Seasonal Periodicity of Periphytic Algae in Relation to Water Quality in Three Florida Experimental Ponds

Spring 1981

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SEASONAL PERIODICITY OF PERIPHYTIC ALGAE IN RELATION TO WATER QUALITY IN THREE FLORIDA EXPERIMENTAL PONDS

Michael J. Gilbrook
B.S., University of Central Florida, 1978

THESIS

Submitted in partial fulfillment of the requirements for the degree of Master of Science: Biological Science in the Graduate Studies Program of the College of Arts and Sciences at the University of Central Florida; Orlando, Florida

Winter Quarter
1981
ABSTRACT

Periphytic algae biomass, periphyton taxonomic composition and water quality were monitored from October, 1978 through October, 1979 in three experimental ponds on the University of Central Florida campus, Orlando, Florida. Differences in the abundance and seasonal periodicity of phytoplankton in the ponds presumably arose from intrinsic differences in the nature of the pond sediments. Ceramic tile and pressboard wood artificial substrates were sampled at two-month intervals to provide estimates of periphyton biomass and productivity; there was no significant difference in algal biomass on wood and tile substrates. Algal productivity on continuous-immersion (cumulative) substrates which supported a large accumulation of periphyton was substantially lower than productivity on uncolonized substrates immersed during the same period, thus indicating the existence of a carrying capacity for the periphyton community. Turbidity, which was largely determined by phytoplankton abundance, was significantly higher in Pond 2 (7.50 FTU) than in Ponds 1 and 3 (2.60 and 2.53 FTU, respectively) and resulted in reduced light penetration and development of a heterotrophic periphyton community in Pond 2. The algal flora of Pond 2 was dominated by small colonial or unicellular green algae characteristic of eutrophic conditions, whereas Ponds 1 and 3 possessed periphyton communities dominated by large, filamentous green algae indicative of "clean" water.
ACKNOWLEDGEMENTS

This study was made possible only by the combined efforts of a number of people to whom I wish to extend my appreciation. I am indebted to Ms. Jackie McDade Fry, Mr. Greg Jubinsky, Mr. Ray Miller, Mr. Larry Sellers and Ms. Gail Sloane for their assistance in periphyton biomass sampling. Mr. Winston Borkowski deserves thanks for his help with the water quality analysis, as does Mr. Jeff Wetherington for lending a hand with the computer processing. I would like to thank Drs. I. Jack Stout and Haven C. Sweet for their advice and their careful review of the manuscript; Dr. Sweet also merits thanks for his assistance in making algal identifications. Dr. John A. Osborne warrants special recognition for his seemingly inexhaustible supply of ideas, materials, funding and time which supported my during the course of this study. Funding for this research was provided by the Bureau of Aquatic Plant Research and Control, Florida Department of Natural Resources, Tallahassee, Florida. Lastly, I would like to thank my parents for pretending to believe it was all worth it, even when they weren't sure.
TABLE OF CONTENTS

List of Tables................................................................. v
List of Figures................................................................. vi
Introduction................................................................. 1
Methods and Materials..................................................... 4
  Description of Experimental Ponds.................................... 4
  Physicochemical Methods................................................. 6
  Periphytic Algae Biomass Methods.................................... 7
  Taxonomic Composition Methods..................................... 12
Results and Discussion................................................... 15
  Experimental Pond Water Quality..................................... 15
  Periphytic Algae Quantitative Results............................... 26
  Periphytic Algae Taxonomic Composition............................ 43
Summary............................................................................. 52
Appendix............................................................................. 54
Literature Cited............................................................... 57
LIST OF TABLES

Table                                                                                                           Page
1. Annual means of selected water quality parameters for experimental ponds, October, 1978 through October, 1979... 16
2. Simple linear correlation coefficients and significance levels (in parentheses) for water quality parameters in Pond 1, October, 1978 through October, 1979.................. 22
3. Simple linear correlation coefficients and significance levels (in parentheses) for water quality parameters in Pond 2, October, 1978 through October, 1979.................. 23
4. Simple linear correlation coefficients and significance levels (in parentheses) for water quality parameters in Pond 3, October, 1978 through October, 1979.................. 24
5. Periphytic algae productivity on tile substrates, measured as mg Chl a/m²/day........................................ 31
6. Periphytic algae productivity on tile substrates, measured as g dry weight/m²/day...................................... 32
8. Simple linear correlation coefficients and significance levels (in parentheses) for periphytic algae and water quality parameters in Pond 1, October 1978-October 1979... 38
9. Simple linear correlation coefficients and significance levels (in parentheses) for periphytic algae and water quality parameters in Pond 2, October 1978-October 1979... 39
10. Simple linear correlation coefficients and significance levels (in parentheses) for periphytic algae and water quality parameters in Pond 3, October 1978-October 1979... 40
11. Coverage values (%) for algal taxa identified on glass slides from Ponds 1, 2 and 3, December, 1978 through October, 1979................................. 44
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Aerial view of the UCF experimental ponds</td>
<td>5</td>
</tr>
<tr>
<td>2. Assembled periphytic algae samplers</td>
<td>9</td>
</tr>
<tr>
<td>3. View of a drained pond showing exposed samplers in place</td>
<td>10</td>
</tr>
<tr>
<td>4. Seasonal trend of water temperature in the three experimental ponds, October 1978-1979</td>
<td>19</td>
</tr>
<tr>
<td>5. Seasonal trend of water color in the three experimental ponds, October 1978-1979</td>
<td>20</td>
</tr>
<tr>
<td>6. Seasonal trends of turbidity and chlorophyll a in the three experimental ponds, October 1978-1979</td>
<td>21</td>
</tr>
<tr>
<td>7. Seasonal trends in chlorophyll a concentrations for bimonthly and continuously immersed artificial substrates in the experimental ponds, October 1978-1979</td>
<td>28</td>
</tr>
<tr>
<td>8. Seasonal trends in dry weight of periphyton for bimonthly and continuously immersed artificial substrates in the experimental ponds, October 1978-1979</td>
<td>30</td>
</tr>
<tr>
<td>9. Simple linear regression of mean chlorophyll a concentration and dry weight of periphyton collected in the experimental ponds, October 1978-1979</td>
<td>34</td>
</tr>
<tr>
<td>10. Seasonal trends in coverage (%) by three algal classes of periphytic algae collected on glass slides in the three experimental ponds, December 1978-October 1979</td>
<td>49</td>
</tr>
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The periphytic algae comprise one component of the biocoenosis known in America as periphyton. Considerable confusion exists concerning the terminology used in reference to aquatic organisms which live attached to a substrate; this confusion has prompted a number of reviews of periphyton nomenclature (Cooke, 1956; Sladečková, 1962; Round, 1964; Wetzel, 1964) which have provided clarification of the variety of terms in use to describe "littoral algae."

The periphytic algae are responsible for much of the primary productivity of freshwater systems. Odum (1957) reported that the periphyton attached to Sagittaria blades accounted for 70% of the primary productivity of Silver Springs, Florida, and primary production by periphytic algae in lakes has been shown to rival or exceed that of phytoplankton (Wetzel, 1964; Olson and Odlaug, 1972). The periphytic algae of the littoral zone may in fact play a major role in lake eutrophication (Wetzel and Hough, 1973).

The study of the periphytic algae has provided a means of assessing changes in water quality associated with pollution or eutrophication. Taxonomic analyses of the periphyton have been used to monitor the water quality of both streams and lakes (Hansmann and Phinney, 1973; Casterlin and Reynolds, 1977; Parker, 1979). Quantitative measures of periphyton populations have also been applied...
to water quality assessment, such as measurements of biomass and productivity in reservoirs (Sladečková, 1965) or radionuclide accumulation by periphyton downstream from a nuclear reactor (Cushing, 1967). The proportion of chlorophyll a to dry weight biomass of a periphyton sample can be used to calculate an Autotrophic Index for a lake or stream, thus providing another means of water quality assessment (Weber, 1973).

Whatever the purpose of the study, most quantitative research of the periphytic algae employs artificial substrates in order to simplify calculations of surface area and to permit more uniform replication. Sladečková (1962) described a number of periphyton sampler designs and discussed the importance of position, immersion duration and means of handling to the quantitative analysis of periphyton from artificial substrates. Although artificial substrates are ideally suited for comparative studies of periphytic algae, there is some doubt as to how well trends in biomass accumulation on artificial surfaces reflect changes in the periphyton biomass of natural substrates (Lowe and Gale, 1980).

A variety of methods have been used to quantitatively describe the periphyton, including $^{14}$C and $^{35}$S assimilation (Clark, et al., 1980), ATP content (Weber, 1973; Perkins and Kaplan, 1978) and measures of upstream--downstream changes in dissolved oxygen (Kevern and Ball, 1965). The most common means of quantitative description is that of biomass, of which there are two basic approaches. The simplest and most direct approach is the measure of dry weight, a technique which has often been used to estimate periphyton biomass.
The measurement of chlorophyll \( a \) is a convenient way to estimate the biomass of algal populations because all algae possess chlorophyll \( a \) (Round, 1973). Like dry weight, this method has been widely used in the study of periphyton (Grzenda and Brehmer, 1960; Waters, 1961; Welch, et al., 1972); unfortunately, its use is complicated by the dependence of chlorophyll content on light intensity, nutrition and algal species (Round, 1973). The accuracy of biomass measurements is also reduced by interference from inactive degradation products of chlorophyll (Tett, et al., 1975).

Although there has been much interest in the periphyton worldwide, very little is known about the freshwater periphytic algae of Florida. In light of the importance of periphytic algae to lake primary productivity and the usefulness of periphyton as an index of pollution, much more work is necessary to describe the intrinsic variation in the composition, biomass and seasonal periodicity of periphytic algae populations in Florida in relation to water quality. In this study, the use of three experimental ponds permitted the study of seasonal trends in periphytic algae under different water quality regimes, while holding the variables of climate and basin morphology constant.
METHODS AND MATERIALS

Description of Experimental Ponds

The three experimental ponds used in the study were located on the University of Central Florida campus, Orange County, Florida (Figure 1). The ponds measured 75 x 15 m; the long axis of each pond was graded along the long axis on a 1:40 slope to simulate a cross section of the littoral zone of a natural lake or pond. Depth ranged from a few cm at the south end to 1.8 m at the north end of each pond.

The ponds were partitioned with fences to restrict the movement of various exotic fish species kept in them. A transverse fence was erected approximately 34 m from the south end of each pond, and the shallow end of each pond was bisected by a longitudinal fence (Figure 1). Fences were constructed of galvanized chicken wire strung between aluminum fence posts positioned about 3 m apart; the fence wire was buried in the sediment. Water depth at the junction of the transverse and longitudinal fences was approximately 1 m throughout the study in all ponds.

Each pond could be drained by removal of an outfall pipe located in a concrete drainage basin at its deepest end. Ponds were refilled with water pumped from a 122 m well; each pond therefore received
Figure 1. Aerial view of the UCF experimental ponds. North is to the top of the photograph. The pond to the far left was not used in this study; the remaining ponds are referred to in the text as (left to right) Ponds 1, 2 and 3.
water of identical quality. Well water was added to the ponds on a fixed schedule (regulated by a timer on the pump) to compensate for water lost by evaporation and seepage.

To eliminate the confounding effect of aquatic macrophytes on the ponds, all submersed and emergent plants were removed from the ponds prior to the study. Pond margins were mowed as necessary to prevent the regrowth of emergent plants. Submersed plants that became re-established were removed when the ponds were drained for sampling.

Individuals of the native fish species *Gambusia affinis*, *Micropterus salmoides* and *Lepomis macrochirus* were able to move freely throughout the ponds. Large centrarchids which could not pass through the fence mesh were removed from the study areas when the ponds were drawn down for periphytic algae sampling.

**Physicochemical methods**

Water quality analysis was performed monthly on the ponds. During those months when the ponds were drained for periphytic algae sampling water quality was analyzed prior to the draining of the ponds. Sampling was conducted between 0800 and 1200 hrs. Two stations were sampled in each pond, one on either side of the longitudinal fence. Due to the small size of the ponds, two samples were considered adequate to assess water quality. Sampling was conducted from a jon boat which was carefully launched into the ponds to prevent disturbing the sediment.

Vertical light transparency was measured to the nearest 0.1 cm with a 20 cm Secchi disc. Light extinction coefficients were
determined using a Kahl Scientific Instrument Corp. Model 268WA310 submarine photometer; the sea cell was submerged to a depth of 0.5 m. Specific conductivity and temperature were measured using a Montedoro-Whitney Model CTU-4A digital conductivity/temperature meter. Temperature (±0.01 C) was measured at the surface and at the bottom at each station. Specific conductivity (±1 micromho/cm @ 25 C) was measured just below the surface. Water samples were collected at the surface with a 1.2 l Kemmerer water sampler. Glass BOD bottles were filled for dissolved oxygen analysis, fixed through the acid stage of the modified Winkler technique (APHA, 1976) and returned to the laboratory for titration. Water samples were collected in 1 l plastic bottles for all other analyses.

Phytoplankton chlorophyll a determinations were performed by the method of Richards with Thompson (1952). Optical densities were measured with a Beckman Model 26 spectrophotometer. Color (Pt-Co units) was determined spectrophotometrically for filtered water samples (filter pore size = 0.45 µm) using a platinum-cobalt standard (APHA, 1976). Turbidity (FTU) was measured spectrophotometrically using filtered water samples as blanks and a formazin solution as the standard (APHA, 1976). Alkalinity (mg/1 CaCO₃) was determined by Standard Methods (APHA, 1976); pH was measured on a Sargeant-Walch Model PBX pH meter to the nearest 0.5 pH unit. Inorganic carbon (mg/1 C) was calculated from pH and alkalinity measurements using the table of Saunders, et al. (1962).

**Periphytic Algae Biomass Methods**

Periphytic algae samplers were constructed using pressboard
and unglazed ceramic tile as artificial substrates. The substrates measured 15 X 15 cm and were held between two 1 X 5 X 15 cm blocks of wood fastened together with aluminum wood screws (Figure 2). Dowels mounted on the underside of one of the blocks were used to secure the samplers in a vertical position to boards set in the sediment of the experimental ponds. Four boards were placed within the study area of each pond, and each board was aligned parallel to the pond's long axis. Each board supported 18 samplers; tile and wood substrates were alternated along the boards (Figure 3). The orientation of the samplers insured that both sides of the artificial substrates would receive roughly the same solar illumination during the course of a day.

The substrates were placed in the ponds in October, 1978 and sampled every two months until October, 1979. The importance of allowing sufficient time for the development of a mature periphyton community on artificial substrates has been previously recognized (Waters, 1961; Sladečková, 1962); an immersion period of two months was felt to be appropriate for the system under study. An immersion period of 60 days has since been found to provide the best approximation to the natural periphytic flora for glass slides in the Everglades (D.R. Swift, personal communication, 1980).

The ponds were sampled over three consecutive days. Ponds were drained only as far as was necessary to collect the artificial substrates (Figure 3); the drawdown took 4 to 6 hrs. The ponds were sampled early in the morning and rapidly refilled after sampling to minimize dessication of the substrates remaining in the ponds.
Figure 2. Assembled periphytic algae samplers. The dark substrate is ceramic tile and the light colored substrate is pressboard. The projecting dowels were inserted into boards placed in the experimental ponds.
Figure 3. View of a drained pond showing exposed samplers in place. The pond has been drained to sampling depth; the samplers on the right-hand (east) side of the longitudinal fence were not used in this study.
The first two samplers on each board (i.e., those at the southernmost end) were removed and replaced with fresh, uncolonized substrates every two months (bimonthly-immersion substrates). A randomly selected pair of samplers was chosen from each board to assess the cumulative algal biomass (continuous-immersion substrates). In all, sixteen samplers were removed from each pond for each sample period, thus providing a sample size of $n = 4$ for continuous and bimonthly immersed wood and tile substrates from each pond.

Substrates were brought to the laboratory in styrofoam containers. The exposed surface area of one side of each substrate was measured, and the attached algae scraped and rinsed into glass beakers. Macroinvertebrates were removed from the samples. Algae from each sample was individually homogenized in a tissue grinder and the homogenate mixed on a magnetic stirrer. A 10 to 25 ml subsample was taken from all samples for phytopigment analysis; a second sample was taken from samples derived from tile substrates for gravimetric analysis. The pressboard substrates proved to be unsuitable for dry weight analysis due to the introduction of wood shavings in the samples during the scraping process. After removal of the subsample(s), the volume of the remaining homogenate was recorded to allow back-calculation of results to the original surface area of the substrate.

Subsamples for dry weight analysis were rinsed into preweighed crucibles, dried at 105°C for 72 hrs and weighed to the nearest 0.1 mg. Subsamples destined for phytopigment analysis were filtered onto glass fiber filters (pore size = 0.45 μm) which were placed in 90% acetone
and ground thoroughly in the tissue grinder. The ground filter suspension was transferred to a 250 ml screw-top Erlenmeyer flask, and a total of 100 ml of acetone was added. The flasks were stored at 4°C in the dark for 48 hrs to fully extract phytopigments. The flasks were briefly agitated after 24 hrs. Pigment extract was decanted into screw-top vials and centrifuged for 10 minutes to remove suspended solids. Supernatant from the vials was decanted into quartz cuvettes, and the pigment extract examined spectrophotometrically at 665, 645 and 630 nm. Chlorophyll a/m² was determined using the equation of Richards with Thompson (1952). After the initial reading, pigment extracts from tile substrates were re-examined at 665 nm before and after acidification with 1 N HCl. Pheophytin a/m² and absorbance ratios were calculated with reference to Standard Methods (APHA, 1976).

**Taxonomic Composition Methods**

To study seasonal trends in community composition, periphytic algae were grown on glass slides. Four 25 X 75 mm glass microscope slides were inserted vertically into rubber stoppers and suspended 0.5 m below the water surface from aluminum fence poles; two poles were positioned within each pond, one on either side of the longitudinal fence.

Slides were immersed for the one month period prior to periphytic algae biomass sampling, and were set out and retrieved concurrently with water quality sampling. Slides were placed in glass jars filled with pond water immediately after retrieval and returned to the laboratory. Four of the eight slides removed from each pond
were selected at random for study. Attached material from one side of each slide was scraped and washed into a beaker. The material scraped from two slides was pooled in a beaker, rinsed into a 40 ml glass screw-top sample bottle with distilled water, and preserved with Lugol's solution (APHA, 1976).

The characterization of periphyton communities by estimating abundance or cover, often involving the use of an arbitrary value scale, has found widespread acceptance (Sladečková, 1962). The coverage scale suggested by Daubenmire (1968) for estimating the cover of terrestrial plants was adopted because the six coverage classes employed were easily visualized within a microscope field, and the coverage estimates made for each taxon were objective and reproducible. The objective nature of the scale permitted a comparison of the abundance of a particular taxon between ponds, and seasonally within any one pond.

The samples were mixed thoroughly in a round-bottomed flask, and a 1 ml subsample removed with a Hensen-Stempel automatic pipette. Two replicate 1 ml aliquots were examined from each sample. The subsamples were placed into a Sedgwick-Rafter counting cell and examined under a binocular light microscope at 100X to estimate coverage. Higher magnifications (to 400X) were used for identifications. Green and blue-green algae were identified to genus using Smith (1950) and Prescott (1970). Diatoms were classified as pennate or centric; the coverage of forms that formed chains or filaments was scored separately from that of unicellular diatoms. Five fields of view (one near each corner and one in the center of the cell) were
examined for each subsample and the cover value for each taxon appearing in a field was scored. From the counts made on two samples per pond (n = 20 fields of view), a mean cover value for each taxon was calculated using the midpoints of the class ranges after Daubenmire (1968). This procedure satisfied the requirements of the two-stage sampling plan advocated by McAlice (1971) for the enumeration of phytoplankton samples using the Sedgwick-Rafter counting chamber.
RESULTS AND DISCUSSION

Experimental Pond Water Quality

The application of Duncan's Multiple Range Test (Helwig and Council, 1979) to the monthly physicochemical data revealed no significant difference ($P \leq 0.05$) in the annual means of water color and dissolved oxygen in the three ponds (Table 1), but some differences in the water quality of the ponds were apparent. The annual mean pH of Pond 2 (8.08) was significantly higher than the pH values of Ponds 1 and 3 (7.84 and 7.82 respectively, Table 1). The annual mean of inorganic carbon in Pond 1 (35.34 mg C/l) was significantly less than that of Pond 3 (38.56 mg C/l); Pond 2, with an annual mean of 37.27 mg C/l, was intermediate between Ponds 1 and 3 (Table 1). Likewise, the annual mean of specific conductivity in Pond 3 was significantly higher than that in Pond 1 (302.7 and 267.6 micromhos/cm, respectively), while Pond 2 again occupied an intermediate position with an annual mean of 285.0 micromhos/cm (Table 1).

Annual mean turbidity was not significantly different in Ponds 1 and 3 (2.60 and 2.53 FTU, respectively), but both ponds had significantly lower annual mean turbidity than that for Pond 3 (7.28 FTU) (Table 1). The trend in the annual mean for chlorophyll $a$ in the ponds paralleled that of turbidity; the mean of Pond 2 (39.32 mg Chl $a$/m$^3$) far exceeded the means for Ponds 1 and 3.
Table 1. Annual means of selected water quality parameters for experimental ponds, October, 1978 through October, 1979. Means with the same letter are not significantly different, $P \leq 0.05$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Pond 1</th>
<th>Pond 2</th>
<th>Pond 3</th>
</tr>
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<tbody>
<tr>
<td>Turbidity (FTU)</td>
<td>2.60$^A$</td>
<td>7.28$^B$</td>
<td>2.53$^A$</td>
</tr>
<tr>
<td>Color (Pt-Co Units)</td>
<td>16.21$^A$</td>
<td>17.76$^A$</td>
<td>17.17$^A$</td>
</tr>
<tr>
<td>Light Extinction (k)</td>
<td>2.19$^A$</td>
<td>2.85$^B$</td>
<td>1.61$^A$</td>
</tr>
<tr>
<td>Dissolved Oxygen (ppm)</td>
<td>6.61$^A$</td>
<td>7.33$^A$</td>
<td>5.94$^A$</td>
</tr>
<tr>
<td>pH</td>
<td>7.84$^A$</td>
<td>8.08$^B$</td>
<td>7.82$^A$</td>
</tr>
<tr>
<td>Inorganic Carbon (mg C/l)</td>
<td>35.34$^A$</td>
<td>37.27$^A$,$^B$</td>
<td>38.56$^B$</td>
</tr>
<tr>
<td>Specific Conductivity (micromhos/cm @ 25 C)</td>
<td>267.6$^A$</td>
<td>285.0$^A$,$^B$</td>
<td>302.7$^B$</td>
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<td>Phytoplankton Chlorophyll (mg Chl a/m$^3$)</td>
<td>11.81$^A$</td>
<td>39.32$^B$</td>
<td>16.21$^A$</td>
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(11.81 and 16.21 mg Chl a/m³) which were not significantly different (Table 1). The annual mean vertical light extinction coefficients (k values) for the three ponds reflected their turbidity differences. Pond 2 was least transparent ($\bar{k} = 2.85$), whereas Pond 1 ($\bar{k} = 2.19$) and Pond 3 ($\bar{k} = 1.60$) were not significantly different with respect to light penetration (Table 1).

The water quality of the ponds was generally very similar to that of many central Florida lakes. The low water color and high pH, alkalinity and specific conductivity values observed in the ponds were similar to that of "alkaline, clear" Florida lakes (Shannon and Brezonik, 1972). The annual mean phytoplankton chlorophyll a values for the three ponds (Table 1) were within the range found in eutrophic Florida lakes (Shannon and Brezonik, 1972). Using the annual mean phytoplankton chlorophyll a biomass values as an index of production, Pond 2 appeared to be the most productive of the ponds, whereas Ponds 1 and 3 were lower in planktonic productivity (Table 1).

In order to provide a more realistic comparison of changes in the periphyton over each two-month period with respect to the prevailing water quality conditions a mean value for each water quality parameter was calculated from observations made during the two water sampling periods immediately prior to periphyton sampling; all subsequent use of physicochemical data will involve bimonthly mean values.

The seasonal trends of temperature and the factors which influence light penetration (color and turbidity) were of interest
because of their potential influence on the metabolism and growth of the periphytic algae. Water temperatures were essentially identical between ponds with the lowest mean temperature of ca. 16 °C observed for the period ending in February while the highest mean temperature of ca. 28 °C occurred in August (Figure 4). Water color trends in the three ponds were fairly similar; all ponds experienced a sharp decline in mean color values for August, followed by a dramatic increase in water color in October (Figure 5). Monthly samples of well water did not change appreciably in water color during the study, so presumably some climatic factor was responsible for the synchronization of water color trends in the three ponds. Bradley and Beard (1969) reported that increases in precipitation during the fall rainy season resulted in increased runoff which elevated water color in Mud Lake, Florida. Correlation of pond water color values with precipitation measurements made by the National Weather Service at the Orlando International Airport revealed no such relationship ($r = 0.0017, P = 0.8683$). However, the NWS rainfall measurements may not have been representative of precipitation received by the ponds due to the distance (ca. 26 km) between the weather reporting station and the experimental pond study area; rainfall induced runoff remains the most viable explanation for the observed trends in water color.

The seasonal trends of turbidity varied widely between the ponds, and in Ponds 1 and 3 were clearly related to changes in phytoplankton abundance (Figure 6). Turbidity and chlorophyll $a$ concentrations were highly correlated in Ponds 1 and 3 (Tables 2 and 4); although an inverse relationship appeared to exist between chlorophyll $a$ and
Figure 4. Seasonal trend of water temperature in the three experimental ponds, October 1978-1979. Points appearing over each date are means for the two-month period prior to that month's periphyton biomass sampling.
Figure 5. Seasonal trend of water color in the three experimental ponds, October 1978-1979. Points appearing over each date are means for the two-month period prior to that month's periphyton biomass sampling.
POND 1

POND 2

POND 3

Pt-Co Units


Pt-Co Units

Pt-Co Units

Pt-Co Units
Figure 6. Seasonal trends of turbidity and chlorophyll a in the three experimental ponds, October 1978-1979. Points appearing over each date are means for the two-month period prior to that month's periphyton biomass sampling.
Table 2. Simple linear correlation coefficients and significance levels (in parentheses) for water quality parameters in Pond 1, October, 1978 through October, 1979.

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Table 3. Simple linear correlation coefficients and significance levels (in parentheses) for water quality parameters in Pond 2, October, 1978 through October, 1979.

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Table 4. Simple linear correlation coefficients and significance levels (in parentheses) for water quality parameters in Pond 3, October, 1978 through October, 1979.

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turbidity measurements in Pond 2 for the first eight months of the study, there was no significant correlation between turbidity and chlorophyll a in Pond 2 (Table 3). Phytoplankton abundance is believed to have been the dominant factor influencing turbidity in all three ponds, and the lack of correlation between phytoplankton density and turbidity in Pond 2 was probably due to interference from other causes of turbidity (e.g., suspended sediments, zooplankton). The seasonal periodicity of phytoplankton abundance in Ponds 2 and 3 was very similar, and the dissimilarity of phytoplankton periodicity in Pond 1 to that in Ponds 2 and 3 suggests the regulatory mechanisms acting on phytoplankton in Pond 1 were different from those in the other ponds (Figure 6).

Light extinction coefficients showed a strong positive correlation with water color values in Ponds 1 and 2, but there were no significant correlations between light extinction coefficients and turbidity, suggesting that water color was the major influence on changes in light penetration in the ponds (Tables 2, 3 and 4). Nevertheless, a comparison of the annual means of turbidity, water color and light extinction coefficients (Table 1) reveals turbidity as the most important factor regulating light penetration in the ponds.

There was a strong negative correlation between dissolved oxygen and temperature in all three ponds (Tables 2, 3 and 4), reflecting the decreased solubility of dissolved gases with increasing temperature (Wetzel, 1975). There were also strong positive correlations between dissolved oxygen and pH in all three ponds (Tables 2, 3 and 4) which can probably be attributed to the interrelationships
which occur between dissolved oxygen, carbon dioxide and pH in freshwater due to plant photosynthesis (Wetzel, 1975). A strong positive correlation existed between specific conductivity and inorganic carbon in Pond 1 (Table 2) but not in Ponds 2 or 3 (Tables 3 and 4); apparently, ionic species other than bicarbonate and carbonate contributed to the seasonal variability of specific conductivity in Ponds 2 and 3. Chlorophyll a concentrations were positively correlated with inorganic carbon in Ponds 1 and 3, but not in Pond 2 (Tables 2, 3 and 4).

Some differences in the water chemistry of the three ponds were probably a result of differences in biological activity. For example, the higher annual mean pH in Pond 2 (Table 1) was probably due to an increased demand on free carbon dioxide by the comparatively large phytoplankton population in Pond 2. The more fundamental differences in the ponds, which were ultimately responsible for the biological patterns observed, can probably be attributed to differences in the pond sediments. Golterman (1973) has shown how the texture and composition of sediments influences the degree to which nutrients become available to algae in the overlying water. Differences in sediment type that occurred during pond construction, or as a result of differences in aquatic vegetation growth in the ponds, may have been responsible for inequities in nutrient availability which influences algal density and periodicity in the experimental ponds (J.A. Osborne, personal communication, 1980).

Periphytic Algae Quantitative Results

To determine the effect of substrate type on biomass estimates,
a two-way analysis of variance (Helwig and Council, 1979) was used to compare the chlorophyll a concentration of periphyton collected from each pair of wood and tile substrates removed from the ponds during the year long study. There was no significant difference between chlorophyll a concentrations on the two substrate types for both bimonthly (df = 137, \( P = 0.6355 \)) or continuously immersed (df = 119, \( P = 0.2150 \)) substrates. Periphyton density has been shown to be relatively independent of substrate type in a recent study of five artificial substrates (glass, frosted glass, Vermont slate, flagstone and acrylic plate) incubated on the bottom of the Susquehanna River, Pennsylvania (Lowe and Gale, 1980). Since periphytic algae biomass on wood and tile substrates was identical, all further discussion will be restricted to data gathered from tile substrates.

There was a strong similarity in the seasonal trends of biomass for continuously and bimonthly immersed tile substrates when chlorophyll a concentration was used as a measure of periphytic algae biomass (Figure 7). Simple linear correlation between bimonthly and continuously immersed substrate chlorophyll a biomass estimates was significant at the \( P \leq 0.01 \) level (\( r = 0.8963 \), df = 18). Periphytic algae biomass on continuously immersed tiles was generally much greater than that on bimonthly immersed substrates, but occasional seasonal variations in biomass indicated that the amount of algal accumulation was not strictly a function of immersion time (Figure 7). The similarity in seasonal trends of biomass for bimonthly and continuously immersed substrates was not as strong
Figure 7. Seasonal trends in chlorophyll $a$ concentrations for bimonthly and continuously immersed artificial substrates in the experimental ponds, October 1978-1979.
when dry weight was used as the estimator of biomass; the simple linear correlation of continuous and bimonthly-immersion biomass estimates by dry weight was significant at the $P \leq 0.05$ level ($r = 0.5545$, df = 18).

Although trends in biomass for bimonthly and continuously immersed substrates were similar, periphyton production on continuously immersed substrates was often quite different from that on bimonthly immersed substrates. When periphyton biomass on continuously immersed substrates was relatively low (Figures 7 and 8) the productivity on those substrates was equal to or greater than that on bimonthly-immersed substrates (Tables 5 and 6). However, at high periphyton densities production on continuous-immersion substrates was almost always less than that of uncolonized bimonthly substrates (e.g., June through October in Pond 3, Figure 7 and Table 5). The onset of reduced productivity on continuous-immersion substrates probably relates to the approach of the periphyton biomass to the current pond "carrying capacity"; negative production values (Tables 5 and 6) occurred when periphyton biomass exceeded the carrying capacity. The idea of a carrying capacity limit for the periphyton community is not new; Waters (1961) demonstrated that colonization of artificial substrates in a Minnesota stream was complete within three to four weeks with the attainment of a stable periphyton biomass ("population saturation") and that periphytic algae biomass on substrates immersed beyond this initial colonization period varied seasonally with environmental conditions.

Periphyton studies using artificial substrates have usually
Figure 8. Seasonal trends in dry weight of periphyton for bimonthly and continuously immersed artificial substrates in the experimental ponds, October 1978-1979. Each point represents the mean of four observations made in each pond for the sample date shown.
Table 5. Periphytic algae productivity on tile substrates, measured as mg Chl $\alpha/m^2$/day. Standard errors appear in parentheses; B = Bimonthly, C = Continuous immersion substrates.

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<td>1.666</td>
<td>0.702</td>
<td>-0.530</td>
<td>2.843</td>
<td>0.666</td>
</tr>
<tr>
<td></td>
<td>(0.134)</td>
<td>(0.126)</td>
<td>(0.107)</td>
<td>(0.580)</td>
<td>(0.398)</td>
<td>(0.650)</td>
</tr>
<tr>
<td>Aug</td>
<td>0.307</td>
<td>-2.289</td>
<td>1.117</td>
<td>1.922</td>
<td>2.572</td>
<td>1.398</td>
</tr>
<tr>
<td></td>
<td>(0.037)</td>
<td>(0.149)</td>
<td>(0.183)</td>
<td>(0.381)</td>
<td>(0.460)</td>
<td>(0.496)</td>
</tr>
<tr>
<td>Oct</td>
<td>1.365</td>
<td>1.352</td>
<td>2.368</td>
<td>4.306</td>
<td>6.655</td>
<td>1.561</td>
</tr>
<tr>
<td></td>
<td>(0.230)</td>
<td>(0.096)</td>
<td>(0.774)</td>
<td>(1.301)</td>
<td>(0.280)</td>
<td>(0.559)</td>
</tr>
</tbody>
</table>
Table 6. Periphytic algae productivity on tile substrates, measured as g dry weight/m²/day. Standard errors appear in parentheses; B = Bimonthly, C = Continuous immersion substrates.

<table>
<thead>
<tr>
<th>Month</th>
<th>Pond 1 B</th>
<th>Pond 1 C</th>
<th>Pond 2 B</th>
<th>Pond 2 C</th>
<th>Pond 3 B</th>
<th>Pond 3 C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec</td>
<td>0.5611 (0.1264)</td>
<td>0.5611 (0.1264)</td>
<td>0.5618 (0.0502)</td>
<td>0.5618 (0.0502)</td>
<td>0.4096 (0.0677)</td>
<td>0.4096 (0.0677)</td>
</tr>
<tr>
<td>Feb</td>
<td>0.2924 (0.1958)</td>
<td>0.2132 (0.2459)</td>
<td>0.1372 (0.0329)</td>
<td>0.7509 (0.3765)</td>
<td>0.4184 (0.0753)</td>
<td>0.5880 (0.1341)</td>
</tr>
<tr>
<td>Apr</td>
<td>0.6395 (0.2379)</td>
<td>0.1755 (0.1598)</td>
<td>0.5491 (0.1800)</td>
<td>0.6749 (0.2323)</td>
<td>0.4516 (0.1227)</td>
<td>0.4041 (0.1911)</td>
</tr>
<tr>
<td>Jun</td>
<td>0.9452 (0.0845)</td>
<td>0.9240 (0.3225)</td>
<td>0.8068 (0.2100)</td>
<td>0.5393 (0.4037)</td>
<td>0.8527 (0.1762)</td>
<td>0.1250 (0.4152)</td>
</tr>
<tr>
<td>Aug</td>
<td>0.0860 (0.0222)</td>
<td>-1.2359 (0.2020)</td>
<td>0.9402 (0.2102)</td>
<td>0.0816 (0.2277)</td>
<td>0.5804 (0.2428)</td>
<td>-0.1703 (0.0804)</td>
</tr>
<tr>
<td>Oct</td>
<td>0.2493 (0.0276)</td>
<td>-0.2452 (0.0994)</td>
<td>1.0553 (0.3790)</td>
<td>3.4935 (0.6393)</td>
<td>1.2818 (0.1458)</td>
<td>0.6671 (0.3953)</td>
</tr>
</tbody>
</table>
used relatively brief immersion periods, from as short as two days (Kevern, et al., 1966) to as long as twelve weeks (Dumont, 1969), with immersion periods of two to four weeks most common. Lowe and Gale (1980) suggested that the use of substrates immersed for short periods of time may not be of value in making reliable inferences about the periodicity of periphyton density after finding that trends in periphyton density on cumulative artificial substrates were similar to those of natural river stones, whereas trends in periphyton colonization rates for monthly artificial substrates were often diametrically opposed to the trends on natural surfaces. The data collected in this study supports the view that production values obtained from substrates immersed for relatively brief periods of time may be widely divergent from the productivity of a dense natural periphyton community because of the constraints imposed upon production by the carrying capacity of the system under study.

A comparison of the seasonal trends of chlorophyll a (Figure 7) and dry weight (Figure 8) reveals how closely these two techniques agreed in reflecting seasonal variations in periphytic algae biomass. The simple linear regression of chlorophyll a against dry-weight biomass was significant at the $P = 0.0001$ level; almost 64% of the variability in chlorophyll a could be accounted for by variations in dry weight (Figure 9). All but one of the points falling above the 95% confidence interval for the mean (Figure 9) were contributed by Pond 3, indicating that the periphyton collected in Pond 3 generally had more chlorophyll a per unit dry weight than periphyton from Ponds 1 or 2. In fact, Pond 3 had the largest annual mean ratio of
Figure 9. Simple linear regression of mean chlorophyll a concentration and dry weight of periphyton collected in the experimental ponds, October 1978-1979. Dashed lines denote 95% confidence interval for the mean.
mg Chla = 32.1 + 1.44 (g Dry Weight)

$r^2 = 0.637$

DRO WEIGHT, g/m²

CHLOROPHYLL a, mg/m²
chlorophyll \( \text{a} \) to dry weight of the three ponds (3.15 mg Chl \( \text{a}/g \) dry weight)(Table 7). Duncan's Multiple Range Test revealed that the annual mean chlorophyll \( \text{a}/\text{dry weight} \) ratio in Pond 1 (2.75 mg Chl \( \text{a}/g \) dry weight) was not significantly different from that of Pond 3 (\( P \leq 0.05 \)); the annual mean chlorophyll \( \text{a}/\text{dry weight} \) ratio in Pond 2 (1.42 mg Chl \( \text{a}/g \) dry weight) was significantly lower than those of the other ponds (Table 7).

Variability in the chlorophyll \( \text{a}/\text{dry weight} \) ratio can be interpreted as an indication of differences in the proportion of algae to heterotrophic organisms in periphyton samples. The Autotrophic Index, for example, is based on the ratio of dry weight (total biomass) to chlorophyll \( \text{a} \) (algal biomass) in the periphyton (Weber, 1973); the relationship between chlorophyll \( \text{a} \) and dry weight has been shown to be sensitive to the relative abundance of inorganic detritus and heterotrophic organisms in the periphyton of streams in central Finland (Eloranta and Kunnas, 1979). Ponds 1 and 3 had a small heterotrophic component, as indicated by annual mean chlorophyll \( \text{a}/\text{dry weight} \) ratios comparable to those of algal dominated stations studied by Eloranta and Kunnas (1979), whereas the low chlorophyll \( \text{a}/\text{dry weight} \) ratio for Pond 2 suggests that the periphyton in that pond was largely heterotrophic. The ratio of optical densities of chlorophyll \( \text{a} \) extractions before and after acidification provides a measure of the "physiological health" of the algae (Weber, 1973), inasmuch as a low ratio indicates the presence of degraded chlorophyll, pheophytin \( \text{a} \). The low annual mean absorbance ratio for Pond 2 indicates that much of
Table 7. Annual means of periphytic algae parameters for experimental ponds, October, 1978 through October, 1979. Means with the same letter are not significantly different, \( P \leq 0.05 \).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Pond 1</th>
<th>Pond 2</th>
<th>Pond 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll Biomass (mg Chl (a/\text{m}^2))</td>
<td>82.57(A)</td>
<td>147.35(B)</td>
<td>184.02(B)</td>
</tr>
<tr>
<td>Dry Weight Biomass (g dry weight/(\text{m}^2))</td>
<td>41.47(A)</td>
<td>61.57(A)</td>
<td>99.41(B)</td>
</tr>
<tr>
<td>Chlorophyll/Dry Weight (mg Chl (a/g) dry weight)</td>
<td>2.75(A)</td>
<td>1.42(B)</td>
<td>3.15(A)</td>
</tr>
<tr>
<td>Absorbance Ratio (OD 665(B/\text{OD 665}_A))</td>
<td>1.64(A,B)</td>
<td>1.60(A)</td>
<td>1.68(B)</td>
</tr>
</tbody>
</table>
the chlorophyll a measured in Pond 2 was degraded and that the chlorophyll a:dry weight ratio may have underestimated the dominance of heterotrophs in the Pond 2 periphyton. Examination of the periphyton's taxonomic composition (discussed in the next section) confirmed the heterotrophic nature of the Pond 2 periphyton relative to the algal dominated periphyton of Ponds 1 and 3.

The effects of light intensity and temperature on periphyton have been well documented. Phinney and McIntire (1965) demonstrated that periphyton metabolism increased logarithmically (Q10 of ca. 2) when light was not limiting and temperature was increased in artificial streams, and Cushing (1967) showed chlorophyll a and dry-weight biomass of periphyton to be positively correlated with temperature in the Columbia River. However, most researchers agree that light intensity, not temperature, is of primary importance in regulating periphytic algae growth (Wetzel, 1964; Kevern and Ball, 1965; Welch, et al., 1972). Positive correlations of periphyton biomass and temperature in Ponds 2 and 3 suggest that periphyton growth was enhanced by increasing water temperatures (Tables 9 and 10), but it is not possible to assign credit to water temperature alone due to the dependence of temperature on solar insolation; there was no correlation of temperature and periphyton biomass in Pond 1 (Table 8). The positive correlation of temperature with the chlorophyll a:dry weight ratio of the periphyton in Pond 3 (Table 10) suggests an increase in the algal component of the Pond 3 periphyton with increasing water temperature; however, the increase in chlorophyll a per unit dry weight was also positively
Table 8. Simple linear correlation coefficients and significance levels (in parentheses) for periphytic algae and water quality parameters in Pond 1, October, 1978 - October, 1979.

<table>
<thead>
<tr>
<th></th>
<th>Chl a/m²</th>
<th>g DW/m²</th>
<th>Abs. Ratio</th>
<th>Chl a/g DW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp.</td>
<td>0.4482</td>
<td>-0.1218</td>
<td>0.0145</td>
<td>0.6185</td>
</tr>
<tr>
<td></td>
<td>(0.1439)</td>
<td>(0.8182)</td>
<td>(0.9783)</td>
<td>(0.1906)</td>
</tr>
<tr>
<td>k</td>
<td>0.6097</td>
<td>-0.3089</td>
<td>-0.0928</td>
<td>0.8195</td>
</tr>
<tr>
<td></td>
<td>(0.0353)</td>
<td>(0.5514)</td>
<td>(0.8613)</td>
<td>(0.0459)</td>
</tr>
<tr>
<td>Color</td>
<td>0.6910</td>
<td>-0.2328</td>
<td>-0.0306</td>
<td>0.7307</td>
</tr>
<tr>
<td></td>
<td>(0.0128)</td>
<td>(0.6571)</td>
<td>(0.9540)</td>
<td>(0.0990)</td>
</tr>
<tr>
<td>Turbid.</td>
<td>-0.4777</td>
<td>0.2315</td>
<td>0.1517</td>
<td>-0.4846</td>
</tr>
<tr>
<td></td>
<td>(0.1163)</td>
<td>(0.6590)</td>
<td>(0.7741)</td>
<td>(0.3300)</td>
</tr>
<tr>
<td>D.O.</td>
<td>-0.3737</td>
<td>0.4258</td>
<td>0.2696</td>
<td>-0.8436</td>
</tr>
<tr>
<td></td>
<td>(0.2314)</td>
<td>(0.3999)</td>
<td>(0.6054)</td>
<td>(0.0348)</td>
</tr>
<tr>
<td>pH</td>
<td>-0.3862</td>
<td>0.3597</td>
<td>0.2361</td>
<td>-0.7151</td>
</tr>
<tr>
<td></td>
<td>(0.2149)</td>
<td>(0.4838)</td>
<td>(0.6524)</td>
<td>(0.1102)</td>
</tr>
<tr>
<td>Sp. Con.</td>
<td>0.0478</td>
<td>0.2922</td>
<td>-0.0575</td>
<td>-0.1850</td>
</tr>
<tr>
<td></td>
<td>(0.8828)</td>
<td>(0.5742)</td>
<td>(0.9138)</td>
<td>(0.7256)</td>
</tr>
<tr>
<td>Inorg. C</td>
<td>0.0710</td>
<td>-0.3191</td>
<td>-0.2569</td>
<td>0.4976</td>
</tr>
<tr>
<td></td>
<td>(0.8454)</td>
<td>(0.6007)</td>
<td>(0.6765)</td>
<td>(0.3936)</td>
</tr>
<tr>
<td>Chl a/m³</td>
<td>0.0325</td>
<td>-0.4745</td>
<td>-0.4104</td>
<td>0.8274</td>
</tr>
<tr>
<td></td>
<td>(0.9291)</td>
<td>(0.4193)</td>
<td>(0.4925)</td>
<td>(0.0838)</td>
</tr>
</tbody>
</table>
Table 9. Simple linear correlation coefficients and significance levels (in parentheses) for periphytic algae and water quality parameters in Pond 2, October, 1978 - October, 1979.

<table>
<thead>
<tr>
<th></th>
<th>Chl (a/m^2)</th>
<th>(g \text{ DW/m}^2)</th>
<th>Abs. Ratio</th>
<th>Chl (a/g \text{ DW})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp.</td>
<td>0.5780</td>
<td>0.9178</td>
<td>-0.0030</td>
<td>-0.0610</td>
</tr>
<tr>
<td></td>
<td>(0.0490)</td>
<td>(0.0094)</td>
<td>(0.9955)</td>
<td>(0.9085)</td>
</tr>
<tr>
<td>(k)</td>
<td>0.5223</td>
<td>0.5507</td>
<td>0.3130</td>
<td>0.2560</td>
</tr>
<tr>
<td></td>
<td>(0.0815)</td>
<td>(0.2575)</td>
<td>(0.5458)</td>
<td>(0.6244)</td>
</tr>
<tr>
<td>Color</td>
<td>0.5401</td>
<td>0.2298</td>
<td>0.1793</td>
<td>0.5404</td>
</tr>
<tr>
<td></td>
<td>(0.0699)</td>
<td>(0.6614)</td>
<td>(0.7339)</td>
<td>(0.2683)</td>
</tr>
<tr>
<td>Turbid.</td>
<td>0.0319</td>
<td>-0.1945</td>
<td>0.6986</td>
<td>0.3714</td>
</tr>
<tr>
<td></td>
<td>(0.9215)</td>
<td>(0.7120)</td>
<td>(0.1225)</td>
<td>(0.4685)</td>
</tr>
<tr>
<td>D.O.</td>
<td>-0.8421</td>
<td>-0.7195</td>
<td>0.1327</td>
<td>-0.4337</td>
</tr>
<tr>
<td></td>
<td>(0.0006)</td>
<td>(0.1070)</td>
<td>(0.8021)</td>
<td>(0.3902)</td>
</tr>
<tr>
<td>pH</td>
<td>-0.7326</td>
<td>-0.5199</td>
<td>0.2447</td>
<td>-0.4456</td>
</tr>
<tr>
<td></td>
<td>(0.0067)</td>
<td>(0.2904)</td>
<td>(0.6403)</td>
<td>(0.3758)</td>
</tr>
<tr>
<td>Sp. Con.</td>
<td>0.3591</td>
<td>0.4239</td>
<td>-0.8594</td>
<td>-0.0953</td>
</tr>
<tr>
<td></td>
<td>(0.2516)</td>
<td>(0.4022)</td>
<td>(0.0283)</td>
<td>(0.8575)</td>
</tr>
<tr>
<td>Inorg. C</td>
<td>-0.0964</td>
<td>-0.4668</td>
<td>-0.3918</td>
<td>0.1987</td>
</tr>
<tr>
<td></td>
<td>(0.7656)</td>
<td>(0.3507)</td>
<td>(0.4423)</td>
<td>(0.7058)</td>
</tr>
<tr>
<td>Chl (a/m^3)</td>
<td>-0.2008</td>
<td>-0.0380</td>
<td>-0.1354</td>
<td>-0.2599</td>
</tr>
<tr>
<td></td>
<td>(0.5314)</td>
<td>(0.9430)</td>
<td>(0.7981)</td>
<td>(0.6189)</td>
</tr>
</tbody>
</table>
Table 10. Simple linear correlation coefficients and significance levels (in parentheses) for periphytic algae and water quality parameters in Pond 3, October, 1978 - October, 1979.

<table>
<thead>
<tr>
<th></th>
<th>Chl a/m²</th>
<th>g DW/m²</th>
<th>Abs. Ratio</th>
<th>Chl a/g DW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp.</td>
<td>0.7900</td>
<td>0.7511</td>
<td>0.2051</td>
<td>0.8285</td>
</tr>
<tr>
<td></td>
<td>(0.0022)</td>
<td>(0.0852)</td>
<td>(0.5978)</td>
<td>(0.0416)</td>
</tr>
<tr>
<td>k</td>
<td>0.5121</td>
<td>0.4286</td>
<td>0.1908</td>
<td>0.8444</td>
</tr>
<tr>
<td></td>
<td>(0.0887)</td>
<td>(0.3965)</td>
<td>(0.7173)</td>
<td>(0.0342)</td>
</tr>
<tr>
<td>Color</td>
<td>0.2177</td>
<td>0.5032</td>
<td>0.8401</td>
<td>-0.2494</td>
</tr>
<tr>
<td></td>
<td>(0.4966)</td>
<td>(0.3089)</td>
<td>(0.0363)</td>
<td>(0.6336)</td>
</tr>
<tr>
<td>Turbid.</td>
<td>-0.4165</td>
<td>-0.4831</td>
<td>-0.6164</td>
<td>-0.3744</td>
</tr>
<tr>
<td></td>
<td>(0.1781)</td>
<td>(0.3317)</td>
<td>(0.1925)</td>
<td>(0.4646)</td>
</tr>
<tr>
<td>D.O.</td>
<td>-0.8856</td>
<td>-0.8489</td>
<td>-0.4196</td>
<td>-0.7946</td>
</tr>
<tr>
<td></td>
<td>(0.0001)</td>
<td>(0.0325)</td>
<td>(0.4075)</td>
<td>(0.0590)</td>
</tr>
<tr>
<td>pH</td>
<td>-0.5981</td>
<td>-0.6350</td>
<td>-0.3328</td>
<td>-0.4704</td>
</tr>
<tr>
<td></td>
<td>(0.0400)</td>
<td>(0.1755)</td>
<td>(0.5192)</td>
<td>(0.3464)</td>
</tr>
<tr>
<td>Sp. Con.</td>
<td>0.0668</td>
<td>0.0017</td>
<td>-0.5787</td>
<td>-0.0413</td>
</tr>
<tr>
<td></td>
<td>(0.8365)</td>
<td>(0.9975)</td>
<td>(0.2289)</td>
<td>(0.9381)</td>
</tr>
<tr>
<td>Inorg. C</td>
<td>-0.6357</td>
<td>-0.6606</td>
<td>-0.2989</td>
<td>-0.7333</td>
</tr>
<tr>
<td></td>
<td>(0.0254)</td>
<td>(0.1532)</td>
<td>(0.5650)</td>
<td>(0.0972)</td>
</tr>
<tr>
<td>Chl a/m³</td>
<td>-0.3403</td>
<td>-0.2253</td>
<td>0.2934</td>
<td>-0.3721</td>
</tr>
<tr>
<td></td>
<td>(0.2790)</td>
<td>(0.6678)</td>
<td>(0.5725)</td>
<td>(0.4676)</td>
</tr>
</tbody>
</table>
correlated with light extinction coefficient values (Table 10) which indicate that the increase in chlorophyll $a$ may have been an adaptation to decreased light availability.

Light availability was the key factor which determined the amounts of periphytic algae observed in Ponds 2 and 3. As was noted previously, the seasonal periodicity of phytoplankton biomass in the two ponds was very similar, but phytoplankton abundance in Pond 2 was much higher than that in Pond 3 and resulted in greater turbidity and light extinction values for that pond. Eloranta and Kunnas (1979) reported that a reduction of light by turbidity hampered the growth of attached algae in Finnish streams; similarly, submersed macrophytes have been shown to grow poorly during phytoplankton blooms in experimental ponds (Mulligan, et al., 1976), and low periphyton densities have been reported in high mountain lakes following the development of phytoplankton blooms after artificial fertilization (Rabe, 1965). Presumably, the light attenuating effects of the greater phytoplanktonic turbidity in Pond 2 were responsible for the inhibition of growth by periphytic algae and the development of a heterotroph-dominated periphyton community in that pond.

Although annual mean water clarity in Pond 1 was virtually identical to that of Pond 3 (Table 1), the seasonal periodicity of periphyton biomass was quite different (Figure 7). Pond 1 periphyton biomass did not continue to increase with rising water temperatures, but declined after a peak in June, giving Pond 1 the appearance of being nutrient limited with respect to Ponds 2 and 3; unfortunately
no nutrient data are available to test this hypothesis. The positive correlation of periphyton chlorophyll a with water color in Pond 1 (Table 8) suggests that the periphytic algae were adapting to changes in light intensity caused by water color variations. This may have been true to some extent, as the chlorophyll a:dry weight ratio in Pond 1 was also positively correlated with water color (Table 8), but the similarity in the trends of chlorophyll a and dry-weight biomass in Pond 1 (Figures 7 and 8) demonstrates that variations in chlorophyll a reflected actual changes in periphyton biomass. In his paper on the seasonal variability of phytoplankton in tropical lakes, Melack (1979) reported that photosynthesis by benthic algae increased after the decline of a persistent phytoplankton bloom in Lake Elmenteita, Kenya. This pattern was evident in the trends of phytoplankton and periphytic algae biomass in Pond 1 (Figures 6 and 7), but without detailed nutrient analysis it is impossible to speculate on the nature of the relationship that may have existed between phytoplankton and periphytic algae.

The physiological health of the periphytic algae in Pond 3 (measured by the pheophytin absorbance ratio) improved with increasing water color (Table 10); the relationship between color and algal physiological health might be accounted for if water color variations were related to changes in available nutrients, perhaps as a result of runoff into the pond. The correlations of water color with periphytic algae biomass in Pond 1 (Table 8) might be similarly explained if water color were an index of nutrient input through runoff. Negative correlations between
Periphytic algae biomass and pH in Ponds 2 and 3 (Tables 9 and 10) might be attributed to the increase in carbon dioxide evolved during respiration by the periphyton in the summer months; dissolved oxygen concentrations were probably most sensitive to temperature changes, but oxygen uptake by respiring periphyton may have further depressed oxygen values in the summer, accounting for the high correlation of dissolved oxygen and periphytic algae biomass in Ponds 2 and 3 (Tables 9 and 10). The strong negative correlation between inorganic carbon and periphytic algae biomass in Pond 3 (Table 10) seems to suggest that periphytic algae photosynthesis may have worked to deplete inorganic carbon in the water and might account for the dependence of phytoplankton abundance on inorganic carbon in that pond (Table 4). Phytoplankton abundance and inorganic carbon were also correlated in Pond 2 (Table 2), although less strongly; however, there was no indication that the periphytic algae in Pond 1 made heavy demands on the available inorganic carbon. In any case, inorganic carbon is rarely limiting in freshwater systems (Wetzel, 1975), and the correlations observed may have been spurious.

**Periphytic Algae Taxonomic Composition**

Twelve genera of green algae (Class Chlorophyceae) and four genera of blue-green algae (Class Cyanophyceae) were identified among the three ponds during the study (Table 11). Although no methodical attempt was made to identify diatoms (Class Bacillariophyceae) to genus, it was apparent that the diatoms were very diverse taxonomically. Centric diatoms were almost unknown in the ponds,
Table 11. Coverage values (%) for algal taxa identified on glass slides from Ponds 1, 2 and 3, December, 1978 through October, 1979. Taxa observed in trace quantities are designated by a plus (+); a dash (-) indicates no observation for that taxon.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>December</th>
<th>February</th>
<th>April</th>
<th>June</th>
<th>August</th>
<th>October</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 2 3</td>
<td>1 2 3</td>
<td>1 2 3</td>
<td>1 2 3</td>
<td>1 2 3</td>
<td>1 2 3</td>
</tr>
<tr>
<td>Bacillariophyceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Filamentous</td>
<td>1.5 2.8 1.5</td>
<td>0.5 0.4 2.1</td>
<td>2.0 0.8 1.9</td>
<td>6.9 1.8 4.0</td>
<td>3.9 1.0 6.3</td>
<td>4.9 0.5 1.4</td>
</tr>
<tr>
<td>Centric</td>
<td>+ - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- -</td>
<td>- -</td>
<td>- -</td>
</tr>
<tr>
<td>Pennate</td>
<td>2.3 6.3 2.5</td>
<td>15. 2.5 3.8</td>
<td>2.5 2.5 2.3</td>
<td>15. 6.9 2.4</td>
<td>24. 6.9 2.4</td>
<td>14. 2.5 15.</td>
</tr>
<tr>
<td>Chlorophyceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cladophora</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>2.3 - 23.</td>
<td>3.0 0.8 8.8</td>
<td>3.5 - -</td>
</tr>
<tr>
<td>Closterium</td>
<td>0.8 - 0.5</td>
<td>0.1 - -</td>
<td>+ - -</td>
<td>+ - +</td>
<td>0.1 0.5 0.8</td>
<td>0.8 0.4 -</td>
</tr>
<tr>
<td>Coleochaete</td>
<td>- 0.2 -</td>
<td>- - -</td>
<td>+ - +</td>
<td>+ - +</td>
<td>- 1.8 - -</td>
<td>- - -</td>
</tr>
<tr>
<td>Mougeotia</td>
<td>1.3 + 3.8</td>
<td>- - 11.</td>
<td>13. 1.0</td>
<td>- - -</td>
<td>1.5 - -</td>
<td>- - -</td>
</tr>
<tr>
<td>Microspora</td>
<td>- - -</td>
<td>2.1 + 3.5</td>
<td>1.8 - -</td>
<td>- - 0.3</td>
<td>- - -</td>
<td>- - -</td>
</tr>
<tr>
<td>Oedogonium</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>2.1 -</td>
</tr>
<tr>
<td>Pedospermum</td>
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<td>- - -</td>
<td>- 1.6</td>
<td>- 1.0</td>
<td>- 1.9</td>
<td>- 1.3</td>
</tr>
<tr>
<td>Pleurotaenium</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>0.3 -</td>
</tr>
<tr>
<td>Scenedesmus</td>
<td>0.8 1.6 0.2</td>
<td>2.5 2.5 0.9</td>
<td>1.2 15. 0.2</td>
<td>1.6 6.9 1.0</td>
<td>2.1 8.1 0.5</td>
<td>- 2.5 -</td>
</tr>
<tr>
<td>Spirogyra</td>
<td>+ 0.3 -</td>
<td>- - 1.0</td>
<td>0.5 - 4.0</td>
<td>27. 0.1 0.2</td>
<td>6.6 0.2</td>
<td>- 7.5 -</td>
</tr>
<tr>
<td>Stigeoclonium</td>
<td>17. 4.4 5.6</td>
<td>4.6 1.9 1.9</td>
<td>4.1 2.1 11.</td>
<td>0.2 3.0 44.</td>
<td>1.8 1.1 4.1</td>
<td>2.1 1.2 3.1</td>
</tr>
<tr>
<td>Treubaria</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>0.2 -</td>
</tr>
<tr>
<td>Cyanophyceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anabaena</td>
<td>1.8 0.8 9.9</td>
<td>- 0.2 1.0</td>
<td>1.5 2.5 1.2</td>
<td>14. - -</td>
<td>1.5 0.5 0.5</td>
<td>- 0.5 -</td>
</tr>
<tr>
<td>Calothrix</td>
<td>2.5 1.0 1.9</td>
<td>- - 0.2</td>
<td>0.8 - 5.4</td>
<td>0.6 1.2 6.9</td>
<td>4.9 3.1 20.</td>
<td>2.9 3.6 5.8</td>
</tr>
<tr>
<td>Gloeocapsa</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>0.5 -</td>
</tr>
<tr>
<td>Oscillatoria</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>- - -</td>
<td>2.0 1.5</td>
<td>1.2 0.2</td>
</tr>
</tbody>
</table>
being observed in trace amounts only once in Pond 1 in December (Table 11); a "trace" value was defined as the observation of a taxon within a sample that, because of its rarity, was not included in a counted field. All of the filamentous diatoms observed were members of the Order Pennales. Unicellular pennate diatoms dominated the diatom flora in the ponds throughout the study except for two occasions, June and August in Pond 3 (Table 11). Unicellular and filamentous diatoms were present in each pond on every sample date, but were generally most abundant in Pond 1 (Table 11).

More than half of the twelve genera of green algae observed in the ponds were filamentous. *Stigeoclonium* was the only genus found in every pond throughout the year, and *Scenedesmus* was the second most frequently observed genus, missing only in Ponds 1 and 3 in October (Table 11). Three genera were observed only once: *Oedogonium* and *Pleurotaenium* in Pond 1, and *Treubaria* in Pond 2 appeared in October (Table 11). *Pediastrum* was observed only in Pond 2 and was present during every sample period except February (Table 11). The most frequently observed blue-green alga was *Calothrix* which was only absent from Ponds 1 and 2 in February and from Pond 2 again in April (Table 11). *Anabaena* was the second most frequently observed blue-green alga and was present in at least one pond every sample date (Table 11). *Oscillatoria* did not appear until late summer in Ponds 1 and 2 and was never observed in Pond 3 (Table 11); *Gloeocapsa* was found only in Pond 1 in August (Table 11).

The composition of the periphytic flora in the experimental ponds was similar to that reported for other bodies of freshwater in
Florida. Crowson (1950) listed Oscillatoria, Coleochaete, Stigeoclonium and Oedogonium as among the most common epiphytic genera in Port Leon Pool, north Florida. As in the experimental ponds, the Chlorophyceae constituted the dominant algal group in Port Leon Pool, and large algal mats that formed during periods of maximum production were composed partly of Spirogyra, Mougeotia and, to a lesser extent, Stigeoclonium (Crowson, 1950); these same genera, plus Cladophora, were responsible for most of the cover by green algae in the three ponds (Table 11). Crowson (1950) also reported the presence of non-filamentous Pleurotaenium and Scenedesmus, and the blue-greens Gloeocapsa and Oscillatoria. Many of the algal genera found in the ponds were among the attached algae of fresh, hardwater springs studied by Whitford (1956), including the green algae Cladophora, Microspora, Mougeotia, Oedogonium, Spirogyra and Stigeoclonium, and the blue-green filament Calothrix. Whitford (1956) noted that the algal community present in shallow water and amongst emergent plants at the edge of a hardwater spring boil resembled "the littoral community typical of Florida ponds and lakes," including the genera Spirogyra, Oedogonium, Mougeotia, Scenedesmus and Closterium, all of which were found in the three ponds (Table 11). Anabaena, which was common in the ponds, was found on both natural and artificial substrates in the Everglades (Swift and Green, unpublished data). Pediastrum, though not reported in Florida by the authorities referenced above, is known to be a common element of the periphytic flora (Round, 1973). Treubaria is a planktonic alga (Prescott, 1970) whose presence in the periphyton
by sedimentation probably reflected its high abundance in the water column of Pond 2.

The absence of an organism from a community can be attributed to dispersal, habitat selection, interaction with other species (e.g., predation), or because of inhospitable physical and chemical factors (Krebs, 1978). The proximity of the experimental ponds to one another rules out dispersal as a reason for differences in their taxonomic composition. Habitat selection can be ignored, and similar herbivorous organisms were present in all three ponds; physicochemical factors (i.e., water quality) must have been ultimately responsible for the presence and relative abundance of the various algal taxa in the ponds.

The persistently high phytoplankton biomass and largely heterotrophic periphyton of Pond 2 gave that pond the appearance of an advanced state of eutrophication which was reflected by the taxonomic composition of the periphytic algae. Total periphytic algae cover was generally lower in Pond 2 than in Ponds 1 and 3 (Table 11). Periphyton examined live on glass slides removed from Pond 2 was generally dominated by individuals of the protozoan genus Vorticella, and sessile rotifers were found in lesser abundance. Large, filamentous green algae were in low abundance in Pond 2 throughout the study, and unicellular or small colonial green algae (Pediastrum, Scenedesmus) predominated (Table 11); the lower surface-to-volume ratios of large algal cells limits their efficiency at nutrient uptake and reduces their turnover rate with respect to small algae, which may be better suited to take advantage of nutrient
rich conditions (Porter, 1977). The only filamentous green alga to attain significant cover in Pond 2, \textit{Stigeoclonium}, appears high on the list of genera tolerant of organic pollution compiled by Palmer (1969). \textit{Scenedesmus}, which dominated the Pond 2 flora, has also been associated with eutrophic conditions (Palmer, 1969), and together with \textit{Pediastrum} (which was found only in Pond 2) has been identified as a dominant member of the "eutrophic chlorococcal plankton" association by Hutchinson (1967).

The taxonomic composition of the periphyton in Ponds 1 and 3 was much alike, reflecting little difference in the water quality of those ponds (Table 11). The "clean water" genera \textit{Cladophora} and \textit{Calothrix} (Palmer, 1962) appeared most frequently and in highest abundance in Ponds 1 and 3. \textit{Oscillatoria}, which ranks second on the list of pollution tolerant genera (Palmer, 1969), may reflect some minor difference in water quality between Ponds 1 and 3 by its presence in Ponds 1 and 2 and its absence from Pond 3 (Table 11).

The total coverage contributed by all the genera within a class was plotted for each sample date and each pond (Figure 10) in order to provide some understanding of seasonal succession in the periphyton within the experimental ponds. No two ponds were alike in their successional patterns (Figure 10). The seasonal succession of periphytic algae generally follows the pattern typical of the plankton: a spring pulse of diatoms followed by the predominance of green algae in summer, blue-green algae in late summer--early fall, and another diatom peak in autumn. Such a pattern has been described for the periphytic algae of both lakes and streams (Butcher, 1932;
Figure 10. Seasonal trends in coverage (%) by three algal classes of periphytic algae collected on glass slides in the three experimental ponds, December 1978-October 1979.
Godward, 1937; Casterlin and Reynolds, 1977), and the seasonal periodicity of algal classes in Ponds 1 and 3 adhered in part to this pattern (Figure 10). In Pond 3 the shift of dominance from green algae to blue-greens in late summer and diatoms in the fall closely followed the classical successional pattern, but in Pond 1 green and blue-green algae peaked simultaneously and the diatom peak that followed arrived two months earlier than the diatom pulse in Pond 3 (Figure 10). The abundance of green and blue-green algae was depressed in February in Pond 1 (Figure 10), presumably due to low water temperatures; diatoms peaked during the same period. Blue-green coverage was depressed in February in Pond 3 as well, but green algae increased in coverage and diatom cover remained largely unchanged, in contrast to the pattern in Pond 1 (Figure 10). Due to the depauperate nature of the periphytic flora in Pond 2, no well-defined successional pattern developed in that pond.

A thorough treatment of the factors which influence algal succession has been rendered by Hutchinson (1967) and Fogg (1975). Temperature effects may account for some of the similarity in successional patterns in the three ponds, such as the near disappearance of the Cyanophyceae with cold water temperatures in February, but temperature obviously can not account for the differences in the successional patterns of the ponds. Although the ponds were subject to the same seasonal variations in incident light, the differences between ponds in light penetration due to turbidity and water color may have influenced the periphytic algae successional patterns; the reduction of light by high turbidity levels was surely
responsible for the meager development of the periphytic algae in Pond 2, and the subsequent lack of significant successional replacement by algal classes with seasonal changes in that pond. Diatoms, green and blue-green algae differ markedly in their nutritional needs (Hutchinson, 1967), and differences in the nature and amount of nutrients available in the ponds may have been responsible for the differences in the seasonal succession of periphytic algae in Ponds 1 and 3.
SUMMARY

The seasonal periodicity of phytoplankton biomass was identical in Ponds 2 and 3 (Figure 6), but annual mean phytoplankton biomass in Pond 2 was almost twice that in Pond 3 (Table 1); phytoplankton biomass in Pond 1 was low throughout most of the study following a "crash" in phytoplankton abundance in December, 1978 (Figure 6). The differences in phytoplankton periodicity and abundance in the ponds were presumably due to differences in nutrient availability. The amount of turbidity in the ponds and its affect on light penetration was directly related to annual mean phytoplankton abundance (Table 1).

Periphyton biomass increased between February and October in Ponds 2 and 3, but declined following a peak in early summer in Pond 1, presumably due to nutrient depletion (Figures 7 and 8). The periphyton in Pond 2 was largely heterotrophic and in poor physiological health, as indicated by a small chlorophyll a:dry weight ratio, a low annual mean pheophytin absorbance ratio (Table 7) and the predominance of Vorticella and sessile Rotifera in live periphyton samples; the dominance of heterotrophs in the Pond 2 periphyton was probably due to the reduction in light availability to the periphyton caused by phytoplankton turbidity. Ponds 1 and 3, which were similar in water clarity and light penetration, possessed
autotroph-dominated periphyton communities (Table 7).

The small amounts of algae found on glass slides in Pond 2 were largely composed of small colonial or unicellular green algae indicative of eutrophic conditions, whereas the algal flora of Ponds 1 and 3 were dominated by large, filamentous green algae typical of "clean" water (Table 11). The similarity in the periphytic floras of Ponds 1 and 3 suggested that light availability, rather than the implied differences in available nutrients, was most important in shaping the taxonomic composition of the periphytic algae communities in the experimental ponds.
APPENDIX

Means and standard errors (in parentheses) of water quality parameters in Ponds 1, 2 and 3 for the two-month periods preceding periphytic algae sampling, October, 1978 through October, 1979. Decimal points (.) signify when Secchi disc was visible on the pond bottom.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Pond</th>
<th>December</th>
<th>February</th>
<th>April</th>
<th>June</th>
<th>August</th>
<th>October</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>1</td>
<td>20.25(1.46)</td>
<td>16.31(1.54)</td>
<td>21.84(0.68)</td>
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<td>28.28(0.60)</td>
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<td></td>
<td>2</td>
<td>20.53(1.44)</td>
<td>16.74(1.72)</td>
<td>21.48(0.68)</td>
<td>27.53(0.69)</td>
<td>28.14(0.67)</td>
<td>27.24(0.29)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>20.67(1.49)</td>
<td>16.64(1.77)</td>
<td>22.30(0.74)</td>
<td>27.72(0.51)</td>
<td>28.21(0.60)</td>
<td>27.47(0.45)</td>
</tr>
<tr>
<td>Temperature (C)</td>
<td>1</td>
<td>20.08(1.53)</td>
<td>16.20(1.53)</td>
<td>22.55(1.42)</td>
<td>27.13(0.70)</td>
<td>28.16(0.63)</td>
<td>27.24(0.30)</td>
</tr>
<tr>
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<td>2</td>
<td>19.89(1.59)</td>
<td>16.29(1.69)</td>
<td>21.09(0.61)</td>
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<td>27.96(0.71)</td>
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</tr>
<tr>
<td></td>
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<td>20.19(1.58)</td>
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<td>22.02(0.70)</td>
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<td>27.98(0.65)</td>
<td>27.26(0.46)</td>
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<tr>
<td>Bottom</td>
<td>1</td>
<td>20.08(1.53)</td>
<td>16.20(1.53)</td>
<td>22.55(1.42)</td>
<td>27.13(0.70)</td>
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<td>Temperature (C)</td>
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<td>19.89(1.59)</td>
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<td>27.96(0.71)</td>
<td>27.12(0.31)</td>
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<td></td>
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<td>20.19(1.58)</td>
<td>16.40(1.82)</td>
<td>22.02(0.70)</td>
<td>27.33(0.62)</td>
<td>27.98(0.65)</td>
<td>27.26(0.46)</td>
</tr>
<tr>
<td>Bottom</td>
<td>1</td>
<td>114.5(2.53)</td>
<td>120.9(1.39)</td>
<td>120.2(1.01)</td>
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<td>105.5(0.96)</td>
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<td>1.34(0.18)</td>
<td>1.73(0.10)</td>
<td>2.17(0.52)</td>
<td>1.88(0.16)</td>
<td>4.26(0.64)</td>
</tr>
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<td>3.16(0.44)</td>
<td>3.44(0.93)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1.05(0.04)</td>
<td>1.16(0.28)</td>
<td>1.40(0.25)</td>
<td>1.96(0.34)</td>
<td>2.48(0.07)</td>
<td>1.62(0.58)</td>
</tr>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Depth (cm)</td>
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<td>66.8(1.8)</td>
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<td>65.1(5.1)</td>
<td>66.0(7.7)</td>
<td>47.0(1.4)</td>
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<tr>
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<td>13.55(1.59)</td>
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<tr>
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<td>19.20(1.04)</td>
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<td>1.82(0.14)</td>
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<td>9.65(2.49)</td>
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<td>8.38(0.91)</td>
<td>7.72(1.56)</td>
<td>7.85(0.32)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>3.55(1.88)</td>
<td>1.75(0.28)</td>
<td>3.22(0.71)</td>
<td>2.55(0.73)</td>
<td>2.32(0.56)</td>
<td>1.78(0.16)</td>
</tr>
<tr>
<td>Parameter</td>
<td>Pond</td>
<td>December</td>
<td>February</td>
<td>April</td>
<td>June</td>
<td>August</td>
<td>October</td>
</tr>
<tr>
<td>-----------------</td>
<td>------</td>
<td>-----------</td>
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<td>-----------</td>
<td>-----------</td>
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</tr>
<tr>
<td>Dissolved</td>
<td>1</td>
<td>7.50(0.41)</td>
<td>9.68(0.11)</td>
<td>7.69(0.65)</td>
<td>7.30(0.19)</td>
<td>5.68(1.46)</td>
<td>1.80(0.14)</td>
</tr>
<tr>
<td>Oxygen (ppm)</td>
<td>2</td>
<td>8.10(0.39)</td>
<td>10.05(0.29)</td>
<td>10.05(1.28)</td>
<td>8.02(0.71)</td>
<td>6.72(0.31)</td>
<td>2.60(0.70)</td>
</tr>
<tr>
<td>pH</td>
<td>3</td>
<td>7.94(0.49)</td>
<td>10.20(0.52)</td>
<td>6.38(0.42)</td>
<td>7.49(0.13)</td>
<td>4.25(0.45)</td>
<td>2.30(0.64)</td>
</tr>
<tr>
<td>Carbonate</td>
<td>1</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>3.50(2.06)</td>
<td>0.00</td>
</tr>
<tr>
<td>Alkalinity (mg/l CaCO₃)</td>
<td>2</td>
<td>0.00</td>
<td>0.00</td>
<td>23.50(9.54)</td>
<td>1.50(1.50)</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Bicarbonate</td>
<td>3</td>
<td>0.00</td>
<td>29.00(6.40)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Alkalinity (mg/l CaCO₃)</td>
<td>1</td>
<td>161.0(2.61)</td>
<td>163.5(3.77)</td>
<td>158.2(0.25)</td>
<td>116.2(10.5)</td>
<td>106.2(4.59)</td>
<td>136.2(0.48)</td>
</tr>
<tr>
<td>Carbon</td>
<td>2</td>
<td>174.8(2.46)</td>
<td>160.8(8.81)</td>
<td>140.5(4.87)</td>
<td>130.5(3.28)</td>
<td>138.0(7.82)</td>
<td>147.8(0.85)</td>
</tr>
<tr>
<td>(mg/l)</td>
<td>3</td>
<td>166.8(2.18)</td>
<td>129.2(15.6)</td>
<td>171.5(2.40)</td>
<td>142.5(4.05)</td>
<td>142.0(3.00)</td>
<td>143.0(5.20)</td>
</tr>
<tr>
<td>Inorganic</td>
<td>1</td>
<td>39.84(0.61)</td>
<td>40.22(0.93)</td>
<td>38.93(0.06)</td>
<td>28.61(2.66)</td>
<td>27.91(1.60)</td>
<td>36.54(1.55)</td>
</tr>
<tr>
<td>Carbon</td>
<td>2</td>
<td>42.98(0.51)</td>
<td>39.06(2.14)</td>
<td>38.83(3.06)</td>
<td>31.46(0.26)</td>
<td>33.80(2.01)</td>
<td>37.50(0.50)</td>
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<tr>
<td>(mg C/l)</td>
<td>3</td>
<td>41.15(0.51)</td>
<td>38.20(2.22)</td>
<td>43.05(0.78)</td>
<td>36.84(0.78)</td>
<td>35.54(0.95)</td>
<td>36.60(1.33)</td>
</tr>
<tr>
<td>Specific</td>
<td>1</td>
<td>297.8(0.63)</td>
<td>246.2(0.95)</td>
<td>290.5(5.48)</td>
<td>250.5(23.5)</td>
<td>231.0(6.36)</td>
<td>289.5(0.87)</td>
</tr>
<tr>
<td>Conductivity</td>
<td>2</td>
<td>333.8(14.8)</td>
<td>250.0(0.71)</td>
<td>274.0(9.24)</td>
<td>273.5(8.09)</td>
<td>276.2(13.7)</td>
<td>302.8(3.35)</td>
</tr>
<tr>
<td>(µmhos/cm @ 25°C)</td>
<td>3</td>
<td>367.0(32.4)</td>
<td>236.2(2.46)</td>
<td>312.2(1.89)</td>
<td>309.0(6.72)</td>
<td>293.8(5.92)</td>
<td>298.0(8.08)</td>
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<tr>
<td>Phytoplankton</td>
<td>1</td>
<td>28.98(9.85)</td>
<td>13.86(2.86)</td>
<td>5.86(0.37)</td>
<td>5.07(0.35)</td>
<td>5.93(1.74)</td>
<td>10.92(3.18)</td>
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<tr>
<td>Chlorophyll a</td>
<td>2</td>
<td>30.89(10.1)</td>
<td>22.22(1.06)</td>
<td>71.14(8.49)</td>
<td>53.55(14.4)</td>
<td>23.58(3.42)</td>
<td>34.56(6.63)</td>
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<tr>
<td>(mg/m³)</td>
<td>3</td>
<td>11.90(1.94)</td>
<td>8.82(1.94)</td>
<td>32.66(7.78)</td>
<td>26.03(3.39)</td>
<td>9.47(3.61)</td>
<td>8.39(1.52)</td>
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LITERATURE CITED


