Factors Affecting the Contribution by Epiphytic Algae to the Primary Productivity of an Oligotrophic Freshwater Lake

RICHARD B. SHELDON AND CHARLES W. BOYLEN*

Department of Chemical and Environmental Engineering, and Freshwater Institute and Department of Biology,* Rensselaer Polytechnic Institute, Troy, New York 12181

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A diatom-dominated population of epiphytic algae was studied in an oligotrophic lake to determine the factors which limit epiphyte growth and to measure their contribution to primary productivity. Algae were collected from plants growing at four sites in Lake George, N.Y., during the spring, summer, and fall of 1974. Samples were taken from 3 m, corresponding to the depth at which macrophytes were most productive. Algae exhibited an optimum temperature for H\textsuperscript{14}CO\textsubscript{3}\textsuperscript{-} uptake at 30 C, although the summer littoral lake temperature ranged from 18 to 25 C. Light saturation occurred at an intensity of 8,608 lux, approximating the environmental intensity at the depth from which algae were taken. Epiphytes exhibited their maximum photosynthetic capacity of 0.6 mg of carbon fixed/m\textsuperscript{2} of macrophyte surface area per h in the early afternoon in mid-August. They assimilated approximately 5% as much inorganic carbon as the macrophytes from which they were taken. Epiphyte population densities followed the seasonal growth patterns of the macrophytes, with maximal leaf colonization remaining essentially constant relative to the leaf position on the plant. There was little change in density between sampling sites at any given time. Productivities of epiphytes from bottom leaves were 10-fold greater than those of epiphytes from top leaves. Addition of PO\textsubscript{4}\textsuperscript{3-}, NO\textsubscript{3}\textsuperscript{-}, NH\textsubscript{3}, Si, and SO\textsubscript{4}\textsuperscript{2-} had no stimulatory effect on photosynthesis. Addition of HCO\textsubscript{3}\textsuperscript{-} stimulated photosynthesis greater than 30%, suggesting that carbon may be a limiting nutrient for epiphytic algae in Lake George.

Investigations attempting to understand the complex ecological interrelationships existing in aquatic environments have frequently overlooked the role of the epiphytic community. The exact meaning of the term "epiphyte" is itself a subject of disagreement, as is illustrated by examination of the literature. Ruttner (23) defines them as unrooted plants which use other plants as a substrate without penetrating into them and without withdrawing nutrient substances from them. A subdivision of the German concept of the entire sessile benthic community known as "Aufwuchs" or of the more Americanized term "periphyton," the term is used to identify the organisms growing upon the free surfaces of submerged objects in water. Other investigations base their terminology on the presence or absence of associations between the individual sessile organisms on the fixed substrata. Wetzel (28) suggests the usage of the term "periphyton" modified by an appropriate adjective such as epipellic (on the surface of sediments), epilithic (on the surface of rocks), and epiphytic (on the surface of submerged aquatic plants). Allen (2) uses Wetzel's term "epiphytic periphyton" to describe both the attached algae and bacteria on aquatic plants.

In many aquatic environments, the epiphytes have been shown to be an important productive component of the ecosystem. A study of the algal epiphytes of Utricularia in the Everglades National Park suggests the possibility that the epiphytes rather than their macrophyte hosts are responsible for most of the primary production (7). The epiphytic algae in the littoral zone of a small shallow lake in Michigan were shown to contribute approximately 31% of the littoral primary production (2). The productivity of the epiphytes in a small English pond were shown to exceed that of the phytoplankton (15), whereas in a marine environment the blue-green epiphyte Dicothrix contributed 15% of the coastal Sargassum community production (9). The epiphytic alga Oedogonium, which forms a surface mat on Myriophyllum spicatum in Lake Wingra, Wisconsin, was also shown to be an important producer (18).

The purpose of this research has been to ascen-
tain the role of the epiphytic algae in the primary productivity of the littoral zone of Lake George, an oligotrophic glacier-formed lake situated in the Adirondack Mountains of Eastern New York State. Objectives have been to determine: (i) the physical and chemical factors which limit or stimulate epiphyte growth; (ii) the variations in the role of the epiphytes due to environmental influences such as season, location, depth, and macrophyte host; (iii) the identity of the organisms comprising the epiphytic algal communities; and (iv) the percentage of the littoral macrophyte community production attributed to the epiphytic algae.

MATERIALS AND METHODS

Sample collection. There are over 40 species of rooted macrophytes commonly found in the littoral zone of Lake George (E. C. Ogden, K. Dean, C. W. Boylen, and R. B. Sheldon, Aquatic Plants of Lake George, New York, in press). The epiphytic populations may be suspected to vary depending on the macrophyte species with which the community is associated. To do a comprehensive study of the communities found on each of the many species would be highly impractical. Therefore, experiments were performed on algal assemblages taken from plants of a single species, Potamogeton amplifolius, common throughout Lake George, predominating at a 3-m depth (6). Data were collected from June through October, 1974.

Lake George consists of two basins partially separated near the middle by an area known as the "Narrows" (Fig. 1). Traditionally the lake has been classified as oligotrophic; however, in recent years with increased urbanization the southern half has become considerably productive. There exists a five-fold difference in rooted macrophyte productivity between the two basins (R. B. Sheldon and C. W. Boylen, submitted for publication). Three experimental sites were chosen for seasonal measurements, one each in the southern and northern basins and a third station near the only outlet for Lake George at TiCorderoga, New York, which supported a heavy growth of macrophytes atypical of the northern basin. Smith Bay, location of the Rensselaer Freshwater Institute, provided a source of epiphyte populations for nonseasonal experimentation.

Leaves from plants of P. amplifolius and associated epiphytes were collected in triplicate by divers at a 3-m depth using self-contained underwater breathing apparatus. Leaves were removed from the fourth to sixth position from the top of the macrophyte and placed in empty, inverted 125-ml Erlenmeyer flasks allowing for minimum loss of epiphytes from the leaves. The flasks were recapped underwater, brought to the surface, and returned to the laboratory. Epiphytes were removed from the leaves by swirling in lake water, followed by rinsing the leaf surface with a water spray. Leaves were fragile and easily torn by more vigorous treatment. It was estimated by microscopic inspection that this procedure removed more than 95% of the algae attached to the leaf surface. The washed leaf was placed in a 160-ml milk dilution bottle containing 100 ml of lake water. The epiphyte solution was adjusted to 100-ml total volume in lake water. Sample water temperature and pH were taken to insure that samples remained at lake values. Samples containing the intact leaf and epiphytic community were placed directly in bottles containing 100 ml of lake water.

For standardization of values all comparisons between macrophyte and epiphyte productivity were expressed as grams of carbon assimilated per hour per unit of surface area of the host macrophyte. The dry weight-to-wet weight ratio was determined experimentally and was used in conversions from wet weight to dry weight and ultimately to leaf surface area (Fig. 2).

Radioactive tracer experiments. The hourly rates of net photosynthesis were determined using a modification of Wetzel (29). After 15 min for thermal equilibration, 1 μCi of NaH\(^{14}\)CO\(_3\) at pH 9.5 (New England Nuclear Corp.; specific activity, 100 μCi of NaHCO\(_3\) per mg) was injected into each bottle. Incubations were run in duplicate with one dark control for 2 h on a rotating drum in an algal growth chamber (Chesapeake Bay Institute, Johns Hopkins University, Annapolis, Md.) equipped with a fluorescent light source rheostat controlled to yield a maxi-

![Fig. 1. Map of Lake George, N.Y., showing the four sampling stations.](image-url)
The validity of laboratory studies in evaluating the role of the epiphytes in their aquatic habitat necessitated a comparison between in situ incubations and incubation in an algal growth chamber. Close agreement in photosynthetic rates were obtained, indicating that environmental parameters such as light intensity, temperature, and agitation could be satisfactorily duplicated in the laboratory.

Photosynthetic rate determination. The photosynthetic rates of the epiphytes and macrophytes were calculated in terms of inorganic carbon fixation. The conversion from radioactivity (disintegrations per minute) to photosynthetic rate was accomplished according to nomographic procedures given in Standard Methods (3). Measurements were made of pH, temperature, and dissolved filtrable residue. Total alkalinity was determined by titration with 0.02 N HCl to pH 4.4. Knowing the volumes of the incubation solutions, the amount of carbon fixed in a given time interval was calculated as follows: milligrams of carbon fixed = sample activity/added activity × milligrams of initial inorganic carbon × 1.064 (isotope effect). The use of alkalinity data to determine inorganic carbon concentrations was substantiated by infrared spectrophotometry, indicating negligible contributions by noncarbon forms of alkalinity.

Nutrient stimulation. Using N as KNO3, NH4Cl, P as KH2PO4, S as K2SO4, Si as Na2SiO3, and C as NaHCO3, nutrients were added to 100-ml suspensions of epiphytic algae in lake water and were incubated with NaH14CO3 for 2 h in the algal growth chamber. Control samples containing no additional nutrients were used to determine the unstimulated photosynthetic rates.

RESULTS

Effect of physical parameters. Temperature has previously been found to be an important variable in algal photosynthesis (2, 5). An experiment was performed in midsummer to determine the effect of temperature variation on the photosynthetic rate of epiphyte communities. The results presented in Fig. 3a indicate a temperature optimum of 30°C. This is slightly higher than the maximum summer environmental temperature of 24°C occurring in early August.

Since epiphytes were always taken from leaves of plants growing at 3 m, it was necessary to determine what effect light intensity had on epiphyte photosynthesis. Photosynthetic rates were determined at various intensities up to 19,368 lux, yielding the curve presented in Fig. 3b. Maximum photosynthesis occurred at approximately 8,608 lux, with a slight decrease thereafter. The decline at higher light intensities may be due to photosynthetic inhibition (13). All subsequent laboratory experiments were carried out at 8,070 lux in the algal growth chamber. The time of day had a notice-

FIG. 2. Relationship among macrophyte dry weight, wet weight, and surface area of leaves from P. amplifolius collected at 3 m. Two independent collections were made. Symbols: O, dry weight-to-surface area ratio; ·, dry weight-to-wet weight ratio.

![Graph](attachment:image.png)
Relative contributions from epiphytes and macrophytes to littoral productivity. For the purpose of comparing the photosynthetic rates of the epiphytes at different locations in Lake George, the epiphyte photosynthetic rate was expressed in terms of the surface area of the macrophyte leaf from which the epiphytes were taken. To ascertain the significance of the epiphytic population in this process, comparisons were made by determining the photosynthetic rates of the macrophyte leaves alone, epiphytes alone, and the intact macrophyte-epiphyte system. The latter determination yielded results which were highly variable, because the epiphyte communities were very small and contributed to the overall photosynthesis in an amount less than the inherent variability in photosynthetic rates of the macrophyte leaves themselves.

The seasonal epiphyte photosynthetic rates at various locations in Lake George are presented in Fig. 4a. All experiments were performed under conditions of light saturation and ambient lake temperature. When the epiphyte photosynthetic rate is expressed as a percentage of the total photosynthetic rate of the leaf plus epiphytes, the extent of the epiphyte contribution to productivity is obtained on a seasonal basis (Table 2). In most instances, the epiphytes contributed a slightly greater percentage of the total productivity in Warner Bay than at the other two stations. The average contribution of the epiphytes was approximately 5% of that for their macrophyte host, P. amplifolius. Epiphyte biomass estimates were performed simultaneously with the photosynthetic rates at the three stations from June to October, 1974 (Fig. 4b). Peak epiphyte biomass was obtained in midsummer for both Warner and Hearts Bay and slightly later for the outlet station.

The epiphytic communities were found to differ in productivity with respect to their position on the macrophyte. The data in Table 3 indicate

![Graph](image.png)

**Fig. 3.** Uptake of H\(^{14}\)CO\(_3\)\(^{-}\) by epiphytes from P. amplifolius as a function of temperature (a) and light intensity (b). Triplicate samples were removed from plants collected at 3 m, and homogeneous aliquots were incubated in the presence of 1 µCi of NaH\(^{14}\)CO\(_3\) for 2 h. Graphs (a) and (b) represent independently collected samples. Graph (a) has been corrected for dark controls. Bars represent range of values obtained.

Table 1. Diurnal variation in epiphyte in situ photosynthetic rate*

| Incubation period | Avg light intensity at 3 m (lux) | Avg \(^{14}\)C uptake (dpm) ± SD | % of maximum |
|-------------------|---------------------------------|---------------------------------|--------------|
| 8 a.m.–10 a.m.   | 5,380                           | 7,696 ± 627                     | 56.4         |
| 12 p.m.–2 p.m.   | 8,070                           | 13,634 ± 2,683                  | 100.0        |
| 4 p.m.–6 p.m.    | 5,918                           | 8,387 ± 3,660                   | 61.5         |

* The experiment was performed in triplicate with corrections for dark controls. Light intensities are low due to cloud cover throughout the experimental period. Surface light intensity ranged from 21,520 to 37,660 lux. SD, Standard deviation.
that the epiphytic algae on lower leaves were more productive than those on upper leaves. Because older leaves of \( P. \) amplifolius were less productive than younger leaves, the relative productivity contribution by the epiphytes increased substantially on older leaves. Although \( P. \) amplifolius was used throughout most of this study, a comparison of the epiphytic communities of three other species of rooted macrophytes was made. Results are presented in Table 4. They indicate that the epiphyte community associated with \( N. \) flexilis was the most highly productive for the four macrophyte species studied. Although \( P. \) amplifolius grows most abundantly at the 3-m depth, the plant does grow at a range between less than 1 to 5 m. The variability in the productivity of the epiphytes taken from plants growing at different depths was investigated. Table 5 indicates that, although the epiphytes were more productive at the 3-m depth, the relative epiphyte biomass contribution was greatest at the 1-m depth.

Nutrient studies. To determine if nutrient limitation exists for epiphytes in Lake George, an experiment was designed in which different amounts of nutrients were added to the lake water in which the epiphyte incubations were performed. Any change in photosynthetic rate was detected by expressing the ratio of the photosynthetic rate of the solutions containing additional nutrients to the photosynthetic rate of a control group of epiphytes which had no added nutrients. The results are presented in Table 6. In this experiment most of the nutrients result in an inhibition of growth, with the exception of bicarbonate, which stimulated the growth rate by as much as 30% in a 2-h period. This would indicate the possibility that carbon is the limiting nutrient for epiphytes in Lake George. The bicarbonate stimulation data are represented graphically in Fig. 5. The slight change in pH (7.4 to 8.3) due to bicarbonate addition probably would not be responsible for the increase in photosynthetic rate, as indicated by studies on carbon limitation by Allen (1), since a pH rise would decrease the available CO\(_2\).

Algal floristic studies. The relative abundances of the various epiphytic diatoms present in the northern and southern basins of Lake George during the investigation period (June through October, 1974) are found in Table 7. The nondiatom algae represented an insignificant contribution to the epiphytic communities. The total concentrations of diatoms present on the middle leaves of \( P. \) amplifolius were highly variable, with densities ranging between \( 3 \times 10^6 \) and \( 1.4 \times 10^6 \) diatoms/m^2 of leaf surface area. The major nondiatom components of the epiphytic community include the green algae Protodera, Scenedesmus, Sporygyra, and Mougeottia, the blue-green algae Nostoc, Spirulina, and Oscillatoria, and the desmid Cosmarium.

**DISCUSSION**

A number of factors have been shown to be of considerable importance in regulating the growth of epiphytic algae in Lake George. Since the temperature optimum for epiphyte growth was 30 C and the maximum lake water temperature was 24 C, it is evident that temperature is a rate-controlling factor for photosynthesis in natural algal assemblages. Canale and Vogel (8) have likewise demonstrated a growth rate optimum of 30 C for diatoms. Any future rise in the seasonal lake water temperature would be expected to increase the productivity of the present epiphyte community (23).
TABLE 2. Relative contribution to littoral production by epiphytic algae

| Station       | Sample          | Sample date          |
|---------------|-----------------|----------------------|
|               |                 | 6/29/74 | 7/18/74 | 8/15/74 | 9/17/74 | 10/24/74 |
| Warner Bay    | Macrophyte      | 7.75 ± 0.05 | 4.51 ± 0.01 | 4.72 ± 0.16 | 5.45 ± 0.53 | 2.21 ± 0.60 |
|               | photosynthetic  |          |          |          |          |          |
|               | rate (mg of C/m² of leaf surface area per h) |          |          |          |          |          |
|               | Epiphyte        | 0.21 ± 0.02 | 0.44 ± 0.02 | 0.39 ± 0.01 | 0.23 ± 0.02 | 0.07 ± 0.02 |
|               | photosynthetic  |          |          |          |          |          |
|               | rate (mg of C/m² of leaf surface area per h) |          |          |          |          |          |
|               | Relative        | 2.64 | 8.89 | 7.63 | 4.05 | 3.07 |
|               | epiphyte        |          |          |          |          |          |
|               | contribution (%) |          |          |          |          |          |
| Hearts Bay    | Macrophyte      | 11.27 ± 0.16 | 7.13 ± 0.25 | 9.18 ± 0.05 | 2.67 ± 1.06 | 1.43 ± 0.74 |
|               | photosynthetic  |          |          |          |          |          |
|               | rate (mg of C/m² of leaf surface area per h) |          |          |          |          |          |
|               | Epiphyte        | 0.02 ± 0.01 | 0.21 ± 0.02 | 0.58 ± 0.14 | 0.21 ± 0.02 | 0.01 ± 0.00 |
|               | photosynthetic  |          |          |          |          |          |
|               | rate (mg of C/m² of leaf surface area per h) |          |          |          |          |          |
|               | Relative        | 0.18 | 2.86 | 5.94 | 7.29 | 0.69 |
|               | epiphyte        |          |          |          |          |          |
|               | contribution (%) |          |          |          |          |          |
| Outlet        | Macrophyte      | 6.58 ± 0.62 | 4.55 ± 1.10 | 8.26 ± 1.59 | 3.77 ± 0.87 | 0.74 ± 0.28 |
|               | photosynthetic  |          |          |          |          |          |
|               | rate (mg of C/m² of leaf surface area per h) |          |          |          |          |          |
|               | Epiphyte        | 0.05 ± 0.02 | 0.12 ± 0.01 | 0.32 ± 0.02 | 0.14 ± 0.02 | 0.09 ± 0.02 |
|               | photosynthetic  |          |          |          |          |          |
|               | rate (mg of C/m² of leaf surface area per h) |          |          |          |          |          |
|               | Relative        | 0.75 | 2.57 | 3.73 | 3.58 | 10.84 |
|               | epiphyte        |          |          |          |          |          |
|               | contribution (%) |          |          |          |          |          |
| Average water | temperature at 3 | | | | | |
| m (C)         |                 | | | | | |

* Relative epiphyte contribution is the percent contribution by the epiphytic algae to the total primary productivity of the leaf and epiphyte constituents. Data from samples taken from Smith Bay under the ice on 3/13/75 indicate that, although P. amplifolius and its algal epiphytes are still viable, the epiphyte contribution to primary productivity during the winter is less than 1%. Data for photosynthetic rates are presented as mean ± standard deviation.

TABLE 3. Variation in epiphyte productivity with leaf position

| Leaf position | Avg photosynthetic rate ± SD* (mg of C/m² of leaf surface area/h) | Relative epiphyte contribution (%) | Epiphyte dry weight (g/m² of leaf surface area) |
|---------------|---------------------------------------------------------------------|------------------------------------|-----------------------------------------------|
| Top           | 4.69 ± 1.20             | 0.02 ± 0.01                        | 0.42                                           |
| Middle        | 4.90 ± 0.14             | 0.12 ± 0.05                        | 2.39                                           |
| Bottom        | 1.82 ± 0.53             | 0.37 ± 0.14                        | 16.89                                          |

* SD, Standard deviation.

TABLE 4. Productivity of four macrophyte species and associated epiphytes

| Species              | Avg photosynthetic rate ± SD* (mg of C/m² of leaf surface area/h) | Relative epiphyte contribution (%) | Epiphyte biomass (g/m² of leaf surface area) |
|----------------------|-------------------------------------------------------------------|-----------------------------------|---------------------------------------------|
| Potamogeton amplifolius | 4.72 ± 0.16               | 0.39 ± 0.00                     | 7.63                                        |
| Potamogeton robbinsi | 2.60 ± 0.30             | 0.05 ± 0.02                     | 1.89                                        |
| Vallisneria americana | 4.16 ± 1.24              | 0.23 ± 0.02                     | 5.24                                        |
| Najas flexilis       | 3.59 ± 0.44             | 0.74 ± 0.44                     | 17.09                                       |

* SD, Standard deviation.

However, a rise in seasonal temperature would not necessarily result in increased activity, since population changes may occur (5). Patrick (22) suggests 30 C as the temperature above which the composition of benthic algae shifts from diatoms to greens. Although light intensity to the 3-m depth indicated saturation for most of the daylight hours, the epiphytic com-
The diurnal effect observed for the epiphytes in situ indicated maximum photosynthesis in the early afternoon. This is not consistent with the theory of midday photosynthetic inhibition (4) but may be explained by the overcast sky during the experimental period or the reduction in light intensity at the 3-m depth. Stross et al. (26) suggest the role of nutrients in affecting daily rhythms in photosynthetic rates of Lake George phytoplankton.

The epiphytes exhibited their maximum photosynthetic capacity in midsummer, which averaged slightly higher in Warner Bay, further suggesting the influence of human activity in the southern basin. The epiphytic algae contributed to the primary productivity of the macrophyte-epiphyte communities a seasonal average of 5.3% in Warner Bay, 3.4% in Hearts Bay, and 4.3% at the outlet (Table 2). The value of 10.8% obtained at the outlet in October can be seen more as a reflection of the faster decline in macrophyte productivity than an indication of increased epiphytic algal growth. The epiphytes were responsible for less than 1% of the macrophyte-epiphyte winter productivity as determined from samples taken under the ice in Smith Bay during the winter of 1975. Winter

![Graph](image-url)

**Fig. 5. Stimulation of epiphytic algal photosynthetic rates by the addition of bicarbonate. Values are based on triplicate determinations and include corrections for radioisotope dilution and dark controls. Rates are expressed as milligrams of C per hour.**

TABLE 5. Variation in epiphyte productivity with water depth

| Depth (m) | Leaf | Epiphytes | Relative epiphyte contribution to productivity (%) | Epiphyte dry weight (g/m² of leaf surface area) |
|-----------|------|-----------|---------------------------------------------------|-----------------------------------------------|
| 1         | 1.73 ± 0.85 | 0.07 ± 0.02 | 3.89 | 3.92 |
| 3         | 4.90 ± 0.14 | 0.12 ± 0.05 | 2.39 | 2.23 |
| 5         | 4.97 ± 1.10 | 0.02 ± 0.02 | 0.46 | 2.78 |

* SD, Standard deviation.

TABLE 6. Nutrient stimulation of epiphyte productivity

| Nutrient added | Conc (mg/liter)* | Ratio photosynthetic rate (nutrient-control) |
|----------------|------------------|---------------------------------------------|
| Control, no additions | N, 0.025 | 1.000 |
| NH₄⁺ | N, 0.075 | 0.810 |
| NH₄⁻ | N, 0.225 | 0.897 |
| SO₄²⁻ | S, 5.000 | 0.803 |
| SO₄²⁻ | S, 15.000 | 1.142 |
| P| P, 0.050 | 0.838 |
| PO₄³⁻ | P, 0.015 | 0.806 |
| NO₃⁻ | N, 0.150 | 0.977 |
| NO₃⁻ | N, 0.500 | 0.943 |
| NO₃⁻ + PO₄³⁻ | N, 0.150, + P, 0.005 | 0.829 |
| NO₃⁻ + PO₄³⁻ | N, 0.500, + P, 0.015 | 0.392 |
| SiO₃²⁻ | Si, 1.00 | 0.480 |

* Concentration per liter does not include the amount present in the lake water prior to nutrient addition.

* 95% confidence limits are ± 0.084 as determined by pooling variances for all nutrient data after verification for Cochran's test (10).
productivity, although still measurable, was greatly reduced because of low temperatures and limited light due to ice cover.

Although excretion of photosynthate can be very high with some algal cells, the epiphytes removed from *P. amplifolius* excreted less than 1% of the carbon fixed during a 2-h incubation at 22 °C. In a study of phytoplankton populations containing diatom species similar to those found in Lake George epiphyte communities, less than 2% of the carbon fixed during short-term experiments was excreted under incubation conditions of population densities and inorganic carbon concentrations similar to those used in this investigation (19).

The photosynthetic rate maximum of 0.6 mg of C/m² of macrophyte surface area per h in mid-August for the Lake George epiphytes is on the order of 50 times less than the values obtained by Allen (2) in his studies on the epiphytes of *Scirpus acutus, Najas flexilis,* and *Chara* sp. in Lawrence Lake, Michigan (258 mg of C/m² of macrophyte surface area per day, average). Such values are typical of lakes more eutrophic than Lake George and can be as great as 2,300 mg of C/m² of surface area per day for the epiphytic community associated with *Myriophyllum spicatum* in Lake Wingra, Wisconsin (18).

The population densities of the epiphytic communities followed the seasonal growth patterns of the rooted macrophytes, with maximal leaf colonization remaining essentially constant relative to the leaf position on the plant. The average seasonal epiphyte biomass in grams (dry weight) of epiphytes per square meter of macrophyte surface area was 1.54 at the outlet, 1.12 in Hearts Bay, and 1.06 in Warner Bay. Both epiphyte and macrophyte productivity (Table 2), as well as population densities at the lake outlet, are atypical for the northern basin. This abundance may have been due to the visibly swift currents leaving the lake through the narrow-CHANNELLED outlet, bathing the plants in a continuous supply of nutrients. The data for Hearts and Warner Bay appear contradictory to the average seasonal productivity data presented in Table 2. This inconsistency may be explained by the inherent variations in dry-weight determinations due to the contribution by detrital materials. Biomass estimates by chlorophyll extraction methods yielded even more variable results due to the low concentrations of epiphytic algae present in all samples collected during the course of this study.

Other studies on epiphyte assemblages have been carried out in more eutrophic habitats than those present in Lake George. However, with increased urbanization of the villages around the southern half of this lake and the marsh areas draining only into the southern basin, nutrient levels can be expected to increase. Such input has already influenced the humic sediment character in the littoral areas of the southern basin (Sheldon and Boylen, unpublished data). These factors have resulted in a fivefold difference in macrophyte and epiphyte standing crops in the two basins (Sheldon and Boylen, submitted for publication). The epiphyte standing crop differences are more a reflection of greater macrophyte substrate area available for colonization than a reflection of greater epiphyte productivity, since epiphyte densities appear similar for all stations (Fig. 4b). Macrophytes have been shown to be the dominant producers in the littoral zone of Lake George (Sheldon and Boylen, submitted for publication). The maximum productivity occurred in Warner Bay and for all macrophytes was 140 mg of C/m² of littoral area per h, 10.4 mg of C/m² of littoral area per h for epiphytes, and 12.9 mg of C/m² of littoral area per h for phytoplankton at the 3-m depth. In deeper regions the contribution by the phytoplankton in-

| Species          | % Diatom populations* | North Basin† | South Basin† |
|------------------|-----------------------|--------------|--------------|
| Achnanthes sp.   | 3.3                   | 0.8          |              |
| Asterionella formosa | 4.6               | 0.0          |              |
| Cocconeis placentula | 2.1               | 1.6          |              |
| Cyclotella sp.   | 8.3                   | 13.1         |              |
| Cymbella cistula | 6.7                   | 8.2          |              |
| Diatoma sp.      | 4.2                   | 13.9         |              |
| Diatomsella sp.  | 4.6                   | 0.8          |              |
| Eunotia sp.      | 2.1                   | 0.0          |              |
| Fragilaria sp.   | 2.9                   | 0.0          |              |
| Gymphonema acuminatum | 3.8             | 4.1          |              |
| Melosira sp.     | 1.7                   | 6.6          |              |
| Meridion circulare | 0.0                | 0.8          |              |
| Nauicula sp.     | 18.8                  | 12.3         |              |
| Nitzschia sp.    | 3.8                   | 4.9          |              |
| Pinularia nobilis | 2.5                  | 1.6          |              |
| Rhizosolenia eternis | 0.4               | 0.0          |              |
| Rhopalodia gibba | 2.5                   | 2.5          |              |
| Stauroeis phoenicentron | 0.4      | 1.6          |              |
| Stephanodesmus astra | 4.6               | 2.5          |              |
| Surirella sp.    | 0.4                   | 0.0          |              |
| Synedra sp.      | 5.4                   | 21.3         |              |
| Tabellaria sp.   | 17.1                  | 3.3          |              |

* Algae were preserved in formalin at a final concentration of 4% and identified by the keys of Ward and Whipple (27) and Needham and Needham (21).
† Percentage is expressed in terms of total numbers of species.
‡ North Basin includes data from Hearts Bay, Smith Bay, and outlet.
§ South Basin includes data from Warner Bay only.

**Table 7. Composition of epiphytic diatom populations in Lake George**

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croases as a result of the greater volume of water, whereas the macrophyte and epiphyte contributions decrease due to light limitation. These hourly productivity values can be extrapolated to daily and seasonal productivities with certain limitations. All productivity data have been calculated from photosynthetic rates determined under conditions of light saturation (Fig. 3b). Since productivity data can vary greatly on a daily basis during a single season because of varying light input, these data indicate the potential contribution to littoral community productivity.

The productivity of epiphytes from the lower leaves was 10-fold greater than from the upper leaves, implicating the role of released nutrients in the decomposition of the lower leaves as well as the longer time available for colonization. The choice of *P. amplifolius* as the representative rooted macrophyte for sampling of epiphytic communities was supported by the determination that the relative epiphyte productivity for *P. amplifolius* fell between the maximum value obtained from *Najas flexilis* and the minimum value obtained from *P. robusta* (Table 4). Considerable morphological variation is exhibited by the four macrophyte species examined. The *Potamogeton* spp. produce single broad leaves born on stems and *V. americana* produces long ribbonlike leaves developing from a single basal position, whereas *N. flexilis* produces abundant, closely clustered leaves less than 1 mm wide and 20 mm long. Such variation may provide substrata for differing degrees of success of epiphyte attachment. The release of materials by these plants, which inhibit or stimulate epiphyte growth, is not known.

Nutrient levels in Lake George are indicative of the lake's current oligotrophic status (11). Phosphate levels throughout the lake are less than 5 μg of P/liter, and nitrate levels range from 4 to 12 μg of N/liter; the higher concentrations are found in the southern basin. Alkalinity ranges from 21 to 25 mg of CaCO₃/liter throughout the lake. A previous investigation on Lake George indicated that phosphorus was the limiting nutrient for *Nitella flexilis* (25). Fuhs et al. (12) found the addition of nitrogen and phosphorus to stimulate Lake George phytoplankton growth when administered simultaneously, but they also hypothesized the possibility of carbon limitation. Williams and Clesceri (31) suggest the possible seasonal variation in limitation by all three of the elements carbon, nitrogen, and phosphorus for the lake's diatom populations. They further suggest the possibility of a shift to other types of algae if the input of these nutrients continues to increase while the levels of silicon and manganese are maintained. The use of the ¹⁴C method of determining photosynthetic rates provides an excellent means of assessing nutrient limitation by evaluating the effects of nutrient additions on photosynthetic rates in algal stimulation studies. The addition of PO₄³⁻, NO₃⁻, PO₄³⁻ + NO₃⁻, NH₃, SiO₃²⁻, and SO₄²⁻ to epiphytic algae resulted in no stimulation of photosynthetic rate and in many cases had an inhibitory effect upon algal growth. In the case of Si, the inhibition may have been due to the rise in pH effected by addition of SiO₃²⁻. It is unlikely that Si is a limiting nutrient for diatoms in Lake George, since concentrations range from 215 μg/liter in the northern basin to 352 μg/liter in the southern basin (11). The addition of bicarbonate to algal epiphytes stimulated photosynthesis greater than 30% (when the decrease in specific radioactivity of the radioisotope was considered), suggesting that carbon may be the limiting nutrient for these communities in Lake George.

According to Liebig's Law of the Minimum, the total crop of any organism will be determined by the abundance of the substance that, in relation to the needs of the organism, is least abundant in the environment (16). Since carbon is the primary constituent of all organisms, it is likely to be a limiting nutrient, although in most instances it has not been found to be deficient since it is readily available as dissolved CO₂ from the atmosphere (24). The consideration of carbon as the limiting nutrient for epiphytes in Lake George would imply that the diffusion rate of atmospheric CO₂ was insufficient to support a maximal rate of photosynthesis. Kuentzel (17) has proposed a similar hypothesis concerning algal blooms resulting from CO₂ produced by bacterial decomposition. Goldman (14) elaborates on the controversy over carbon limitation. The possibility does exist that the bicarbonate stimulation observed in the epiphytes was actually a manifestation of luxury carbon uptake, a phenomenon that may occur in P-limited as well as N-limited algae (12). However, the epiphytes were found to be neither P nor N limited.

The low nutrient levels in Lake George are suggested to be a major factor maintaining a large species diversity of epiphytic algae. The heavier nutrient load in the southern basin is reflected by the decrease from 21 predominant diatoms in the northern basin to 17 predominant diatoms in the southern basin. A percent increase in the more eutrophic-associated diatom of the genus *Synedra* has occurred in the
southern basin in the short time since Williams and Clesceri (31) first suggested the shift in diatom populations due to trophic changes occurring in the lake. Genera common to oligotrophic freshwaters such as Cyclotella, Navicula, and Tabellaria are prevalent in the epiphytic communities of Lake George. In 1922, Needham et al. reported only four species of diatoms but included a greater relative abundance of green and blue-green algae (20).

The epiphytic algae of Lake George contribute a small amount to the total primary productivity of this aquatic ecosystem. For the present time their contribution is almost negligible, since the epiphytes are responsible only for approximately 5% of the littoral macrophyte-epiphyte component of the total lake primary productivity. The role of the epiphytes as food for grazing forms in the littoral zone is important. Should nutrient or other factors in the lake change so as to increase algal growth, the role of the epiphytes could be considerably enhanced. The results of this study in an oligotrophic lake and similar studies in more eutrophic environments (2, 7, 15, 18, 28) suggest that the role of algal epiphytes in primary productivity becomes more important as the trophic level of the aquatic ecosystem approaches the eutrophic state.

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