THE PRODUCTIVITY OF THE MACROPHYTES OF MARION LAKE, B.C.

by

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in the Department of Zoology

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THE UNIVERSITY OF BRITISH COLUMBIA

April, 1968
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Department of \underline{Zoology}

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Date \underline{May 17, 1965}
ABSTRACT

The in situ productivity of both the phytoplankton and the macrophytes in Marion Lake, B.C., was determined from April 1966 through September 1966, by using $^{14}$C techniques. The uptake of NaH$^{14}$CO$_3$ was measured in selected macrophytes by enclosing them in plexiglass chambers. These plants were then combusted in oxygen, and the $^{14}$CO$_2$ was absorbed in toluene-POPOP-ethanolamine. Radioassay was accomplished by liquid scintillation. In addition to the $^{14}$C method, an organic weight method was used to measure macrophytic productivity.

The productivity of the macrophytes was always higher than that of the phytoplankton. There was a considerable difference in the estimates of the macrophyte productivity arrived at by the two different methods, and reasons for this are discussed.

The total productivity of the lake is very low when compared with lakes of similar latitudes because of low phytoplankton productivity. It is concluded that in Marion Lake the macrophytes are more important primary producers than the phytoplankton.

The difficulty of comparing data between this and other studies is discussed, and the need for standardization of methods is emphasized.
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ACKNOWLEDGMENTS

I wish to thank Dr. Ian E. Efford for his help and encouragement with all aspects of the study. Dr. R. G. Wetzel of Michigan State University offered much good advice and his correspondence was greatly appreciated. Drs. D. Chitty, C. V. Finnegan, P. A. Larkin, and E. B. Tregunna critically read the manuscript and made many helpful suggestions. Dr. C. T. Beer of the Cancer Research Institute of the University of British Columbia made available an oxygen combustion flask which was used during the study, and he was most generous with his time in discussing the handling and assay of radioisotopes.

Many people assisted in the field observations and collections but I especially thank Mr. Kanji Tsumura who assisted in almost all the practical aspects of the study. Messrs. M. Dickman, J. Mathias, R. Armstrong, and P. Richerson provided much in the way of help and discussion.

My wife, Anita Davies, made the illustrations and assisted in all phases of the preparation of the manuscript.
INTRODUCTION

In most of the limnological studies dealing with primary productivity, the emphasis has been placed on the productivity of the phytoplankton. Recently Wetzel (1964) and others have noted that in shallow lakes the contribution of the periphyton and higher vascular aquatics may be vastly underrated. The present study attempts to evaluate the role played in primary productivity by the macrophytes of Marion Lake, B.C. and is part of a detailed investigation which will describe the flow of energy through a small freshwater lake.

The primary productivity of this lake for 1965 was recently described by Efford (1967), but since phytoplankton productivity is apt to fluctuate a great deal from year to year, it was again determined in the course of the present study.

The productivity of the macrophytes was determined by making periodic biomass determinations and also by using a $^{14}$C method.
METHODS

The Study Area

Marion Lake is located 16 km. north of Langley, B.C. in the University Research Forest. The lake lies in a long narrow valley 300 m. above sea level, bordered on the west by a steep ridge 300 m. above the lake level and on the east by the southern slopes of the Coastal Mountains.

The basin of the lake is 800 m. long and about 200 m. wide at its maximum. At standard water level the lake has an area of 13.3 ha., one half of which is less than 2 m. deep (Fig. 1). The major inlet stream enters from the north and drains a watershed of 6.5 km.$^2$ including nearby Eunice Lake. The outlet at the south end feeds into the North Alouette system which is 1 km. away. Both inlet and outlet streams are gravelled, whereas the bottom of the lake consists of a uniform brown ooze.

In winter the lake is isothermal, but from spring through fall it is weakly stratified. The winters in the lower mainland of British Columbia are relatively mild and consequently the lake does not regularly have a permanent ice sheet but is covered with a thick layer of slush.

A detailed physical description of the lake is given elsewhere (Efford, 1967).
Fig. 1. Morphometric map of Marion Lake, British Columbia, showing Stations A, B, D, and E.
The phytoplankton contains over 200 species (Dickman, MS, 1967) and of these the dominant forms are microflagellates of the Chlorophyceae and Chrysophycae. Efford (1967) attributes 95 percent of the phytoplankton productivity to the nannoplankton. He separated the nannoplankton productivity from that of the macroplankton by regularly filtering half a sample normally and half through a #25 net (0.064 mm. diameter). He further states that spring blooms in the macroplankton appear not to change productivity significantly.

The periphyton are dominated in the summer by the algae Mougeotia spp. which are found in dense mats over the bottom ooze in shallow water and adhering to the stems of Nuphar sp. and Potamogeton natans.

There are only four rooted aquatics of numerical significance: Vallisneria sp. and Isoetes occidentalis (submerged), and Potamogeton natans and Nuphar sp. (floating). Dense beds of Chara spp. are found in association with the main spring of the lake and also with several of the smaller ones. Isoetes occidentalis is distributed in water over 2 m. in depth, while the other macrophytes are generally found in more shallow areas.

**Phytoplankton**

In order to compare the productivity of the phytoplankton with that of the rooted aquatics, the $^{14}$C technique introduced by Steeman-Nielsen (1952) and modified by Goldman (1963) was used. Paired
samples of water were collected from several depths in a polyethylene bottle and transferred to clear and opaque glass stoppered bottles. Each sample was inoculated with 4μc of $^{14}$C in the form of NaH$^{14}$CO$_3$. The samples were then incubated at the depths from which they were obtained for a period of 4 to 6 hours. This period is considered adequate for significant carbon uptake but brief enough to minimize bottle effects (Vollenweider and Nauwerk, 1961).

Ideally, productivity measurements should have been taken at suitable increments from dawn to dusk each day of the study period, but this was impractical. Instead, a four hour mid-day incubation period was selected in order to average out the variations in the diurnal curve caused by changing meteorological conditions which could influence the photosynthetic pattern. The assumption was made that productivity is directly proportional to light with full realization that this correlation is not always exact; minimal rates might be obtained, for example, if the measured rates were at maximal intensity. Daily light curves were obtained at Marion Lake with a recording pyrheliometer and the area under these curves was determined by planimetry. The ratio of the area under that portion of the curve representing the incubation period to the total area of the light curve gives a diurnal correction factor which was used to extrapolate daily production values.

After incubation, aliquots of the samples were filtered under vacuum at the lakeside onto HA Millipore filters of a porosity of 0.45 ± 0.02 μ. The activity of the samples was determined at the International Agency for $^{14}$C Determination in Denmark.
The method involves difficulties (Thomas, 1961), but it is probably
the most sensitive now available for measuring carbon fixation rates
under natural conditions and is thought to give values which approxi-
mate net productivity (Strickland, 1960).

All observations were made at Stations A and E, the assumption
being that Station A would be typical of that part of the lake deeper
than 2 m., and Station E of the shallower portion (Fig. 1). The areas
represented by A and E were equal, so the productivity of the lake on
any given day was taken to be the average of the productivities at A
and E.

Rooted Aquatics

There is a vast literature on the investigations of the productivity
of higher aquatic plants, much of which has been reviewed by Penfound
(1956), Westlake (1963), and Wetzel (1964). Until recently when
Wetzel (1963) devised a technique for measuring the in situ prod-
uctivity of aquatic macrophytes with $^{14}$C, most of the studies have been
cconcerned with biomass determinations and, less frequently, techniques
involving the changes in dissolved oxygen in the water surrounding
the plants.

Hartman and Brown (1966) have shown that dissolved oxygen con-
centrations in the water surrounding vascular plants are not proportional
to the production of internal oxygen because of the storage of oxygen
in the internal lacunae. Errors involved when using the oxygen
technique may be 200 percent or higher (Wetzel, personal communication). The above considerations plus the added technical difficulty of obtaining samples while operating at depths of up to 4 m. necessitated eliminating the oxygen technique.

Two methods were used to determine the seasonal productivity of the macrophytes; one was based on the calculation of in situ $^{14}$C fixation rates, the other on the rate of increase in organic carbon as determined by periodic cropping. In both cases, periodic measurements were made throughout the growing season. Although the organic weight method was used to describe each of the four important macrophytes in the lake, the $^{14}$C investigations were carried out only on the two submerged aquatics.

With the aid of SCUBA, light and opaque plexiglass chambers were placed over individual plants (Fig. 2). The cylinders were similar to those designed by Wetzel (1964) and were calibrated so that the enclosed volume of water was known. Depending on the size of the plants, the volumes used were 1.5 or 2.0 l. A known amount of $^{14}$C (10-20 μc/l. of water) was injected into the chamber as NaH$^{14}$CO$_3$, by means of a hypodermic syringe. After 4 hours of incubation (10:00 A.M. until 2:00 P.M.), the entire plant was removed and epiphytes were stripped from the leaves since they will also fix carbon. The plant was then blotted, weighed, and placed on dry ice.

In the laboratory the plants were dried at 60°C and then ground in a mill to pass through a #20 mesh (0.25 mm. diameter) sieve. Ten mg. aliquots of each plant were then combusted in an oxygen
Fig. 2. Light and opaque chambers used for determining productivity of macrophytes.
flask designed by Dr. C. T. Beer of the Cancer Research Institute of the University of British Columbia (Fig. 3).

When the combustion was complete, the flask was water-cooled in order to reduce the internal pressure. The capillary tube of the flask was then inserted in a liquid scintillation vial which contained a toluene-POPOP-ethanolamine mixture. When the stopcock of the flask was opened, the scintillation-absorbent mixture was drawn up, because of the vacuum, into the flask, where it was trapped by closure of the stopcock. The apparatus was agitated intermittently and after 20 minutes the fluid was returned to the scintillation vial for counting.

The efficiency of the above assay (38%) was determined by comparing the counts of replicate samples where one of the plants was placed in an induction furnace, combusted and the $^{14}\text{CO}_2$ evolved flushed into an evacuated 500 ml. ionization chamber. This second assay was made with a Dynacon Electrometer which is accurate within 1% by comparison with the American National Bureau of Standards samples.

The raw data which are in counts per minute are converted to mgC in exactly the same way as they are for the phytoplankton. In order to express these values as mg C·m$^{-2}$·day$^{-1}$, it is necessary to know the biomass distribution. All the productivity values given in the paper are expressed as mg C·m$^{-2}$ of lake surface.

All observations on *Isoetes occidentalis* were made at Station B while those on *Vallisneria* sp. were made at Station D (Fig. 1). On a given sampling day, three light and one opaque chamber measurements were made for each species.
Fig. 3. Oxygen combustion flask showing:

A - platinum carriage holding encapsulated sample,
B - stopcock, and
C - capillary tube.
The collection of the biomass data was complicated by the heterogeneous distribution of the plants. Accordingly, with the use of SCUBA, a thorough map was made of the submergent distribution (Fig. 4). Samples were then collected along transects within 1 m² quadrats. Great care was taken to obtain extensive samples for each time period and, further, to obtain the roots or rhizomes where possible as these may represent a considerable portion of the biomass. SCUBA greatly facilitated this, although the productivity of Potamogeton natans may be underestimated because the roots of this plant break very easily.

From these samples wet and organic weights were obtained. The organic weight is calculated by subtracting the ash weight from the dry weight. It is assumed to be the best criterion of biomass since it is free from errors due to variable water and ash contents (Westlake, 1963). Carbon analyses were performed on the four species of macrophytes in order to determine the percentage of organic carbon when related to organic weight. All the values obtained fitted in the range published by Westlake (1963), and it was decided that the value of 47% was representative. This figure, therefore, was used to convert the biomass figures to mg C.

The weighing, drying, and ashing methods used agree with those outlined by Westlake (1965a).
Fig. 4 Vegetation map of Marion Lake, British Columbia, 1966.

The lake was surveyed with the aid of SCUBA.
RESULTS

The average productivity of the phytoplankton in Marion Lake was 8.04 mg C m\(^{-2}\) day\(^{-1}\). The average productivity of the submerged macrophytes was 33.2 mg C m\(^{-2}\) day\(^{-1}\), determined by using the \(^{14}\)C method. The organic weight method indicated that the combined productivities of the submerged and floating macrophytes was 18.8 mg C m\(^{-2}\) day\(^{-1}\), this value being obtained by finding the area under the productivity curve shown in Fig. 5. All values are corrected for the total lake area.

The \(^{14}\)C method of measuring the productivity of the macrophytes yields consistently higher results than does the organic weight method, but no matter which method is considered, the productivity of the macrophytes is always higher than that of the phytoplankton (Table I). The values shown in the third column of the table represent the ratio of the productivities as measured by the two methods.

Table II records, for each of the species of macrophytes, the initial and maximum biomass in g C m\(^{-2}\) of lake surface. A cumulative net productivity is derived for each species at the time when the total organic weight was at a maximum (mid-August). Although the area covered by each species of plant was comparable, it can be seen that the productivity of the floating aquatics is greater than that of the submerged plants by a factor of ten.

A measure of reliability of the sampling program used in the field, and in the laboratory analyses, is given in Tables III, IV, and
V. A standard error equal to 10% of the mean is considered tolerable in most ecological studies (Watt, 1968) and it can be seen that this value is never greatly exceeded. Some of the variability in the Vallisneria sp. material may be attributed to the fact that this species grew throughout the time of the study by vegetative means, and it was often a subjective decision as to what constituted an individual plant.

There was a unimodal temporal pattern in the primary productivity of the phytoplankton in Marion Lake, with the peak of production occurring in early August (Fig. 6). It is also evident that differences in productivity between closely occurring days was sometimes considerable. Although the productivity of the macrophytes was based on fewer determinations, a peak was observed in late June followed by a steady decline, until by mid-September there was relatively little productivity (Fig. 6).

The temporal variation in productivity values derived from the organic weight data is somewhat clearer. There is a bimodal curve of productivity with a minor peak occurring in early June followed by a rapid increase in productivity to a major peak in mid-August. The individual curves for three of the species (Potamogeton natans, Nuphar sp., and Vallisneria sp.) reflect, with minor variations, the overall pattern (Fig. 7). Isoetes occidentalis apparently reverses this pattern, exhibiting a major peak in its productivity in late May and a minor peak in mid-August.
Fig. 5. Productivity of the aquatic macrophytes in Marion Lake, April to September, 1966, as determined by organic weight method.
MACROPHYCE PRODUCTIVITY

PRODUCTIVITY IN mgC·m⁻²·day⁻¹

APRIL  MAY  JUNE  JULY  AUGUST  SEPTEMBER
Fig. 6. Comparison of the productivity of the phytoplankton and macrophytes as determined by $^{14}$C method.
Fig. 7. Comparison of the productivities of the four important macrophytes in Marion Lake, April to September, 1966, as determined by the organic weight method.
Table I. Comparison of productivity of macrophytes and phytoplankton in Marion Lake, 1966. Blank values indicate that net respiration equals or exceeds photosynthesis.

Productivity in mg C $\cdot$ m$^{-2}$ $\cdot$ day$^{-1}$

<table>
<thead>
<tr>
<th>Date</th>
<th>Submerged aquatics C-14 method</th>
<th>Submerged aquatics organic wt. method</th>
<th>Ratio</th>
<th>Phytoplankton C-14 method</th>
<th>Total Macrophytes organic wt. method</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 28</td>
<td>44.2</td>
<td>4.2</td>
<td>11/1</td>
<td>2.2</td>
<td>10.8</td>
</tr>
<tr>
<td>June 10</td>
<td>40.7</td>
<td>3.2</td>
<td>12/1</td>
<td>1.4*</td>
<td>22.9</td>
</tr>
<tr>
<td>June 30</td>
<td>73.8</td>
<td>2.4</td>
<td>31/1</td>
<td>2.3*</td>
<td>16.4</td>
</tr>
<tr>
<td>July 17</td>
<td>31.5</td>
<td>1.7</td>
<td>17/1</td>
<td>2.2*</td>
<td>21.3</td>
</tr>
<tr>
<td>Aug. 4</td>
<td>32.9</td>
<td>2.7</td>
<td>12/1</td>
<td>2.9*</td>
<td>42.1</td>
</tr>
<tr>
<td>Aug. 18</td>
<td>18.1</td>
<td>2.9</td>
<td>6/1</td>
<td>2.7*</td>
<td>34.3</td>
</tr>
<tr>
<td>Sept. 5</td>
<td>2.2</td>
<td>-</td>
<td></td>
<td>2.1*</td>
<td>-</td>
</tr>
<tr>
<td>Sept. 15</td>
<td>2.6</td>
<td>-</td>
<td></td>
<td>0.8</td>
<td>-</td>
</tr>
</tbody>
</table>

* Values marked with an asterisk are from day closest to sampling date.
Table II. Distribution and cumulative net productivities of the four species of macrophytes in Marion Lake, 1966. Numbers in parentheses represent number of plants involved in determination.

<table>
<thead>
<tr>
<th>Species</th>
<th>Area % of total</th>
<th>Depth Range in meters</th>
<th>Biomass (gC/m²)</th>
<th>Productivity (mgC·m⁻²·day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potamageton natans</td>
<td>7.0</td>
<td>0-2.0</td>
<td>0.5 (10)</td>
<td>12.2 (10)</td>
</tr>
<tr>
<td>Nuphar sp.</td>
<td>5.0</td>
<td>0-2.5</td>
<td>4.2 (10)</td>
<td>34.2 (10)</td>
</tr>
<tr>
<td>Isoetes occidentalis</td>
<td>4.4</td>
<td>1.0-4.0</td>
<td>0.8 (10)</td>
<td>4.2 (10)</td>
</tr>
<tr>
<td>Vallisneria sp</td>
<td>5.8</td>
<td>0-3.0</td>
<td>0.4 (10)</td>
<td>2.2 (10)</td>
</tr>
<tr>
<td>Total</td>
<td>22.2</td>
<td>5.9</td>
<td>52.8</td>
<td>22.5</td>
</tr>
</tbody>
</table>
Table III. Variability in numbers of macrophytes between quadrats of one square meter.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of quadrats counted</th>
<th>Average number of plants per m²</th>
<th>Standard error as % of mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>May</td>
<td>Sept.</td>
</tr>
<tr>
<td>Isoetes occidentalis</td>
<td>10</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>Vallisneria sp.</td>
<td>10</td>
<td>29</td>
<td>45</td>
</tr>
<tr>
<td>Potamogeton natans</td>
<td>10</td>
<td>3</td>
<td>16</td>
</tr>
</tbody>
</table>
Table IV. Variability in fresh weights of individual plants.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of plants weighed</th>
<th>Average Weight (mg)</th>
<th>Standard Error as % of mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>April</td>
<td>Aug.</td>
</tr>
<tr>
<td>Potamogeton natans</td>
<td>10</td>
<td>2.4</td>
<td>10.9</td>
</tr>
<tr>
<td>Nuphar sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>deep</td>
<td>10</td>
<td>667.4</td>
<td>3644.6</td>
</tr>
<tr>
<td>shallow</td>
<td>10</td>
<td>265.0</td>
<td>1812.0</td>
</tr>
<tr>
<td>Isoetes occidentalis</td>
<td>10</td>
<td>2.6</td>
<td>13.6</td>
</tr>
<tr>
<td>Vallisneria sp.</td>
<td>10</td>
<td>0.4</td>
<td>0.6</td>
</tr>
</tbody>
</table>
Table V. Variability in drying and ashing techniques. Each percentage represents a mean value obtained from ten plants.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dry weight as % of fresh</th>
<th>Standard Error as % of mean</th>
<th>Ash weight as % of dry</th>
<th>Standard Error as % of mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potamogeton natans</td>
<td>15.0</td>
<td>14.1</td>
<td>2.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Nuphar sp.</td>
<td>10.5</td>
<td>7.7</td>
<td>9.7</td>
<td>7.3</td>
</tr>
<tr>
<td>Isoetes occidentalis</td>
<td>11.2</td>
<td>10.7</td>
<td>8.1</td>
<td>8.1</td>
</tr>
<tr>
<td>Vallisneria sp.</td>
<td>13.9</td>
<td>13.0</td>
<td>3.6</td>
<td>4.5</td>
</tr>
</tbody>
</table>
Table VI. Comparisons of the annual mean primary productivity of Borax Lake, California (Wetzel, 1964) to the values for Marion Lake, British Columbia; data in parentheses are values for the growing season and are in mg C·m$^{-2}$·day$^{-1}$.

<table>
<thead>
<tr>
<th></th>
<th>Borax Lake</th>
<th>Marion Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual Mean Productivity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mgC·m$^{-2}$·day$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>249.3</td>
<td>&lt;2.0</td>
</tr>
<tr>
<td>Periphyton</td>
<td>731.5</td>
<td>-</td>
</tr>
<tr>
<td>Macrophytes</td>
<td>76.5 (372.3)</td>
<td>7.1 (18.8)</td>
</tr>
</tbody>
</table>
DISCUSSION

Marion Lake may be characterized by a very low level of phytoplankton productivity and a relatively high macrophytic productivity. The rates obtained in this study are only estimates, but it is clear that there is agreement between the $^{14}$C method and the organic weight method, as to the relative importance of the macrophytes in the lake.

There is, however, considerable difference between the estimates of the productivity of the macrophytes made by the two different methods. The $^{14}$C method gives an instantaneous measure of net productivity and there is no correction for respiration in the dark. The organic weight method, since it involves longer periods of time, corrects for rapidly changing environmental conditions which might influence the rate of carbon fixation and also allows for respiration in the dark. This method is considered to give an estimate of net productivity if the community experiences a marked annual fluctuation in its biomass and if it suffers few losses from grazing or death (Westlake, 1963). There is no quantitative evidence from Marion Lake to justify the acceptance of the latter two assumptions, but repeated observations indicated that there was little damage done by grazing. According to Westlake (1965a), some aquatic macrophyte communities are scarcely subject to grazing and their production is mostly consumed by bacteria and detritus feeders. This would appear to be the case in Marion Lake, since most of the herbivores found on the plants appeared to be browsing on the attached algae.
It is now clear from a number of phytoplankton studies, where the $^{14}\text{C}$ method has been used, that there is considerable variation in productivity both within days and between days (Rhodhe et al., 1958). It is possible, therefore, to explain the lack of a clear temporal pattern in the data, by the infrequent nature of the sampling periods. It is better to sample every day, or where this is not possible, for several consecutive days each month, in order to make a reasonable estimate of productivity. Another source of variability in estimating the productivity of the phytoplankton, arises from the fact that the variability between stations at one time is nearly the same as the variability at one station and one depth over a period of ten days (Efford, 1967). The two index stations used for the phytoplankton tend to give somewhat higher values than the stations farther south, therefore giving a somewhat exaggerated estimate of the productivity.

The same kind of variability is inherent in the rates determined by measuring the productivity of the macrophytes with $^{14}\text{C}$. These values are further influenced by the probability that, with few replicates, the experimental plants could be in different physiological states.

The productivity of the phytoplankton in Marion Lake, however, is surprisingly low when compared with that of other temperate zone lakes. Recent unpublished data supports the hypothesis that the rapid flushing of the lake (sometimes within two to three days) prevents any substantial increase in the phytoplankton population, thereby reducing the rate of carbon fixation (Dickman, personal communication).

It is very difficult to compare the data from Marion Lake with that obtained from studies on other lakes because of the wide variety of
techniques and sampling procedures involved. Westlake (1965b) has recently made an appeal to standardize observational procedures and suggests that one of the main functions of the International Biological Programme should be to recommend methods based on common principles and to obtain internationally comparable observations of the basic biological parameters.

Of all the freshwater productivity studies, there is only one that lends itself to comparison with the Marion Lake study, that of Wetzel (1964). From his study, Borax Lake is more productive than Marion Lake, but the relative importance of the macrophytic productivity is greater in Marion Lake (Table VI).

A considerable growth of the periphytic algae, Mougeotia spp., was observed in Marion Lake throughout the summer, but their productivities were not monitored owing to the difficulty of placing the experimental chambers over the algae without displacing them or covering them with bottom sediments. It is possible that the periphyton is very important in fixing energy; its importance in supporting a large crop of herbivores has already been observed.

Emergent communities are generally considered to be more productive than submerged ones (Westlake, 1963). Much of the littoral zone of Marion Lake is covered with emergent plants and it is likely that a consideration of their productivity, as well as that of the periphyton, would increase considerably the total estimated productivity. Organic weight criteria would have to be used as no convenient way has yet been devised to measure accurately the in situ carbon fixation for these plants.
LITERATURE CITED


