

AQUATIC VEGETATION AS THE CAUSE OF  
CONTINUOUSLY HIGH pH VALUES

by

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A Thesis Submitted to the Faculty of the  
SCHOOL OF RENEWABLE NATURAL RESOURCES  
In Partial Fulfillment of the Requirements  
For the Degree of  
MASTER OF SCIENCE  
WITH A MAJOR IN FISHERIES SCIENCE  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

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Dedicated to my wife Sharlet, son Glen and daughter Jill  
for their patience at being husbandless and fatherless  
during the period of time I was a graduate student

## ACKNOWLEDGMENTS

Dr. Jerry C. Tash served as my major advisor and assisted in the field work and preparation of the thesis project in every way possible. I am in great debt to him for his guidance not only on the thesis project, but also for his patience and ability to instill in me the personal gratification to be gained through a fuller understanding of the philosophy of science.

The Department of the Army provided financial support and allowed me the time to undertake the schooling and thesis. My supervisor, Mr. Clark Derdeyn, assisted in the laboratory work and data collection as well as arranging my work schedule to allow time for me to attend school and complete the thesis project. The Arizona Cooperative Fisheries Unit personnel: Dr. Jerry C. Tash, Mr. Chuck Ziebell and Mrs. Esther Ayers, helped in every way possible and granted me unlimited support and use of Unit facilities and equipment.

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## ABSTRACT

The occurrence of continuously high pH values with little, none or inverse diel fluctuations were documented in the field and duplicated under laboratory conditions. This phenomenon was caused by various species of common aquatic vascular plants and filamentous algae, but not by unicellular planktonic algae. Information from the separate fields of plant physiology and limnology were analyzed to determine the mechanism by which the photosynthetic activity of the aquatic vegetation produce the phenomenon. The implications of this phenomenon as related to fisheries management and evolutionary consequences are discussed.

## INTRODUCTION

The pH value of a body of water has been recognized as one of the significant parameters in interpreting the physical, chemical and biological processes occurring in that water (Hutchinson 1957; Reid 1961; Ruttner 1963; Welch 1952; Wetzel 1975). The pH value of the water directly affects and is in turn affected by the aquatic organisms inhabiting that water. When used in combination with other limnological data the pH value is an important indicator regarding the productivity and suitability of that water for aquatic life.

Chemical mechanisms involving the pH of water are well documented and comprise a section of most textbooks on limnology (Hutchinson 1957; Reid 1961; Ruttner 1963; Stumm and Morgan 1970; U.S. Department of Interior [USDI] 1959; Welch 1952; Wetzel 1975). Effects of organisms on the maintenance and regulation of the pH of the water is not entirely clear despite extensive work on the subject (Bostrum 1967; Boyd 1972, 1973; Cole 1975; Holm-Hansen 1962; Lee and Hoadley 1967; Russell-Hunter 1970; Wright 1961). Effects of pH on aquatic organisms, particularly fish, have received some attention (Johnson 1968; McCarragher 1971; Trama 1954; Wiebe 1931) and optimal pH values have been recommended for the protection of aquatic organisms (Cleary 1955; European Inland Fisheries Advisory Commission [EIFAC] 1969; Finnell and Reed 1969; McKee and Wolf 1963; Stroud 1967; Swingle 1961).

The well documented phenomenon of diel fluctuating pH values associated with the photosynthetic activity of aquatic vegetation is

presently accepted as evidence that when aquatic vegetation is present, diel pH fluctuations usually occur (George 1961; Hutchinson 1957; Philip 1927; Reid 1961; Sreenivasan 1976; Welch 1948, 1952). Diel activities of aquatic vegetation would therefore elicit selective pressure on the cohabiting aquatic organisms resulting in the evolution of aquatic life adapted to diel pH fluctuations. In response to the diel fluctuating pH values, aquatic organisms have evolved the capability to tolerate brief periods during the daylight hours when the pH is at or above values that would otherwise be lethal to them for prolonged periods of time (Daye and Garside 1975; Eicher 1946; Jordan and Lloyd 1964; Lagler 1952; Steemann Nielsen 1952b; Weatherley 1972).

During recent limnological investigations of fishing impoundments in Arizona, I observed continuously high pH values in waters with abundant aquatic vegetation and other aquatic organisms. Continuously high pH values are not an isolated phenomenon and have been observed in African waters by Schütte and Elsworth (1954), in Indian waters by George (1961) and by Hasler and Jones (1949) in North American waters. An extensive search of the available literature could not entirely account for the mechanisms involved in producing the observed phenomenon. Something was occurring that could not adequately be explained by the information available and was, in fact, contrary to the basic premise of normal diel pH fluctuations so well documented. Plant physiologists have proven experimentally that the assimilation of carbon during photosynthesis by certain aquatic vegetation can create continuously high pH values (Raven 1970; Steemann Nielsen 1960). However, the information available from plant physiologists has not been

related to the observed limnological phenomenon of continuously high pH values.

The purpose of this study was to document the occurrence of continuously high pH values observed in the field and to determine the cause of and duplicate this phenomenon in the laboratory.

## MATERIALS AND METHODS

A Horizon Ecology Mini-Digital pH meter or a VWR pH master was used to measure the pH. Dissolved oxygen and temperature were measured with a Yellow Springs Instrument Co. Model 54 ARC meter. Alkalinity, hardness and CO<sub>2</sub> tests were measured with a Model AL 36 WR HACH kit. Weights <5.0g were made on a Model P Mettler balance and weights >5.0g on an HOMS Model 28 scale.

### Field Studies

The pH and alkalinity were measured at daybreak and midday in nine lakes in the White Mountains Region of east-central Arizona (A-1, Bootleg, Cooley, Horseshoe Cienega, Nelson Reservoir, Rainbow, Show Low, Shush-Be-Zahze and Sunrise Lakes) and two lakes on the Fort Huachuca Military Reservation in southeastern Arizona (Golf Course and Officers Club Lakes) once during the summer of 1977 and once during the summer of 1978. The pH values in Gravel Pit and Pan Am Lakes at the Fort Huachuca Military Reservation were measured weekly from June 1977 through May 1978. Visual estimates were made of the percentages of the surface areas of the lakes that were covered by aquatic vegetation. Samples of the vegetation were placed in plastic bags under ice and brought back to the laboratory for identification and experiments. Plants were identified using keys by Bold and Wynne (1978), Correll and Correll (1975) and Stodola (1967).

### Laboratory Experiments

Twelve 20-liter glass tanks and two 1,000-liter earthen tanks lined with plastic were used to hold the water and plants during the experiments. All vegetation in the experiments was from lakes sampled in field studies. Commercial fertilizer containing 10% N (0.8% nitric, 6.1% ammonia and 3.1% organic), 10% phosphoric acid, 10% potash, 0.29% Zn, 0.47% Mn, 10% Fe and 10% S was added to the tanks in excess of the values given by Fogg (1962) to provide most of the macro-nutrients required for normal plant growth.

Experiments were conducted on: (1) filamentous algae (Oedogonium sp. and Rhizoclonium sp.); (2) vascular plants (Myriophyllum spicatum); and (3) a combination of filamentous algae (Oedogonium sp.) and vascular plants (M. spicatum). The combination of the three major groups of experiments is displayed in Table 1. Tap water was obtained from Fort Huachuca which had a pH of 7.3 and total alkalinity of 205 ppm as  $\text{CaCO}_3$ . Gravel Pit Lake water from Fort Huachuca had a pH of 9.8, a total alkalinity of 130 ppm as  $\text{CaCO}_3$  and approximately 1,000 cells/ml of planktonic algae. The 20-liter tanks were refilled with the same type of water they contained to replace water loss due to evaporation after approximately 10% was lost. The 1,000-liter tanks were not refilled to replace water lost by evaporation. All of the tanks were outdoors and the illumination was from sunlight, averaging 14 hours during the experimental period from June 1, through July 21, 1978.

The pH in the tanks was measured twice daily; once at sunrise, approximately 5:00 AM, and once at midday, approximately 1:00 PM.

Table 1. Composition of experimental tank setups.

Species of Plants	Ratio	Grams/liter	Water	Tank Size (liters)	No. of Tanks
<u>Oedogonium:Rhizoclonium</u>	3:1	4.0	Tap	20	3
<u>Oedogonium:Rhizoclonium</u>	3:1	4.0	Gravel Pit	20	2
<u>M. Spicatum:Oedogonium</u>	4:1	1.4	Tap	1,000	2
<u>M. Spicatum</u>		3.2	Tap	20	3
<u>M. Spicatum</u>		11.0	Gravel Pit	20	2
Control			Tap	20	1
Control			Gravel Pit	20	1

Dissolved oxygen, temperature, alkalinity,  $\text{CO}_2$  and hardness tests were measured on an intermittent basis. Preliminary investigations indicated that the pH within the filamentous algal mats varied as much as 2-3 units from the pH in the open water areas that were free of vegetation. Therefore, pH values were always measured in an open water section of the tank and occasionally additional measurements were taken in the midst of the filamentous algal mats. During a 24-h period, 13 measurements at 2-h intervals were taken to record the entire diel cycle. Vegetation was weighed after light sponging with a paper towel.

Continuously high pH values are defined as those exceeding 8.5 throughout a 24-h diel cycle, in contrast to values that fluctuate to levels under 8.5 units during a 24-h period; the latter phenomenon has been the condition most often reported (Dineen 1953; Dunn 1967; George 1961; Philip 1927; Sreenivasan 1976).

## RESULTS

Continuously high pH values were found in two lakes in the White Mountains (Bootleg and Rainbow Lakes) and one at the Fort Huachuca Military Reservation (Gravel Pit Lake). All of these lakes had large amounts of aquatic plants and/or filamentous algae. In the other lakes studied, some had only small amounts of aquatic vascular vegetation and/or filamentous algae, or some contained only planktonic algae, and in these lakes the pH fluctuated below 8.5 during a 24-h period. Plants from lakes having continuously high pH values were used in experiments in the laboratory.

### Field Studies

Of the 13 lakes in which observations were made, only two in the White Mountains and Gravel Pit Lake at Fort Huachuca had greater than 20% of their surface areas covered by aquatic vascular vegetation and/or epiphytic filamentous algae. These three lakes exhibited continuously high pH values during the early summer of 1977 and 1978, prior to the rainy season.

The highest pH values occurred in Gravel Pit Lake, a two ha reservoir on Fort Huachuca. The sunrise and midday pH values observed at Gravel Pit Lake over the one year period of June 1, 1977 through May 31, 1978 were above 8.5 for six months of the year (Fig. 1). During the summer months, approximately 40% of the surface area of Gravel Pit Lake was covered by M. spicatum. A mixture of Oedogonium sp.

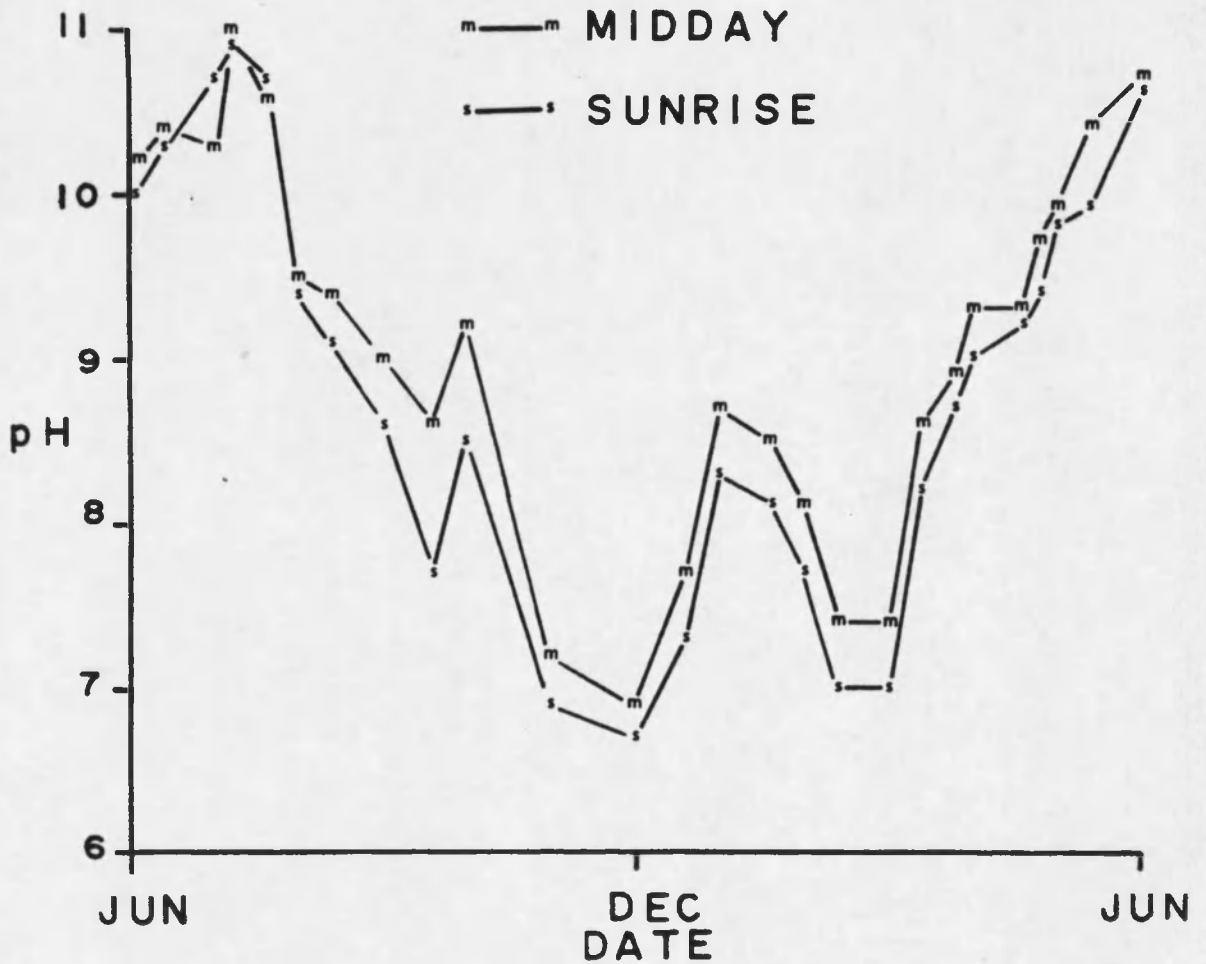


Figure 1. Sunrise and midday pH values at Gravel Pit Lake, Fort Huachuca, from June 1, 1977 through May 31, 1978.

(90%) and Rhizoclonium sp. (10%) formed an algal mat that was epiphytic on as much as 50% of the M. spicatum. This algal mixture also formed dense carpets on the bottom and on the M. spicatum in the illuminated littoral zone. The M. spicatum was measured at a density of 420 g/m<sup>2</sup> of total surface area and the filamentous algae at 260 g/m<sup>2</sup> of total surface area during a period of their greatest abundance in the summer of 1977. The percentage of each of these groups was approximately 60% M. spicatum, 35% Oedogonium sp. and 5% Rhizoclonium sp.

Vertical stratification in Gravel Pit Lake during the period of continuously high pH values consisted of less than 1 pH unit of change in the deepest portion of the lake which was free of vegetation (Fig. 2). Average vertical temperatures during this period were 24.2 C at the surface and 17.1 C at 10m. Total alkalinity ranged between 100 and 130 mg/l as CaCO<sub>3</sub> during the entire study period at Gravel Pit Lake.

Pan Am Lake, a one ha reservoir at Fort Huachuca, contained no vascular plants or filamentous algae, but had >100,000 cells/ml of planktonic algae during the spring-summer periods of 1977 and 1978. The sunrise and midday pH values in Pan Am Lake from June 1, 1977 through May 31, 1978 fluctuated markedly (Fig. 3). There was less than 1 unit of change in the vertical pH values at Pan Am Lake as measured on July 27, 1977 (Fig. 4); vertical temperature stratification on this date was 23.0 C at the surface and 14.6 C at 4m. Total alkalinity ranged between 86 and 103 mg/l as CaCO<sub>3</sub> during the entire study period at Pan Am Lake.

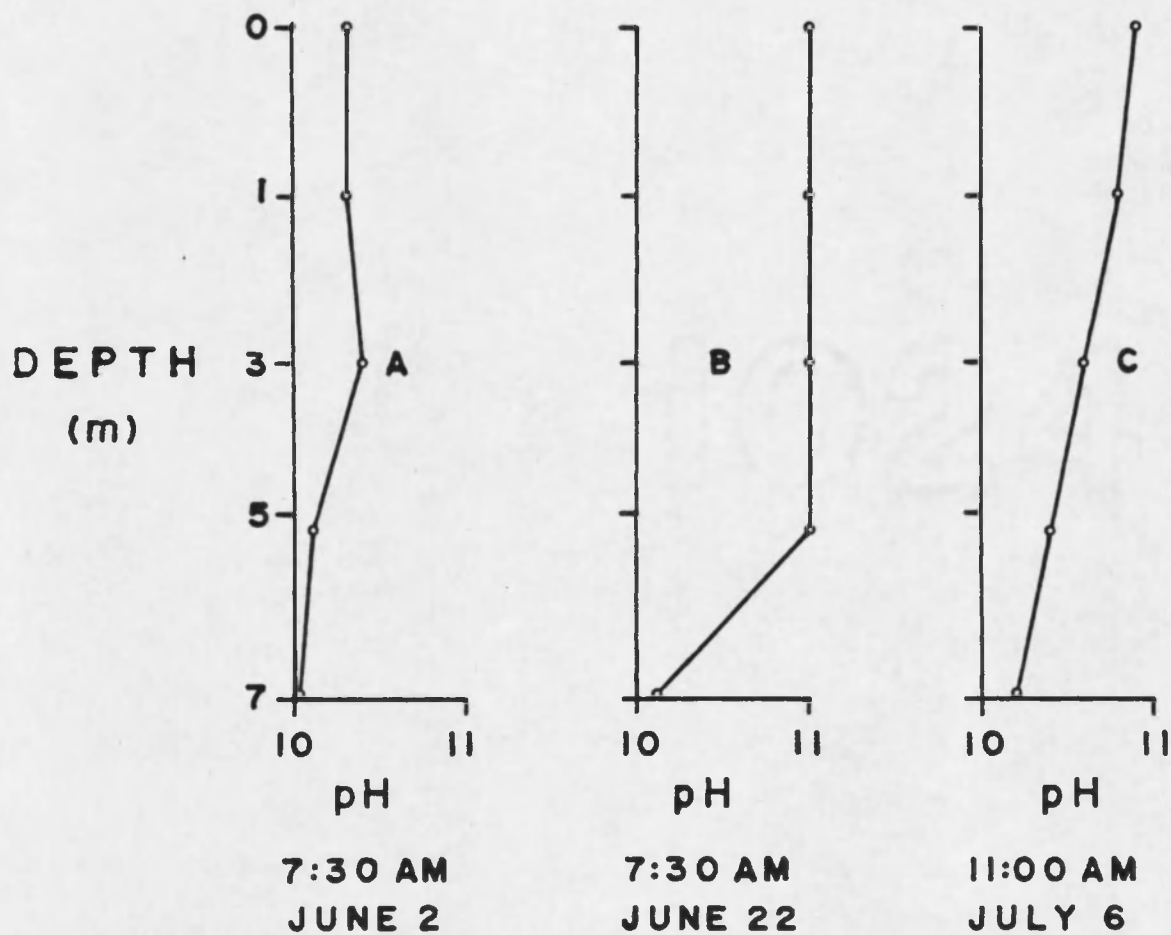


Figure 2. Vertical pH values in the deepest region of Gravel Pit Lake, Fort Huachuca, during June and July 1977.

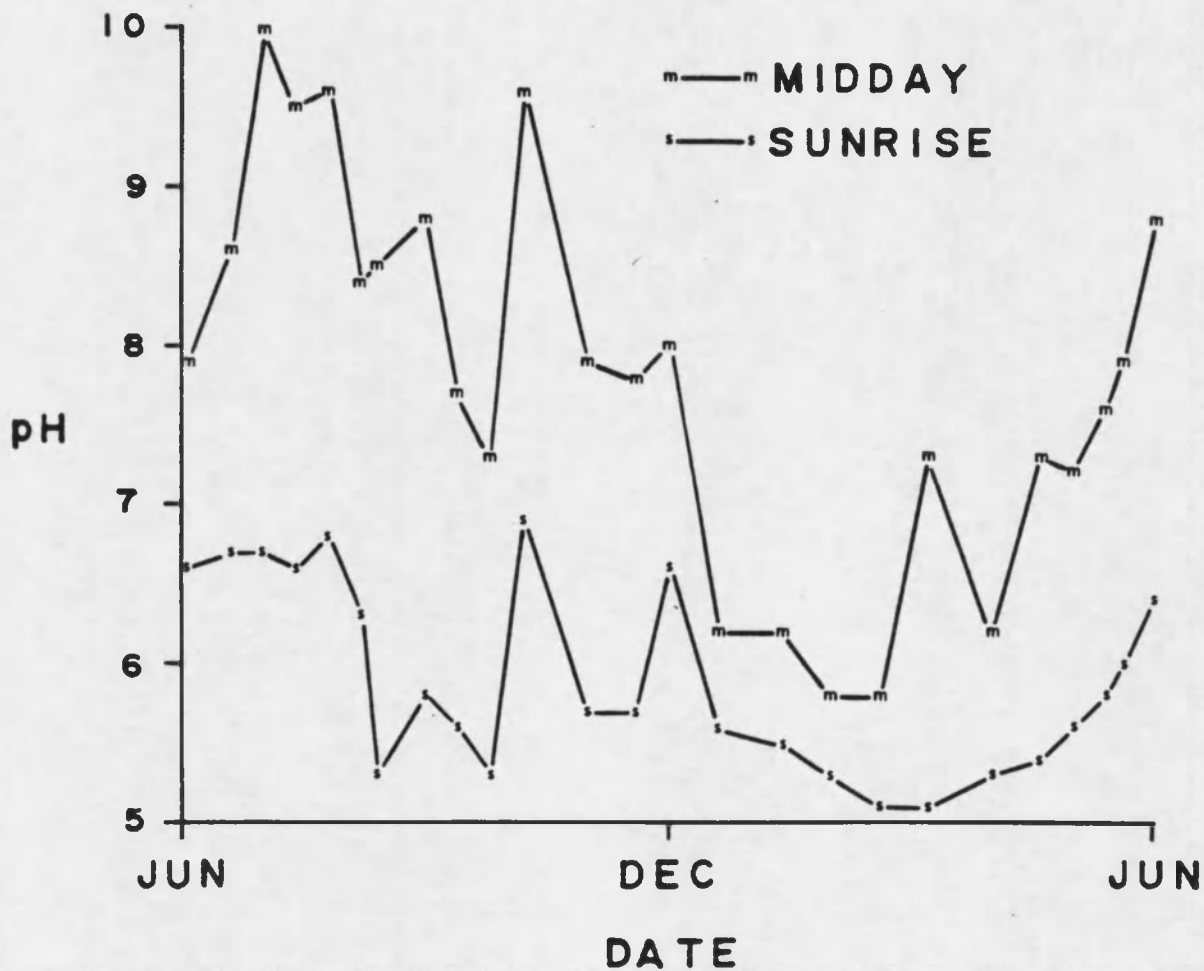


Figure 3. Sunrise and midday pH values at Pan Am Lake, Fort Huachuca, from June 1, 1977 through May 31, 1978.

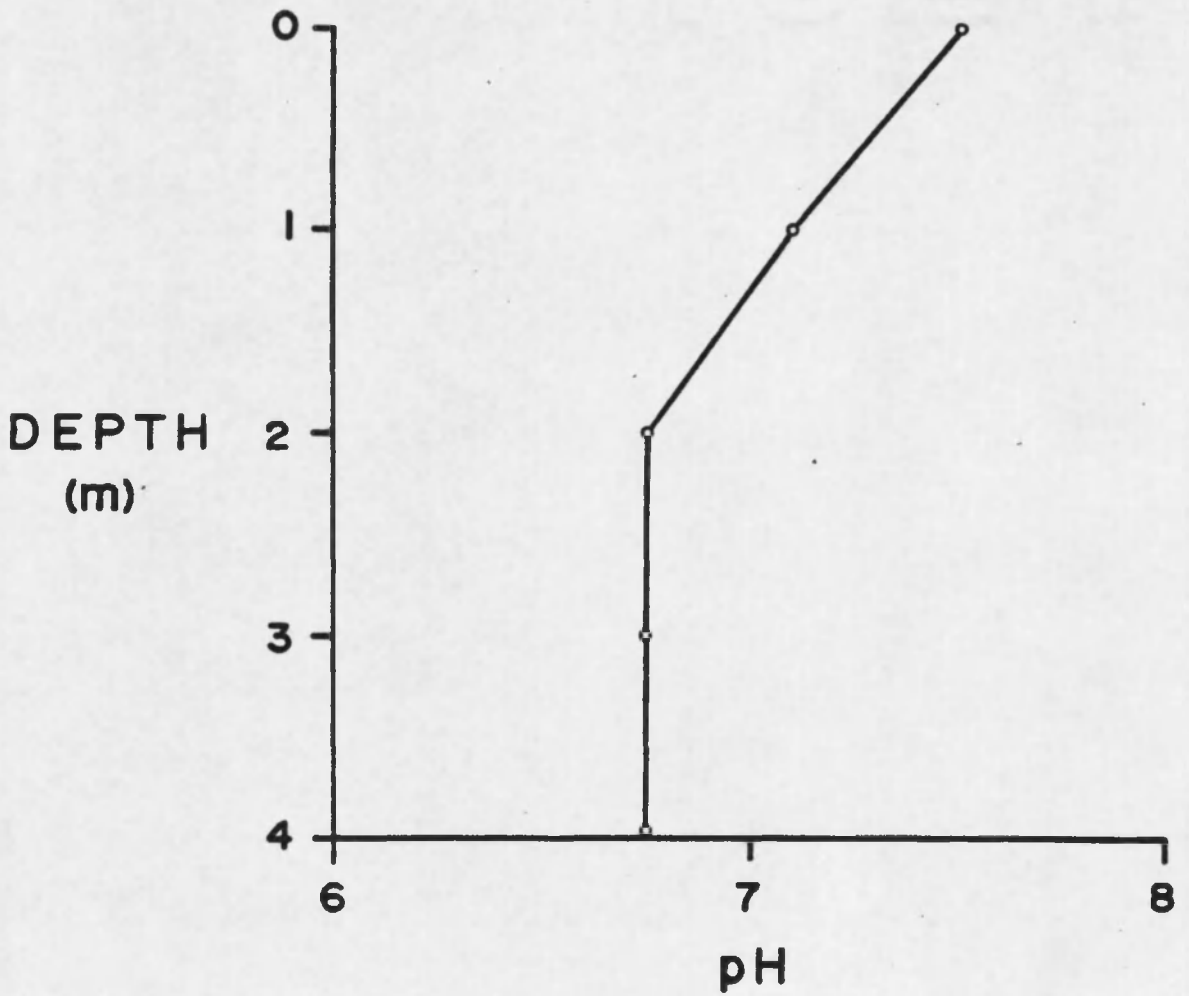


Figure 4. Vertical pH values in the deepest region of Pan Am Lake, Fort Huachuca, at 11:00 AM, July 27, 1977.

### Laboratory Experiments

Continuously high pH values were duplicated under laboratory conditions using the various types of vegetation collected during the field studies. The average sunrise and midday pH values measured in the three 20-liter tanks containing tap water with Oedogonium sp. and Rhizoclonium sp. exhibited continuously high values (Fig. 5A). The pH rose from 7.3 to  $\bar{9}.5$  within 5 days and remained at this high level for the duration of the experiment, except when the tanks were refilled. The reductions in pH on days 8, 12, 16, 21, 28 and 34 displayed in Fig. 5A, were days when the tank was refilled. These temporary reductions in pH were typical of all experimental tanks after being refilled with tap water.

The average sunrise and midday pH values measured in the two 20-liter tanks containing Gravel Pit Lake water with Oedogonium sp. and Rhizoclonium sp. maintained continuously high values (Fig. 5B). As the pH of the Gravel Pit Lake water used to refill these tanks was approximately the same value as the tank water, there were no temporary reductions in pH on being refilled. The reduced pH values on days 24 through 28 occurred as a result of a ground squirrel entering the tank and becoming entangled in the filamentous algae, stirring the water and probably allowing atmospheric CO<sub>2</sub> to diffuse into the tank and lower the pH.

The average sunrise and midday pH values measured in the two 1,000-liter tanks containing tap water with M. spicatum and Oedogonium sp. exhibited the same continuously high values measured in the 20-liter tanks (Fig. 5C). The pH rose from 7.3 to  $\bar{9}.5$  within 9 days and

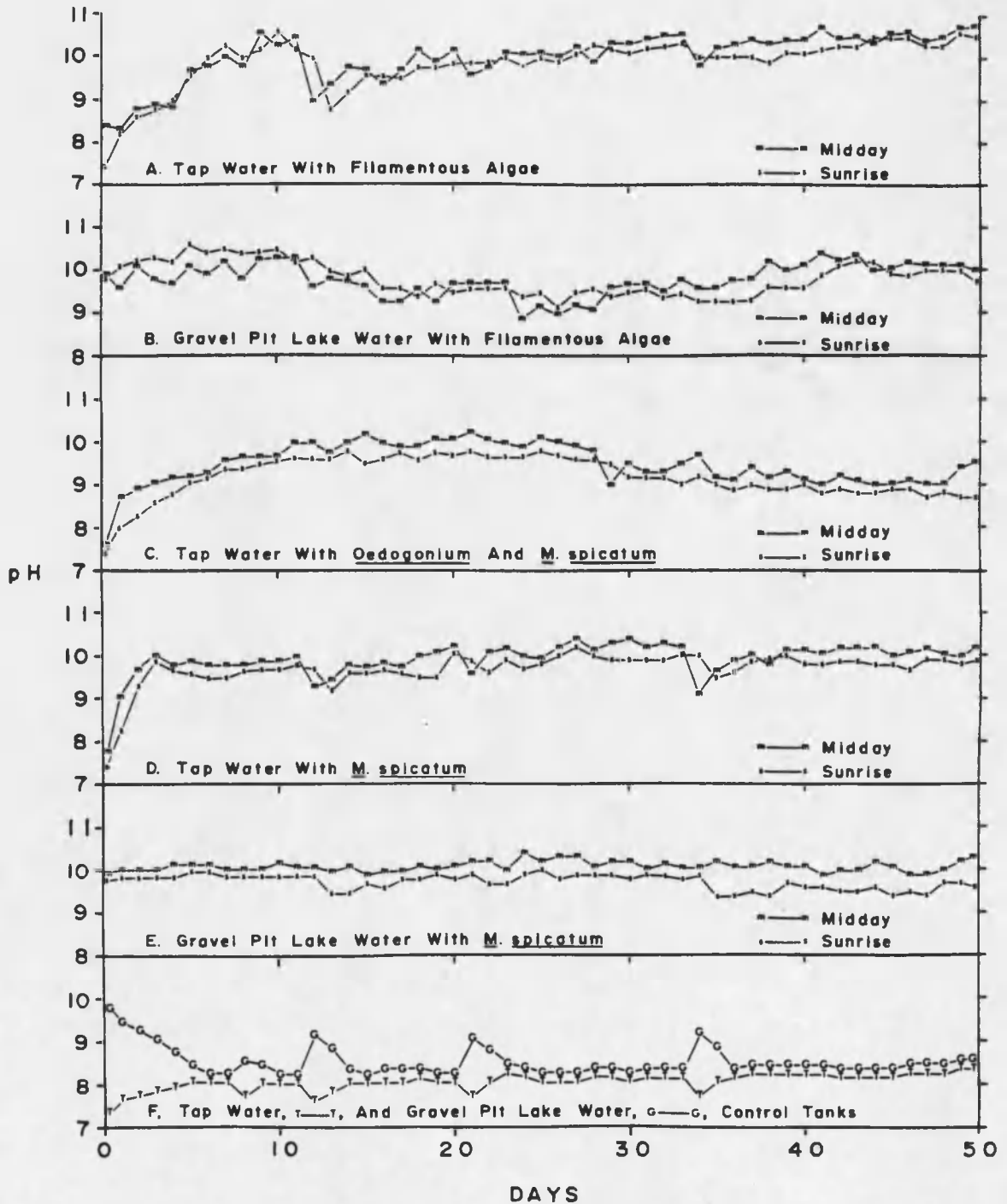


Figure 5. Average sunrise and midday pH values in the open water portions of the experimental tanks and the average daily pH values in the control tanks, from June 1 through July 21, 1978.

remained at this high level until the onset of the rainy season on day 28 after which the pH did not reach the previously high levels.

The average sunrise and midday pH values measured in the three 20-liter tanks containing tap water with M. spicatum exhibited continuously high values (Fig. 5D). The pH rose from 7.3 to  $\geq 9.5$  within 3 days and remained at this high level during the remainder of the experiment except when refilled and then returned to  $\geq 9.5$  within 2 days after refilling.

The average sunrise and midday pH values measured in the two 20-liter tanks containing Gravel Pit Lake water with M. spicatum maintained continuously high values (Fig. 5E). The rains beginning on day 28 and continuing throughout the experiment did not have as measurable an effect on the 20-liter tanks as on the 1,000-liter tanks. The slight reduction in sunrise pH values beginning on day 35 and continuing throughout the experiment was probably caused by the rainfall which usually occurred during the late afternoon or evening.

The average daily pH values measured in the two 20-liter tanks used as controls reached values of 8.3 after 51 days and remained within 0.2 units of this value except for every two days after being refilled on days 8, 12, 21 and 34 (Fig. 5F). The pH of the Gravel Pit Lake control tank was temporarily increased after being refilled with the fresh Gravel Pit Lake water and the tap water control tank was temporarily reduced after being refilled with fresh tap water. After 40 days both control tanks became contaminated with a growth of Oedogonium sp. and they exceeded 8.3 for the last 5 days of the experiment.

Measurements over the 24-h period from 6:00 AM, July 20 through 6:00 AM, July 21, 1978 in the three 20-liter tanks containing tap water with filamentous algae showed a continuously high pH and a very large dissolved oxygen diel fluctuation (Fig. 6). The slight pH fluctuations and large D.O. fluctuations were typical of all the experimental tanks containing vegetation. The pH and D.O. values measured over the 24-h period were homogeneous throughout the open water portion of the 20-liter tanks and within the filamentous algal mats. Near the conclusion of the experiment, several days of heavy rainfall occurred, saturating the 1,000-liter tanks with CO<sub>2</sub> and reducing the pH. The 24-h pH and D.O. values measured in the 1,000-liter tanks following the rainfall were not homogeneous throughout the diel cycle. The pH within the filamentous algal mat reached values >10.5 during midday, dropping to <9.0 during the night; 15cm away in the open water portion of the tank the pH was a constant 9.0 over the 24-h period. Measurements of pH taken in the tanks containing only M. spicatum were homogeneous among the plants and in the open water area. The composition of the filamentous algal mats containing mixed amounts of Oedogonium sp. and Rhizoclonium sp. changed from a ratio of approximately 75% Oedogonium sp.: 25% Rhizoclonium sp. at the start of the experiment to 100% Oedogonium sp. at the conclusion.

During the course of the experiment, bubbles were blown underneath the filamentous algal mats through a one ml plastic pipet. It was observed that these bubbles, of approximately the same size as bubbles escaping from vascular plants during photosynthesis, were

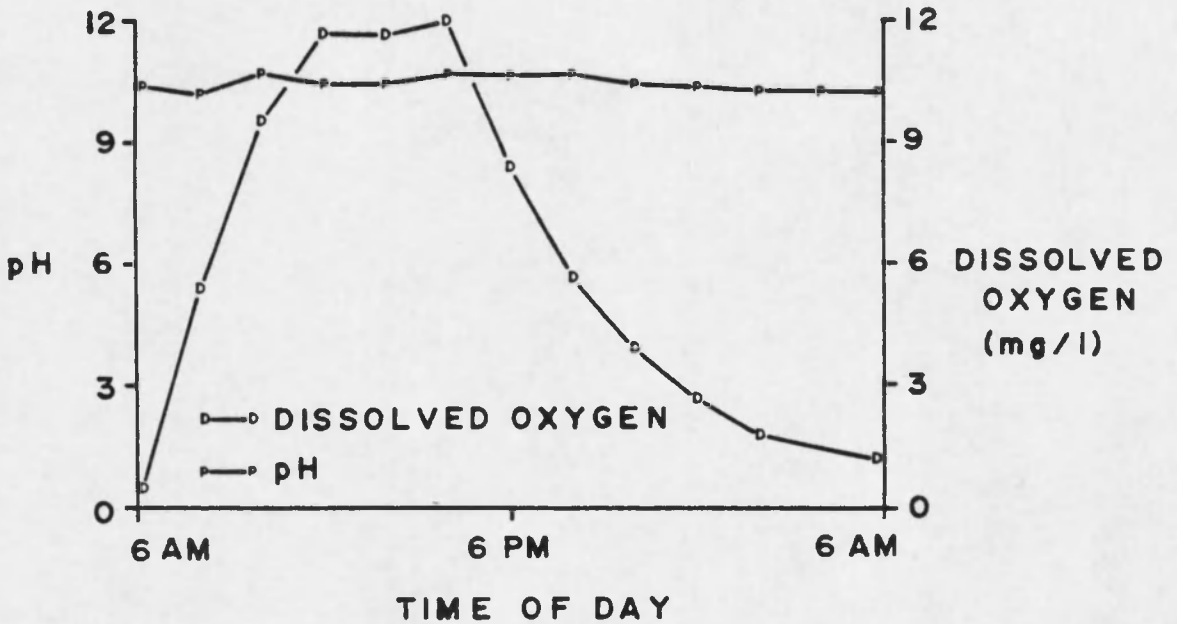


Figure 6. Average pH and dissolved oxygen in three 20-liter tanks containing tap water with filamentous algae from 6:00 AM, July 20 through 6:00 AM, July 21, 1978.

mechanically entrapped underneath and within the floating filamentous algal mat.

The laboratory experiments were designed to reveal the minimum biomass of aquatic vegetation required to produce continuously high pH values. However, even at a biomass of 0.30 g/liter of filamentous algae, continuously high pH values occurred, but a minimum amount of vegetation required to produce continuously high pH values was not determined.

## DISCUSSION

Continuously high pH values associated with aquatic vegetation have been recorded by other workers during their limnological investigations (Castenholz 1960; Dineen 1953; Dunn 1967; Gasaway 1962; George 1961; Goulder 1969; Hasler and Jones 1949; Kimball and Kimball 1977; Knight and Ball 1962; Mason 1965; Schütte and Elsworth 1954; Tash and Keister 1974). However, the exact mechanisms involved in creating the continuously high pH values and the consequences resulting from the phenomenon were not elaborated upon. Plant physiologists have proven that most filamentous algae and aquatic macrophytes are capable of depleting the water of  $\text{CO}_2$  and then utilize  $\text{HCO}_3^-$  as the carbon source which could create continuously high pH values (Brown and Tregunna 1967; Gavis and Ferguson 1975; Gibbs 1962; James 1928; Kroes 1971; Osterlind 1951; Raven 1970; Steemann Nielsen 1946; Steemann Nielsen 1960). However, information gathered by plant physiologists has not been directly related to the field of limnology to explain the continuously high pH values encountered in the field.

Field studies and laboratory experiments provide evidence for the existence of continuously high pH values over prolonged periods of time in natural waters containing extensive amounts of aquatic vegetation. The pH value is regarded as a valuable limnological indicator of the suitability of the water for fish and other aquatic organisms (Dendy 1963), degree of eutrophication (Hutchinson 1957),

redox-reduction reactions (Anderson 1975) as well as affecting the toxicity of herbicides, pesticides (Matsumura 1975) and other pollutants (Doudoroff and Katz 1950; Mount 1966). Aquatic organisms have apparently evolved mechanisms to adapt to normal diel fluctuating pH values but their ability to survive and adapt to continuously high pH values is uncertain.

#### Recognition of Continuously High pH Values

Continuously high pH values were first observed by this investigator during routine limnological investigations of the Gravel Pit Lake at the Fort Huachuca Military Reservation. The period of continuously high pH values occurred for six months of the year (Fig. 1). During this six month period the lake was considered unsuitable for sport fish and remained idle. This is a serious problem in an area where surface water suitable for sport fishing is rare. It was considered imperative that the mechanisms involved in causing the problem were identified and a solution be determined to allow the lake to be utilized for stocking with sport fish.

Although only two of the nine lakes sampled in the White Mountains exhibited continuously high pH values, it is normal for all nine of the lakes to reach a pH in excess of 10 during the summer (Hanson, personal communication 1978). The probable reason that only two of the lakes in the White Mountains were found with continuously high pH values during the 1977 sampling is that the samples were taken following a heavy flood during the winter of 1977 and all of the lakes had been completely flushed and much of the vegetation destroyed. All nine

of the lakes in the White Mountains are treated with  $\text{CuSO}_4$  during the summer months to destroy the unwanted vegetation which also created reduced pH values. Under natural conditions it is impossible to attain high pH values in natural bodies of water without the presence of aquatic vegetation. Aquatic vegetation appears to be the only naturally occurring entity with the capability of reducing the  $\text{CO}_2$  content of the water so as to create high pH values.

The pH of the 20-liter control tanks would indicate that in the absence of aquatic vegetation the equilibrium pH value would be approximately 8.3 given the present experimental conditions (Fig. 5F). The pH of the Gravel Pit Lake water control tank tended towards this value in the absence of vegetation as did the tap water control tank (Fig. 5F).

It was observed that during the laboratory experiments the 20-liter tanks exhibited temporary reductions in pH after being refilled with tap water, but quickly regained their previously high levels (Fig. 5A, C, D, and E). When the Gravel Pit Lake at Fort Huachuca was refilled with 15% to 20% of its volume in rainfall and natural runoff, it also exhibited a reduced pH but did not regain its previously high levels (Fig. 1). The probable explanation for this discrepancy is that the runoff entering Gravel Pit Lake is supersaturated with  $\text{CO}_2$  and is extremely turbid with silt particles. The silt particles inhibit light penetration to the aquatic vegetation, which is now one to two feet below the new surface of the lake. The silt particles then settle out on the plants themselves, further inhibiting light penetration and possibly killing the plants. If the plants die, they no longer deplete

the water of  $\text{CO}_2$  but instead release  $\text{CO}_2$  to the water while dying and decomposing. If the plants survive, reduced photosynthetic activity caused by the reduction in light penetration would not be sufficient to offset the incoming  $\text{CO}_2$  from the rainfall and runoff.

Although the pH value of the water during the laboratory experiments did not exhibit normal diel fluctuations, dissolved oxygen values showed the normal diel fluctuations associated with plant photosynthetic activity (Fig. 6). This would indicate that the plants used in the experiment were physiologically active and assimilating carbon through photosynthesis.

The observation of diel fluctuating pH values within the filamentous algal mat, compared to continuously high pH values in the open water section of the 1,000-liter tanks would indicate that once the  $\text{CO}_2$  requirements of the algae have exhausted the  $\text{CO}_2$  supply from the open water, that any  $\text{CO}_2$  released by the algae is mechanically entrapped within the mat. Here it is recycled or diffused through the surface to the atmosphere, and does not reach the open water portion.

The observation of homogeneous pH values throughout the tanks containing only vascular plants would indicate that the  $\text{CO}_2$  produced during respiration by these plants is not being released to the water. Hartman and Brown (1966, 1967) have reported that the lacunal system of aquatic vascular plants serves as a reservoir for gases produced during photosynthesis and respiration. Laing (1940) found that the internal  $\text{CO}_2$  content of certain aquatic vegetation was greater in the dark than in the light. Wetzel (1975) reported that aquatic angiosperms with large intercellular gas lacunae effectively refix their

CO<sub>2</sub> of respiration. The entrapped gases can then be recycled by the plant (McGahee and Davis 1971; Steemann Nielsen 1953) without having any measurable effect on the pH of the water.

There is experimental evidence available to prove that almost all filamentous algae and aquatic vascular plants, as well as some unicellular planktonic algae, can utilize HCO<sub>3</sub><sup>-</sup> as the carbon source in the absence of CO<sub>2</sub> at high pH's (Gavis and Ferguson 1975; Hough and Wetzel 1972, 1977; James 1928; Osterlind 1951; Raven 1968, 1970; Stanley and Naylor 1972; Steemann Nielsen 1946, 1951, 1952a, 1960; Steemann Nielsen and Jensen 1958). Golterman (1975) reported that Felföldy has shown that certain green algae may be able to utilize CO<sub>3</sub><sup>=</sup> as well as HCO<sub>3</sub><sup>-</sup> as the carbon source for growth. Under certain conditions the CO<sub>2</sub> content of the water can limit growth because of non-availability (Wright 1961) or overabundance (Steemann Nielsen 1955b). Therefore, the ability of aquatic vegetation to deplete the water mass of CO<sub>2</sub> and entrap their own CO<sub>2</sub> of respiration for recycling, would prove beneficial to the plants in controlling the highly fluctuating aquatic environment and inhibiting competition from those organisms unable to adapt to continuously high pH values.

The dark reaction of carbon assimilation prevalent among terrestrial plants is apparently quite common among aquatic vegetation as well. Brown and Tregunna (1967), Carr (1969), and Saunders (1972), all measured photosynthetic and respiration rates in aquatic vegetation and obtained results that were comparable to terrestrial plants performing the dark reaction. Other workers (Hartman and Brown 1967; Hough 1974; Morris, Yentsch and Yentsch 1971a, 1971b; Nalewajko 1966; Ouellet and

Benson 1952; Steemann Nielsen 1955c) have proven that the dark reaction does occur in most aquatic vegetation, and Fogg (1963) states that the dark reaction probably occurs in all forms of life. The ability to perform the dark reaction of carbon assimilation, refixing entrapped  $\text{CO}_2$ , would not allow for release of  $\text{CO}_2$  to the water and would create the continuously high pH values observed.

#### Fisheries Management Implications

The occurrence of lakes with continuously high pH values has distinct fisheries management implications. Values exceeding a pH of 8.5 are usually detrimental to fish if the fish are exposed to these values for relatively long periods, and high mortalities of fish occur from pH shock if fish are transferred from pH 7 to pH's 2-3 units higher (Daye and Garside 1975; Eicher 1946; Swingle 1961). The occurrence of continuously high pH values during the spring and summer could have adverse effects upon many species of fish which are laying eggs, young are hatching and the fish are actively feeding during this same period (Powers 1936).

The main source of food for fish, in the form of vegetation, insects and other types of organisms, is predominant in the littoral region of lakes and ponds and is associated with aquatic vegetation where continuously high pH values can be expected. Wetzel (1975) emphasizes the fact that most lakes are small and the littoral zone is generally a greater portion of the lake than is the pelagic. High pH in the littoral zone creates a condition in which the food source for the fish is nonavailable and the fish must reside in an area of

reduced pH. However, I found at the Gravel Pit Lake that the pH of the entire body of water was greater than 10 units and had less than 1 unit of pH difference throughout the vertical column (Fig. 2). The homogeneously high pH values throughout the vertical column of the water are contradictory to what McIntire and Bond (1962) and Sreenivasan (1976) observed but is in agreement with what Sreenivasan (1964) observed. Homogeneously high pH values throughout the vertical column of the water would indicate that the lake is predominated by the littoral zone where the aquatic vegetation and associated organisms occur. As Wetzel (1975, p. 404) states, "In most lakes, the littoral complex of macrophytes and associated microflora is foremost in regulation of rates of eutrophication and in functional impact on the system as a whole."

#### Evolutionary Implications

Selective pressures generated by aquatic vegetation which causes the continuously high pH values to occur throughout a body of water have definite evolutionary implications. The ability of the filamentous algae to form mats and entrap gas within their vacuoles and within the mat, allowing them to float and cover the surface, would reduce competition for nutrients and sunlight from the rooted vascular plants and planktonic algae (Fogg 1962; Gibbs 1962; Hoshaw 1968; Round 1973; Steemann Nielsen 1955a). The high pH values generated by the filamentous algae and vascular plants, which eliminates  $\text{CO}_2$  from the water, leaving only  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$  as the carbon sources would inhibit any species able to utilize only  $\text{CO}_2$  as the carbon source (Wetzel 1969).

Hasler and Jones (1949) have concluded that vascular plants, through elevating the pH of the water, effectively inhibited growth and production of phytoplankton and rotifers. While Hasler and Jones did not notice a decrease in the crustacean zooplankton in their experiments, O'Brien and DeNoyelles (1972) found that a high pH created by aquatic vegetation caused extensive mortality among the crustacean population. After investigating the relationship between two species of green algae, Kroes (1971) found that the ability of one species to elevate the pH of the water and continue normal growth, had an adverse effect on the growth and survival of the cohabiting second species.

Results observed in the laboratory experiments, which began with mixed cultures of Oedogonium sp. and Rhizoclonium sp. but ended with only Oedogonium sp. present was also observed by Crawford (1977). Although Crawford did not consider Oedogonium sp. and Rhizoclonium sp. important, the death of Rhizoclonium sp. and the growth of Oedogonium sp. I observed, would indicate that Oedogonium sp. may be better adapted to the high pH values, as well as other growth factors, than was Rhizoclonium sp.

Wetzel (1975) states that inhibition of phytoplankton in the presence of submerged macrophytes is probably a result of competition for light and nutrients. Although not proven, Wetzel discusses the possibility of submerged macrophytes excreting organic substances that would inhibit phytoplankton production. He also states that increasing the pH of the water amongst dense strands of submerged macrophytes inhibited phytoplankton productivity. The inhibition could be eliminated

completely by adding  $\text{CO}_2$  to the water. The possible inhibition of phytoplankton growth caused by an increased pH in the presence of submerged macrophytes was one of the objectives of the present project. As previously mentioned in this paper, it has been proven that most aquatic angiosperms and filamentous algae can utilize  $\text{HCO}_3^-$  as the carbon source for growth. However most investigators (Crawford 1977; Fogg 1963; Gibbs 1962; Golterman 1975; Goulder 1969; Hasler and Jones 1949; Holm-Hansen 1962; Kimball and Kimball 1977; Kroes 1971; Nalewajko 1966; Osterlind 1951; Raven 1970; Round 1973; Steemann Nielsen 1952b, 1953, 1955a, 1960; Wright 1961) have found that many phytoplankton species cannot utilize  $\text{HCO}_3^-$  as the carbon source for growth. The inability of phytoplankton to utilize  $\text{HCO}_3^-$  as the carbon source for growth could explain their inhibition in the presence of submerged macrophytes which deplete the water of  $\text{CO}_2$  and raise the pH to a level where only  $\text{HCO}_3^-$  is the available carbon source.

The aquatic angiosperm M. spicatum provides a typical example of the adverse effects that can occur when exotic species are introduced into previously uninhabited areas. M. spicatum was introduced to the United States in the 19th century (Adams, Titus and McCracken 1974) and now occurs throughout the country. The ability of M. spicatum to elevate the pH to continuously high levels through  $\text{CO}_2$  recycling,  $\text{CO}_2$  absorption through the roots (Wium-Anderson and Anderson 1972) and utilize  $\text{HCO}_3^-$  as the carbon source as well as provide a substrate for epiphytic algae could have adverse evolutionary effects on the native aquatic fauna and flora of this country.

The geographical occurrence of continuously high pH values is undoubtedly more widespread than the area I investigated in Arizona. It is important that other areas and other species of aquatic vegetation be examined for the occurrence of continuously high pH values. Halstead (1978) has found that the vascular plant Myriophyllum pinnatum and the filamentous algae Spirogyra sp. are also capable of creating continuously high pH values either alone or in association with other aquatic vegetation. The limnological practice of taking one pH measurement at a random time of the day will not reveal the existence of this phenomenon. Based on the information available on the chemical and biological mechanisms involved in aquatic photosynthesis, the necessary conditions where continuously high pH values could possibly occur appears to be worldwide.

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