Epiphyton Biomass is Related to Lake Trophic Status, Depth, and Macrophyte Architecture

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The relationship between epiphyton biomass and water column total phosphorus concentration (TP) was studied in macrophyte beds in 11 lakes covering a wide range of trophic status (TP = 5.8–72.8 μg L⁻¹). Phosphorus concentration was a poor predictor of epiphyton biomass when considered alone. Our data do not agree with previous studies that found that epiphyton biomass increased continuously with TP. Instead, we found a very weak, nonlinear relationship between TP and epiphyton biomass, where epiphyton biomass increased up to TP ≈ 39 μg L⁻¹, and decreased at higher TP. Season and sampling depth accounted for significantly more variation in epiphyton biomass than did TP. Epiphyton biomass increased with depth in oligotrophic lakes but decreased with depth in eutrophic lakes. Seven common species of macrophytes of differing architecture developed significantly different epiphyton biomass. Macrophytes with flexible, ribbon-like leaves supported lower epiphyton biomass than species of broad-leaved or whorled architecture. The effect of host type on epiphyton algae biomass was not, however, as great as the influence of environmental variables.

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Epiphytic algae contribute significantly to the primary production of littoral zones colonized by aquatic macrophytes. For example, Kajak et al. (1972) found that epiphytic algae were responsible for 28% of the production in the littoral zone of Mikolajskie Lake, while Cattaneo and Kalff (1980) estimated that epiphytic algae contributed as much as 82% of the primary production in the littoral zone of Lake Memphremagog. Epiphytic algae are an important source of food for phytophilous invertebrates (Soszka 1975; Dvořák and Best 1982; Cattaneo 1983), which are a major food source for littoral fish and waterfowl (Keast 1984; Danell and Sjöberg 1980). The biomass of algae attached to substrates (periphyton, f. Wetzel 1983) has been suggested as a potential indicator of point-sources of nutrient enrichment (e.g. Patrick 1973; Ennis 1975; Collins and Weber 1978; American Public Health Association et al. 1985; Biggs 1989) because it is sensitive to variations in phosphorus availability and because it grows fixed to a physical substrate. Periphytic algae can become a nuisance, decreasing recreational use of water bodies (Horner et al. 1983). Although it is of practical and theoretical interest to determine factors limiting epiphyton biomass in lentic ecosystems, epiphytic algae are difficult to study because they have a heterogeneous spatial distribution (Pieczyńska and Szczepańska 1966; Brown and Austin 1973) and are difficult to separate from their macrophyte substrate (Cattaneo and Kalff 1978, Wetzel 1983).

Conflicting evidence exists about the relationship between periphytic algae and phosphorus. While single-lake studies and mesocosm enrichment experiments have found that periphyton biomass is influenced by nutrient concentration (Phillips et al. 1978; Cattaneo and Kalff 1980; Sand-Jensen and Søndergaard 1981; Krewer and Holm 1982; Fairchild et al. 1985; Osenberg 1989), interecosystem comparisons find weak correlations between phosphorus concentration and periphyton (Stevenson et al. 1985; Cattaneo 1987; Hansson 1988). Cattaneo and Kalff (1980) found that epiphyton biomass increased linearly with water column total phosphorus concentration (TP) in a single lake with a trophic gradient (TP from 10 to 40 μg L⁻¹). They further suggested (Cattaneo and Kalff 1980, p. 287) that the relationship they found could be used to predict the effects of phosphorus enrichment on the dynamics of macrophyte beds. Other authors (e.g. Moss 1976; Hansson 1988) have suggested, however, that phosphorus enrichment leads to decreased peri-
phyton biomass because of light attenuation caused by dense phytoplankton growth at high TP. There is, therefore, reason to believe that correlations between epiphyton biomass and TP should not be linear, but that epiphyton biomass is reduced at high TP.

Factors other than nutrient concentration may also influence the biomass of algae growing on the surfaces of aquatic macrophytes. In a mesotrophic lake, on the one hand, Cattaneo and Kalff (1980) found that macrophyte beds in deeper waters supported higher epiphyton biomass, but that within one bed, the leaves of plants closest to the water surface had the greatest epiphyton productivity. On the other hand, Allen and Ocevski (1981) found that the vertical distribution of epiphyton abundance in an oligotrophic lake was uniform, while Young (1945) showed that epiphyton on deeper macrophytes in an oligotrophic lake was less subject to surface turbulence, and therefore more abundant than that found on shallower macrophytes. These results, taken together, suggest that epiphyton abundance at different depths will be influenced differently by factors such as light and turbulence and that these effects might be different, even reversed, in lakes of various trophic status.

Architecture of macrophytes might also influence epiphyton abundance. It is widely accepted that different macrophyte species support different amounts of epiphyton (Young 1945; Prowse 1959; Cattaneo and Kalff 1980; Allen and Ocevski 1981), and several authors have suggested that macrophytes with finely dissected leaves (e.g. Myriophyllum spp.) develop the greatest epiphyton biomass (Foerster and Schlichting 1965; Kowalczewski 1975; Cattaneo and Kalff 1980; Dvofak and Best 1982; Gregg and Rose 1982) because of their high surface to biomass ratio. We therefore expect that macrophyte species with finely dissected leaves should support the greatest epiphyton biomass. Few quantitative, interspecies comparisons have been attempted on submerged plants, however.

The first objective of this study was to test the hypothesis that TP and epiphyton biomass covary in a series of lakes of different trophic status. Such interlake studies of the periphyton–phosphorus relationship are rare (e.g. Cattaneo 1987, for epilithon; Stevenson et al. 1985 and Hansson 1988, for epipelton) and we know of no previous study of epiphyton that has tested this hypothesis. Next, we tested the hypothesis that macrophyte beds in deeper waters support higher epiphyton biomass. We also examined the simultaneous roles of light attenuation and turbulence by examining how epiphyte abundance covaries with the distance below the water surface in lakes of different trophic status. We hypothesize that epiphyton biomass should increase with depth below the water surface in oligotrophic lakes (due to the effect of turbulence) but should decrease with depth in eutrophic lakes (due to light attenuation by phytoplankton). Therefore, both total depth and depth below water surface should be positively correlated with epiphyton biomass. We also examined the simultaneous roles of light attenuation and turbulence by examining how epiphyte abundance covaries with the distance below the water surface in lakes of different trophic status. We hypothesize that epiphyton biomass should increase with depth below the water surface in oligotrophic lakes (due to the effect of turbulence) but should decrease with depth in eutrophic lakes (due to light attenuation by phytoplankton). Therefore, both total depth and depth below water surface should be positively correlated with epiphyton biomass. Finally, we tested the hypothesis that the biomass of...
epiphytic algae colonizing the surfaces of macrophytes varies significantly among macrophytes of differing architecture.

Methods

The epiphyton found on seven species of submerged aquatic macrophytes (Fig. 1) was sampled in 11 lakes in southern Quebec, Canada (Fig. 2). Samples were collected throughout the months of July and August in two successive years. Lakes and macrophyte beds were selected to represent a wide range of macrophyte species diversity, epiphyton abundance, and trophic status in order to maximize our ability to detect significant effects of phosphorus concentration, water depth, and macrophyte architecture.

Samples of epiphyton were taken at random points along a 50-m transect installed parallel to the shore in one macrophyte bed in each lake. Between 20 and 30 samples of macrophytes were collected at each site using a 6-L Plexiglas box that was closed gently around macrophytes without disturbing the epiphytic flora and fauna (Downing 1986). At each site, samples were taken at different, randomly chosen distances below the water surface (Zv, metres), i.e. at different distances from the top of the macrophytes which did not all grow to the water's surface. The total water depth (Zf, metres) at each epiphyton sampling point was also noted. All samples were carefully collected by divers. After each sample was sealed in the plastic box sampler and brought to the boat, a random subsample of epiphyton was withdrawn through an opening in the side of the sampler. Each epiphyton sample was then placed gently into a clean jar containing 200 mL of filtered lake water. All samples were refrigerated until laboratory analysis which was performed within 24 h of collection.

The epiphyton biomass (EPI, micrograms chlorophyll a per gram dry mass of plant) was determined using Cattaneo and Kalff's (1978) method. Each sample jar was vigorously shaken 100 times to dislodge the epiphytes from the macrophytes. This technique samples the loosely attached algal community without contaminating the samples with macrophyte tissue (Cattaneo and Kalff 1978). A subsample of 20–200 mL of epiphyte suspension was filtered (Millipore AP40 04705) and the filters were frozen. Chlorophyll a was later extracted from these filters by soaking them in 96% ethanol for 24 h in the dark and under refrigeration. This chlorophyll solution was subsequently filtered to reduce turbidity and was read spectrophotometrically (Spectronic 21, Bausch and Lomb) at wavelengths of 665 and 649 nm (Bergman and Peters 1980). Macrophytes from which epiphyton was removed were identified (Fassett 1957) and dried to constant mass (60°C; ±0.1 mg).

A 1-L water sample was taken by a diver using an opaque, acid-washed plastic bottle approximately 30 cm beneath the water surface at 10 m intervals along each 50-m transect (six 1-L samples per site). TP (micrograms per litre) in this sample was determined by persulfate digestion followed by the ascorbic acid colorimetric method (American Public Health Association et al. 1985). Because variations in TP within macrophyte beds are generally very low (Table 1; Cyr and Downing 1988), TP estimates were not paired with epiphyton samples, but represented a macrophyte bed mean.

The literature suggests that, in general, epiphyton abundance is greatest in spring, stable or decreasing slowly throughout the summer, and increasing in autumn (Pieczynska and Szczepanska 1966; Cattaneo and Kalff 1980; Cattaneo 1983). Our study was performed during the shortest possible period (July and August) to avoid as much seasonal variation as possible. The sampling date, however, was employed as an independent variable in the statistical analyses to ensure that seasonal variation would not confound analyses. These indices of season varied from 1 (first day of sampling) to 44 (last day of sampling).
Table 1. Average characteristics of 11 macrophyte beds sampled (standard deviation in parentheses). TP, total phosphorus concentration of the water surrounding the macrophytes; S, phytoplankton abundance (chlorophyll a) in each macrophyte bed; EPI, epiphyton biomass per unit dry mass of macrophyte; Z, mean depth of sampling site. The principal macrophyte species that represented more than 1% of the total macrophyte standing biomass are listed in decreasing order of abundance for each macrophyte bed. Cd, Ceratophyllum demersum; Ch, Chara sp.; Cla, Cladophora sp.; Ec, Elodea canadensis; Hd, Heteranthera dubia; J, Juncus sp.; M, Myriophyllum spicatum (except in Lac Des Iles, where M. humile was found); N, Nitella sp.; Pa, Potamogeton amplifolius; Pr, Potamogeton robbinsii; Pric, Potamogeton richardsonii; Ppr, Potamogeton praetangus; P, Potamogeton sp.; S, Sagittaria sp.; Va, Vallisneria americana.

<table>
<thead>
<tr>
<th>Lake</th>
<th>TP (µg L⁻¹)</th>
<th>S (µg Chl a L⁻¹)</th>
<th>EPI (µg Chl a g⁻¹)</th>
<th>Z (m)</th>
<th>Dominant macrophytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Des Iles</td>
<td>5.8 (0.7)</td>
<td>1.5 (1.1)</td>
<td>480.3 (615.9)</td>
<td>1.6 (0.1)</td>
<td>M, Pa, Pr, Ni, P</td>
</tr>
<tr>
<td>Orford</td>
<td>6.9 (1.8)</td>
<td>1.5 (0.6)</td>
<td>235.4 (195.8)</td>
<td>2.0 (0.3)</td>
<td>Pa, Ec, Ni</td>
</tr>
<tr>
<td>Fournelle</td>
<td>7.0 (1.1)</td>
<td>2.6 (1.0)</td>
<td>466.1 (382.4)</td>
<td>1.6 (0.3)</td>
<td>Pr, Ec</td>
</tr>
<tr>
<td>Quenouilles</td>
<td>11.2 (2.8)</td>
<td>1.6 (0.6)</td>
<td>217.3 (216.6)</td>
<td>1.3 (0.1)</td>
<td>Pa, J, Ch, S, Va</td>
</tr>
<tr>
<td>Echo</td>
<td>12.8 (5.8)</td>
<td>8.3 (7.6)</td>
<td>141.5 (127.1)</td>
<td>1.6 (0.1)</td>
<td>Ch, Pa, Pr, Ppr</td>
</tr>
<tr>
<td>D'Argent</td>
<td>13.2 (2.6)</td>
<td>7.5 (2.3)</td>
<td>209.1 (164.4)</td>
<td>1.5 (0.3)</td>
<td>M, Ni, Va</td>
</tr>
<tr>
<td>Memphremagog</td>
<td>17.5 (3.9)</td>
<td>3.3 (0.8)</td>
<td>114.0 (82.5)</td>
<td>2.2 (0.1)</td>
<td>M, Va, Hd, Ec</td>
</tr>
<tr>
<td>(Cove Island Bay)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Champlain</td>
<td>23.3 (4.1)</td>
<td>3.5 (2.3)</td>
<td>120.0 (88.7)</td>
<td>2.0 (0.0)</td>
<td>Va, Cla, Pric</td>
</tr>
<tr>
<td>(Baie de Venise)</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Massawippi</td>
<td>23.9 (9.2)</td>
<td>15.9 (12.4)</td>
<td>995.4 (484.2)</td>
<td>2.2 (0.4)</td>
<td>M</td>
</tr>
<tr>
<td>Magog</td>
<td>57.5 (20.5)</td>
<td>19.8 (12.9)</td>
<td>413.7 (310.4)</td>
<td>1.6 (0.1)</td>
<td>Ec, M, Pr, Cd</td>
</tr>
<tr>
<td>Waterloo</td>
<td>72.8 (17.4)</td>
<td>41.7 (11.0)</td>
<td>121.6 (52.0)</td>
<td>1.1 (0.1)</td>
<td>M, Va</td>
</tr>
</tbody>
</table>

The correlation between epiphyton biomass and phosphorus concentration was tested by calculating Pearson's correlation coefficient (r) between epiphyton biomass and TP. We tested the hypothesis that epiphyton biomass and TP were nonlinearly related with polynomial regression analysis. Bivariate correlations between epiphyton biomass and macrophyte bed characteristics were examined using Pearson's correlation coefficient. The hypothesis that several of these characteristics might influence epiphyton biomass simultaneously was further tested by multiple, linear, stepwise regression analysis. Candidate variables in this analysis were total phosphorus concentration (TP), water depth (Z), distance between sample and water surface (Z), and the sampling date (D). In addition to these variables, we included the square of the total phosphorus concentration (TP²) to test for the probable negative influence of high concentrations of phosphorus on epiphyton biomass. We also included the interaction term of phosphorus and distance below water surface (TP·Z) to test for the reversal of the effect of depth on epiphyton biomass at high TP. Because measures of TP were not directly paired with epiphyton estimates, we followed Draper and Smith's protocol (1981, p. 241) for the calculation of regression coefficients, degrees of freedom, and significance of effects when using dummy variables with more than two levels (i.e. TP). An analysis of variance and a multiple comparisons test (Student–Newman–Keuls) were subsequently performed on the residuals of the multiple regression to determine whether the epiphyton biomass differed among species of aquatic macrophytes after accounting for the effects of season, lake trophic status, and depth. Epiphyton data were transformed to their fourth root for entry into polynomial and multiple regression analyses to normalize residuals. All statistical analyses were performed using SPSS.

Results and Discussion

The TP of the 11 study lakes varied between 5.8 and 72.8 µg L⁻¹ (Table 1), ranging from oligotrophic to eutrophic conditions (Wetzel 1983). Variation of TP within macrophyte beds was low (Table 1). Although Cattaneo and Kalff (1980) found a linear relationship between epiphyton biomass and TP, our results (Fig. 3) indicated that, in our range of TP, there was no significant relationship between these variables (r = -0.066, p = 0.85, n = 11), and in the range of TP observed by Cattaneo and Kalff (1980) (<40 µg L⁻¹), the weak positive correlation we observed between TP and epiphyton biomass was not statistically significant (r = 0.21, p = 0.58, n = 11). At high TP, epiphyton biomass appeared to decrease, but a polynomial regression analysis performed on macrophyte bed
average values of epiphyton biomass and TP \((n = 11)\) indicated that this relationship was not statistically significant \((p = 0.85)\). Our results therefore disagree with Cattaneo and Kalff’s (1980) hypothesis that eutrophication results in a linear increase in epiphyton biomass. Although this is an unexpected result for epiphytic algae, other interlake comparisons of epipelic (Stevenson et al. 1985; Hansson 1988) and epilithic (Cattaneo 1987) algae have found weak, often conflicting relationships between periphyton biomass and TP.

The lack of relationship between epiphyton biomass and TP was not due to a lack of phosphorus limitation in the lakes that we studied, as the logarithm of the concentration of chlorophyll \(a\) in the suspended phytoplankton was significantly correlated with log TP (Lalonde 1988: \(r^2 = 0.75, \text{slope} = 1.2\)) in a way that was similar to that found elsewhere in the littoral zone (Cattaneo 1987: \(r^2 = 0.89, \text{slope} = 1.33\)) and in the pelagic zone (Pace 1984: \(r^2 = 0.93, \text{slope} = 1.09\); Dillon and Rigler 1974: \(r^2 = 0.90, \text{slope} = 1.45\)).

Epiphyton biomass varied widely at all phosphorus concentrations (Fig. 3), suggesting that variables other than phosphorus had a significant impact on epiphyton biomass (Table 2). Multiple regression analysis showed that epiphyton biomass (EPI) varied as

\[
(1) \quad \text{EPI}^{0.25} = -0.0435(D) + 1.1412(Z_s) - 0.0013(TP^2) + 0.1151(TP) - 0.0367(TP-Z_s) + 3.1002
\]

\(R^2 = 0.40, F = 34.2, p < 0.0001, n = 260\) where \(D\) is the sampling date, \(Z_s\) is the distance between the water surface and the sample, TP is the concentration of total phosphorus in the water column, and TP-\(Z_s\) is the product of TP and the depth below the water surface at which the sample was taken. All of the regression coefficients in Eq. 1 differ significantly from zero \((p < 0.0001)\) and the variables are listed in decreasing order of the significance of their partial \(t\)-values. The total water depth \((Z_s)\) at each epiphyton sampling point had no significant effect.

Equation 1 shows that after accounting for the significant effects of other variables by multiple regression, TP had a weak
but significant positive effect on epiphyton biomass up to 39 \( \mu g \cdot L^{-1} \), above which epiphyton biomass decreased (negative effect of TP\(^2\)). Equation 1 reconciles the conflicting results of Cattaneo and Kalff (1980) and Hansson (1988). Within the range of low phosphorus concentrations studied by Cattaneo and Kalff (10–40 \( \mu g \cdot L^{-1} \)), our results agree with the positive correlation between epiphyton biomass and TP that they observed. Our analysis of Hansson’s (1988) data showed that epipelon biomass decreased at high TP \( (p = 0.052) \) in his 20 study lakes only when two lakes with TP > 100 \( \mu g \cdot L^{-1} \) were considered.

The sign of the coefficient for the TP-Z\(_s\) interaction term shows that the form of the relationship between epiphyton biomass and sampling depth depends on TP. Therefore, at low TP, epiphyton biomass increases with distance below the water surface whereas at high TP, this relationship is reversed due to light attenuation, and higher biomasses of epiphyton are found closer to the water surface (Fig. 4). The lower biomass of epiphyton closer to the water surface in oligotrophic lakes could be attributable to shorter colonization times on younger parts of macrophytes, or greater turbulence at the surface. Evans and Stockner (1972) have observed similar reversed relationships between depth and epiphyton biomass in oligotrophic versus eutrophic lakes.

Season explained the most variance in epiphyton biomass, even considering data from lakes of different trophic status, sampled within a short period of time. As in other studies (e.g. Pieczyńska and Szczepańska 1966; Cattaneo and Kalff 1978, 1980; Sand-Jensen 1983), epiphyton biomass decreased as the season progressed. This systematic decrease of epiphyton during the summer has been linked to grazing by phytophilous invertebrates (Cattaneo 1983; Kairesalo 1984). Besides grazing, other factors such as nutrient depletion (nitrogen and silicon), temperature and light variations, and macrophyte age and condition could be linked to seasonal variations in epiphyton biomass.

The seven macrophyte species that we collected (Fig. 1) did not support an equal biomass of epiphyton when expressed per unit dry mass of macrophyte (Table 3). Our results agree with those of other authors who found that different macrophyte species were colonized differentially by epiphytic algae (Kowalczewska 1975; Cattaneo and Kalff 1980; Allen and Ocevski 1981; Gregg and Rose 1982). None of the seven macrophyte species that we studied was present in all lakes (Table 3); thus, apparent differences in epiphyton biomass on different macrophyte species could have arisen from different environmental characteristics prevailing at the different sites colonized by these macrophyte species.

Analysis of the residuals of Eq. 1 shows that the different macrophyte species supported significantly different biomasses of epiphyton, even after compensation for the effects of lake trophic status, depth, and season (ANOVA: \( F = 6.486, p < 0.0001 \); Table 4). Average residuals appear to be related to macrophyte architecture: the two whorled macrophytes *Myriophyllum spicatum* and *Elodea canadensis* had the highest residuals, the broad-leaved macrophyte *Potamogeton amplifolius* had the next highest residuals, and the ribbon-leaved macrophytes had three of the four lowest residuals (Table 4). The only outlier to this pattern was *Potamogeton richardsonii* which was sampled in only one lake \( (n = 5) \) and had very young leaves (i.e., green leaves with no signs of senescence), which are often associated with low epiphyton biomass (Sand-Jensen and Søndergaard 1981; Rogers and Breen 1983; Sand-Jensen 1983). A Student–Newman–Keuls multiple comparisons test (Table 4) showed that only *Vallisneria americana, Potamogeton sp.*, and *P. richardsonii* had epiphyton biomasses that were significantly different from those found on other species. None of the other architecturally diverse macrophyte species supported significantly eccentric epiphyton biomass. Therefore, even though plants such as *Myriophyllum* and *Elodea* seemed to have more abundant epiphyton than other macrophyte species (Table 3), part of the difference in colonization of the different macrophyte species appeared to reflect specific characteristics of different habitats in which certain macrophyte species grow (Tables 1 and 3). Once these specific characteristics were accounted for, differences in epiphyton biomass were less obvious. Thus, environmental and seasonal factors seemed to have a greater influence on epiphyton biomass than the architecture of the macrophyte species on which it grows.

This study concludes, therefore, that several factors, including lake trophic status, influence the development of epiphyton biomass. The macrophyte bed characteristics that we measured explained 40% of the variation in transformed epiphyton biomass, and a small additional amount of the residual variance was explained by differences in epiphyton biomass among seven macrophyte species. Our multivariate analyses showed that phosphorus concentration accounted for only a very small fraction of the total variation in epiphyton biomass in 11 lakes (Eq. 1) and that this relationship was nonlinear, showing a decrease in epiphyton biomass at high phosphorus concentrations. The effect of phosphorus enrichment was, however, to decrease light penetration in the water column, making it difficult to measure changes accurately.

Table 4. Tests for differences in the epiphyton biomass found on several species of macrophytes, made using a Student–Newman–Keuls multiple comparisons test on the residuals of Eq. 1. *Significant difference \( (p < 0.05) \); ns, no significant difference. Where significant differences exist, the greater epiphyton biomass was found on the species with the greatest mean residual. Sample size \( (n) \) is not the same as in Table 3 because some values of \( Z_s \) are missing (see Eq. 1).

<table>
<thead>
<tr>
<th>Macrophyte Species</th>
<th>Myriophyllum spicatum</th>
<th>Elodea canadensis</th>
<th>Potamogeton amplifolius</th>
<th>Vallisneria americana</th>
<th>Potamogeton richardsonii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean residual</td>
<td>0.2390</td>
<td>0.0919</td>
<td>-0.0561</td>
<td>-0.2012</td>
<td>-0.3925</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.7923</td>
<td>0.9307</td>
<td>0.8778</td>
<td>0.6157</td>
<td>0.6309</td>
</tr>
<tr>
<td>( n )</td>
<td>117</td>
<td>11</td>
<td>82</td>
<td>23</td>
<td>12</td>
</tr>
</tbody>
</table>

impossible for epiphyton to grow at depth. Therefore, the pattern of increasing epiphyton biomass with distance below water surface in oligotrophic lakes was reversed in more eutrophic lakes. Although this model has a coefficient of determination too low to be useful in making predictions, it demonstrates that epiphyton biomass is more appropriately described by multivariate analysis and, unlike phytoplankton, cannot be simply predicted from TP, a finding corroborated by studies of other periphytic algae.

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