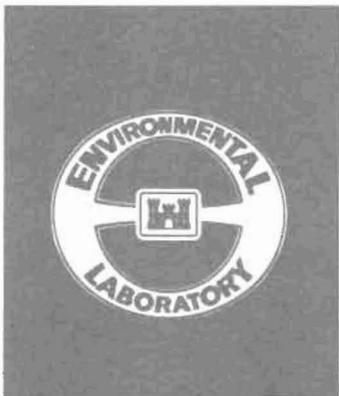




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TECHNICAL REPORT A-88-11

EFFECTS OF SUBMERSED AQUATIC MACROPHYTES ON PHYSICAL AND CHEMICAL PROPERTIES OF SURROUNDING WATER

by

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<p>Studies were conducted to characterize physical and chemical gradients in submersed macrophyte beds located in limnologically contrasting environments--Eau Galle Reservoir, Wisconsin, and the Potomac River near Washington, DC. Various environmental factors were examined over specific periods at discrete depths to elucidate the effects of aquatic macrophytes on habitat conditions.</p> <p>Submersed aquatic macrophytes had both passive and active roles in influencing the physical and chemical attributes of their environment. Mixing of surface-heated water to lower depths was reduced as macrophytes became more abundant during the growing season. Intense metabolic activity significantly altered profiles of oxygen and pH within macrophyte beds as compared with open waters.</p>					
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In both study areas (Eau Galle Reservoir and Potomac River), depthwise gradients in water temperature, dissolved oxygen, and pH exhibited strikingly greater variations over daily cycles in macrophyte beds than in adjacent open water. Variability in these parameters was apparently related to macrophyte biomass. Water clarity was considerably greater, while chlorophyll-a concentration was significantly lesser in macrophyte beds than in the open water. Current velocity, measured within a particularly dense *Hydrilla* bed in the Potomac River, was about one third that measured in the open water.

From results of these studies it is apparent that submersed macrophytes create distinct physical and chemical conditions that may influence the local distribution of other organisms. The steepening of environmental gradients by submersed macrophytes over both depth and time adds significantly to the complexity of the aquatic habitat.

Preface

The studies reported herein were sponsored by the Headquarters, US Army Corps of Engineers (HQUSACE), Directorate of Civil Works (DAEN-CW), through the Aquatic Plant Control Research Program (ARCRP). Funds were provided by DAEN-CW under Department of the Army Appropriation No. 96X3122 Construction General. The APCRP is managed by the US Army Engineer Waterways Experiment Station (WES). Technical Monitor for HQUSACE was Mr. E. Carl Brown.

Principal investigator for these studies was Dr. John W. Barko, Environmental Laboratory (EL), WES. Experimental design, data analysis, and interpretation were provided by Dr. Barko and Dr. Gordon L. Godshalk of the EL, and by Dr. Virginia Carter and Ms. Nancy B. Rybicki of the US Geological Survey (USGS). The report was prepared by the authors, based on articles submitted previously to technical journals. Reviews of this report were provided by Drs. Thomas L. Hart and William D. Taylor, EL.

Technical assistance in conducting the study at the Eau Galle Laboratory, Wisconsin, was provided by Mr. P. Bradley, Ms. Y. Hartz, Mr. R. Kuta, Ms. K. Mueller, and Mr. R. Olewinski, Jr., of the EL. Dr. R. L. Chen and Mr. P. Bradley of the EL and Mr. R. T. Anderson of the USGS provided technical assistance in the study on the Potomac River, Washington, DC. The Potomac River studies were a collaborative effort of WES and the USGS. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory.

This investigation was performed under the general supervision of Dr. John Harrison, Chief, EL, and Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, and under the direct supervision of Dr. Thomas L. Hart, Chief, Aquatic Processes and Effects Group. Manager of the APCRP was Mr. J. Lewis Decell, EL.

COL Dwayne G. Lee, EN, was the Commander and Director of WES. Dr. Robert W. Whalin was Technical Director.

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EFFECTS OF SUBMERSED AQUATIC MACROPHYTES ON PHYSICAL AND
CHEMICAL PROPERTIES OF SURROUNDING WATER

Introduction

1. Considerable past research has focused on properties of the aquatic environment affecting the growth and distribution of submersed aquatic macrophytes. Factors of primary consideration have included light, temperature, and nutrients (reviewed in Barko, Adams, and Clesceri 1986). These studies have collectively advanced the current understanding of the physiological ecology of aquatic macrophytes. However, relatively little attention has been focused on the reciprocal effects of these plants on the environment (Carpenter and Lodge 1986). This information is necessary for a better understanding, within a management context, of the role of aquatic macrophytes in influencing the habitat value and functioning of aquatic ecosystems.

2. Aquatic macrophytes affect the environment at many levels, resulting from both their structure and metabolism (Carpenter and Lodge 1986). It is generally recognized that submersed aquatic macrophytes can have important effects on dissolved oxygen (DO) concentration and pH (see, for example, Van, Haller, and Bowes 1976; Bowes, Holaday, and Haller 1979; Reddy 1981; Halstead and Tash 1982; Ondok, Pokorny, and Kvet 1984). Effects of macrophytes on temperature gradients have also been identified (Dale and Gillespie 1976, 1977, 1978). These effects have been shown to vary with macrophyte community density and productivity, but have not been investigated extensively over daily or seasonal cycles. Limited attention has been given to the effects of macrophytes on dissolved nutrient concentrations, although it is clear that these plants may play a central role in lacustrine nutrient budgets (Prentki et al. 1979; Barko and Smart 1980; Carpenter 1980; Purohit, Sinhg, and Upreti 1986).

3. As part of an extensive project dealing with the influence of submersed aquatic macrophytes on the environment, studies were conducted during the summer of 1986 to characterize gradients in physical and chemical properties of water in submersed macrophyte beds located in Eau Galle Reservoir, Wisconsin, and in the Potomac River near Washington, DC. The objective of these studies was to elucidate the effects of aquatic macrophytes on

surrounding habitat conditions over specific periods (daily and seasonal in Eau Galle; daily in the Potomac).

4. Eau Galle Reservoir has abundant and diverse submersed aquatic vegetation in its shallow waters (Filbin and Barko 1985; Godshalk and Barko, unpublished data). The vegetation is quite typical of that of most north-temperate, hardwater, eutrophic lakes. *Potamogeton nodosus* Poir. and *Ceratophyllum demersum* L. are the dominant species, with combined densities in some areas as high as 500 g dry wt·m⁻² during the study period. *Potamogeton foliosus* Raf., *Potamogeton pectinatus* L., *Heteranthera dubia* (Jacquin) MacM., *Najas flexilis* (Willd.) Rostk. & Schmidt, and *Elodea canadensis* Michx. are also present.

5. Carter and Rybicki (1986) reported the resurgence of submersed aquatic vegetation in the tidal Potomac River in 1983 following a 4-decade absence from this system. By 1986, there were 1,460 ha of plants, including *Vallisneria americana* Michx., *C. demersum* L., *H. dubia*, *Myriophyllum spicatum* L., and *Najas guadalupensis* (Spreng.) Morong, with dominance by the exotic species *Hydrilla verticillata* (L.f.) Caspary. The biomass of *Hydrilla* is distributed throughout the water column and becomes very dense at low tide. The Potomac River provided an opportunity to investigate effects of a near-monotypic stand of *Hydrilla* on water quality in a flowing-water system.

Methods and Materials

Eau Galle protocol

6. Diel sampling was conducted at three littoral sites in the reservoir (Figure 1); a fourth sampling site was located near the center of the reservoir to allow comparison of littoral and pelagic (open-water) characteristics and processes. Each of the littoral sites had a depth of ca. 1.6 m and was marked by a metal fencepost driven into the sediment. Site B in the mouth of the northwest bay was the least densely colonized site with respect to macrophyte biomass throughout the growing season. It was also the site closest to the edge of the littoral zone and therefore subject to greatest mixing with water from the pelagic zone of the reservoir. Site C (just north of the mouth of Lohn Creek) and site D (well into the protected southwest bay) had much denser macrophyte stands and were physically removed from open-water influences. *In situ* measurements were made approximately every 2 weeks; water

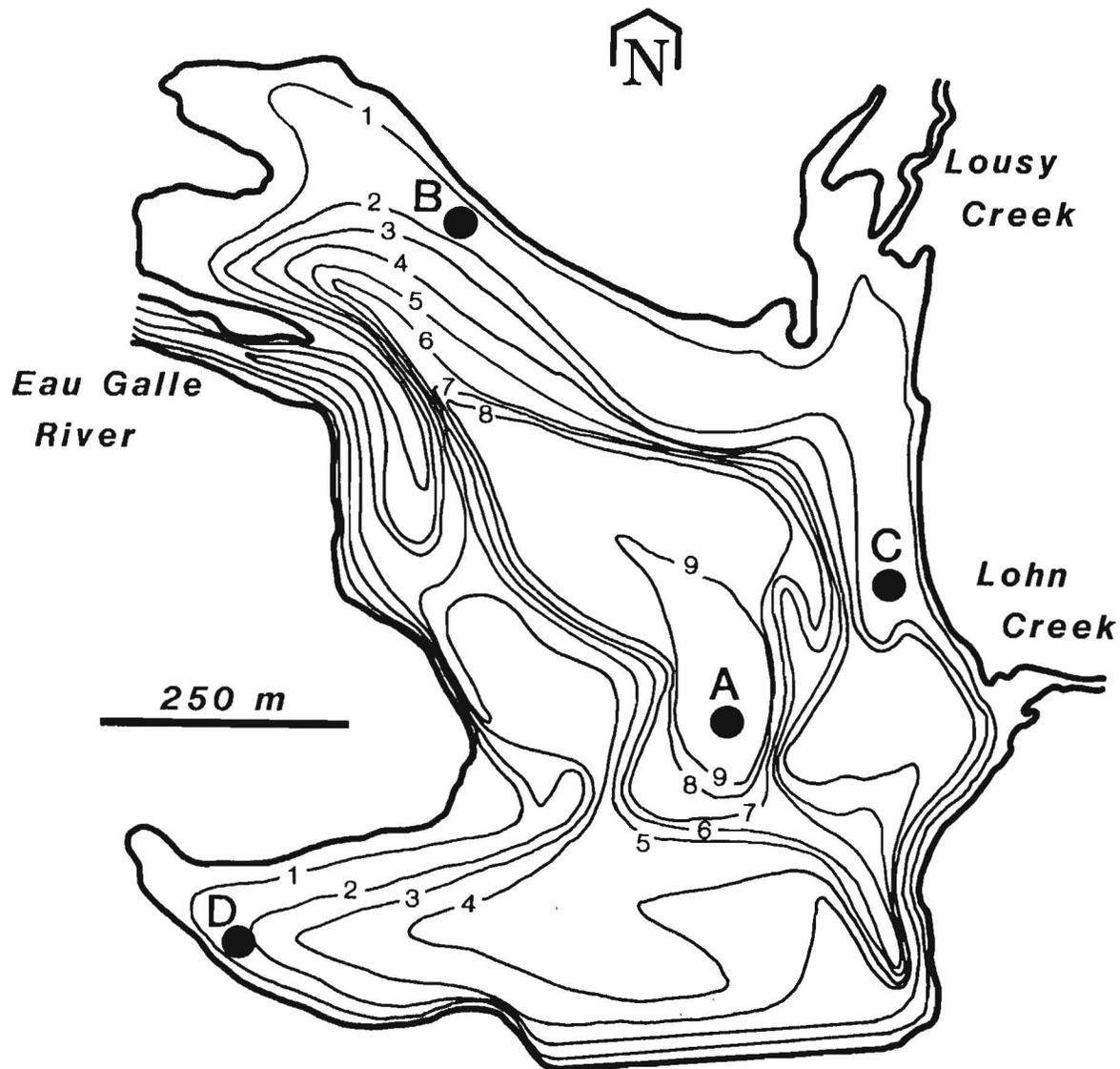


Figure 1. Morphometric map of Eau Galle Reservoir, with depth contours (1-m intervals) and sampling sites (A, B, C, D) indicated

samples for chemical analyses in the laboratory were collected monthly. Sampling was intentionally performed during clear, calm weather to maximize potential diel variations in values of parameters measured.

7. On the day before each sampling run, a plastic pipe (polyvinyl chloride, 3.8-cm inside diameter (ID) was slipped over the fencepost at each site with minimal disturbance to the adjacent vegetation. Each pipe was equipped at intervals of 30 cm with horizontal ports (opening, 3.5-mm diameter) attached to Tygon R3603 tubing through the pipe to the surface. The six tubes from the ports extended 6 m downwind of the sampling site. The ends of

the tubes were kept at the surface with a small buoy. The midlake site was sampled with a similar apparatus suspended from a boat at each time of sampling.

8. Samples were taken at each site three times during a 24-hr period: just before dawn ("morning"), "midday," and just before dusk ("evening"). The workboat slowly approached each sampling station from the downwind site and was moored just close enough so that the tubing from the sampling ports could be attached to peristaltic pumps on the boat. Water was pumped through each tube for 1 min, the time previously determined to provide complete flushing of the sampling tube. Then, enough water was pumped to fill a 0.5-ℓ brown plastic bottle that was chilled until return to the laboratory (2 hr maximum). Following pumping, the boat was pulled to the sampling site, and the sonde unit of a Hydrolab Surveyor II was lowered in 30-cm intervals to measure *in situ* temperature, pH, DO, and specific conductance. The Hydrolab unit was calibrated at least daily using standard solutions according to the manufacturer's instructions.

9. The bottled sample was vacuum-filtered (<200 mm Hg) in the laboratory through cellulose nitrate membrane filters of pore size 0.45 μm (Millipore HA or Micro Filtration Systems A045A). Filtered water was assayed for ammonium using Nessler reagent (American Publication Health Association (APHA) 1975, Method 418 B) and for soluble reactive phosphorus (APHA 1975, Method 425 F). An aliquot of filtered water was digested with potassium persulfate and sulfuric acid (APHA 1975, Method 425 C III) and subsequently analyzed for total nitrogen and total phosphorus on a Technicon AutoAnalyzer. A final portion of each filtered sample was acidified (pH <2) with nitric acid and later analyzed for Na⁺, K⁺, Ca²⁺, and Mg²⁺ by flame photometry.

10. Approximately every 2 weeks, additional water samples integrated over the top 1.25 m of the water column were taken with a pipe sampler (Barko et al. 1984) and then split into two portions. One portion of the integrated sample was vacuum-filtered as described above through glass fiber filters (Micro Filtration Systems GF75 or Gelman Type A/E), which were then frozen until analyzed for chlorophyll a (Wetzel and Likens 1979, p 152). The second portion of the midday integrated sample was preserved with Lugol's solution (APHA 1975, p 1016) for later enumeration of algae (data are not presented here).

Potomac protocol

11. Water quality measurements were made on 6 August 1986, at four stations transecting a dense bed of submersed macrophytes located in the tidal Potomac River just south of Washington, DC. Stations were selected perpendicular to shore with three of the four stations located within the bed: station 1, nearshore; station 2, middle of bed; and station 3, near the outer edge of the bed. Station 4 was positioned in the open river about 10 m outside the bed. Water depth at high tide ranged from about 1 m at station 1 to about 2.5 m at station 4. All sampling was done from a canoe to avoid disturbance of bottom sediment. Water depth was determined at each sampling time by reference to a calibrated stake placed at station 2. Species composition of submersed aquatic vegetation at stations 1, 2, and 3 was determined by visual estimates of percent cover by species. Percentages are the average of estimates made by three observers.

12. *In situ* measurements of temperature, pH, DO, and conductivity were made using a Hydrolab Surveyor II. Sampling was conducted from dawn (0600 hr) to early evening (1800 hr) at each of the four stations at depth intervals of 0.3 m and time intervals of approximately 90 min. Sampling was ended before sunset because of deteriorating weather conditions. Each site was sampled 10 times during the day.

13. Depth-integrated samples for chlorophyll-a and suspended-particulate matter analyses were taken at each station at high, low, and mean tide; samples were taken with a 3-m section of 7.6-cm ID plastic pipe equipped with a check valve at the basal end (Barko et al. 1984). The sampler was lowered vertically through the water column to a depth just above the sediment; the integrated sample was then withdrawn and mixed in a plastic container. Five replicate samples were obtained at each site. Chlorophyll-a was extracted from 4.25-mm-diam glass microfiber filters (effective retention 1.2 μ m) with a 90-percent acetone solution. Chlorophyll-a, corrected for phaeophytin, was determined according to the fluorometric procedures of Strickland and Parsons (1972) as modified by Blanchard, Coupe, and Woodward (1982). Modifications included elimination of magnesium carbonate during filtration and use of hydrochloric acid for the acidification step. Suspended-particulate samples were vacuum-filtered through tared 4.25-mm-diam glass microfiber filters, freeze-dried for 3 hr, and reweighed to obtain total suspended-particulate mass. Filters were combusted in a muffle oven for

2 to 3 hr at 500° C and reweighed to determine the mass of the organic fraction. The SAS GLM statistical package was used to analyze chlorophyll-a and suspended-particulate data. Results reported as statistically significant were examined at the 5-percent probability level.

14. Light penetration measurements were made at low, mean, and high tide in a gap within the macrophyte bed located near station 3 and outside the bed at station 4. Photosynthetically active radiation was measured with a LICOR photometer; readings were made in air, just below the water surface, and at 0.25-m intervals throughout the water column. Extinction coefficients for the upper 0.5 m of the water column were calculated according to Champ et al. (1980):

$$I_z = I_o e^{-kz}$$

where

I_z = average light intensity at depth z , W/m^2

I_o = average light intensity just below the water surface

k = extinction coefficient (ln/m)

Secchi-disk transparency and light measurements were made simultaneously. Current velocity measurements were made 1 week later, on 11 August 1986, at ebb, maximum ebb, flood, and maximum flood tides near stations 3 and 4 at depths of 0.2, 0.6 and 0.8 m. Velocity measurements were made with a Price AA current meter using the "three-point method" (Rantz et al. 1982, p 135).

Results

Eau Galle Reservoir

15. On most sampling days at the open-water site, water was nearly isothermal from the surface to at least the 1.0-m depth, where relatively slight diel changes in temperature occurred (Figure 2). Surface waters at the littoral sites often showed diel temperature fluctuations greater than 5° C, in contrast to the 2° to 3° C of daily warming and cooling observed in open water. At midday after several hours of direct solar radiation with little mixing, there was a temperature gradient of up to 5° C from the surface to the bottom at the littoral sites. However, this gradient typically began to break down by the time of evening sampling, and no longer was apparent at the morning sampling. By midsummer (July), when littoral vegetation was most

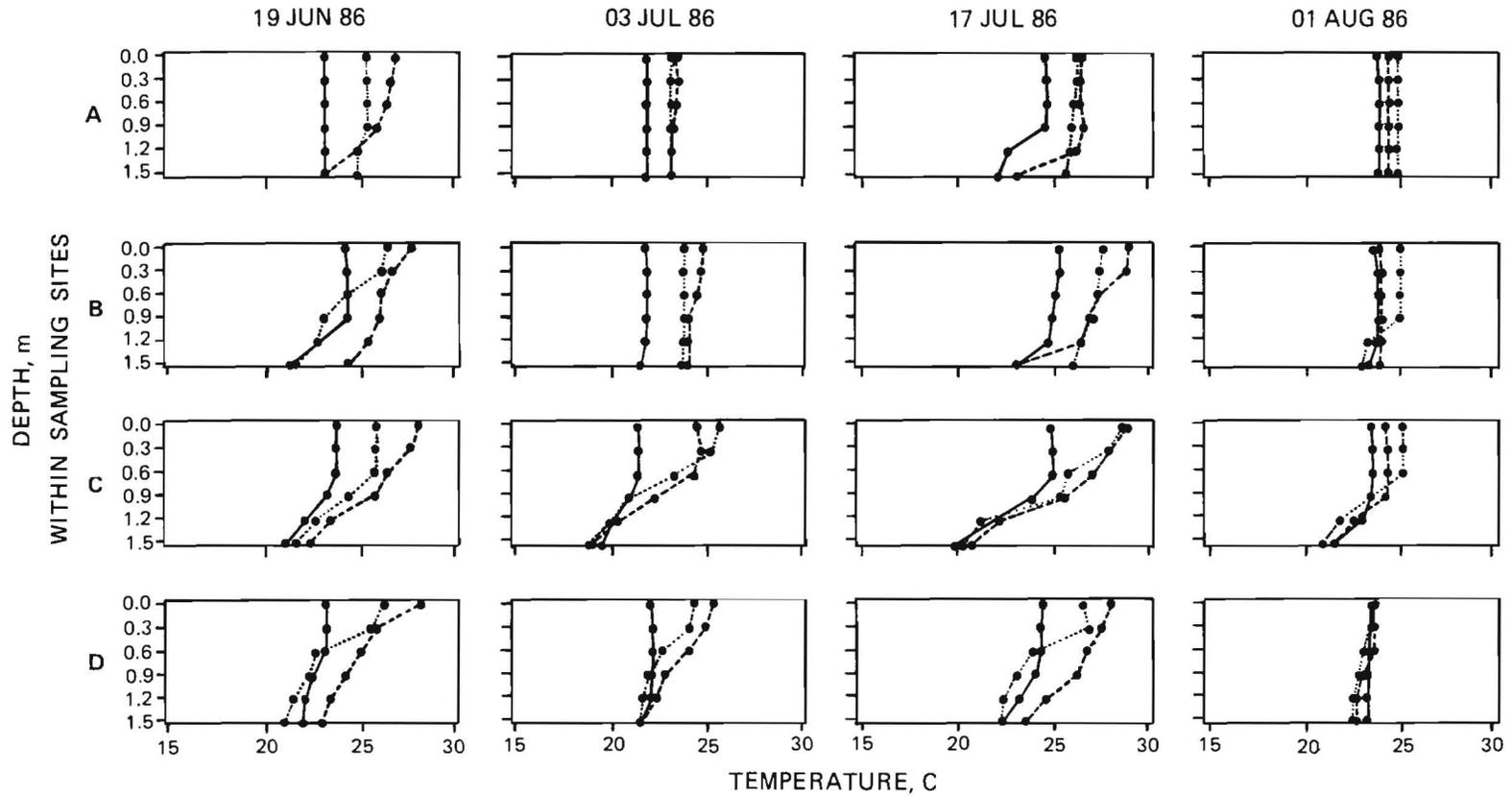


Figure 2. Diel temperature data after onset of macrophyte growth during early summer in Eau Galle Reservoir (solid line, morning; dotted line, midday; broken line, evening)

abundant, depthwise temperature gradients in the plant beds were much steeper, with as much as 9° C change from the surface to the 1.5-m depth. While the water above the 0.9-m depth did undergo a daily heating/cooling cycle of 2° to 4° C, water temperatures near the bottom remained essentially unchanged.

16. During the summer, highest oxygen values usually were found at the surface, with secondary peaks often occurring at middepths (Figure 3). The middepth oxygen peaks appeared as macrophyte abundance increased, but then disappeared later in the season near the time of macrophyte senescence. Subsurface peaks in oxygen concentration occurred earlier in the season at sites most densely colonized with macrophytes (sites C and D in June) than at less densely colonized sites (site B in July). Throughout the summer, morning samples showed an increasingly steep gradient of declining oxygen concentration and degree of saturation with depth, indicative of an acute demand for oxygen at the bottom of the littoral zone. During late summer, dense mats of filamentous algae developed on the surface of the macrophyte beds, coincident with macrophyte senescence.

17. As the macrophyte standing crop increased through the season, diel changes in pH became quite pronounced, especially at depths close to the top and bottom of the water column (Figure 4). By late summer, highest pH values were measured at depths near 0.5 m, with slightly lower values closer to the surface and the bottom.

18. As with other parameters, specific conductance behaved in the littoral sites during early summer as it did all summer in the open water; there was little change with time of day or with depth (Figure 5). Later in the season, surface waters at all littoral sites showed minor declines in specific conductance from morning to evening, while increases near the sediment surface became most pronounced.

19. Concentrations of Na^+ , K^+ , and Mg^{2+} exhibited no discernible trends over time of day or season, but generally increased at the lowest sampling depth (Table 1). The Ca^{2+} concentration quite often decreased from morning to evening in surface waters but only to a minor extent. Concentration of Ca^{2+} was positively correlated with specific conductance ($r = 0.89$, $p < 0.0001$, $n = 108$) and negatively with pH ($r = -0.82$, $p < 0.0001$, $n = 108$).

20. As a rule, ammonium-N and soluble reactive P were barely detectable (practical detection limits were $0.05 \text{ mg ammonium-N} \cdot \ell^{-1}$ and $10 \text{ } \mu\text{g P} \cdot \ell^{-1}$), although concentrations of both increased in the water just above the

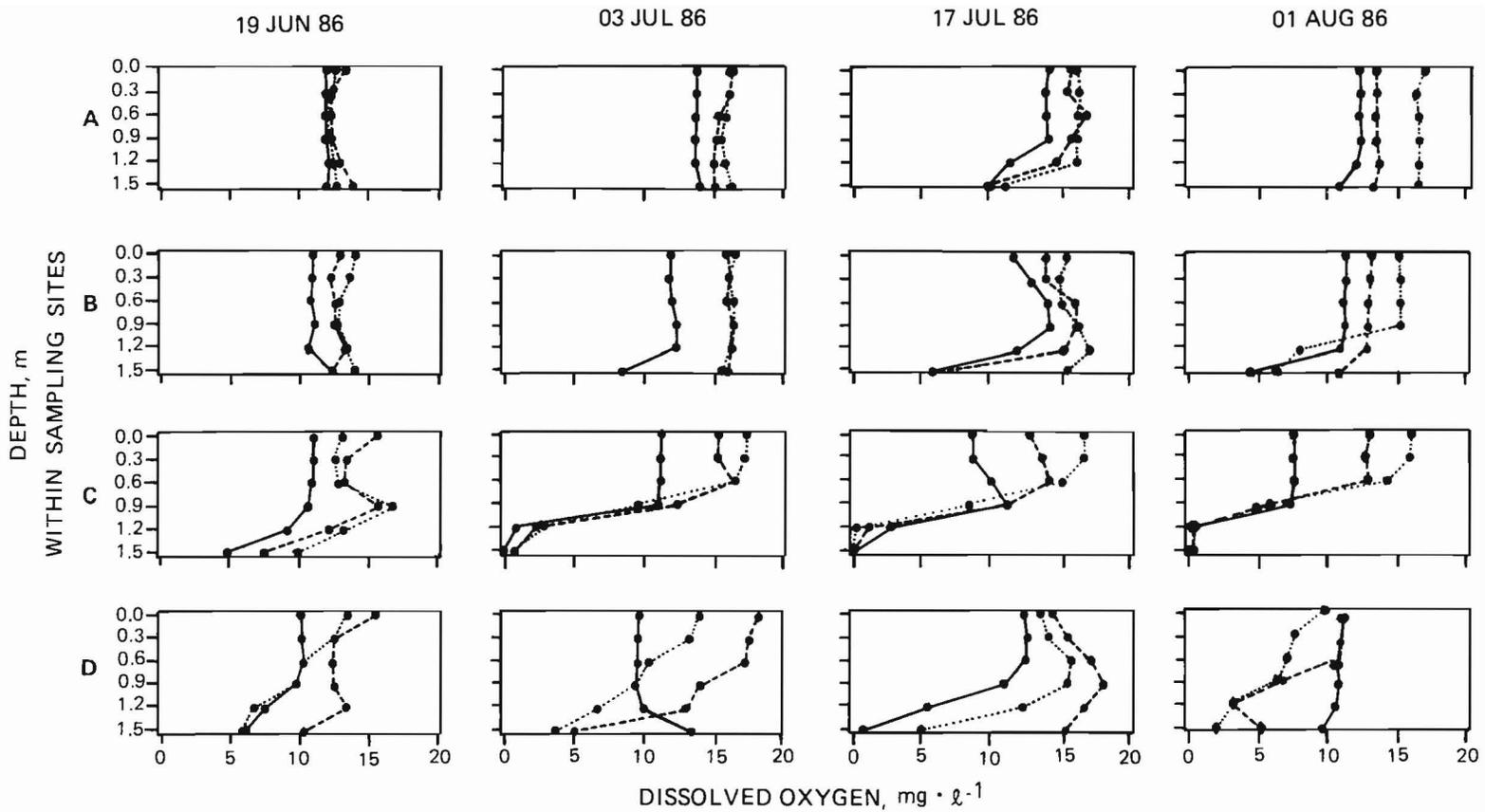


Figure 3. Diel profiles of oxygen concentration in Eau Galle Reservoir ($\text{mg} \cdot \text{l}^{-1}$) (solid line, morning; dotted line, midday; broken line, evening)

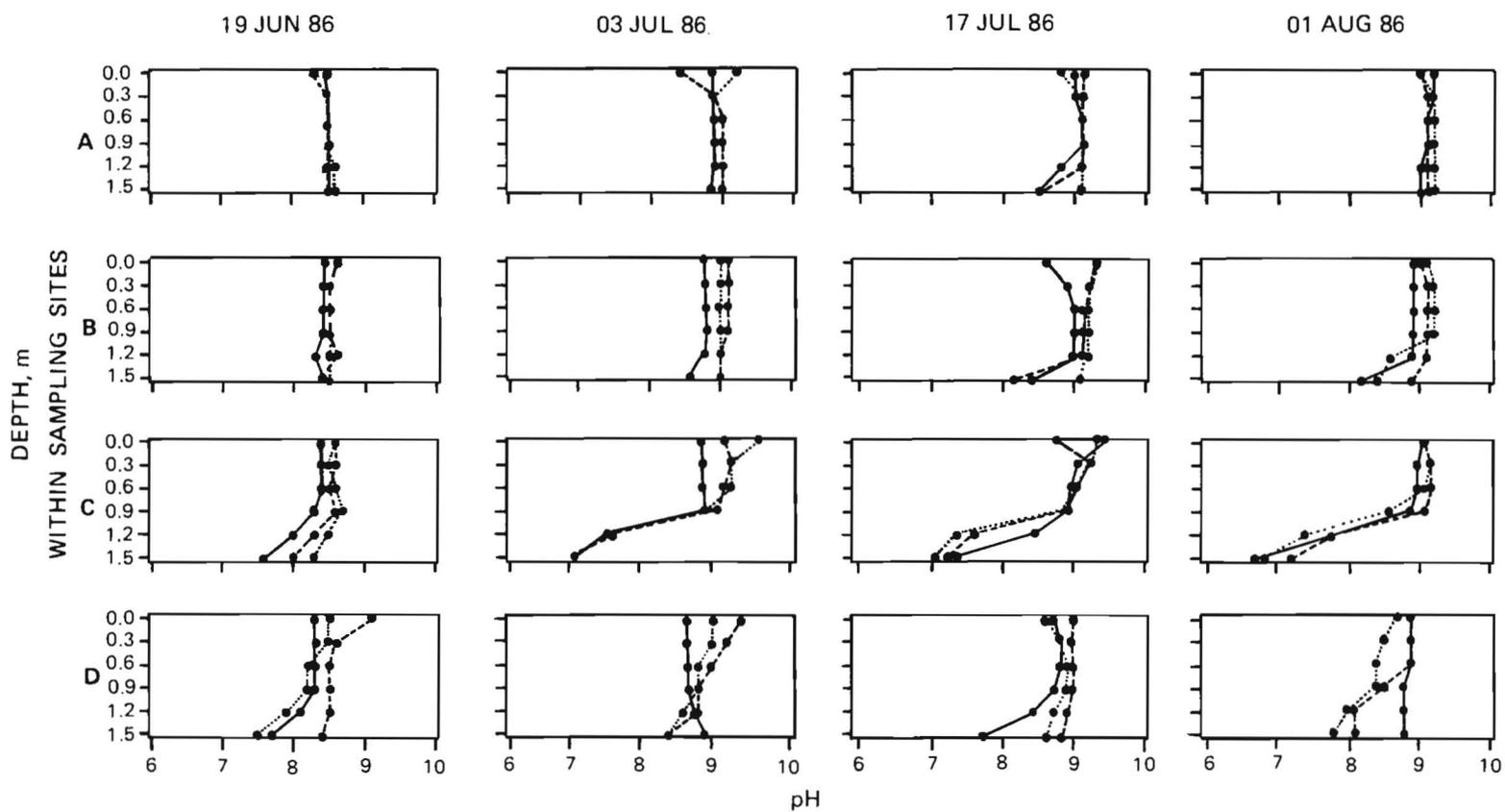


Figure 4. Diel pH values in Eau Galle Reservoir (solid line, morning; dotted line, midday; broken line, evening)

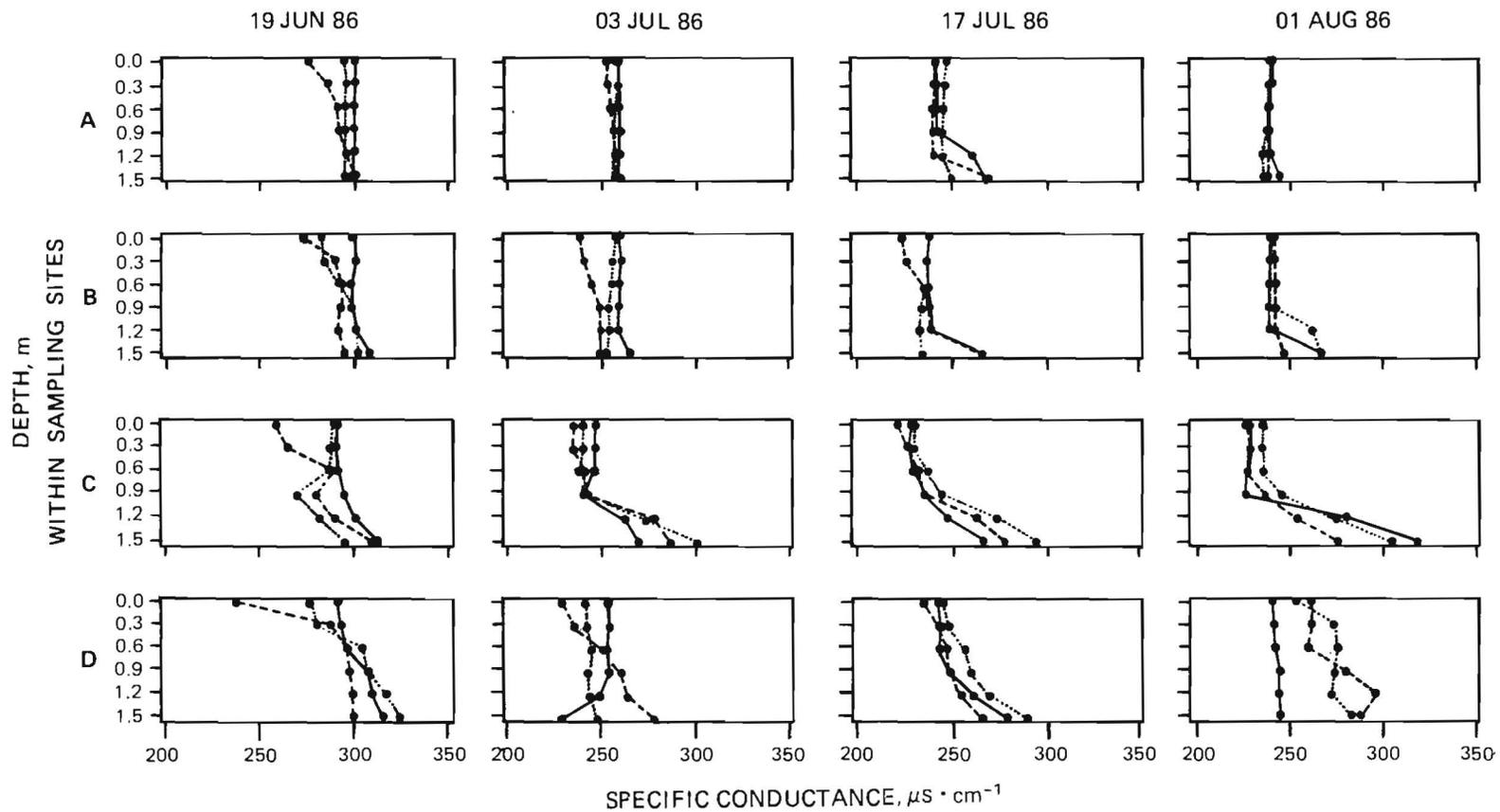


Figure 5. Diel measurements of specific conductance in Eau Galle Reservoir ($\mu\text{S} \cdot \text{cm}^{-1}$ at 25°C) (solid line, morning; dotted line, midday; broken line, evening)

Table 1
Representative Concentrations of Cations in Samples Taken
from Different Depths in Eau Galle Reservoir

Depth, cm	Cation			
	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺
0	2.0 (1.2-2.9)	1.9 (1.2-2.4)	24.4 (16.5-30.3)	17.6 (10.4-21.6)
30	2.1 (1.5-2.9)	1.9 (1.2-2.4)	25.1 (17.3-32.0)	17.4 (10.6-21.3)
60	2.1 (1.3-3.0)	1.9 (1.2-2.5)	25.5 (17.9-31.2)	17.4 (10.4-21.6)
90	2.1 (1.0-3.0)	1.9 (1.2-2.5)	25.9 (18.3-32.2)	17.5 (10.2-21.6)
120	2.1 (1.0-2.9)	1.9 (1.2-2.3)	27.2 (18.5-33.0)	17.6 (10.1-21.9)
150	2.8 (1.5-5.2)	2.1 (1.3-3.0)	31.4 (19.2-39.9)	20.0 (10.7-26.4)

Note: Values, expressed in milligrams per liter, represent the mean (with minimum-maximum in parentheses). Value of n varies from 30 to 36.

sediments (Table 2). Such increases were particularly great (up to 11 mg ammonium-N·ℓ⁻¹ and nearly 0.2 mg P·ℓ⁻¹) when it was visibly apparent that the sampling pumps had taken some particulate materials off the sediment surface with water through the lowest port. There were no apparent trends in these variables over time of day and season.

21. Total dissolved nitrogen and total dissolved phosphorus exhibited no discernible trends with depth or sampling day, except for occasional large increases in concentrations within samples from the bottom sampling port. Often, concentrations in the morning were higher than those later in the day, but differences were small and did not occur consistently.

22. Early in the study period there were no trends among sites in amounts of chlorophyll a suspended in the top 1.25 m of water, with all measured concentrations averaging about 5 µg·ℓ⁻¹ (Table 3). Later in the growing season (after 17 July) when phytoplankton blooms (*Ceratium hirundinella*) were occurring in the open water, pelagial concentrations of chlorophyll a suspended in the surface waters were up to fivefold greater than at littoral sites. Site B in the northwest bay had appreciably greater concentrations of chlorophyll a in the water among the macrophytes than did the other two littoral sites, again due to its close proximity to the open-water region of Eau Galle Reservoir.

Table 2
Representative Concentrations of Nutrients in Samples Taken
from Different Depths in Eau Galle Reservoir

<u>Depth, cm</u>	<u>Ammonium-N</u>	<u>Soluble Reactive P</u>
0	0.16 (0.00-0.50)	0.017 (0.000-0.095)
30	0.16 (0.00-0.49)	0.016 (0.000-0.076)
60	0.16 (0.00-0.50)	0.019 (0.000-0.108)
90	0.16 (0.00-0.43)	0.069 (0.000-1.694)
120	0.16 (0.00-0.44)	0.036 (0.002-0.314)
150	2.12 (0.00-11.6)	0.095 (0.001-0.880)

Note: Values, expressed in milligrams per liter, represent the mean (with minimum-maximum in parentheses). Value of n varies from 30 to 36.

Table 3
Measurement of Chlorophyll a ($\mu\text{g}\cdot\text{L}^{-1}$) Suspended in the Water Column
at Each of the Eau Galle Reservoir Sampling Sites at Midday

<u>Date</u> 1986	<u>Site</u>			
	<u>A</u>	<u>B</u>	<u>C</u>	<u>D</u>
22 May	3.5	3.6	4.5	2.6
5 Jun	5.6	6.2	4.2	6.7
19 Jun	2.3	2.7	1.5	3.1
3 Jul	27.9	31.3	2.1	11.0
17 Jul	52.0	38.5	9.2	20.7
1 Aug	78.1	52.6	39.1	38.0

Potomac River

23. Among vegetated stations, station 1 had the greatest species diversity and the least dense macrophyte community--65 percent *H. verticillata*, 25 percent *V. americana*, 5 percent *M. spicatum*, and 5 percent *H. dubia*. Vegetation at stations 2 and 3 was very dense and consisted of 90 percent *Hydrilla*, 5 percent *Myriophyllum*, and 5 percent *Heteranthera*. Biomass measurements made at several sites in conjunction with other studies being

conducted in the tidal Potomac River (Rybicki et al. 1988; Carter et al., in press; Killgore, Morgan, and Rybicki, in press) suggest that biomass at station 1 in August was approximately $300 \text{ g dry wt} \cdot \text{m}^{-2}$, and biomass at stations 2 and 3 was probably between 500 and $1,000 \text{ g dry wt} \cdot \text{m}^{-2}$.

24. Water quality was remarkably different inside and outside the macrophyte beds; however, differences in water quality among vegetated stations were relatively minor. The greatest diel fluctuation in temperature (26° to 34° C) occurred at the shallow nearshore site, station 1 (Figure 6). The water column at this site was nearly isothermal in both early morning and late afternoon and had the steepest vertical temperature gradient at 1500 hr, just before low tide. Temperature patterns at stations 2 and 3 were similar to those at station 1, with the steepest thermal gradients occurring in midafternoon (Figure 6). Thermal stratification was the result of solar insolation combined with very slow movement of water in plant beds near low slack tide. At station 4, only slight heating of the water was detected during the day. Absorbed solar energy was efficiently mixed by riverflow and turbulence, both longitudinally and throughout the water column outside the plant beds. The river at station 4 was virtually isothermal over depth throughout the day, with slightly lower temperatures at the bottom.

25. Conductivities inside and outside the bed were very similar (data not presented). Station 1 had a greater range of conductivity (400 to $460 \mu\text{S}$) than other stations, which varied between 410 and $450 \mu\text{S}$. Conductivity generally increased slightly with depth at all sites, especially during the midafternoon low tide.

26. Dissolved oxygen concentrations at all vegetated sites increased from about $3 \text{ mg}/\ell$ at dawn to a maximum of $17 \text{ mg}/\ell$ during low tide in midafternoon (Figure 6). Concentrations of DO at all stations were nearly uniform with depth in the morning and highly stratified by midafternoon. Stratification of DO was greatest at vegetated stations. The DO concentrations at station 4 increased only moderately, from $5 \text{ mg}/\ell$ at dawn to $>9 \text{ mg}/\ell$ in midafternoon.

27. The pH at all vegetated stations ranged from 7 to 10 (Figure 6). At station 4, pH ranged from 7 to 8. Vertical gradients of pH in the water column were steepest at stations 2 and 3. Maximum pH values occurred in the afternoon at approximately low tide.

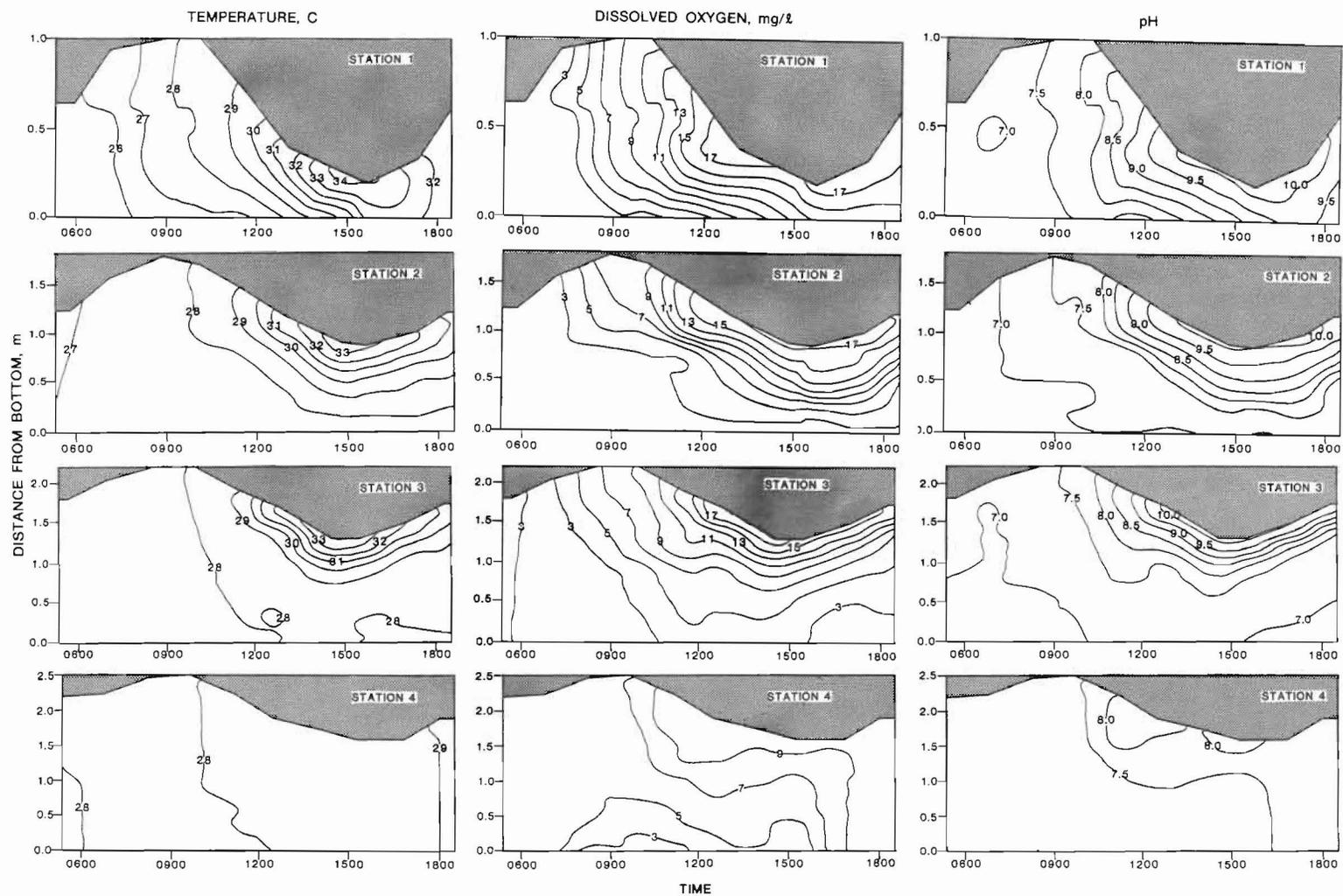


Figure 6. Diel variations (with depth) in temperature, DO, and pH at vegetated stations (1, 2, and 3) and at an unvegetated station (4) in the tidal Potomac River. (Data were collected 6 August 1986)

28. Secchi depth transparency within the macrophyte bed was always >130 cm. The exact reading was dependent upon water depth because the Secchi disk was resting on the bottom or on vegetation for all determinations. Mean Secchi depth at station 4 was 83 cm, with the least transparency (70 cm) occurring at high tide in the early morning. Extinction coefficients in the vegetated bed ranged from 1.1 to 1.7, whereas extinction coefficients at the open-water site ranged from 2.1 to 3.2.

29. Suspended-particulate concentrations at station 4 were significantly greater than at stations 1, 2, and 3 (Table 4). Within the bed, suspended-particulate concentrations were lowest at station 2 and highest at station 1; concentrations at station 1 were significantly greater than at stations 2 and 3 at low tide. Suspended-particulate concentrations at given

Table 4
Summary of Suspended-Particulate and Chlorophyll-a Concentrations Inside and Outside Macrophyte Beds in the Tidal Potomac River

Site/Tidal Stage	Suspended Particulates		Suspended-Particulate Organic Carbon, mg/l			Chlorophyll-a	
	mg/l		Percent of Suspended Particulates			µg/l	
	Mean	SE	Mean	SE		Mean	SE
Station 1							
High	11.6	2.99	6.8	1.97	59	19.01	2.481
Mean	12.2	0.44	5.1	0.27	42	11.77	0.773
Low	14.9	1.21	6.0	0.69	40	13.50	1.900
Station 2							
High	9.9	1.26	4.3	0.79	43	11.69	1.953
Mean	9.6	0.86	4.7	0.74	49	9.34	0.476
Low	9.0	1.67	3.2	0.58	36	8.91	0.454
Station 3							
High	10.1	1.51	4.3	0.55	43	10.95	1.167
Mean	10.7	1.50	3.1	0.32	29	15.10	0.811
Low	10.7	1.77	3.4	0.81	32	9.36	1.367
Station 4							
High	20.5	0.44	3.9	0.35	19	25.40	0.875
Mean	24.3	0.53	3.7	0.36	15	21.54	3.914
Low	19.7	0.44	3.9	0.59	20	16.90	2.403

Note: SE is standard error of the mean.

stations did not differ significantly with tidal stage or time of day. Organic carbon constituted between 29 and 59 percent of the suspended-particulate mass in the vegetated sites and only 15 to 20 percent of the suspended-particulate mass at the open-water site (Table 4).

30. Chlorophyll-a concentrations (Table 4) were lowest at station 2 and highest at station 4 at all three sampling times. Chlorophyll-a concentrations in the open water (station 4) were significantly greater than those at stations 2 and 3 in the macrophyte bed. Chlorophyll-a concentrations at station 1 were always between those at station 4 and stations 2 and 3. The T-test showed that station 1 was significantly different from all other stations at high tide, significantly lower than station 4 and similar to stations 2 and 3 at mean tide, and similar to all other stations at low tide. Chlorophyll-a decreased slightly with decreasing tidal elevation except at station 3, where chlorophyll-a concentrations were significantly higher at mean tide than at low or high tide.

31. Current velocities inside the macrophyte bed were $\leq 0.05 \text{ m}\cdot\text{sec}^{-1}$ and ranged from 0.12 to $0.17 \text{ m}\cdot\text{sec}^{-1}$ at station 4. Very little movement of water occurred within the bed at any stage of the tide.

Discussion

32. Based on observed development of thermal gradients in both Eau Galle Reservoir and the Potomac River, the most readily apparent effect of submersed macrophytes on environmental characteristics was resistance to mixing afforded by the macrophytes. Impedance of water movement by macrophytes has been noted by others as well (e.g., Sculthorpe 1967, Gregg and Rose 1982, Madsen and Warncke 1983, Fonseca and Fisher 1986). Open water in both systems heated and cooled quite uniformly with depth. In Eau Galle Reservoir, the proximity to shore, especially in more protected bays, decreased the exposure of littoral waters to wind in the afternoons and evenings, and as a result, the shallower waters gained more heat during daytime even without the effect of macrophytes. In the Potomac River, the shallow nearshore site, station 1, was most protected, least affected by tidal exchange, and exhibited greatest diel fluctuations in water temperature.

33. Temperature gradients in the littoral zone of Eau Galle Reservoir were steepened as plant biomass increased through the season, as has been

demonstrated by others as well. Dale and Gillespie (1976) found that floating macrophytes significantly affected the diel range of temperatures of surface waters. They further demonstrated depthwise temperature gradients to be steepened proportionately to the leaf area index of submersed macrophytes (Dale and Gillespie 1977, 1978). This is apparently caused both by heat absorption at the leaf surfaces, with subsequent warming of surrounding surficial water, and by shading of lower waters.

34. The distribution of macrophyte leaves within the water column affects the depth distribution of absorbed solar energy. Middepth temperature maxima have been experimentally induced by placing artificial macrophyte beds near the bottom (Dale and Gillespie 1978). The middepth peaks in water temperature observed in Eau Galle Reservoir were probably caused by light absorbance at middepth, with shading of lower waters by the plants. Thermal maxima at the surface in the Potomac River reflect the influence of canopy formation in *Hydrilla* on vertical temperature gradients.

35. Concentrations of dissolved oxygen in the waters of dense plant stands in Eau Galle Reservoir and in the Potomac River were very much influenced over daily time periods by the plants' photosynthetic production (daytime) and respiratory depletion of oxygen (nighttime and daytime). Large diel variations in DO have been reported by Halstead and Tash (1982), Ondok, Pokorny, and Kvet (1984), and Wylie and Jones (1987). From the literature it is apparent that the diel variations in DO observed in the tidal Potomac River are exceptionally large. These extremes appear to be related to the very high biomass of vegetation in this *Hydrilla*-dominated system (Rybicki et al. 1988; Carter et al., in press; Killgore, Morgan, and Rybicki, in press). Daily and seasonal dynamics of DO in a Danish river were also shown to be strongly dependent upon seasonal biomass (Kelly, Thyssen, and Moeslund 1983).

36. In the tidal Potomac River, the effects of submersed macrophytes on temperature, DO, and pH as well are probably greatest during the period August through October, corresponding with peak system-wide biomass. Sunny days with little wind are likely to result in the highest measurements. Although wind speed was relatively high on 6 August, the east-west orientation of the transect caused it to be sheltered and thus very calm.

37. In Eau Galle Reservoir during early summer, middepth oxygen peaks in the littoral zone appeared to occur at sites of greatest photosynthetic activity of macrophytes, i.e., at the top of the developing shoots. By

midsummer the macrophytes had reached the surface, yet during the evening, oxygen concentrations remained greatest near the middle of the water column, producing a positive heterograde pattern.

38. Littoral macrophytes have been the presumed cause of positive heterograde oxygen curves in whole lakes (e.g., Dubay and Simmons 1979) and in littoral zones by investigators studying vertical gradients. Morin and Kimball (1983) found significant differences in DO concentration with depth from June through September in stands of *Myriophyllum heterophyllum* in a lake in New Hampshire. Positive heterograde oxygen curves were observed in dense beds of *Ceratophyllum* in Lake Vechten, The Netherlands, by Gons (1982) and in dense *Elodea* stands in a Colorado alpine lake by Buscemi (1958). Actual mechanisms by which these profiles occur are not precisely known.

39. In Eau Galle Reservoir there are two potential causes of the occurrence of middepth oxygen maxima, and these probably occur in combination. First, oxygen gradients established by the macrophytes are likely to be made even steeper by loss during the day of oxygen to the atmosphere from warmer surface waters. At night, the atmosphere potentially serves as a source rather than as a sink, with oxygen reentering the cooling surface water. Bottom sediments have large biological (and chemical) demands that consume molecular oxygen; thus, the substratum serves as a sink for oxygen during both day and night (e.g., Gons 1982).

40. Second, algae attached to submersed macrophytes may contribute to the development of positive heterograde profiles of oxygen. Epiphytic algae exhibited the same general succession in Eau Galle Reservoir as exhibited elsewhere (Hooper-Reid and Robinson 1978, Morin and Kimball 1983), namely from an attached flora dominated by diatoms (especially *Fragilaria* spp.) and green algae in early summer, to blue-green algae (*Oscillatoria* spp., *Anabaena* spp.), followed by green filamentous algae (*Oedogonium* spp., *Spirogyra* spp.) in late summer and autumn.

41. Sand-Jensen, Revsbech, and Jorgensen (1985) found epiphytes to be capable of producing as much DO under saturating light as did the macrophyte *Potamogeton crispus* studied in their experiments, although the epiphytes inhibited movement of DO away from the macrophyte. Adams, Titus, and McCracken (1974) hypothesized that occasional subsurface photosynthetic maxima of shoots of *M. spicatum* at various depths in Lake Wingra, Wisconsin, were induced mainly by sloughing of biomass from the plant tips, with consequently

lesser community metabolic activity at the top of the canopy late in the growing season. Since the macrophytes in Eau Galle Reservoir, largely *Ceratophyllum*, in July were already undergoing some senescence below the canopy, as evidenced by leaf loss and color change, the high oxygen concentrations well below the water's surface may have been created partly by photosynthetic activity of populations of epiphytes. Photosynthesis in these algae was potentially stimulated by nutrients lost from senescing portions of vascular plants, and by nutrient diffusion upward from the sediments. Others have also observed the photosynthetic capacities of macrophytes and their epiphytes to be greater at middepth in the water column than at the water's surface (Sheldon and Boylen 1975, Gons 1982, Morin and Kimball 1983).

42. Changes in pH also demonstrate the importance of aquatic macrophytes in modifying the chemical environment of surrounding water. High rates of photosynthesis in both studied systems were evidenced not only by daytime accumulation of DO but also by concomitant increases in pH. The same has been observed in other studies (Brown et al. 1974; Van, Haller, and Bowes 1976; Bowes, Holaday, and Haller 1979). Morin and Kimball (1983) observed a pH increase from the surface to middepth in a *M. heterophyllum* bed, and then a decline near the bottom at all sampling times except early in the growing season (early June) and late in the season (September). As in the case of DO, gas exchange was probably a contributing factor to diel variability in pH, both near the surface and at the bottom. The midday maxima of pH observed in surface waters of both Eau Galle Reservoir and the Potomac River indicate declining rates of net photosynthesis during late morning and early afternoon.

43. Decreases in both conductivity and calcium concentration noted in Eau Galle Reservoir during the day, coincident with increasing pH, suggest the occurrence of carbonate precipitation. This may account in part for reductions in phosphorus due to coprecipitation, as described for hardwater lakes (Otsuki and Wetzel 1972, Wetzel 1983a). The frequent absence of detectable soluble reactive phosphorus in the littoral zone of Eau Galle Reservoir during this investigation may have contributed directly to reduced planktonic chlorophyll concentrations in the littoral zone.

44. Reduced concentrations of suspended chlorophyll in both Eau Galle Reservoir and the Potomac River reflect lesser population densities of phytoplankton, as noted--based on direct determinations made earlier in Eau Galle Reservoir (Barko et al. 1984). Lower concentrations of suspended-particulate

matter, in addition to chlorophyll-a in the Potomac River at vegetated stations, clearly contributed to much improved water clarity, in contrast with the adjacent open-water station.

45. Lower chlorophyll-a concentrations in the macrophyte beds may result partially from settling of algal cells due to reduced turbulence or losses due to grazing (Kairesalo 1980, Lemly and Dimmick 1982, Timms and Moss 1984). Additional possible explanations for reduced phytoplankton populations in macrophyte beds include shading, presence of allelopathic substances, and competition for nutrients (Brammer 1979, Planas et al. 1981, Wetzel 1983b). Currently, there is no consensus as to the mechanisms regulating phytoplankton dynamics within submersed macrophyte beds.

Conclusions and Recommendations

46. Because of the intense metabolic activity of submersed macrophyte communities, daily fluctuations in oxygen concentration and pH were much more intense in vegetated areas of both Eau Galle Reservoir and the Potomac River than in adjacent open water. In the Potomac River within a near-monotypic community of *Hydrilla*, diel variations in pH indicated a three-order of magnitude change in hydrogen ion activity. In Eau Galle Reservoir and in the Potomac River, DO concentration varied between 10- and greater than 200-percent saturation on a daily basis during midsummer. These fluctuations were considerably greater than those normally attributed to plankton metabolism and provided uniquely diverse environmental conditions.

47. The steepening of environmental gradients by submersed macrophytes over both depth and time (both daily and seasonally) adds significantly to the complexity of the aquatic habitat. In addition to their importance in the productivity of aquatic systems, submersed macrophytes clearly create distinct physical and chemical conditions that may influence the distribution of other organisms. As evidenced in the studies reported here, gradients in water temperature, pH, and DO in macrophyte beds can be quite pronounced. Fluctuations in these variables and others undoubtedly have far-reaching effects on the activity of animals, as well as on biogeochemical processes. Whereas measurements of these events and processes are difficult, such determinations are necessary to develop an unbiased perception of the role of submersed macrophytes in the functioning of aquatic ecosystems.

48. Major reductions in concentrations of suspended-particulate matter and chlorophyll within submersed macrophyte beds indicate the effectiveness of these communities in improving localized water quality conditions. Notably, these improvements were roughly comparable in both Eau Galle Reservoir and in the Potomac River, despite distinct differences in respective macrophyte species composition. Mechanisms contributing to reductions in chlorophyll concentration in macrophyte beds are essentially unknown; these should be elaborated, since high chlorophyll (phytoplankton) concentrations often constitute a significant water quality problem.

49. Reduced concentrations of suspended sediment in submersed macrophyte beds of the Potomac River illustrate the potential importance of these communities as sediment traps. Enhanced sedimentation in these macrophyte beds, presumably from reduced turbulence, suggests that such areas may function as nutrient sinks during the growing season. Given the potential for nutrient releases from tissues of aquatic macrophytes upon senescence and decay, it is important to evaluate nutrient source-sink relationships within submersed macrophyte communities over annual cycles. As a prerequisite to these evaluations, it is necessary to first improve the current rudimentary understanding of hydraulic exchange between submersed macrophyte beds and adjacent open water.

50. In the studies described herein, only a portion of the potentially significant effects of aquatic macrophytes on the environment have been addressed. Additional studies are recommended to determine the effects of submersed macrophyte communities on geochemical conditions and to couple biological activity with physical and chemical gradients imposed by these plants on both the sediment and water column of aquatic systems. In the context of aquatic plant management, future studies should concentrate on the role of aquatic macrophyte communities in the functioning of aquatic ecosystems.

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