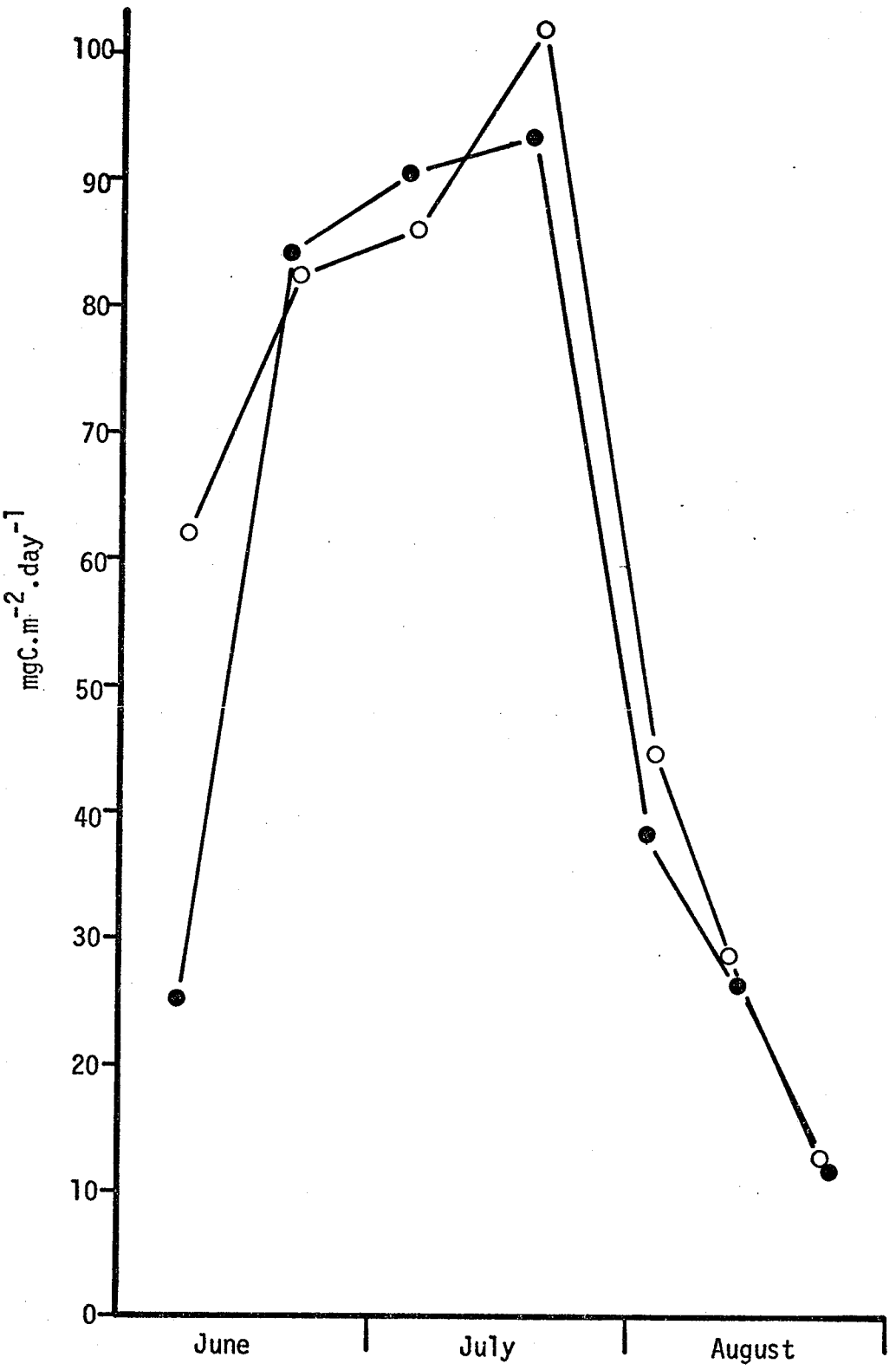
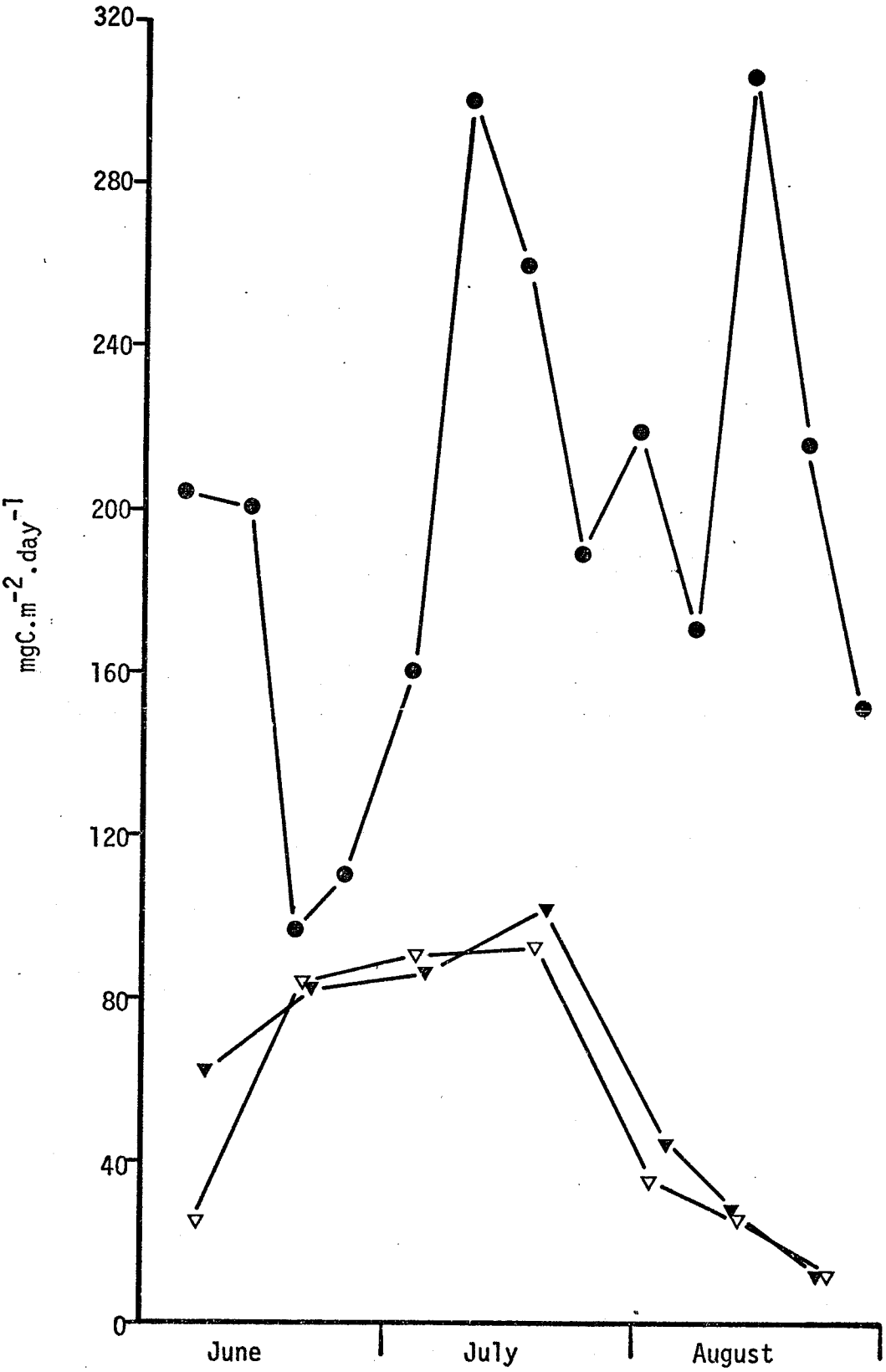

100
90
80
70
60
50
40
30
20
10
0
mgC.m-2.day-1
June
July
August

Figure 27: Comparison of the productivities of the macrophytes and phytoplankton in West Blue Lake, Manitoba, as determined from ^{14}C uptake.

▽ ——— ▽ Macrophytes: Summed transect

▼ ——— ▼ Macrophytes: Random

● ——— ● Phytoplankton


320
280
240
200
160
120
80
40
0
mgC.m-2.day-1
June
July
August

on the plants. The mean value of 46.5% given by Westlake (1965) was employed, although this figure may not be representative.

The submerged macrophytes in West Blue Lake covered an area of 52,736 m^2, which is equivalent to 3.3% of the total lake area. Several species may occupy the same area. When mapped, the area of the entire bed was delineated. The area of each species occurring within the bed was considered to be the total area of that bed. Therefore, when the heterogeneity of the beds was taken into account the areas of individual species total to 7.5% (Tables 2 and 3). The maximum cumulative net production was taken as the point of maximum biomass divided by the number of days in the growing season. The maximum cumulative net productivities determined by both methods are presented in Tables 2 and 3. If the biomass of C. vulgaris is interpolated to the sampling dates of the other species, the total maximum cumulative net productivity for the summed transect becomes 9.4 mg C m^{-2} day^{-1} and for the random method 8.0 mg C m^{-2} day^{-1}. If taken on an annual basis (365 days), both productivities become 2.3 mg C m^{-2} day^{-1}.

Since loss of volatiles may occur upon drying of plant material, the magnitude of this loss was examined in the four submerged angiosperms. Results are expressed as DPM mg wet $weight^{-1}$ and loss as a percentage of the mean of five replicate samples (Table 4). Loss ranged

from 0% in P. pectinatus to 4.1% in P. Richardsonii. A test of significance on the extent of the loss (t-test) indicated no loss was significant at the level tested (95% confidence).

Turnover times for the submerged macrophytes are presented for the summed transect (Table 5) and random (Table 6) methods. In each case turnover times were rapid when production was high and decreased as respiration subsequently increased.

Results of factorial calculations designed to test for significant differences between sampling techniques are presented in Table 7. The calculated "F" value of 0.20 did not exceed the critical value of 3.96, $P < 0.05$. Hence, the null hypothesis that there was no significant difference between sampling techniques could not be rejected.

Table 1: Percent carbon and variability in dry and ash weights of 5 macrophyte species in West Blue Lake, Manitoba.

Species	Dry as % Wet June	Dry as % Wet Aug	Standard Error June	Standard Error Aug	Ash as % Dry June	Ash as % Dry Aug	Standard Error June	Standard Error Aug	Carbon as % organic
Chara vulgaris	21.68	25.43	1.39	0.93	54.20	47.16	2.34	1.77	46.5*
Potamogeton Richardsonii	13.61	10.22	0.71	1.08	14.35	18.21	1.48	1.07	45.5
Potamogeton pectinatus	10.40	9.31	2.22	3.01	16.64	15.92	1.30	0.72	46.9
Megalodonta Beckii	11.97	11.47	2.46	1.06	16.35	23.46	0.99	2.11	41.2
Myriophyllum alterniflorum	11.03	13.82	1.41	1.90	18.80	19.84	2.85	2.20	40.0

* from Westlake (1965)

Table 2: Distribution and cumulative net productivities of 5 macrophyte species in West Blue Lake, Manitoba. Biomass determined from the summed transect samples.

Species	Area % of total	Biomass ($gmC\ m^{-2}$) Initial	Maximum	Productivity ($mgC\ m^{-2}\ day^{-1}$)
Chara vulgaris	1.9	159.2	179.0	3.6
Potamogeton Richardsonii	1.7	-	10.8	2.1
Potamogeton pectinatus	1.2	-	0.9	0.1
Myriophyllum alterniflorum	1.2	-	18.1	2.5
Megalodonta Beckii	1.5	-	3.1	0.5
Total	7.5			8.8

Table 3: Distribution and cumulative net productivities of 5 macrophyte species in West Blue Lake, Manitoba. Biomass determined from random samples.

Species	Area % of total	Biomass (gmC m^{-2}) Initial	Maximum	Productivity (mgC m^{-2} day^{-1})
Chara vularis	1.9	166.3	176.8	2.1
Potamogeton Richardsonii	1.7	-	14.4	2.4
Potamogeton pectinatus	1.2	-	1.3	0.2
Myriophyllum alterniflorum	1.2	-	5.6	0.8
Megalodonta Beckii	1.5	-	14.8	2.1
Total	7.5			7.6

Table 4: Loss of activity upon drying for 4 macrophyte species in West Blue Lake, Manitoba. Results are expressed as the mean of 5 replicate samples.

Species	DPM mg wet weight^{-1}		Standard Error		Loss on Drying	
	Wet	Dry	Wet	Dry	DPM	%
Potamogeton Richardsonii	997	957	30.6	13.9	40	4.1
Potamogeton pectinatus	276	278	4.0	5.0	-	-
Myriophyllum alterniflorum	690	683	14.6	13.1	7	0.7
Megalodonta Beckii	668	659	7.6	13.2	9	1.1

Table 5: Tunrover times for the submerged macrophytes in West Blue Lake, Manitoba. Biomass and productivity from summed transect samples.

Date	Biomass $mgC\ m^{-2}$	Productivity $mgC\ m^{-2}\ day^{-1}$	turnover time (days)
June 8	166.3	25.2	6.6
June 21	316.3	84.3	3.8
July 5	507.2	90.7	5.6
July 20	695.6	93.7	7.4
August 3	815.6	38.0	21.5
August 12	838.5	26.4	31.7
August 23	823.9	12.0	68.4

Table 6: Turnover times for the submerged macrophytes in West Blue Lake, Manitoba. Biomass and productivity from random samples.

Date	Biomass mgC m^{-2}	Productivity mgC m^{-2} day^{-1}	turnover time (days)
June 8	222.3	61.9	3.6
June 21	348.7	82.4	4.2
July 5	495.5	86.2	5.8
July 20	660.8	102.0	6.5
August 3	774.7	44.6	17.4
August 12	805.0	28.9	27.8
August 23	824.0	12.6	65.4

Table 7: Results of factorial calculations designed to test for significance between sampling procedures.

Source of variation	df.	ss.	ms.	F
Total	99	290.28		
Replications	9	74.71		
Species	4	120.34	30.09	28.66*
Sampling procedure	1	0.21	0.21	0.20
Interaction	4	9.76	2.44	2.32
Error	81	85.26	1.05	

DISCUSSION

Research into macrophyte productivity at West Blue Lake was undertaken with the aim of comparing the results of random and fixed sampling procedures utilizing biomass and carbon uptake criteria for the predominant submerged plant species.

The mapping procedure employed, although a fairly rapid method, did not produce an exact picture of total area covered. Both M. alterniflorum and P. Richardsonii reproduced extensively by vegetative means during the summer. It was noted that by July 18th the beds had extended beyond original boundaries, and therefore total macrophyte area was somewhat underestimated.

The distribution of submerged macrophyte species in West Blue Lake appears contradictory to reports of other investigators (Grøntved 1958, Forsberg 1960, Rich, Wetzel and Van Thuy 1971). Species which thrive in shallow waters at other localities do not do well at depths less than 2 meters in West Blue Lake. C. vulgaris and M. Beckii did not appear at all in areas of 1 meter or less, while P. Richardsonii and M. alterniflorum appeared stunted at this depth. Rich, Wetzel and Van Thuy (1971) found the majority of Potamogeton, Myriophyllum and Chara between 0 and 2 meters. The high percent light transmittance due to low turbidity in West Blue

Lake may restrict the majority of macrophyte growth to waters greater than 1 meter in depth. Light inhibited growth did not occur in P. pectinatus which obtained maximum growth at 1 meter.

Although there is agreement between organic weight and ^{14}C methods as to the relationship between depth and productivity, there is little agreement between biomass and ^{14}C, employing either summed transect or random sampling, on the magnitude of the difference between both estimates. The ^{14}C method gives an instantaneous measure of approximate net production, although there is no correction for respiration or excretion during the experimental period. Hough and Wetzel (1972) found significant respiratory losses and subsequent refixation of respired CO_2 in Najas flexilis. Wetzel and Manny (1972) found excretion rates between 1 - 10%, and it appears the combination of respiration and excretion could seriously alter production values obtained in four hour experiments. The dilution effect of the large incubators used in this study precluded the possibility of obtaining reliable excretion values, which perhaps would have produced values in stronger agreement with biomass results.

The organic weight procedure, since it involves extended periods of time, reduces the influence of environmental conditions which play a more defined role

in carbon fixation experiments. Estimates of net production are dependent upon grazing losses and it would appear that losses to herbivores were minimal. It seems likely that grazing was restricted mainly to epiphytic algae rather than to macrophytes themselves.

Since macrophyte production was depth dependent, the depth distribution of all plant species became extremely important when determining production by either ^{14}C or biomass. The sampling procedure must be tailored to suit the distribution encountered. Although no quantitative data are available the extent of each species at each depth cannot be said to be identical. When the area colonized at one depth greatly exceeds areas at other depths, or depth greatly restricts a species in its development, random sampling may produce misleading results. Such was the case with P. pectinatus which was restricted to a depth of 1 meter or less. A greater number of samples would probably have corrected the oscillating production values, but time and manpower limited the number of samples at any one time. Despite the non-rejection of the hypothesis that the two sampling procedures are equal, it is probable that if the productivity of P. pectinatus was large it would have resulted in a significant difference between sampling procedures.

Inherent in the ^{14}C procedure, as outlined previously, was error involved in incubation times. When dealing with

a large number of samples the amount of time required to install incubation chambers was considerable. Although ^{14}C was administered after all plants had been enclosed, the difference in time of enclosure between first and last samples could seriously have altered metabolic rates. A quicker procedure, short of removing plants from the substratum, would be preferable to manual manipulation of incubation chambers under water.

^{14}C results indicated major and minor production peaks for all but one macrophyte species tested. The benthic alga Cladophora demonstrates this phenomenum although much more pronounced (Whitton 1971). These marked fluctuations are thought to be temperature controlled. However, since these maxima appeared only in random samples it would seem that they are more an artifact of sampling procedure than a physiological phenomenon.

The percentages of dry and ash weights (Table 1) fell within values found by previous workers (Westlake 1963, Wetzel 1964a). The percentage carbon of the ash-free organic weight deviates considerably from mean values given by Westlake (1963, 1965). No carbon analysis was performed on C. vulgaris due to large deposits of of $CaCO_3$ encrusted on the plants. Although the mean value of 46.5% given by Westlake (1965) was employed for C. vulgaris, this value may not be representative in view of the range of values (25%) found for other species.

When biomass and productivity are in identical or convertible units, it is possible to calculate a turnover time. This procedure has been used in phytoplankton studies (Schindler and Holmgren 1971). In the shield lakes studied by Schindler and Holmgren (1971) phytoplankton biomass remained constant, and turnover time was used as an index of transfer to higher trophic levels. One of the criteria for the use of biomass in macrophyte studies is that grazing losses be negligible or accountable. Visual estimates indicated mechanical destruction through grazing was negligible and therefore turnover time was then an indicator of time required for the doubling of population biomass. The actual and theoretical doubling times are not in close agreement at any time during the experimental period (Tables 5 and 6). It must be remembered that theoretical turnover time is calculated on the basis of ^{14}C fixation which does not take into account photorespiration nor nocturnal respiration. With a population in exponential growth there is a difference between actual and theoretical biomass at the end of the actual doubling time. For example, consider a population with a theoretical turnover time of 4 days and actual turnover time of 28 days. The turnover times are related by a factor of 7. If the initial biomass was B_o the theoretical final biomass would be $B_o 2^{28/4}$ while actual biomass would be $B_o 2^{28/28}$. The magnitude

of the difference is $2^{28/4} / 2^{28/28} = 2^{7}$.

This figure of 2^7 cannot be considered indicative of the true difference in growth. The errors involved with the ^{14}C procedure (respiration, excretion, mechanical damage) are magnified exponentially over time and the actual difference in growth rates would be considerably less than the above mentioned figure. If the exponential equations are simultaneously reduced to 0 time the difference between them would be the amount of carbon fixed that was not available to growth.

Two previous studies (Wetzel 1964 and Davies 1968) lend themselves to comparison with the West Blue Lake study. The research at West Blue Lake deviated considerably from the former macrophyte studies in that those were performed on relatively shallow lakes in which the macrophytes occupied a large percentage of total lake area. Glacial scouring at West Blue Lake had resulted in deep basins with steep sloping shorelines. Consequently macrophytes exist in relatively few areas where the bottom does not recede so rapidly as the inhibit growth due to insufficient light penetration, and turbulence at shallow depths.

Wetzel (1964a) found on an annual basis that two of the producer components, periphyton and phytoplankton, overshadowed the importance of macrophyte production, yet on the growing season basis macrophyte importance

was enhanced considerably. The restrictive water chemistry of Borax Lake limited the macrophytes to a single species (Wetzel 1964a) while the macrophytes in Marion Lake were composed of four dominant species (Davies 1968). On a comparative basis, the importance of the macrophytes to Borax Lake greatly exceeds macrophyte importance in either Marion Lake or West Blue Lake. Macrophytes occupied a large percentage of the Marion Lake area (11.2%), yet the productivity of the submerged macrophytes was higher in West Blue Lake. This reduced production in Marion Lake is probably a result of rapid flushing times. The annual mean production was higher in Marion Lake (7.1 mgC m^{-2} day^{-1}) than in West Blue Lake (2.3 mgC m^{-2} day^{-1}) due to the presence of two emersed species. Emergent and emersed species are rare in West Blue Lake and it is doubtful if the inclusion of their production would add significantly to the figure mentioned above.

West Blue Lake contains a relatively simple phytoplankton community structure. Cliff (1972) identified thirty five species. Mean daily average phytoplankton production from mid-May to late August was 340 mgC m^{-2} day^{-1} in 1971 and 320 mgC m^{-2} day^{-1} in 1972 (Ward and Robinson 1974). In 1973 mean daily phytoplankton production from mid-May to late August was 218 mgC m^{-2} day^{-1}. Mean daily macrophyte productivity for the same period was 63 mgC m^{-2} day^{-1} and 72 mgC m^{-2} day^{-1} determined from

summed transect and random sampling methods respectively. Although phytoplankton production was depressed in 1973 compared to the two previous years, phytoplankton appear to be the most important contributor to the primary productivity of West Blue Lake. Phytoplankton contribution would assume even more significance if productivity was expressed on a yearly (365 days) basis.

SUMMARY

Primary productivity of five submerged macrophytes was monitored from biomass estimates from May, 1973 to September, 1973. Species areas were mapped with floats and quantified by planimetry. Species distribution was obtained from quadrat samples. Biomass samples were taken along transects through the littoral zone by summed transect and random methods. Results from the summed transect method indicated optimal productivity at 2 meters. Both methods showed the majority of macrophyte productivity to be attributable to 3 species, Chara vulgaris, Potamogeton Richardsonii and Myriophyllum alterniflorum. There was no significant differnce between sampling methods.

Carbon analysis was performed on four of the five species and results were lower than values published previously. When percentage carbon was applied to dry weight figures, the cumulative net productivities for random and summed transect methods were 8.0 mgC m^{-2} day^{-1} and 9.4 mgC m^{-2} day^{-1} respectively.

Productivity was also determined from ^{14}C experiments conducted in situ by the random and summed transect procedures mentioned above. Both procedures produced higher results than their counterparts from biomass data. In order to relate ^{14}C production to biomass and "in-vial" combustion procedure was developed which allowed

an estimate of activity lost upon drying. The losses ranged from 0 - 4.1% of ^{14}C fixed (Table 4) and no loss was considered significant.

The compilation of ^{14}C and biomass data allowed the calculation of turnover times (tables 5 and 6). These ranged from less than four days in the beginning of the summer when productivity was high to greater than sixty days at the end of the summer when productivity was low.

CONCLUSIONS

1. The carbon-14 technique is superior to the biomass technique in sensitivity, but corrections should be made for respiration and excretion.
2. The optimal depth for photosynthesis in West Blue Lake was 2 m. Photoinhibition at lesser depths and increased light attenuation at greater depths considerably reduced production.
3. The majority of macrophyte production was attributable to three species, although this amount in combination with other species is probably not a significant portion of the energy budget of the lake.
4. The ^{14}C technique was found to be time consuming when employed in situ. The difference in enclosure times would probably influence results significantly.
5. A mean carbon value from published literature should not be used to determine production. In this study, published results were higher than actual values for certain species. It is possible that environmental conditions could affect values from different locations.
6. The calculation of turnover times required estimates of respiration, excretion and mechanical losses. Errors involved in calculating theoretical values are magnified by the nature of exponential growth

and theoretical values must therefore be regarded sceptically.

7. Production values were higher where envirnonmental conditions were stable and lake flushing times were extended.

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Appendix 1: Seasonal productivity values for the submerged macrophyte species in West Blue Lake, Manitoba.

Seasonal productivity of Chara vulgaris at 4 depths, as determined from changes in biomass.

Date	Productivity ($mgC\ m^{-2}\ day^{-1}$)				
	2m	3m	4m	5m	mean
May 29	3.1	2.0	0.2	1.7	1.8
June 13	8.2	3.5	4.2	1.7	4.4
June 27	8.9	7.7	3.5	0.9	5.3
July 11	9.7	5.5	2.6	1.7	4.9
July 25	7.9	5.5	1.7	1.4	4.1
August 8	8.2	6.2	1.7	1.2	4.3
August 22	4.2	3.6	0.5	0.5	2.2
September 13	-1.2	0.2	-0.5	0.1	-0.4

Seasonal productivity of *Chara vulgaris* as determined from changes in biomass by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
May 29	2.9
June 13	3.8
June 27	3.3
July 11	3.4
July 25	2.0
August 8	1.2
August 22	1.6
September 13	0.6

Seasonal productivity of Potamogeton Richardsonii at 4 depths as determined from changes in biomass.

Date	Productivity (mgC m^{-2} day^{-1})				
	1m	2m	3m	4m	mean
May 25	1.2	0.1	1.4	-	0.7
June 14	0.3	1.4	2.9	0.8	1.4
June 28	1.6	9.6	3.1	2.4	4.2
July 12	1.1	7.0	2.4	1.6	3.0
July 18	1.2	5.3	1.5	1.0	2.3
July 25	1.1	5.4	1.2	1.2	2.2
August 1	-	2.7	1.3	0.7	1.2
August 8	-0.4	1.6	0.2	0.9	0.6
August 22	-1.5	-2.0	-1.3	-0.2	-1.3
September 13	-1.2	-3.0	-2.5	-1.4	-2.0

Seasonal productivity of Potamogeton Richardsonii as determined from changes in biomass by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
May 25	0.9
June 14	3.1
June 28	2.8
July 12	2.3
July 18	4.4
July 25	3.5
August 1	3.6
August 8	2.0
August 22	1.0
September 13	-1.2

Seasonal productivity of Potamogeton Richardsonii at 4 depths as determined from ^{14}C uptake.

Date	Productivity (mgC m^{-2} day^{-1})				
	1m	2m	3m	4m	mean
June 8	4.2	3.5	6.2	12.7	6.7
June 21	19.6	39.9	11.7	13.0	21.1
July 5	14.9	82.8	25.6	8.7	33.0
July 20	26.3	55.9	30.6	14.1	31.7
August 3	3.4	21.5	12.7	11.2	12.2
August 12	6.4	7.8	9.6	9.8	8.4
August 23	1.0	2.1	10.0	6.0	4.8

Seasonal productivity of Potamogeton Richardsonii as determined from ^{14}C uptake by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
June 8	18.4
June 21	48.0
July 5	36.1
July 20	48.1
August 3	28.4
August 12	8.2
August 23	7.9

Seasonal productivity of Potamogeton pectinatus at 2 depths as determined from changes in biomass.

Date	Productivity (mgC m^{-2} day^{-1})		
	1m	2m	mean
May 25	0.2	-	0.1
June 14	0.5	-	0.3
June 28	0.5	-	0.3
July 12	0.6	-	0.3
July 18	0.6	-	0.3
July 25	0.5	-	0.3
August 1	0.6	-	0.3
August 8	0.3	-	0.3
August 22	-0.1	-	-0.1
September 13	-0.2	-	-0.1

Seasonal productivity of Potamogeton pectinatus as determined from changes in biomass by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
May 25	-
June 14	0.2
June 28	-0.2
July 12	0.5
July 18	0.1
July 25	-
August 1	0.7
August 8	-1.3
August 22	0.6
September 13	-0.4

Seasonal productivity of Potamogeton pectinatus at 2 depths as determined by ^{14}C uptake.

Date	Productivity (mgC m^{-2} day^{-1})		
	1m	2m	mean (4)
June 8	3.0	-	0.8
June 21	3.6	0.2	1.0
July 5	10.4	0.2	2.7
July 20	6.8	0.2	1.8
August 3	6.6	0.2	1.7
August 12	2.2	0.1	0.6
August 23	0.2	0.1	0.1

Seasonal productivity of Myriophyllum alterniflorum at 4 depths as determined from changes in biomass.

Date	Productivity (mgC m^{-2} day^{-1})				
	1m	2m	3m	4m	mean
May 25	0.5	0.4	-	0.2	0.3
June 14	3.3	1.7	0.6	0.9	1.6
June 28	6.3	5.4	2.7	0.3	3.7
July 12	3.7	10.5	2.5	1.0	4.4
July 18	5.1	8.9	6.2	0.8	5.3
July 25	2.7	6.3	2.6	0.8	3.1
August 1	1.5	7.0	1.5	0.6	2.7
August 8	-5.1	3.6	1.8	0.4	0.2
August 22	-3.1	-3.4	0.4	0.2	-1.5
September 13	-3.6	-3.6	-0.6	-	-2.0

Seasonal productivity of Myriophyllum alterniflorum as determined from changes in biomass by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
May 25	0.2
June 14	2.7
June 28	1.8
July 12	2.8
July 18	5.1
July 25	4.2
August 1	1.6
August 8	2.0
August 22	0.7
September 13	-0.3

Seasonal productivity of *Myriophyllum alterniflorum* at 4 depths as determined from ^{14}C uptake.

Date	Productivity (mgC m^{-2} day^{-1})				
	1m	2m	3m	4m	mean
June 8	9.4	15.2	3.2	7.4	8.8
June 21	79.0	69.9	42.6	19.1	52.6
July 5	70.0	67.7	20.1	9.9	41.9
July 20	54.3	100.9	41.3	20.6	54.3
August 3	4.9	44.7	19.8	6.6	19.0
August 12	14.7	17.2	19.3	9.0	15.1
August 23	1.2	8.9	12.3	2.9	6.3

Seasonal productivity of Myriophyllum alterniflorum as determined from ^{14}C uptake by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
June 8	15.5
June 21	12.9
July 5	29.7
July 20	18.8
August 3	4.3
August 12	8.1
August 23	1.1

Seasonal productivity of Megalodonta Beckii at 3 depths as determined from changes in biomass.

Date	Productivity ($mgC\ m^{-2}\ day^{-1}$)			
	2m	3m	4m	mean
May 25	1.1	0.4	-	0.4
June 14	2.5	0.4	-	0.7
June 28	3.0	0.6	-	0.9
July 12	1.3	0.8	0.1	0.6
July 18	1.0	1.3	-	0.6
July 25	-0.9	0.8	-	-
August 1	-0.4	0.6	0.1	0.1
August 8	-0.5	0.3	-	-0.1
August 22	-0.9	-0.2	-	-0.3
September 13	-1.0	-0.5	-	-0.4

Seasonal productivity of Megalodonta Beckii as determined from changes in biomass by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
May 25	0.5
June 14	1.2
June 28	0.9
July 12	0.7
July 18	0.8
July 25	0.8
August 1	-
August 8	0.4
August 22	-1.7
September 13	-0.3

Seasonal productivity of Megalodonta Beckii at 3 depths as determined from ^{14}C uptake.

Date	Productivity (mgC m^{-2} day^{-1})			
	2m	3m	4m	mean
June 8	26.9	4.2	2.0	8.3
June 21	21.4	10.2	3.1	8.7
July 5	30.9	7.9	2.9	10.4
July 20	7.1	6.3	3.1	4.1
August 3	8.0	9.0	1.2	4.5
August 12	2.4	1.1	1.7	1.3
August 23	2.1	0.1	1.0	0.8

Seasonal productivity of Megalodonta Beckii as determined from ^{14}C uptake by random sampling methods.

Date	Productivity (mgC m^{-2} day^{-1})
June 8	15.5
June 21	11.1
July 5	11.6
July 20	13.5
August 3	5.6
August 12	3.0
August 23	1.6

Appendix 2: Turnover times of 4 macrophyte species in West Blue Lake, Manitoba.

Turnover times for Potamogeton Richardsonii as determined from summed transect methods.

Date	Biomass $mgC\ m^{-2}$	Productivity $mgC\ m^{-2}\ day^{-1}$	turnover time (days)
June 8	35.5	6.7	5.3
June 21	71.1	21.1	3.4
July 5	122.8	33.0	3.7
July 20	161.9	31.7	5.1
August 3	182.1	12.2	14.9
August 12	181.7	8.4	21.6
August 23	167.7	4.8	34.8

Turnover times for Potamogeton Richardsonii as determined from random sampling methods.

Date	Biomass $mgC\ m^{-2}$	Productivity $mgC\ m^{-2}\ day^{-1}$	turnover time (days)
June 8	58.1	18.4	3.2
June 21	94.5	48.0	2.0
July 5	127.0	36.1	3.5
July 20	175.1	48.1	3.6
August 3	224.4	28.4	7.9
August 12	238.0	8.2	29.0
August 23	248.2	7.9	31.4

Turnover times for Potamogeton pectinatus as determined from summed transect methods.

Date	Biomass $mgC\ m^{-2}$	Productivity $mgC\ m^{-2}\ day^{-1}$	turnover time (days)
June 8	2.6	0.7	3.7
June 21	4.3	1.0	4.3
July 5	6.1	2.7	2.3
July 20	8.3	1.8	4.6
August 3	10.3	1.8	5.9
August 12	10.7	0.6	17.8
August 23	10.4	0.1	104.0

Turnover times for Myriophyllum alterniflorum as determined from summed transect methods.

Date	Biomass $mgC\ m^{-2}$	Productivity $mgC\ m^{-2}\ day^{-1}$	turnover time (days)
June 8	27.0	8.8	3.1
June 21	58.7	52.6	1.1
July 5	110.1	41.9	2.6
July 20	187.6	54.3	3.5
August 3	222.1	17.8	12.5
August 12	217.0	15.5	14.0
August 23	200.1	6.3	31.8

Turnover times for Myriophyllum alterniflorum as determined from random sampling methods.

Date	Biomass $mgC\ m^{-2}$	Productivity $mgC\ m^{-2}\ day^{-1}$	turnover time (days)
June 8	40.5	28.0	1.5
June 21	68.0	23.4	2.9
July 5	102.1	38.5	2.7
July 20	160.4	40.4	4.0
August 3	196.7	10.6	18.6
August 12	209.4	17.8	11.8
August 23	216.0	3.1	69.7

Turnover times for Megalodonta Beckii as determined from summed transect methods.

Date	Biomass mgC m^{-2}	Productivity mgC m^{-2} day^{-1}	turnover time (days)
June 8	16.4	8.3	2.0
June 21	27.2	8.7	3.1
July 5	37.5	10.4	3.6
July 20	44.8	4.1	10.9
August 3	45.0	4.5	10.0
August 12	43.7	1.3	33.6
August 23	40.7	0.8	50.9

Turnover times for Megalodonta Beckii as determined from random sampling methods.

Date	Biomass mgC m^{-2}	Productivity mgC m^{-2} day^{-1}	turnover time (days)
June 8	24.6	15.5	1.7
June 21	38.4	11.1	3.5
July 5	50.0	11.6	4.3
July 20	61.5	13.5	4.6
August 3	66.5	5.6	11.9
August 12	61.4	3.0	20.4
August 23	43.7	1.6	27.3