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Effects of emergent vegetation on wetland microbial processes

by

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A dissertation submitted to the *graduate faculty*

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Water Resources

Major Professor: William G. Crumpton

Iowa State University

Ames, Iowa

1996

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CHAPTER 1. GENERAL INTRODUCTION

Dramatic, usually cyclic, changes in vegetation dynamics in prairie pothole wetlands due to water level fluctuations and other environmental factors are well recognized (van der Valk and Davis 1976, van der Valk 1981, Kantrud et al. 1989). Yet, relatively little work has been done on the effects of wetland vegetation on the physical environment of the bulk water phase and subsequent effects on microbial metabolism (in prairie pothole or other wetlands).

The relationship between depressed concentrations of dissolved O_2 and the presence of submerged and floating-leafed vegetation has been noted in many studies (Buscemi 1958, Lewis and Bender 1961, Carpenter and Gasith 1978, Duffield 1981, Pokorný and Rejmanková 1983, Ondok et al. 1984, Bican et al. 1986, Carpenter and Lodge 1986, Frodge et al. 1990). Few studies have found low dissolved O_2 associated with emergent macrophyte stands (Carter and Beadle 1932; Ulehlova and Pribil 1978, Reddy 1981, Suthers and Gee 1986, Murkin et al. 1992, Hamilton, et al. 1995). Some of these studies have emphasized the importance of dissolved O_2 patterns in wetlands to the distribution of invertebrates and fish and the resulting effects on predator-prey dynamics (Suthers and Gee 1986, Murkin et al. 1992) while other studies have focused primarily on moderately exposed margins of emergent beds and generally demonstrated periodic depression of dissolved O_2 primarily at night (Ulehlova and Pribil 1978, Reddy 1981). None of these studies have reported long periods of anoxia within the water column of wetlands. Submerged, floating-leafed, and emergent plants may affect basic physical parameters such as light, temperature and dissolved O_2 concentrations in the water column directly through their photosynthesis and respiration, and indirectly by shading the water column, contributing organic matter and substratum for periphytic algae and bacteria, and by interfering with gas transfer across the air/water interface. But emergent plant communities generally have higher productivity and are more persistent than submerged plants (Godshalk and Wetzel 1978, Wetzel 1983) and therefore could have a greater effect on these physical processes.

Both aerobic (photosynthesis and respiration) and anaerobic metabolism may be affected by the physical effects of persistent plant structure. In freshwater systems, under anaerobic conditions, methanogenesis is usually the most important carbon metabolic process (Capone and Kiene 1988). Despite the potential importance of these processes, rates of methanogenesis or methane flux have not been reported in prairie pothole wetlands. Since biogeochemical cycles and possibly contaminant fates with links to carbon metabolism may also be affected, more information is needed on these physical effects, in part, to make better decisions about the management of wetlands and to understand their role in the landscape. The papers in this dissertation examine the temporal and spatial patterns of temperature, dissolved O_2 , aquatic aerobic metabolism, and methanogenesis in prairie pothole wetland systems dominated by *Typha* spp. using both a natural marsh and experimental wetland mesocosms.

Dissertation Organization

This dissertation consists of two manuscripts written for journals, describing the effects of emergent aquatic plants on the dissolved oxygen, temperature, and carbon metabolic dynamics of the water column in prairie pothole wetland systems.

The first paper will be published in the journal *Wetlands* in December 1996. Charles Rose is the principle author and William G. Crumpton is the co-author. This paper describes how synoptic surveys, monitoring of different wetland zones with microprocessor-based continuous temperature and dissolved O₂ probes, and detailed transect studies were used to describe the dynamics of dissolved O₂ in a large prairie pothole marsh.

The second paper is written for submission to the journal *Limnology and Oceanography*. Charles Rose will be the first author; William G. Crumpton will be the second author. This paper describes measurements of dissolved O₂, temperature dynamics, aerobic carbon metabolism, and CH₄ flux in a natural prairie pothole wetland and some experiments using wetland mesocosms.

A General Summary follows the two papers; references cited in the General Introduction and General Summary are listed following the General Summary.

CHAPTER 2. EFFECTS OF EMERGENT MACROPHYTES ON DISSOLVED OXYGEN DYNAMICS IN A PRAIRIE POTHOLE WETLAND

A paper accepted by the the journal Wetlands

Charles Rose, William G. Crumpton

ABSTRACT

Transect measurements, continuous monitoring, and synoptic surveys were used to examine patterns in light availability, temperature, and dissolved oxygen concentrations within and outside emergent vegetation zones in Goose Lake Marsh, a natural prairie pothole wetland in central Iowa. Water column light availability was less than 2% of ambient light in emergent vegetated areas due to canopy cover, small floating plants (lemnids), and plant litter. Water temperatures and dissolved oxygen concentrations were significantly lower and varied less diurnally in vegetated areas. Three habitat zones could be identified based on patterns in vegetation and dissolved oxygen: (1) a zone of dense emergent macrophytes providing significant submerged structure but with nearly or completely anoxic water, (2) a transition zone of sparse emergent macrophytes providing less structure but with more aerobic water, and (3) an open water zone with consistently aerobic water but with little submerged structure. Vegetation patterns are likely to control major aspects of wetland biogeochemistry and trophic dynamics, and wetlands should be viewed as complex mosaics of habitats with distinct structural and functional characteristics.

Key Words: prairie pothole marsh, wetlands, dissolved oxygen, aerobic, anaerobic, emergent macrophyte, litter accumulation, nutrient cycling, biogeochemistry

INTRODUCTION

Seasonal and long-term changes in vegetation structure are a common characteristic of most wetland ecosystems. The vegetation dynamics of prairie pothole wetlands have been the subject of considerable research in recent years, and it is now recognized that these wetlands undergo dramatic, sometimes cyclic changes in response to water-level fluctuations and other environmental factors (van der Valk and Davis 1976, van der Valk 1981, Kantrud et al. 1989). However, there has been comparatively little work on the response of environmental factors to changes in wetland vegetation.

Aquatic vegetation can significantly affect the physical and chemical characteristics of sediments and overlying waters, including such critical factors as temperature and availability of dissolved oxygen. Aquatic macrophytes transfer oxygen to the rhizosphere, with important biogeochemical consequences for energy flow

and nutrient cycling (Carpenter and Lodge 1986, Reddy et al. 1989), and they can significantly alter oxygen availability in the water column (Reddy 1981, Carpenter and Lodge 1986, Frodge et al. 1990). The concentration of oxygen in equilibrium with a body of water in contact with the atmosphere varies primarily with temperature (Mortimer 1981). However, nonequilibrium concentrations are typical of wetlands as a result of atmospheric exchange rate and metabolic O₂ consumption and production. Aquatic vegetation can alter dissolved oxygen (D.O.) dynamics in the water column directly by reducing gas exchange at the water's surface, by root respiration, indirectly by reducing light available for photosynthesis, by providing a substratum for periphytic algae, and by providing a carbon source and substratum for microbial respiration.

Most studies of aquatic vegetation and D.O. relationships have dealt with effects of submersed and floating-leafed vegetation (Buscemi 1958, Carpenter and Gasith 1978, Duffield 1981, Pokorny and Rejmankova 1983, Ondok et al. 1984, Bican et al. 1986, Carpenter and Lodge 1986, Frodge et al. 1990). There have been far fewer studies of D.O. dynamics in emergent macrophyte stands, and these have focused primarily on moderately exposed margins of emergent beds (Ulehlova and Pribil 1978, Reddy 1981, Suthers and Gee 1986, Murkin et al. 1992). In general, results demonstrate periodic depression of D.O., primarily at night, but not prolonged periods of anoxia. However, anoxia might be much more persistent deep within emergent macrophyte stands where vegetation and litter densities are high. The primary objective of this study was to examine the spatial and temporal dynamics of water-column D.O. in relation to the distribution of emergent vegetation in a natural prairie pothole wetland, including interior zones of living and dead emergent stands.

METHODS

Study Site

Goose Lake Marsh (also known as Anderson Lake) is a natural prairie pothole wetland that has been the subject of a variety of research efforts over the past century (Pammel 1898, Errington 1963, Weller and Spatcher 1965, Davis and van der Valk 1978a,b, Roosa 1981). The wetland is located northeast of Jewell, Iowa (42° 22' north latitude, 93° 30' west longitude), near the southern end of the prairie pothole region (van der Valk 1989). The marsh's surface area is about 65 ha, and its maximum depth is near 1.5 m. Water depth is regulated by a dam at the southwestern outlet. Goose Lake Marsh has been classified as a hard water, semi-permanent wetland (Davis and van der Valk 1978a). It has a small watershed (Weller and Spatcher 1965), much of which is agricultural (mainly corn and soybean production). A base map of the marsh was constructed by digitizing the image from an aerial 35-mm slide in September 1993. We used about 325 depth measurements recorded from a canoe to create depth isopleths (Figure 1). Interpolations were made with a Kriging method using Surfer software (Golden Software, Inc., Golden, Colorado, USA). Sampling locations were determined by triangulation of compass bearings.

Continuous Data Collection

Continuous water quality monitors (AQUA 2000 prototypes, Biodevices Inc., Ames, Iowa, USA) recorded temperature and D.O. at five locations (Figure 1) in the marsh during the ice-free period in 1994. Sites 1 and 2 were within a mixed cattail stand dominated by *Typha x glauca* Godr. with occasional *Typha angustifolia* L. Site 3 was at the edge of the *Typha* spp. stand. Site 4 was open water early in the year but developed into a stand of *Scirpus fluviatilis* (Torr.) Gray during the middle of the growing season. We refer to this as the fluctuating vegetation site. Site 5 was open water throughout the study. Sites 1 and 4 were monitored from late March through November, sites 2 and 3 were monitored from May through October, and site 5 from July through September. All monitors recorded temperature and D.O. at 15-cm depth every 6 minutes. Prior to deployment, temperature sensors were calibrated using a two-point calibration between 4° C and 35° C. The D.O. sensors were calibrated using air-saturated water and an O₂ saturation value calculated using the formula of Mortimer (1981). At approximately two-week intervals, monitors were serviced and D.O. and temperature reference values were collected using a field portable meter to check for sensor drift. Sensors drifted less than < 5% and correction was not necessary.

Transects

On six dates from 3 June to 27 September 1994, water, plant, and microenvironment samples were taken near mid-day at three sites along each of four transects from a nearshore, vegetated area to an open water area. Different transects were sampled on each date. On each transect, the first site was 2 to 5 meters into an emergent stand, the second site was within 3 meters of the emergent-open water boundary (stand margin), and the third site was in open water. Vegetation type was recorded, and integrated composites from the water column at each site were collected. Unfiltered and 0.45- μ m filtered aliquots were preserved for nutrient determination. Nitrate was assayed using second derivative spectroscopy (Crumpton et al. 1992), ammonium was assayed using the indophenol method (Scheiner 1976), and soluble reactive phosphorus was assayed using the ascorbic acid method (APHA 1989). Following persulfate digestion, total nitrogen was assayed using second derivative spectroscopy (Crumpton et al. 1992), and total phosphorus was assayed using the ascorbic acid method (APHA 1989). For particulate organic carbon (POC) and particulate organic nitrogen (PON), water samples were filtered through 26- μ m Nitex filters and GF/F filters. Particles were washed off the 26- μ m filters onto GF/F filters. POC and PON were determined by high temperature combustion and thermal conductivity detection using a Carlo-Erba NA1500 elemental analyzer. Floating plant samples were collected by inserting a 15-cm-diameter acrylic cylinder into the water, covering the bottom of the cylinder below the mixture of small floating plants (lemnids), then transferring the contents to a plastic bag. In the laboratory, the plants were freeze-dried and weighed. D.O. and temperature data were measured *in situ* using a field portable meter. Light levels within the water column were recorded at each location using an underwater quantum sensor (model LI-192S, LI-COR, inc., Lincoln, Nebraska, USA). On five dates (excluding June 3), samples to determine dissolved methane were collected; 5-10 mL of water were

drawn into a 10-ml syringe with a 18-gauge needle, then injected into an evacuated, 20-mL gas chromatography (GC) vial through a butyl-rubber septum. The procedure took place under water to prevent air contamination. Methane standard and sample concentrations were measured on a Tremetrics 540 gas chromatograph (helium carrier) configured for head space sampling, a 3.05-m x 3.18-mm stainless steel Haysep D column (at 80 °C), and a Tremetrics 706 discharge ionization detector. Methane concentrations in the vial were corrected for gas partitioning between the head space and water (Stumm and Morgan 1981). These data were analyzed by ANOVA (with contrasts among date and area compared by LSD). On several dates in August, detailed D.O. transects were run across the transition zone between emergent and open water zones with D.O. and temperature measurements at 0.5 m horizontal and 0.1 m vertical intervals. These were plotted using the Kriging method with Surfer.

Synoptic Surveys

The distributions of D.O. and living and dead emergent vegetation in Goose Lake Marsh were surveyed at 160 to 200 locations each month from May through October 1994. At each location, daytime oxygen concentrations were measured at a depth of 15 cm using the portable field meter, and the dominant vegetation types (nearly always *Typha* spp.) were recorded. Sampling locations were sited on the base map by triangulation of compass bearings in order to map D.O. and plant cover. Oxygen isopleths were mapped using the Kriging method.

During September and October 1994, litter samples were collected at 37 sites by inserting a 60-cm-high, 37.5-cm-diameter (0.1 m^2) cylinder into the water column and removing all dead plant material above the sediment (including aerial parts), cutting the litter at the edge of the cylinder where necessary. Water depths were recorded at each site so that litter densities could be calculated on both areal (kg/m^2) and volumetric (kg/m^3) bases. Litter samples were placed in plastic bags, transported back to the lab, oven-dried at 65° C to a constant mass in paper bags, and weighed.

RESULTS

There were striking differences in plant material and water column characteristics of open water and emergent stands, with stand margins that were intermediate in character (Table 1). Often associated with the emergent vegetation was a thick growth of small floating plants (lemnids) including *Lemna minor* L., *Spirodela polyrhiza* L. Schleiden, *Lemna trisulca* L., *Riccia fluitans* L. and *Wolffia columbiana* Karst. Greater amounts of litter and lemnid biomass were found in the emergent zone. Edge-of-stand sites were more subject to intrusion of wind-blown water from open water areas and to variable cover by floating plants and debris, which were irregularly redistributed by wind and wave action.

Emergent macrophyte stands had lower light levels, higher nutrient levels, higher dissolved methane

levels, and higher particulate organic matter than open water areas (Table 1). The C:N ratio of particulates did not differ among zones but were different (at $p < 0.05$) and were of 9.6 ± 1.9 and 8.4 ± 2.5 (mean \pm S.D.) for the large and small size fractions, respectively. Temperatures were generally lower and displayed less diurnal variation at sites within the emergent stand than at stand margin and open water sites. In late August, for example, water temperature at within-stand sites varied 3–4 °C around a mean of about 20 °C, whereas the temperature at open water and edge-of-stand sites varied 8–10 °C around a mean of about 25 °C (Figure 2). Sites within the emergent stand had extremely low oxygen concentrations and were almost continuously anoxic (Figure 2), while sites at the edge of the stand had higher dissolved oxygen concentrations, with significant daytime increases in D.O. on about half of the days. The open water site maintained consistently higher dissolved oxygen concentrations and had diurnal changes in D.O. of up to 10 mg/L.

Temperature and D.O. differences between open water and emergent macrophyte zones persisted throughout the study. Although the sites displayed similar seasonal temperature patterns, temperatures throughout the ice-free season were lower and varied less diurnally at emergent stand sites than open water sites. Emergent sites were generally anoxic until the marsh began to freeze in November, whereas open water sites were rarely anoxic, even at night. The emergent and fluctuating vegetation sites with the longest continuous records are illustrated in Figure 3. The fluctuating vegetation site began as open water, but *S. fluviatilis* emerged near and around this site by June. From that time until the disappearance of *S. fluviatilis* in October, the site displayed a mixture of oxygen and temperature dynamics characteristic of stand and stand edge sites. In July, for example, when the *S. fluviatilis* stand reached its maximum development, the site displayed the depressed D.O. and lower, less diurnally variable temperatures characteristic of stand interiors.

The D.O. transects demonstrated sharp transitions between open water and emergent zones (Figure 4). High dissolved oxygen concentrations were associated with the open water zones, and at sites even a few meters into the emergent zones, surface D.O. concentrations were usually < 2 mg/L, declining to less than 0.2 mg/L in the lower half of the water column. At one sampling area on 15 August 1994, D.O. was 0.9 mg/L in a *Typha* spp. stand and 11.4 mg/L just 2 m toward the open water (both measurements at 10 cm below the water surface). Temperature and oxygen data frequently demonstrated stratification of the water column in the emergent stands. Open water areas near the stand margins tended to show oxygen stratification (Figure 4), but except in very calm periods, tended to be well-mixed further from stand margins.

The quantity and distribution of lemnids varied greatly depending on wind speed and direction, but lemnids were found in only two open water samples, and their mean dry mass for open water sites was 0.5 g/m^2 (Table 1). In contrast, floating plant dry mass averaged 139 g/m^2 at sites on stand margins and 316 g/m^2 at sites within the stands. The combination of *Typha* spp. plants, litter, and floating plants usually resulted in less than 2% ambient light at 5 cm below the water surface, even in sparse canopies or dead emergent zones. Within stands of both living and dead emergent plants, water-column anoxia persisted regardless of the presence or density of

floating plants. Anoxic conditions also persisted in the absence of floating plants early and late in the growing season (Figure 3).

Synoptic surveys confirmed that low dissolved oxygen concentrations were consistently associated with the emergent macrophyte zone around the margins of the marsh and islands (Figure 5). In May, this zone consisted primarily of standing dead shoots and fallen litter rather than live plants and covered about 45% of the marsh's surface area. Live vegetation was first recorded in June and emerged primarily within zones of standing dead shoots. Coverage by live emergent vegetation increased to a peak of 19% of the wetland area by July, after which coverage by live vegetation slowly decreased. The open water area had scattered patches of submersed plants (primarily *Potamogeton* spp.) and water lilies (*Nuphar microphyllum* (Pers.) Fernald. and *Nymphaea tuberosa* Paine). During the growing season, there was a slight increase in the open water area of the marsh from about 55 % in May to 61 % in October. From May to July, the $< 2.0 \text{ mg O}_2/\text{L}$ area in the southeast margin expanded (probably due to increasing temperatures). Higher D.O. returned to those areas by October. Some areas dominated by standing dead vegetation changed to open water between July and October at locations around the islands and along the south and southeast margins. D.O. generally increased in those areas concomitant with the conversion to open water.

DISCUSSION

At least three major habitat zones could be identified in Goose Lake Marsh based on patterns in vegetation and physical parameters: (1) a zone of dense emergent macrophytes providing significant submerged structure and with nearly or completely anoxic water, (2) a transition zone of sparse emergent macrophytes providing less structure but with more aerobic water, and (3) an open water zone with little or no structure and with consistently aerobic water. These zones can be expected to differ greatly with regard to biogeochemical dynamics, biota, and trophic dynamics. For example, areas with low-to-intermediate oxygen levels might be especially important as a refuge for invertebrates adapted to low oxygen conditions (Murkin et al. 1992). These zones may represent a few of this wetland's complex mosaics of habitats.

Much of the difference in dissolved oxygen and temperature patterns between the vegetated and open water zones (Figures 2, 3, 4, and 5) can be attributed to the physical effects of vegetation on O_2 supply. Compared to the open water zone, the emergent zone would have lower rates of O_2 supply because of reduced photosynthesis and reduced O_2 flux from the atmosphere. In emergent stands, much of the ambient light is intercepted by the emergent canopy, lemnids, or plant litter, thereby reducing temperature and photosynthetic production of O_2 in the water column.

Gas exchange between the atmosphere and surface water is controlled primarily by the gas concentration gradient and the boundary layer thickness (Liss and Slater 1974, Broecker and Peng 1982). The boundary layer thickness controls the maximum rate of gas exchange and is primarily a function of shear forces across the air-

water interface. Shear forces and gas transfer rates are decreased by factors that decrease wind velocity (such as a dense plant canopy) or decrease mixing of the water column (such as dense accumulations of living or dead macrophyte shoots and leaves within the water column). These factors can be expected to influence oxygen and methane transfer differentially in live emergent and dead emergent zones. Reduction of light and wind velocity by the plant canopy would obviously be most important in the live emergent zone. Reduction of light and water-column mixing due to submerged structure would be important in both live and dead emergent zones. Floating plants block light and inhibit oxygen transfer by blocking the air-water interface (Morris and Barker 1977) and can contribute to low oxygen concentrations in both emergent and open water zones as may be the case in Figure 4 (b).

In addition to lower rates of O_2 supply from the atmosphere, the emergent zone would likely have higher rates of O_2 demand because of the tremendous annual contribution of the emergent macrophytes to detritus. Litter densities in the emergent vegetation zone were approximately an order of magnitude greater than in the open water zone and presumably represented several years of accumulation. Davis and van der Valk (1978b) reported about $1.3 \text{ kg m}^{-2} \text{ year}^{-1}$ of above-ground production of *Typha x glauca* in Goose Lake Marsh with about 0.95 kg/m^2 remaining after 525 days. The elevated methane concentrations in the emergent zone are comparable to those previously reported for *Typha* sp.-dominated wetlands in agricultural areas (Schipper and Reddy 1994) and may reflect both greater anaerobic production rates and lower air-water flux coefficients in dense emergent stands.

Many of the effects of emergent macrophytes on their environment are similar to those of submersed macrophytes (Carpenter and Lodge 1986). However, we found much more extreme and persistent oxygen depression in emergent stands (Figures 2, 3, 4, and 5) than has been reported for beds of submersed and floating leafed macrophytes. This can largely be attributed to restriction of most photosynthesis to the emergent leaves, as well as to the greater amount and persistence of plant structure in emergent stands. Emergent plant communities have higher potential production rates than submersed communities (Wetzel 1983). Emergent macrophytes produce much more structural material (lignin, cellulose, and hemicellulose) than do submersed and floating leafed plants, and this material decomposes relatively slowly (Godshalk and Wetzel 1978). As was clearly the case in Goose Lake Marsh (Figure 5), standing dead shoots and fallen litter can limit oxygen availability years after the dieback of emergent plants such as *Typha* spp. Effective aeration of the water column seems to require removal of dead as well as live vegetation, for example by muskrats or by physical erosion due to wind and waves, as was observed in the southeastern section of Goose Lake Marsh after July 1994 (Figure 5). These considerations are particularly important given the longer-term (5-20 year) vegetation cycles of prairie pothole wetlands in response to water-level fluctuations and other environmental factors (Weller and Spatcher 1965, van der Valk and Davis 1978, Roosa 1981, Kantrud et al. 1989). These cycles can be quite dramatic, with changes

from near 100 % cover by emergent macrophytes to near 100 % open water within just a few years (Weller and Spatcher 1965).

Temporal and spatial patterns of emergent vegetation are likely to control major aspects of wetland energy flow, nutrient cycling, and food web structure. Depressed O₂ concentrations and supply rates would limit aerobic metabolism in emergent zones and could increase the relative importance of energy flow through anaerobic pathways such as denitrification, sulfate reduction, and methanogenesis. In addition, juxtaposition of aerobic and anaerobic zones in the rhizosphere or between the bulk water phase and biofilms in wetlands is thought to provide tight coupling of various aerobic and anaerobic reactions such as nitrification-denitrification and methanogenesis-methane oxidation. However, in anoxic emergent stands, the potential for coupling of aerobic and anaerobic reactions would be virtually eliminated from the bulk water phase and restricted to the rhizosphere. Either directly or indirectly, vegetation dynamics are likely to control many of the complex biogeochemical transformations involved in wetland nutrient cycling and may help explain why a wetland may act as a nutrient sink one year and a nutrient source another. Additionally, the interplay between O₂ distribution and vegetation structure in wetlands is important to the dynamics of aquatic invertebrates and their predators (Suthers and Gee 1986, Murkin et al. 1992) and may affect diversity and secondary production. If we are to understand functional processes in prairie pothole wetlands, we must recognize these wetlands as complex spatial and temporal mosaics of habitats with distinct structural and functional characteristics.

ACKNOWLEDGMENTS

This study was funded by the United States Environmental Protection Agency Cooperative Agreement # CR 820078 and by a USDA National Needs Fellowship in Water Sciences supporting C. Rose's dissertation work. We thank Marley Ayres, Steve Fisher, Sue Gambera, Elliot Hill, Jennifer Owens, Michelle Ricklefs, Jana Stenback, Jay Turner, and Matt Ueltzen for field and laboratory assistance and Tim Parkin for assistance with methane analyses. We thank Gary Atchison, Tom Jurik, Arnold van der Valk, and anonymous reviewers for their comments on previous drafts, Mike Gipple for his artwork, and the owners of Goose Lake Marsh for allowing us access.

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Manuscript received 2 February 1996; revision received 10 May 1996; accepted 28 July 1996.

Table 1. Means \pm SEM (n) for various parameters in wetland zones in Goose Lake Marsh. Planned comparisons indicated differences at $p < 0.05$ either among all three zones (*) or between the emergent and open water zones (**), but indicated no effect of sampling date except for dissolved methane on one date.

Parameter	Emergent Stand	Stand Margin	Open Water
Plant Litter*			
(kg/m ²)	2.34 \pm 0.18 (24)	1.19 \pm 0.21 (8)	0.35 \pm 0.12 (5)
(kg/m ³)	5.5 \pm 0.5 (24)	2.3 \pm 0.4 (8)	0.45 \pm 0.16 (5)
Lemnids* g/m ²	316 \pm 64 (24)	139 \pm 28 (24)	0.5 \pm 0.1 (24)
Light* (% Surface Irradiation at 5 cm depth)	1.5 \pm 0.5 (24)	29 \pm 6 (24)	61 \pm 6 (23)
Total Nitrogen* (mg/L)	5.5 \pm 0.7 (24)	3.4 \pm 0.4 (24)	1.58 \pm 0.12 (24)
NH ₄ ⁺ -Nitrogen (μ g/L)	450 \pm 70 (24)	390 \pm 50 (24)	330 \pm 70 (24)
NO ₃ ⁻ -Nitrogen (μ g/L)	Not Detected (24)	Not Detected (24)	Not Detected (24)
Total Phosphorus (μ g/L)	258 \pm 28 (23)	280 \pm 30 (24)	200 \pm 40 (23)
Soluble**	102 \pm 14 (24)	88 \pm 13 (24)	66 \pm 8 (24)
Reactive Phosphorus (μ g/L)			
Particulate Carbon*	11.0 \pm 1.4 (24)	6.8 \pm 1.0 (24)	1.9 \pm 0.3 (24)
> 26 μ m (mg./L)			
Particulate Nitrogen*	1.1 \pm 0.1 (24)	0.71 \pm 0.11 (24)	0.20 \pm 0.03 (24)
> 26 μ m (mg./L)			
Particulate Carbon**	2.7 \pm 0.3 (22)	1.9 \pm 0.2 (21)	1.6 \pm 0.2 (20)
GF/F (mg./L)			
Particulate Nitrogen	0.33 \pm 0.04 (22)	0.25 \pm 0.02 (21)	0.17 \pm 0.02 (20)
GF/F (mg/L)			
Dissolved Methane*	6.6 \pm 1.0 (19)	2.9 \pm 0.6 (19)	0.7 \pm 0.1 (19)
(mg/L)			

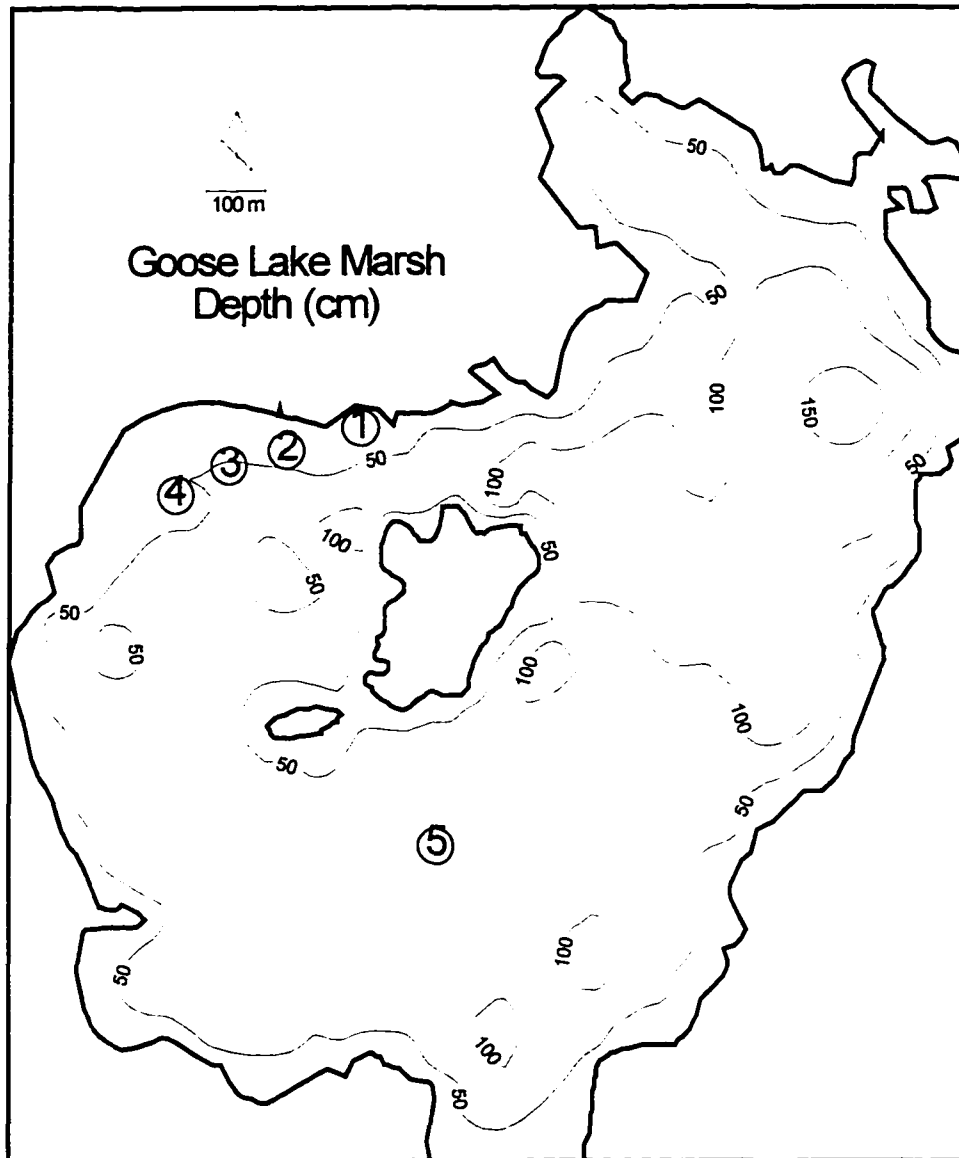


Figure 1. Depth (cm) isopleths of Goose Lake Marsh in central Iowa. The numbers mark locations of continuous water quality monitors.

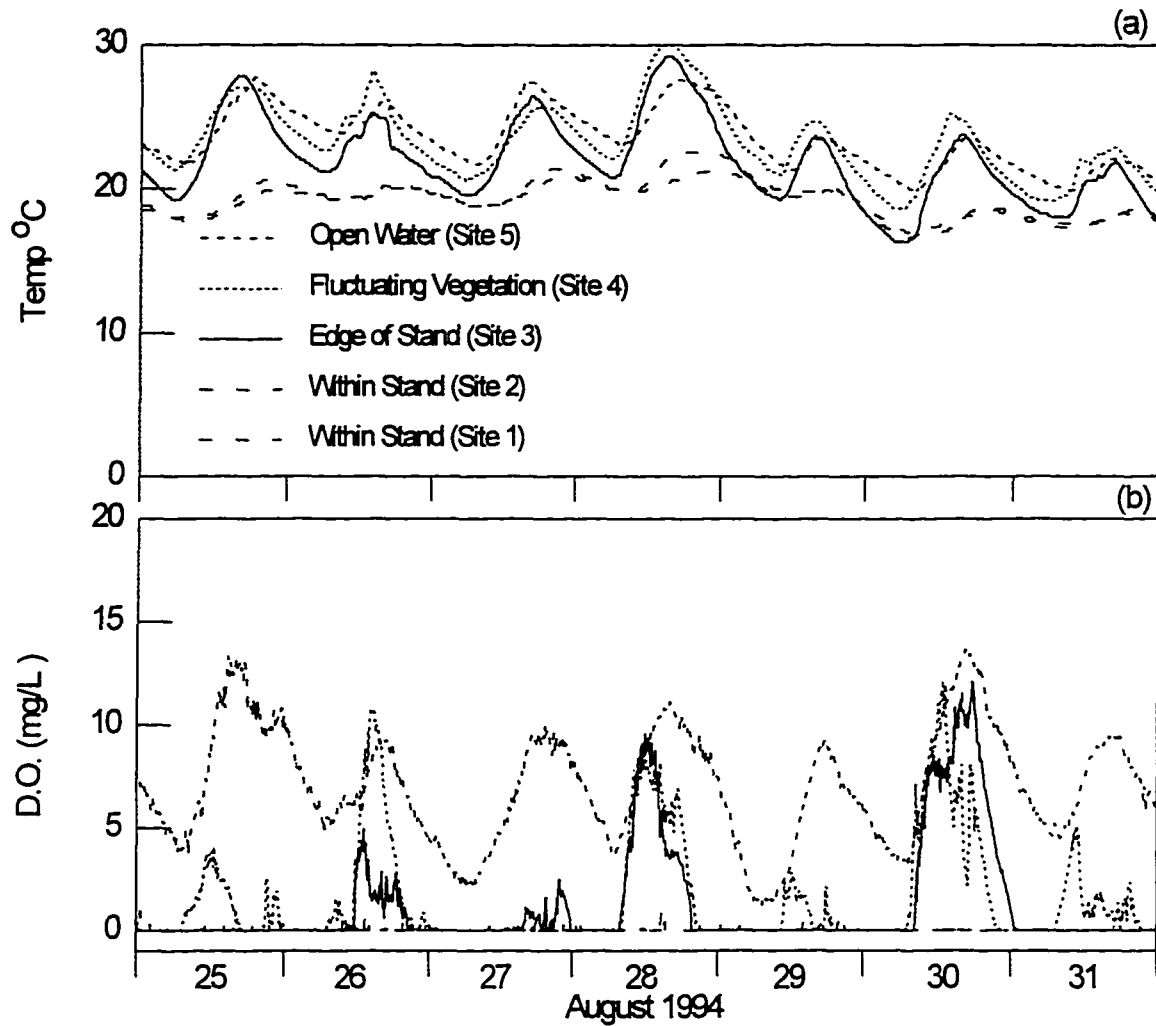


Figure 2. Diurnal variations in water column (a) temperature and (b) D.O. within an emergent stand (sites 1-2), at the edge of an emergent stand (sites 3-4), and in open water (site 5). D.O. was nearly always below 0.2 mg/L at sites 1 and 2.

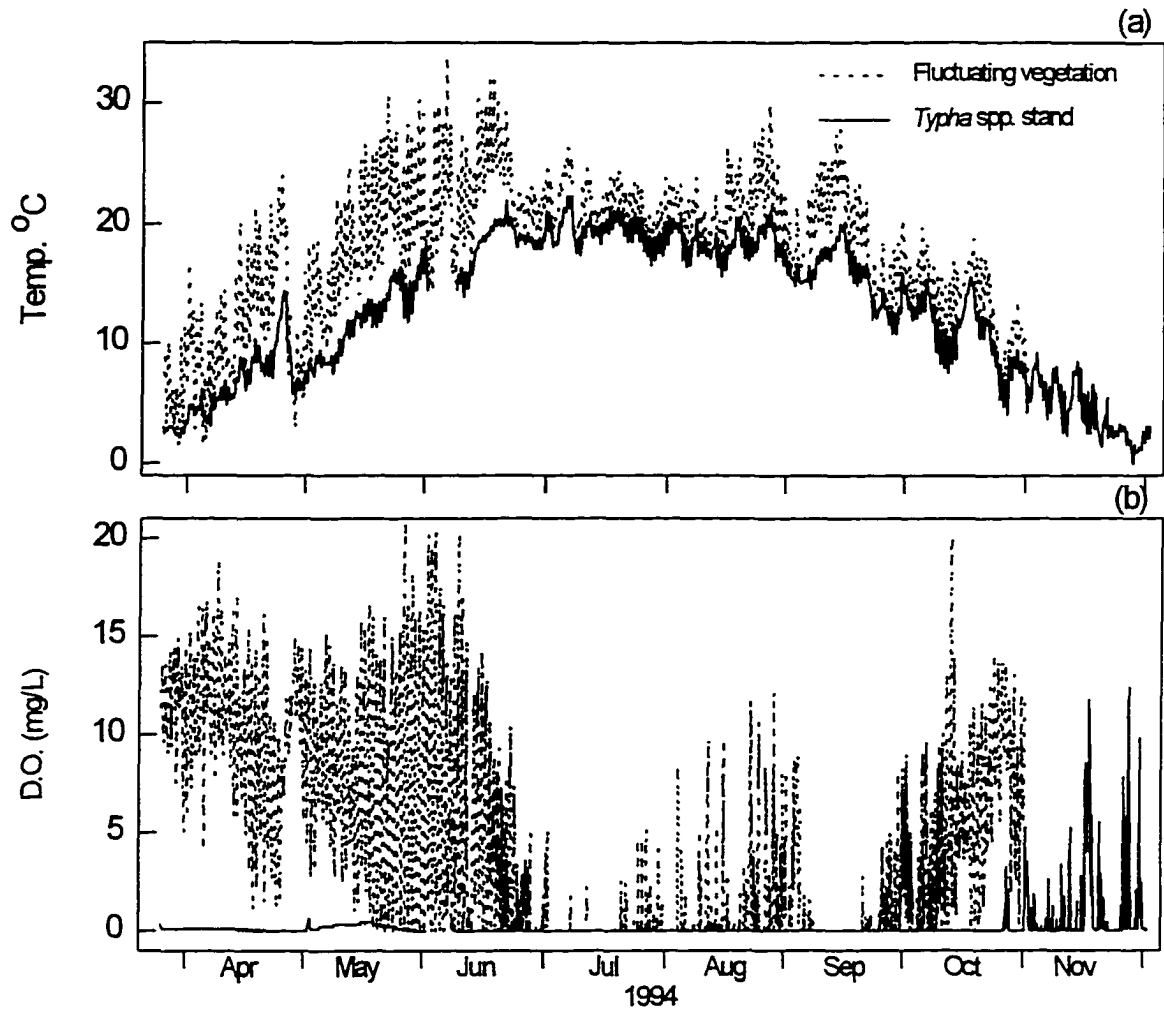


Figure 3. Long-term (a) temperature and (b) D.O. changes at site 1 (*Typha* spp. stand) and site 4 (fluctuating vegetation). Site 4 was in open water through June → *Scirpus fluviatilis* stand or stand edge July through September → open water after September. Due to monitor failure, there are no data for site 4 for November.

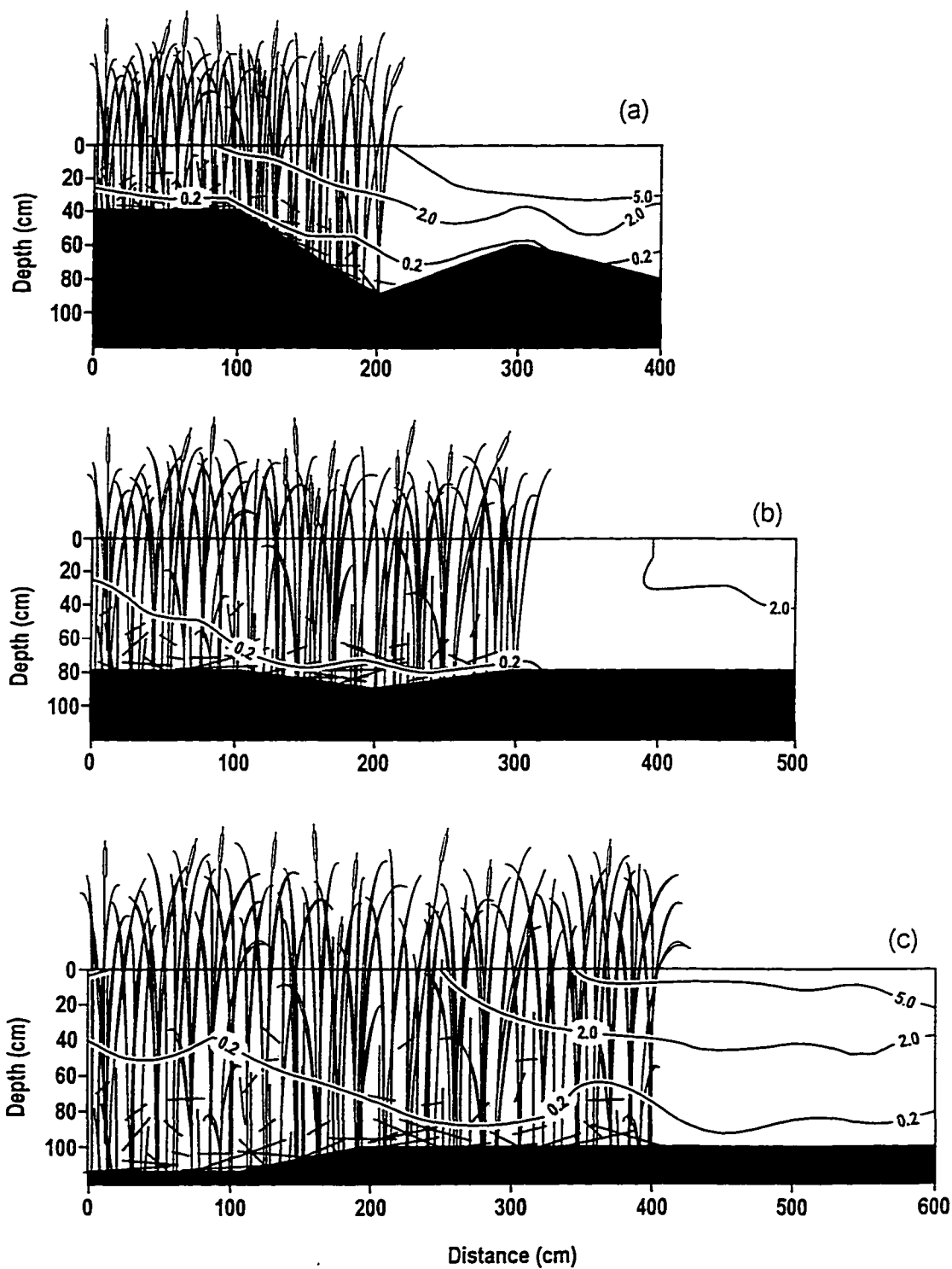


Figure 4. Changes in D.O. isopleths (mg/L) along horizontal gradients from areas of emergent vegetation to open water areas during August 1994. Vegetation and litter present at these sites was *Typha* spp. The transects (b) and (c) also had lemnids present among the emergent plants and open water areas.

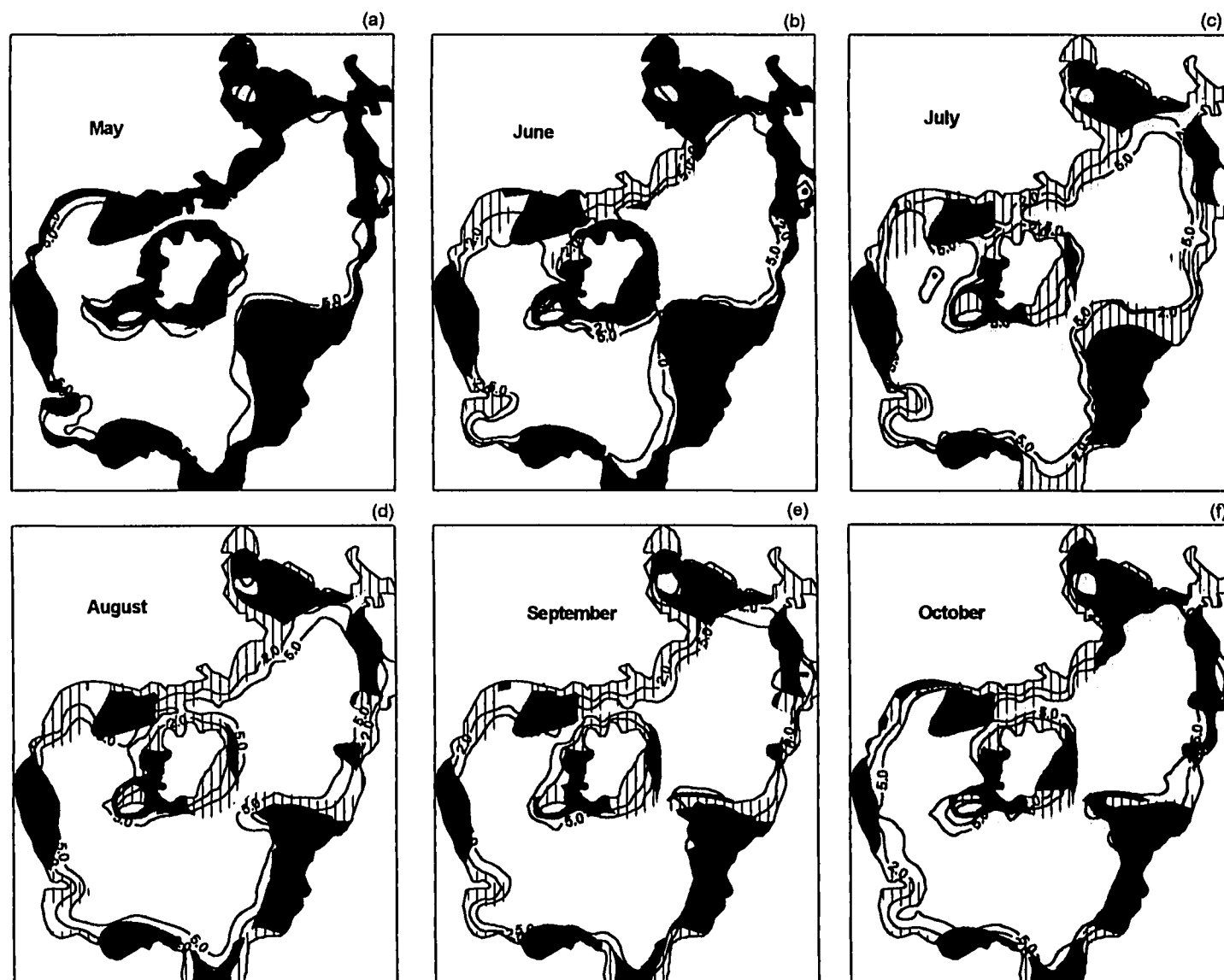


Figure 5. Monthly D.O. isopleths (mg/L) and areas of emergent vegetation in Goose Lake Marsh recorded during 1994. Vertical hatches indicate live emergent plants (predominantly *Typha* spp.), dark grey areas represent dead, emergent macrophytes and light grey areas indicate open water areas.

CHAPTER 3. PATTERNS OF AQUATIC AEROBIC METABOLISM AND METHANOGENESIS IN A PRAIRIE POTHOLE WETLAND

A paper to be submitted to the journal *Limnology and Oceanography*

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Abstract

In a prairie pothole wetland, diurnal oxygen curve analyses were used to determine water column photosynthesis and respiration in open water, transitional, and emergent vegetation zones, while CH₄ flux due to diffusion and ebullition was measured at the air/water interface in these zones. Dissolved O₂, temperature, light, dissolved CH₄, plant densities, and litter densities were measured in transects from open water to emergent vegetation zones. Water column temperature, light penetration, photosynthesis, and aerobic respiration rates were much greater in open water than in emergent vegetation zones. CH₄ concentrations in the water column were much lower in open water than in emergent vegetation zones, but CH₄ flux rates were similar. As a result, methanogenesis is a relatively more important carbon pathway in emergent vegetation than in open water zones. A summary of the carbon budget of different zones suggests that the emergent zone typically has production in excess of consumption while the open water zone may have greater consumption than production. Obviously, organic matter to support the open water zone's consumption is due to production during previous years and possibly to imports from the emergent vegetation zone.

Introduction

Emergent macrophytes are likely to affect major aspects of carbon metabolism and biogeochemistry of wetlands. The transfer of oxygen to the rhizosphere via emergent macrophytes is one example. In addition, macrophytes may affect many aspects of the physical and chemical characteristics of the water column (Ulehlova and Pribil 1978; Reddy 1981; Bican et al. 1986; Murkin et al. 1992; Hamilton et al. 1995). Aquatic plants can increase dissolved O₂ in the water column directly through photosynthesis and indirectly by providing substratum for periphytic algae. They can also decrease dissolved O₂ concentrations by shading the water column (which reduces photosynthesis and heat transfer), by their own respiration, by contributing organic matter and substratum for bacteria, as well as by disrupting gas transfers across the air/water interface. In some cases, these alterations of the physical environment reduce dissolved O₂ concentrations to anaerobic levels (Lewis and Bender 1961; Ulehlova and Pribil 1978; Rose and Crumpton 1996).

Previously, we have reported very different dynamics of dissolved O₂ and temperature in different zones of a prairie pothole wetland (Rose and Crumpton 1996). Open water areas had diurnal O₂ changes of up to 10 mg L⁻¹ while vegetated areas consistently had dissolved O₂ below 1.0 mg L⁻¹. Temperatures were greater and diurnal temperature changes were greater in open water areas compared to vegetated areas. At least three habitat zones have been identified in Goose Lake Marsh based on patterns in vegetation and dissolved oxygen: (1) an emergent macrophyte zone providing significant submerged structure but with nearly or completely anoxic water, (2) a transition zone of sparse emergent macrophytes providing less structure but with more aerobic water, and (3) an open water zone with consistently aerobic water but with little submerged structure. To further explore the consequences of these dynamics, this study used both *Typha* spp.-dominated natural and experimental wetland systems to examine patterns of aquatic aerobic carbon metabolism and methanogenesis among areas with different plant structure levels.

Methods

Study sites—Goose Lake Marsh is a natural, 65 ha, semi-permanent, prairie pothole wetland located in central Iowa (42° 22' north latitude, 93° 30' west longitude) near the southern end of the prairie pothole region (van der Valk 1989). A base map of the marsh was constructed by digitizing the image from an aerial 35 mm slide taken in September, 1993 (Fig. 1). During April, 1995, the marsh's owners lowered the elevation of the dam resulting in an approximately 20 cm drop in the water level in an attempt to increase the extent of emergent vegetation (personal communications, George Clark, Ames, IA.). However, vegetation and dissolved oxygen patterns (measured as in Rose and Crumpton 1996) remained similar to the previous year with low dissolved oxygen concentrations associated with stands of emergent vegetation. The open water zone had submersed plants (primarily *Potamogeton* spp.) and water lilies (*Nuphar microphyllum* (Pers.) Fernald. and *Nymphaea tuberosa* Paine). During 1995, most of the live emergent plants were *Typha glauca* with occasional patches of *Typha angustifolia*; litter of dead plants in the emergent areas was mainly *Typha* spp. Before July, small floating plants (lemnids) including *Lemna minor*, *Spirodela polyrhiza*, *Lemna trisulca*, *Riccia fluitans*, and *Wolffia columbiana* were commonly growing on top of the plant litter of these areas (and scattered across the open water areas). After July, 1995 other plants started to grow there, rooted in the plant litter. This community was dominated by *Helianthus* sp., *Polygonum* sp., and *Scirpus validus* with plants reaching heights of up to 2 m.

Iowa State University's experimental wetland mesocosm facility is described in Crumpton et al. (1993). Briefly, the facility consists of 48 polyethylene tanks, 90 cm deep and 3.35 m in diameter (9 m² surface area). About 60 cm of wetland sediment were placed in the tanks, they were planted with *Typha glauca* Godr. rhizomes in 1989 and flooded. Each tank is individually valved, water is supplied through spray nozzles around the outer edge. Water levels are controlled by variable height stand pipes located in the center

of the tank. By 1994, plant density had reached 60-80 stems/m² (levels typical of field populations) and litter density was about 0.7 kg dry mass/m².

Field sampling—On six dates from 27 July to 26 August 1995, environmental and water quality parameters were measured along transects from near shore, vegetated areas to open water areas using a canoe, separate transects were used on each date (Fig. 1). Transect lengths ranged from 6 to 20 m. Dissolved O₂, temperature, and light measurements were made at 0.5-1.0 m horizontal and 0.1 m vertical intervals. Dissolved O₂ and temperature data were measured *in situ* using a YSI model 51B meter. Light levels within the water column were recorded at each location using an underwater quantum sensor (model LI-192S, LI-COR, Inc., Lincoln, Nebraska, USA). Interpolations were made with a Kriging method. Duplicate lemnid (small free-floating plants), plant shoot densities, and plant litter densities were collected at five to nine locations along the transects. Lemnid samples were collected by inserting a 15 cm diameter acrylic cylinder into the water, covering the bottom of the cylinder below the plants, then transferring the contents to a plastic bag. In the laboratory, the plants were freeze dried and weighed. Live and dead shoot densities were measured using 0.1 m² quadrats. Litter samples were collected by inserting a 60 cm high, 37.5 cm diameter (0.1 m²) cylinder into the water column and removing all dead plant material above the sediment (including aerial parts), cutting the litter at the edge of the cylinder where necessary. Water depths were recorded at each site so that litter densities could be calculated on both areal (kg m⁻²) and volumetric (kg m⁻³) bases. Litter samples were placed in plastic bags, transported back to the lab, oven-dried at 65° C to a constant mass in paper bags, and weighed.

Dissolved oxygen and temperature monitoring—During 1995 and 1996, continuous water quality monitors (AQUA 2000 prototypes, Biodevices Inc., Ames, Iowa, USA) recorded temperature and dissolved O₂ at 15 cm depth every 6 minutes at three sites (in emergent vegetation, transitional and open water zones) in the marsh (Fig. 1). During part of July and August 1996, additional monitors were placed near the bottom (35-40 cm depth) of the water column at the open water and emergent vegetation sites. Prior to deployment, temperature sensors were calibrated using a two-point calibration between 4 °C and 35 °C. Dissolved O₂ sensors were calibrated using air-saturated water with the O₂ saturation value calculated using the formula of Mortimer (1981). At approximately two-week intervals, monitors were serviced and dissolved O₂ and temperature reference values were collected using a field meter to check for sensor drift, which were < 5% and therefore were not corrected.

Calculation of aquatic aerobic metabolic rates—Diurnal oxygen patterns were analyzed to provide estimates of production and respiration (Odom 1956) using the first derivative of the dissolved O₂ concentration based on a moving least-squares convolutes procedure (Savitzky and Golay 1964). Net community production (NCP) in g O₂ m⁻³ h⁻¹ was calculated using the following equation:

$$\text{NCP} = (dC/dt - D) \quad (1)$$

where dC/dt was the rate of change in dissolved O_2 in $g\ O_2\ m^{-3}\ h^{-1}$ and D is the diffusion rate in $g\ O_2\ m^{-3}\ h^{-1}$ and is estimated as described below. The community respiration (CR) rate was estimated from nighttime respiration rates based on the following equation:

$$CR = (dC/dt - D) \quad (2)$$

where CR is in $g\ O_2\ m^{-3}\ h^{-1}$. Gross primary production (GPP) was calculated from the following equation:

$$GPP = NCP - CR \quad (3)$$

which assumes that daytime and nighttime respiration rates are equal. Rates of NCP and CR were converted to $g\ C\ m^{-3}\ h^{-1}$ assuming a photosynthetic quotient of 1.2 and a respiratory quotient of 1.0 (Strickland and Parsons 1972). Areal rates of NCP and CR were calculated from volumetric rates and the depth of each site.

Estimating rates of photosynthesis, aerobic respiration, and methane flux from water may depend on measurements or assumptions about the rate at which O_2 or CH_4 crosses the air/water interface (Owens 1974). The thickness of stagnant boundary layers (SBL) at the air/water interface (along with gas concentrations and temperature) controls the diffusion rates of gases into and out of the water column (Liss and Slater 1974; Broecker and Peng 1974, 1982). Diffusion of oxygen was estimated as follows:

$$D = K_t (C_s - C)/z \quad (4)$$

where K_t is the flux rate constant in $m\ h^{-1}$, C_s is dissolved O_2 at saturation in $g\ O_2\ m^{-3}$ (Mortimer 1981), C is the mean dissolved O_2 in $g\ O_2\ m^{-3}$ over the 6 minute time period dt and z is the depth in meters (Owens 1974). K_t was calculated as follows:

$$K_t = D_t/SBL \quad (5)$$

where D_t is the temperature-dependent diffusivity of the gas in water is ($length^2\ time^{-1}$) and SBL units are length. D_t for dissolved O_2 in water at different temperatures were calculated using the formulas of Broecker and Peng (1974). K_t values for open water areas are better studied than areas with a matrix of *Typha* spp. litter above, at and below the water surface. Therefore, we concentrated on measuring K_t in the emergent vegetation. The SBL were measured in the experimental wetland mesocosms using a Clark-style oxygen micro electrode with an 80 μm tip (Diamond General Development Corp., Ann Arbor, MI, USA). The electrode was lowered into the water with a micromanipulator at 125 μm intervals, and values recorded after 30 seconds was allowed for readings to stabilize. The boundary layer thickness was from the top of the water column to where the dissolved oxygen values were no longer changing (mixed layer). SBL thicknesses in the mesocosms were $1700 \pm 600\ \mu m$. For open water areas of Goose Lake Marsh, a K value of $1.5\ cm\ h^{-1}$ for O_2 (Owens 1974) was used. In the emergent zone, a mean K value of $0.5\ cm\ h^{-1}$ was used. For transitional areas, the mean of the open water and emergent K values ($1.0\ cm\ h^{-1}$) was used.

Methane flux—Methane dissolved in the water was measured at each end and at the midpoints of the transects; duplicate samples were collected near the top, midpoint, and bottom of the water column at each point. From 5-10 mL of water was drawn into a 10-mL syringe with an 18-gauge needle, then injected into an

evacuated 20-mL gas chromatography (GC) vial through a butyl-rubber septum with the procedure taking place under water to prevent air contamination. Methane concentrations in the vial were corrected for gas partitioning between the head space and water (Stumm and Morgan 1981). Methane fluxes from the surface were determined near each end and at the midpoint of the transects, duplicate samples for flux due to diffusion and to diffusion plus bubbles were collected. Samples to determine flux rates due to diffusion were collected by inverting a 20-mL GC vial on the water's surface (Fig. 2). The vials were held by a foam flotation device equipped with a wire and aluminum foil shield to prevent collection of bubbles. Flux rates due to diffusion and bubbles were collected by inverting a GC vial held by a foam float and inserting a 10 cm funnel—which increased the bubbles collection area (Fig. 2). Bubble fluxes were estimated by difference. These rates were scaled by estimating the fraction of free surface where maximum flux could take place since water surface cover such as *Lemna* spp. serves as at least a partial barrier to gas diffusion (Morris and Barker 1977). Methane standard (Scott Specialty gases, Wakefield, MA, USA) and sample concentrations were measured on a Tremetrics 540 gas chromatograph (helium carrier) configured for head space sampling, a 3.05-m x 3.18-mm stainless steel Haysep D column (at 80 °C), and a Tremetrics 706 discharge ionization detector.

Mesocosm experiments—During September, 1995, plants and litter were physically removed from three mesocosms to create experimental units similar to the open water areas of prairie pothole marshes. In October 1995, chl-*a* in mesocosm water samples were analyzed spectrophotometrically (APHA, 1995) and analyzed by ANOVA. During 1996, the dissolved O₂ and temperature patterns were recorded in the three open water and three normal (emergent vegetation) mesocosms using the continuous water quality monitors.

In October, 1994, effects of plant litter quantity on dissolved O₂, temperature, and methane were studied using polyethylene cylinders 90-cm tall, 75-cm diameter (0.44-m²); the cylinders were inserted into the sediment to a depth of about 15-20-cm to isolate a water column of about 110-L. The following treatments were used: (1) normal litter levels remained in the enclosures, (2) half the normal litter level was removed, (3) all the litter was removed, and (4) normal litter level was placed in the enclosure after a plastic barrier was placed on the bottom of the cylinder to isolate the sediment. One cylinder of each treatment was randomly placed in three mesocosms resulting in a randomized block design. After a two week period to allow disturbance effects to be minimized, water samples to determine methane concentrations were taken as described above. Duplicate samples were taken from each enclosure on 24 October, triplicate samples on 26 October. A K value of 0.25 cm h⁻¹ for CH₄ was calculated from the measured stagnant boundary layer and the diffusivity of CH₄ (Broecker and Peng 1974) and was used to model the flux from treatments with litter. A K of 1.2 cm h⁻¹ for CH₄ (temperature adjusted value based on Sebach et al. (1983) value of 1.7 cm h⁻¹ at 20 °C) was used for the sediment-only treatment. Daytime temperature and dissolved O₂ were taken using a field meter. After water sampling, litter was removed, oven-dried at 65° C to a constant mass in paper bags, and

weighed. Data were analyzed by ANOVA (with contrasts compared by least significant differences at $p < 0.05$).

Results

Physical and chemical conditions—In comparison to open water areas, emergent vegetation areas had lower light, lower temperatures, lower concentrations of dissolved O_2 , and higher concentrations of dissolved CH_4 (Figs. 3-8). Light penetrated deeper into the water column in open water areas, but in the emergent macrophyte zone light was blocked by above water plants and litter at or near the top of the water. Temperatures were up to 5 °C lower in emergent macrophyte areas than in open water areas. Dissolved O_2 ranged from anoxia in emergent macrophyte areas to supersaturation in open water areas. Methane concentrations were greater in emergent macrophyte areas than in open water areas. In most cases, there were more dead *Typha* spp. stalks than living. Lemnid and litter density was higher in emergent macrophyte zones than in open water zones. Continuous monitors revealed that temperatures were generally higher and diurnal temperature changes were greater at the open water site than at the emergent vegetation site during June and throughout the 1995 and 1996 growing seasons. Diurnal changes in dissolved O_2 of up to 20 mg L^{-1} were recorded at the open water site while anoxic conditions prevailed at the emergent vegetation site (Fig. 9). Measurements during July 1996 revealed that temperature and dissolved O_2 patterns at the bottom of the water column were similar to those of the upper emergent site with only the upper part of the water column at the open water site having any measurable dissolved O_2 (Fig. 10).

Removing vegetation from mesocosms to simulate open water conditions resulted in diurnal oxygen and temperature patterns similar to those found in Goose Lake Marsh (Fig. 11). Open water mesocosms had warmer water, higher dissolved O_2 , and larger diurnal changes in those parameters than mesocosms with emergent vegetation. Algal growth was apparent in the open water mesocosms where phytoplankton chl-*a* concentrations reached up to 362 ± 93 $\mu g/L$ (mean \pm S.D.) compared to 34 ± 11 $\mu g/L$ in the normal mesocosms during October 1995. *Oedogonium* sp. was the dominant alga at that time. In addition, one of the open water mesocosms developed a population of *Potamogeton pectinatus* during 1996. In Fig. 11, the open water mesocosm with lower dissolved O_2 values was an algal-dominated mesocosm.

Patterns in vegetation and aquatic metabolism—The diurnal oxygen curve analyses indicated that the emergent zone had no measurable water column GPP and had very low rates of CR for a period in August 1995 (Fig. 12). In contrast, the highest photosynthetic rates were in the open water zone. The transitional zone had intermediate photosynthetic rates, but the highest mean respiration rates during the time periods available for data analyses. Methane fluxes among zones were not significantly different as summarized in Table 1. Though caution was taken, disturbing the sediments while sampling from the canoe may cause release of gas bubbles or wind may play a role in releasing bubbles from the sediment.

Mesocosm plant litter manipulation experiments indicated that all treatments had effects on methane levels and the sediment-only (open water) treatment had significantly higher dissolved O_2 (Table 2). The plant litter densities were $2.2 \pm 1.2 \text{ kg m}^{-2}$ (mean \pm S.D.). Diffusive methane fluxes from the normal and half-litter treatments were generally higher than the other treatments. The litter-only and sediment-only treatments had flux rates about 40-60% of the normal litter rate.

Discussion

Many factors are responsible for the different carbon flow pathways in the water column of different zones in this wetland, including the physical effects of plant structure. The combination of litter, emergent plants, and lemnids lead to shading of the water column and reduce wind effects on the air-water interface (resulting in thicker SBLs). Each of those physical processes also affects dissolved O_2 and temperature, as demonstrated by the transect data (Figs. 3-8). Anaerobic conditions exist throughout the water column in the emergent zone. Most of the water column in the open water zone is aerobic during the day while near-sediment water is anaerobic (Figs. 9 and 10). As a result, in the open water and transitional zones, both aerobic respiration and methanogenesis are important metabolic pathways. In contrast, methanogenesis is the dominant carbon flow pathway in the emergent zone. The transitional zone's carbon pathways are similar to the open water zone during the time analyzed. However, at other times, the dissolved O_2 and temperature patterns found in transitional zone has shown greater resemblance to the patterns in the emergent zone (Rose and Crumpton 1996 and unpublished data). This is likely due to the spatial (Figs. 3-8) and temporal variability of plant cover during the growing season (Rose and Crumpton 1996) and the subsequent effect on physical processes in the transitional zone.

Mesocosm studies confirm the role of emergent plants in regulating the temperature and dissolved O_2 of the water column. Creating open water mesocosms resulted in diurnal changes in dissolved O_2 and temperature similar to those found in the open water zone while the vegetated mesocosms had diurnal changes similar to the emergent zone of Goose Lake Marsh (Figs. 9-11). The litter and sediment manipulations also produced methane concentrations and diffusive methane flux similar to the patterns found in different zones of Goose Lake Marsh. Those results also indicate that methanogenesis can take place in an anaerobic water column as well as the sediment. Altogether, the mesocosm results support the idea that as emergent vegetation communities develop and plant litter accumulates, this biological community alters the physical environment and as a result affects microbial processes.

There were consistently great differences in dissolved CH_4 concentrations along the transects (Figs. 3-8). These differences were due to the balance among methanogenesis, methane oxidation, and the methane flux to the atmosphere. The elevated methane concentrations in the emergent zone are higher than those reported by many researchers, but are comparable to those previously reported for shallow, *Typha* sp.-

dominated wetlands in agricultural areas (Schipper and Reddy 1994). Other anaerobic pathways (such as denitrification) are likely to be limited by availability of terminal electron acceptors (in the absence of external inputs). Nitrate was not measurable in water column of any of the wetland zone during the 1994 growing season (Rose and Crumpton 1996). Despite CH_4 concentration differences along the transects (Figs. 3-8) the diffusive CH_4 flux rates were not different (Table 1) due to the thicker SBL and cover by litter and lemnids in the emergent zone. Other researchers have generally found higher methane flux rates in vegetated areas of wetlands than in open water areas (Delaune et al. 1983; Bartlett et al. 1988; Wilson et al. 1989). Methane flux through plants (which we did not measure in this study) would be responsible for some of differences among different wetland areas. Bartlett et al. (1988) found no significant differences for air/water diffusive flux among vegetated and open water habitats. Some studies have found greater ebullition in open water areas (Chanton et al. 1989; Chanton and Dacey 1991), other studies have found greater ebullition in macrophyte covered areas (Bartlett et al. 1988; Devol et al. 1988). The net CH_4 flux rates measured in Goose Lake Marsh probably represent the seasonal peak rates. Other researchers have found that methane flux peaks in the middle of the growing season in wetlands (Schutz et al. 1991). There could be diurnal methane flux patterns in this system especially in the open water zone where diurnal temperature and dissolved O_2 changes are most dramatic (Figs. 9-10). Diurnal measurements were not made. However, Fig. 10 shows that near the sediment (where much of the methanogenesis would take place) had very small diurnal temperature changes and no dissolved O_2 changes, so diurnal CH_4 flux rates may not vary dramatically.

In some aquatic systems, much of the methane generated is consumed by methane oxidation at the aerobic/anaerobic interface at the surface of the sediment (Rudd and Taylor 1980) or in the rhizosphere of emergent macrophytes (Gerard and Chanton 1993). In Goose Lake Marsh, the sediment and part or all of the water column is anaerobic (Fig. 10). Other researchers have noted that oxygen-depleted water restricts methane oxidation (Lidstrom and Somers 1984; Yavitt et al. 1992). Methane oxidation of gas dissolved in bubbles is unlikely in this shallow system since it has been shown that bubbles lost < 10% of their methane while transversing a 10m water column (Hesslein 1976; Robertson 1979). In addition to diffusion and ebullition, another important CH_4 flux pathway is through emergent aquatic plants. In many systems, it is the dominant CH_4 flux pathway (Cicerone and Oremland 1988; Chanton and Dacey 1991; Schutz et al. 1991; Schipper and Reddy 1994). But, during this study in this system, there was a predominance of dead stalks (Figs. 1 and 3-8), most of which were flooded (personal observation) probably due to high water in the spring and during previous years. The flooded stalks would not be gas conduits for methane out of the sediment nor oxygen into the rhizosphere. As a result, both plant-mediated methane flux and methane oxidation would have been minor contributors to the methane budget in Goose Lake Marsh during this study and therefore the measured methane fluxes should be a reasonable estimate of methanogenesis.

Combining analyses of GPP, aerobic respiration, and methanogenesis reveals intriguing patterns in the relative importance of different metabolic pathways (Table 3). Microbial photosynthesis and respiration were much more important pathways in the transitional and open water zone than in the emergent zone. The GPP rates for the open water and transitional zones are within the expected range for eutrophic aquatic systems (Wetzel 1983). If just aerobic respiration rates were considered, the transitional and open water zones would be considered autotrophic, but were clearly heterotrophic when methanogenesis was also considered. A complete carbon budget must obviously include production from free-floating plants (which may shift position among zones due to wind) and emergent plants (both above and below ground production). Prairie pothole wetlands undergo dramatic, often cyclic vegetation changes, with the period of the cycle typically ranging from 5-20 years in response to water-level fluctuations and other environmental factors (Weller and Spatcher 1965; van der Valk and Davis 1978). During this cycle, total annual shoot production may change 18-fold; net average above ground primary production of emergent vegetation may be as high as $23 \text{ g dry mass m}^{-2} \text{ d}^{-1}$ (van der Valk and Davis 1978). Assuming dry biomass values were roughly 45% carbon (Westlake 1965) this represents over $10 \text{ g C m}^{-2} \text{ d}^{-1}$. The productivity of emergent vegetation and their physical effects on the water column likely result in the the emergent zone being a net producer and storer of carbon. While the emergent zone's productivity was relatively low during this study period due to low densities of living plants, it had a large reserve of organic material in the form of litter (due to past production) relative to the other zones (Figs. 1 and 3-8). Once those areas become open water, the greater potential aerobic respiration rates and continued decomposition due to methanogenesis in the sediment combine to allow the open water zones to be net carbon consumers. Aerial photographs show that the much of the area that was the open water zone in 1995 was covered with emergent vegetation from 1985-1992. The relative importance of the metabolic processes associated with the rhizosphere would also vary during the cycle and likely be most important when emergent vegetation productivity is high and least important in the open water zone. This cycle has been well documented in Goose Lake Marsh (Weller and Spatcher 1965; Roosa 1981).

As emergent plant stands develop, alterations in the physical and chemical environment of the bulk water phase take place. For example, in 1990 when the wetland mesocosms were newly established, diurnal dissolved O_2 and temperature patterns were similar to those found in the open water zone of Goose Lake Marsh. Over the years, *Typha x glauca* shoot densities have increased and litter has accumulated. During 1991, the diurnal dissolved O_2 and temperature patterns were similar to the patterns found in the transitional zone. During 1993, the dissolved O_2 and temperature were similar to the emergent zone of Goose Lake Marsh (Crumpton et al., in prep.). It may be assumed that an accumulation of several growing seasons of plant litter may be necessary to create anaerobic conditions in wetlands. This could be an important pattern in restored and created wetlands.

This study deals with a small part of the carbon cycle. Yet, the results suggest that food webs, bioenergetics, and biogeochemical cycles should vary spatially and temporally within wetlands. Anaerobic metabolic pathways are less efficient than aerobic respiration, resulting in lower bacterial growth yield and generally lower ratios of nutrient assimilation relative to mineralization. As a result, assimilation is a less effective nutrient sink under anaerobic conditions and nutrients (such as NH_4^+) tend to accumulate (Gale and Gilmour 1988). Anaerobic conditions can also affect other nutrient sinks including chemical complexation of PO_4^{3-} and “coupled” reactions such as nitrification-denitrification. To better understand the long-term dynamics of aerobic and anaerobic metabolism in prairie pothole wetlands, studies over additional systems and additional stages will be needed. Experiments using mesocosms may allow scientists to better study the dominant microbial processes at different stages of the prairie pothole cycle. Either directly or indirectly, vegetation dynamics are likely to control many of the complex biogeochemical transformations in wetlands.

Acknowledgments

This study was funded in part by the United States Environmental Protection Agency Cooperative Agreement # CR 820078 and by a USDA National Needs Fellowship in Water Sciences supporting C. Rose's dissertation work. We thank Marley Ayres, Steve Fisher, Eric Scherff, and Laura Wendling for field assistance. We thank Tim Parkin for assistance with methane analyses. We thank Gary Atchison, James Baker, and Arnold van der Valk for their comments on previous drafts. We thank the owners of Goose Lake Marsh for allowing us access.

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Table 1. Comparison of methane flux ($\text{mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$) in different wetland zones. Data are means from all days available during July and August 1995. Different superscripted letters indicate significant differences among zones at $p < 0.05$ after accounting for date effects. Date effects were significant on several dates for diffusion, but not for bubbles.

	Zone			
	Emergent	Transitional	Open Water	MSE
Diffusion	25	34	37	385
Bubbles	124	98	72	3238

Table 2. Mean values for various parameters in wetland mesocosms. Different superscripted letters indicate differences among treatments at $p < 0.05$ after accounting for mesocosm effects.

Parameter	Treatments				MSE
	Normal litter and sediment	Half litter and sediment	Litter only	Sediment only (open water)	
Temperature (°C)	5.8 ^a	7.2 ^a	6.0 ^a	7.2 ^a	0.6
Dissolved O ₂ (mg L ⁻¹)	0.4 ^a	0.6 ^a	0.3 ^a	1.2 ^b	0.04
24 October					
Methane (mg L ⁻¹)	2.6 ^a	2.3 ^a	1.3 ^b	0.3 ^c	0.4
Estimated Dissolved Methane Flux (mg m ⁻² h ⁻¹)	6.5 ^a	5.8 ^{ab}	3.9 ^{bc}	3.2 ^c	2.5
26 October					
Methane (mg L ⁻¹)	3.5 ^a	2.1 ^b	1.3 ^c	0.4 ^d	0.3
Estimated Dissolved Methane Flux (mg m ⁻² h ⁻¹)	8.6 ^a	5.5 ^b	3.3 ^c	4.5 ^{bc}	1.7

Table 3. Summary of water column metabolism ($\text{g C m}^{-2} \text{d}^{-1}$) in different wetland zones. Data are means from all days available during July and August, 1995.

	Emergent	Zone Transitional	Open Water
Gross Primary Productivity	0.0	3.5	3.9
Aerobic Respiration	0.15	2.4	2.3
Methanogenesis ($\text{CH}_4 + \text{CO}_2$)	5.4	4.8	3.9
Dates Analyzed	July 1-Aug. 31	Aug. 19-Aug. 31	July 1-Aug. 10 Aug. 17-Aug. 31

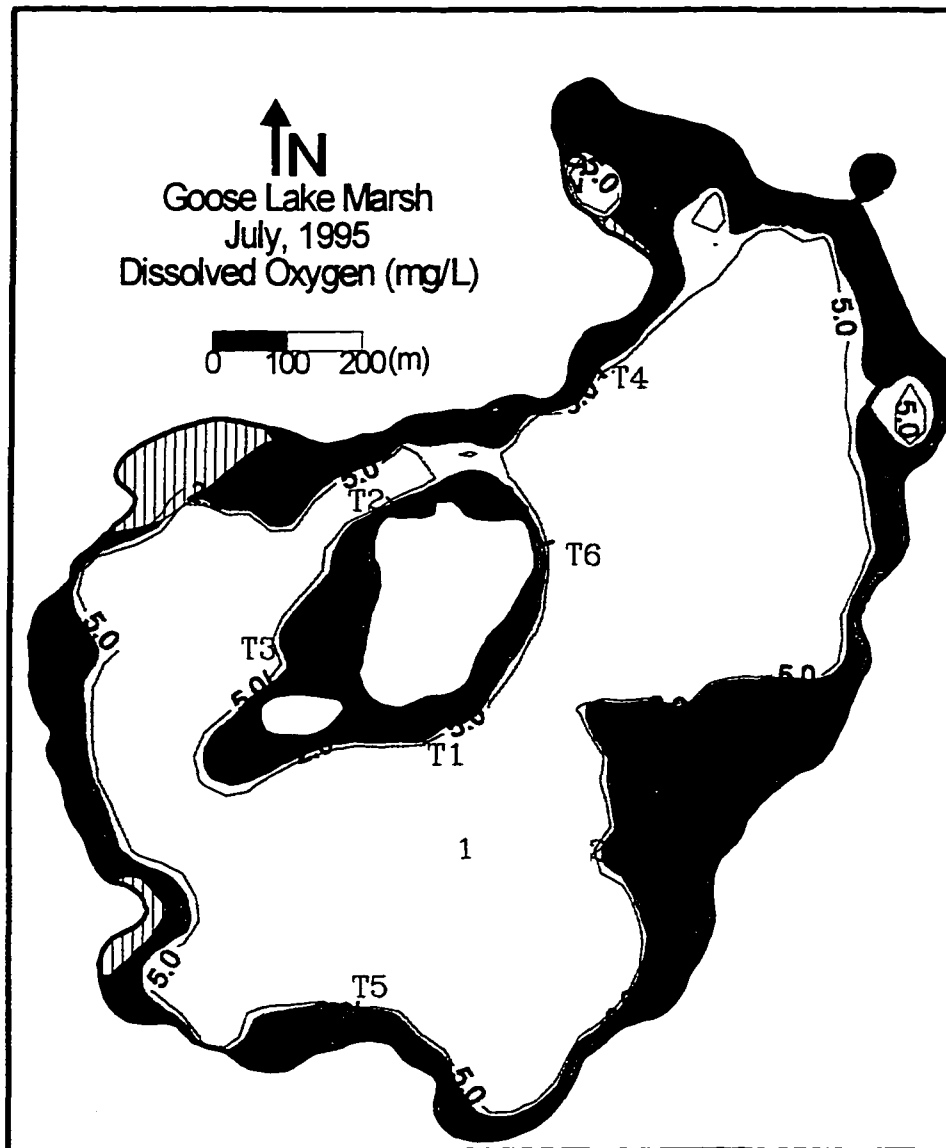


Fig. 1. Vegetation patterns in Goose Lake Marsh recorded during July 1995. Vertical hatches indicate live emergent plants (predominantly *Typha* spp.), dark grey areas represent dead, emergent macrophytes, and the light grey areas indicate open water areas. Locations of sampling transect are marked by (T1, T2 etc.), and the locations continuous dissolved oxygen and temperature are marked by numbers (1, 2, 3).

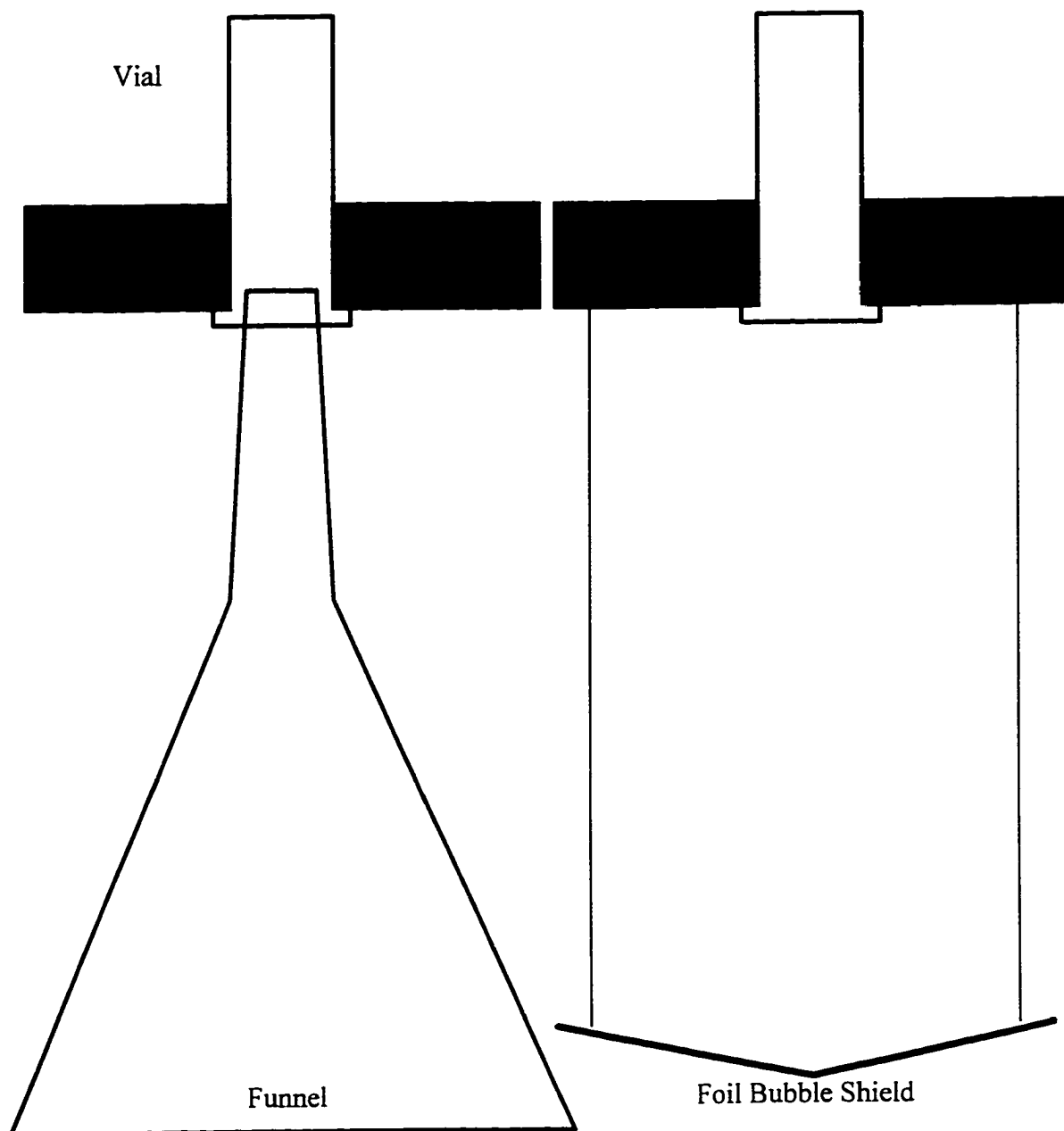


Fig. 2. Methane sampling apparatus. GC vial with funnel captured gas flux due to both bubbles and diffusion while the shield on the left prevented bubbles from entering the second vial.

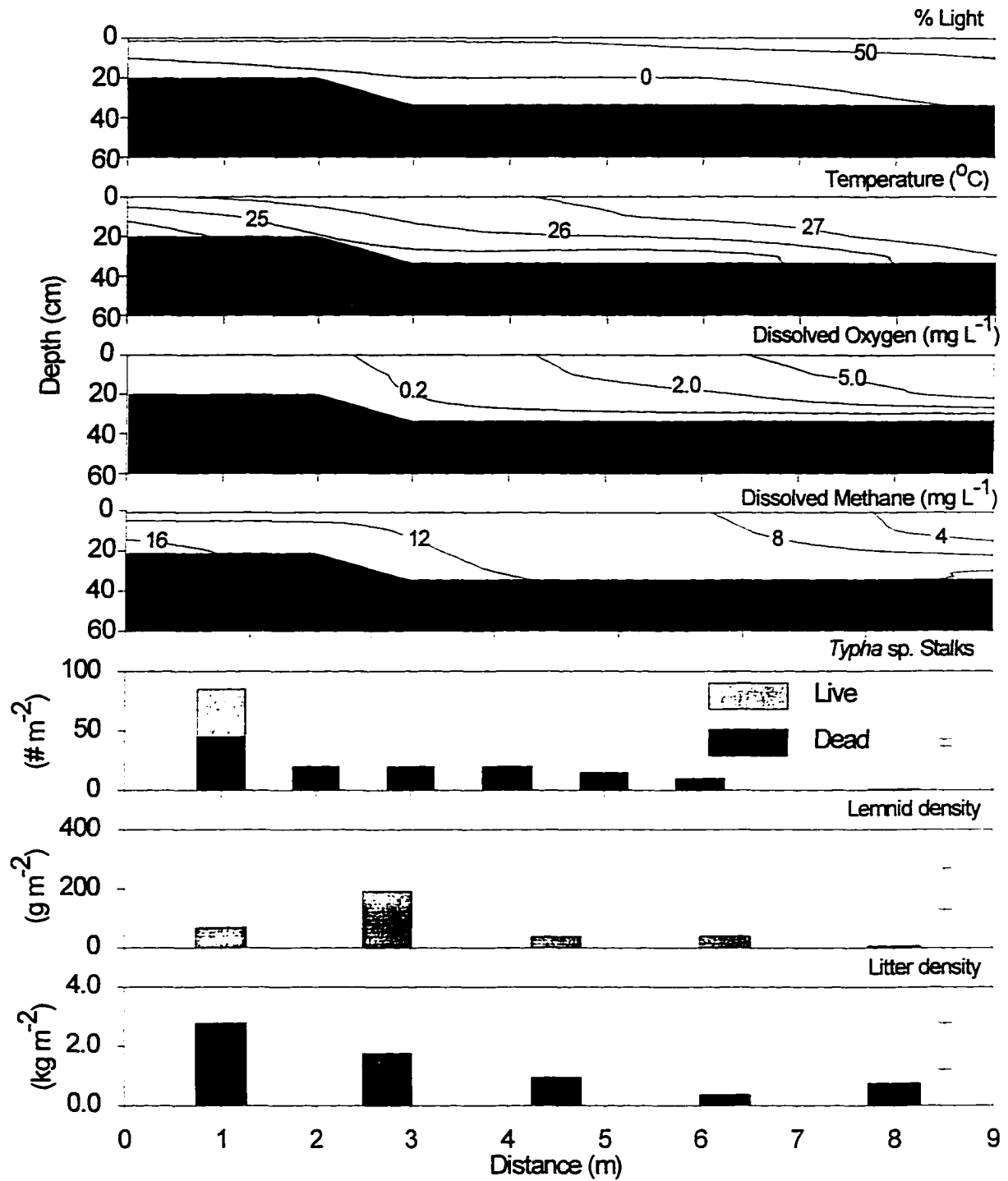


Fig. 3. Physical and chemical parameters along transect 1 (July 27, 1995). Error bars represent the least significant differences. Black areas on upper isopleth graphs represent sediment.

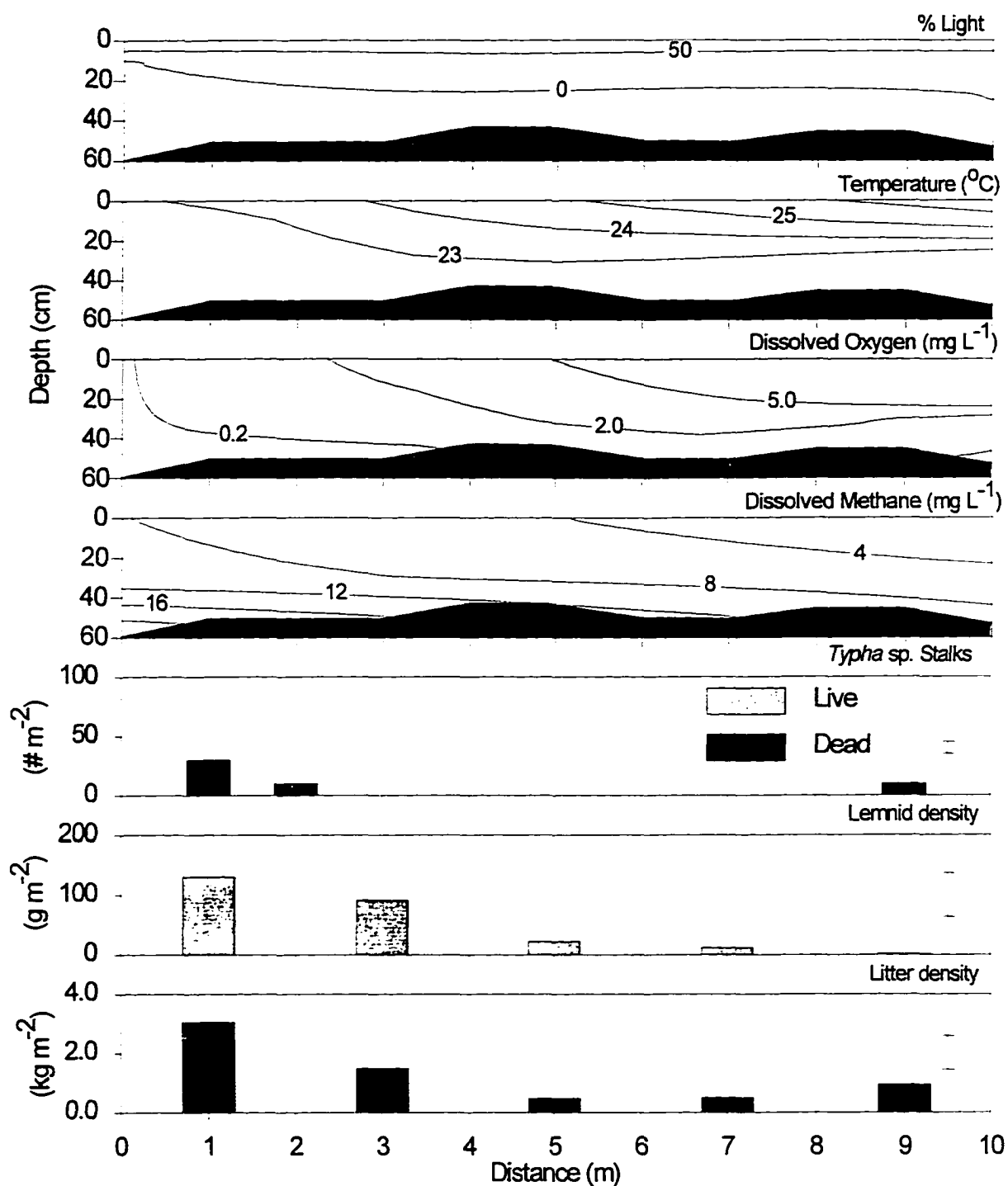


Fig. 4. Physical and chemical parameters along transect 2 (August 1, 1995). Error bars represent the least significant differences. Black areas on upper isopleth graphs represent sediment.

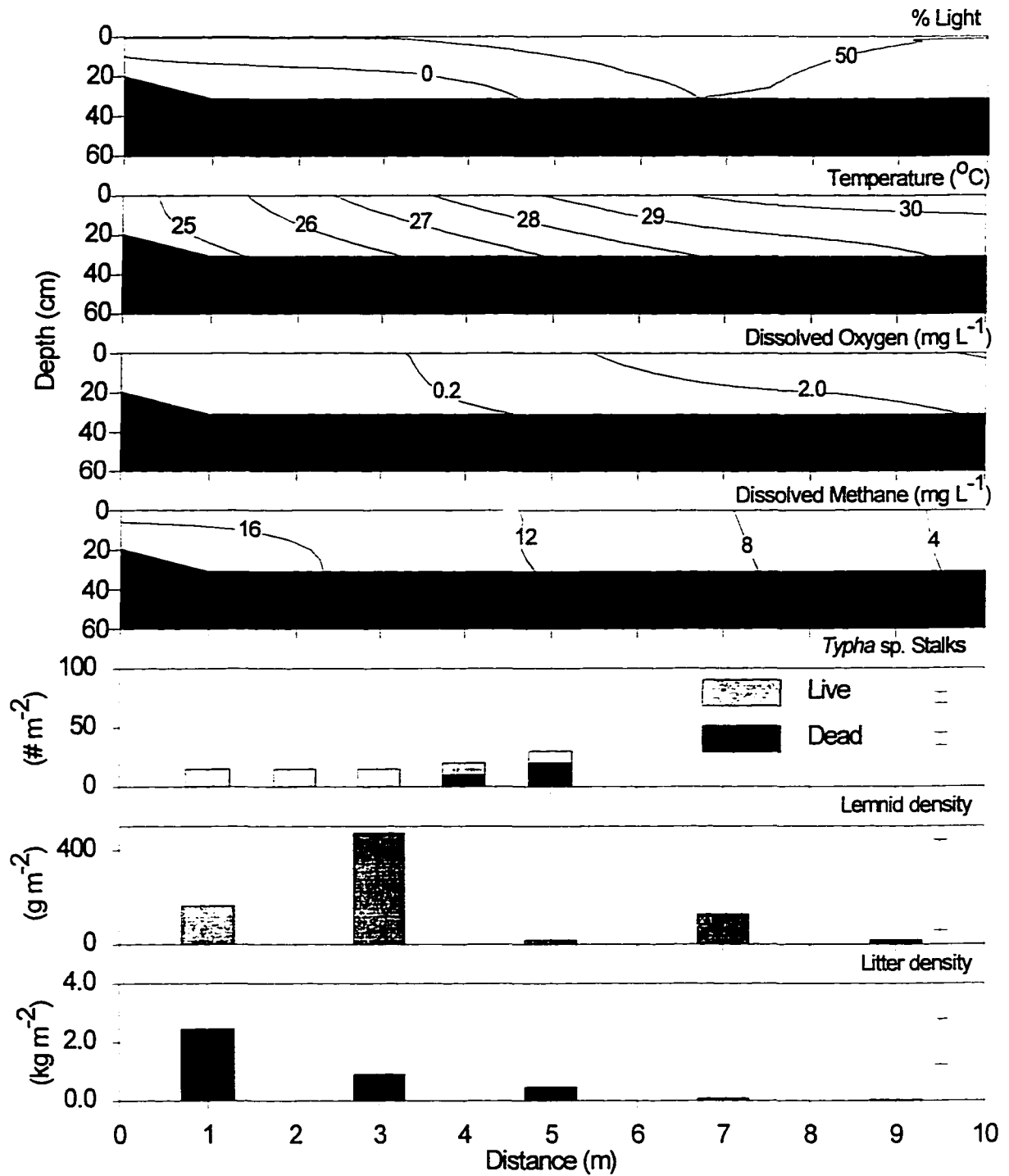


Fig. 5. Physical and chemical parameters along transect 3 (August 8, 1995). Error bars represent the least significant differences. Black areas on upper isopleth graphs represent sediment.

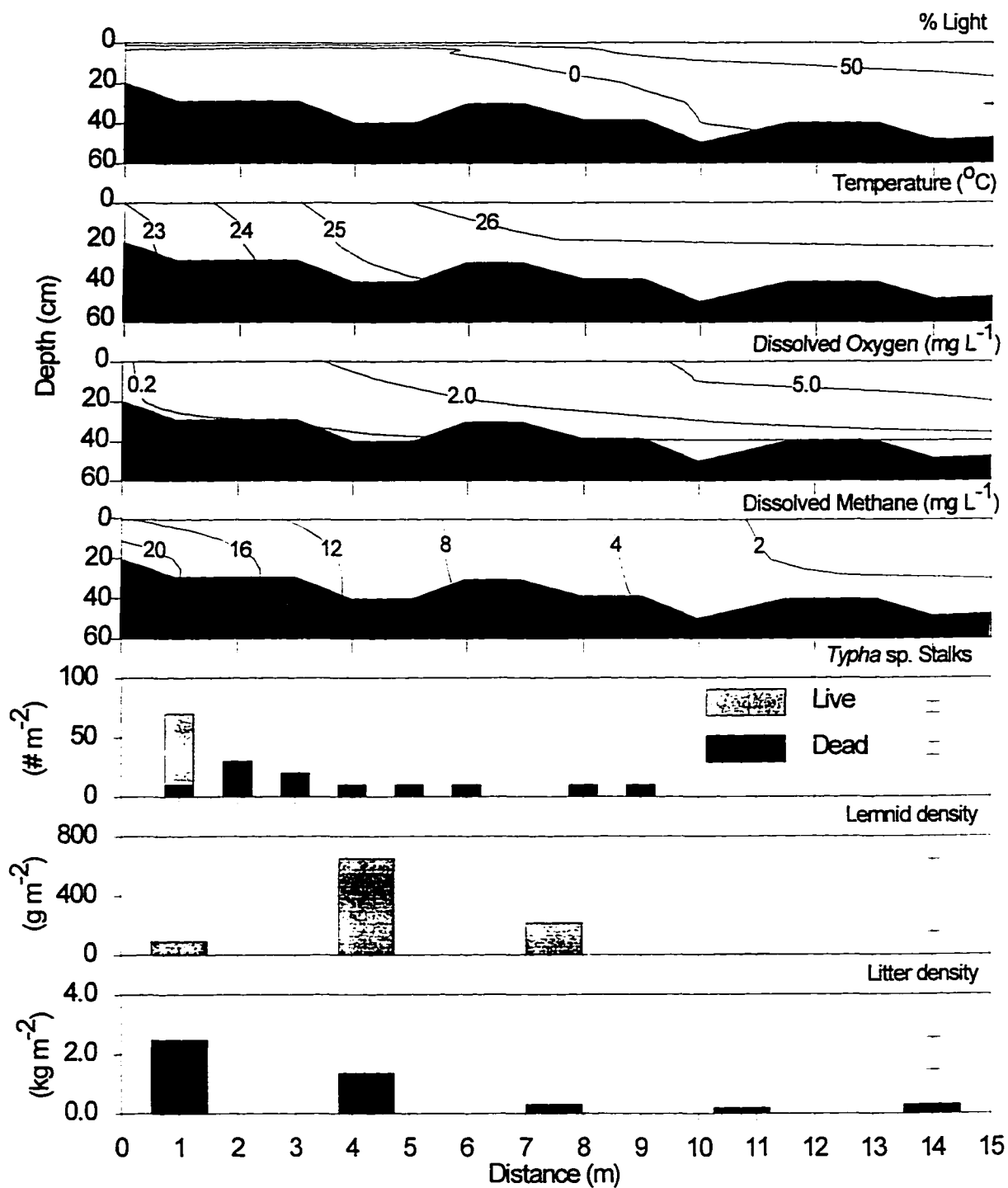


Fig. 6. Physical and chemical parameters along transect 4 (August 15, 1995). Error bars represent the least significant differences. Black areas on upper isopleth graphs represent sediment.

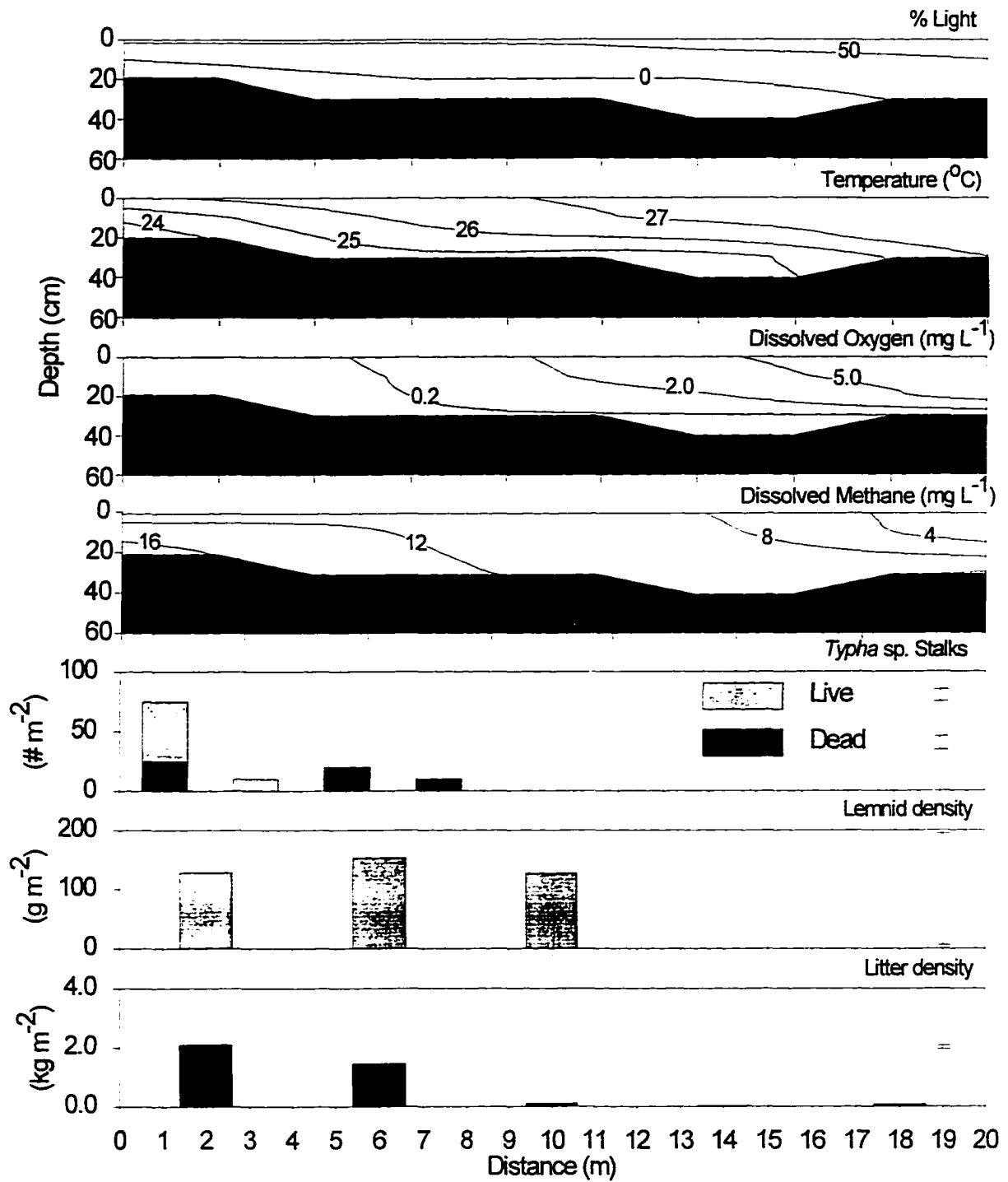


Fig. 7. Physical and chemical parameters along transect 5 (August 18, 1995). Error bars represent the least significant differences. Black areas on upper isopleth graphs represent sediment.

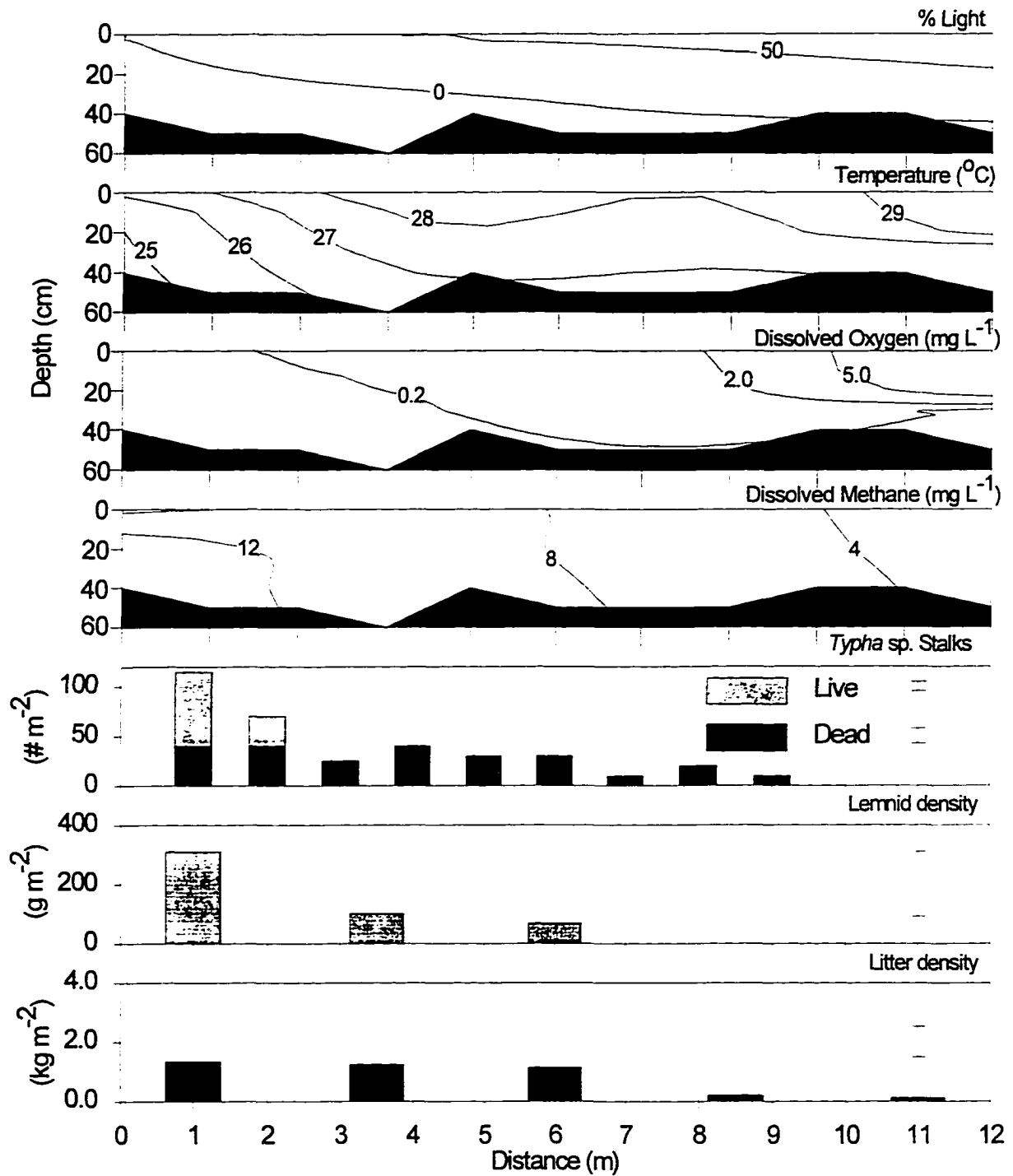


Fig. 8. Physical and chemical parameters along transect 6 (August 26, 1995). Error bars represent the least significant differences. Black areas on upper isopleth graphs represent sediment.

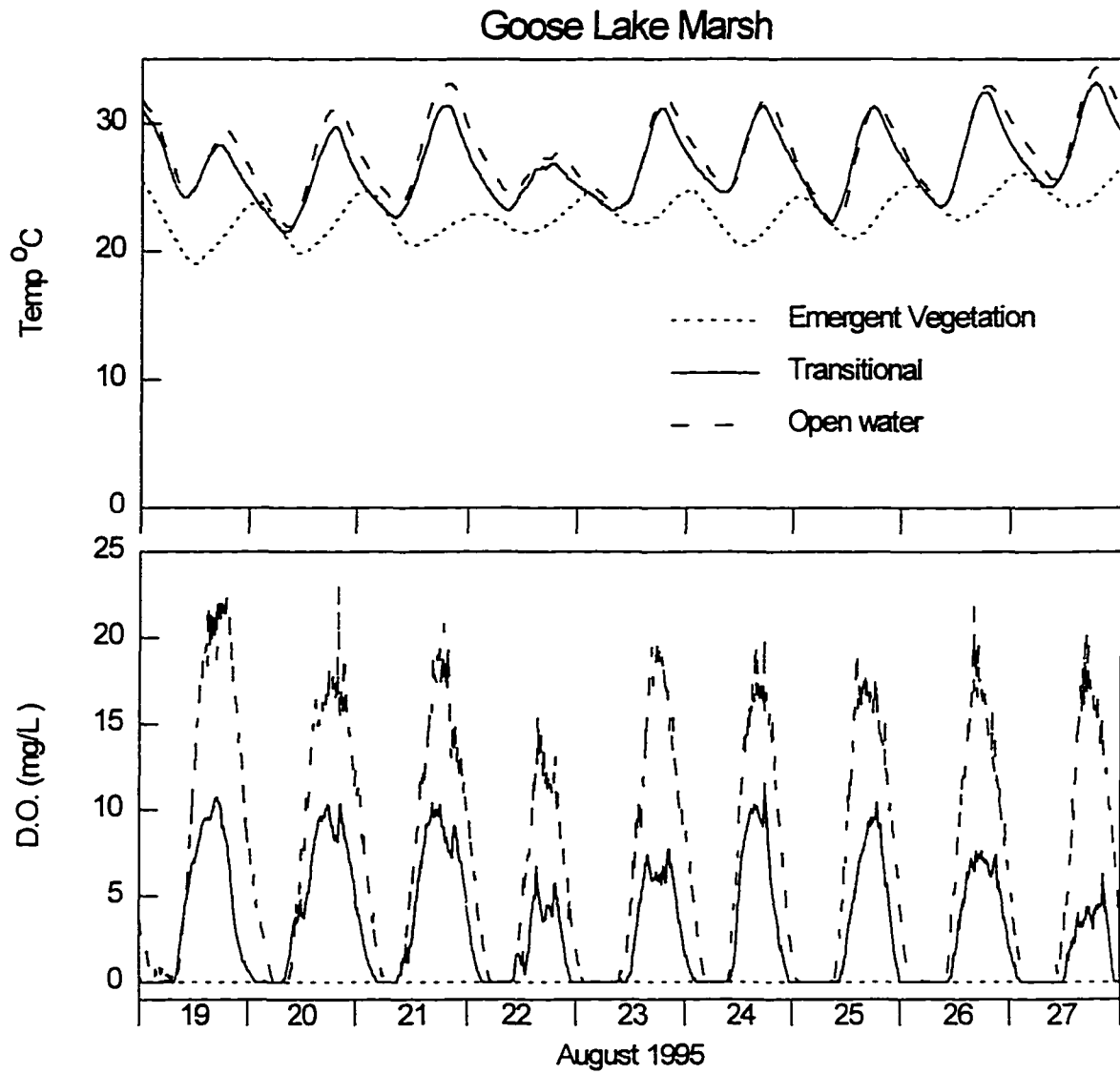


Fig. 9. Temperature and dissolved O₂ changes through time at open water), transitional, and emergent vegetation sites.

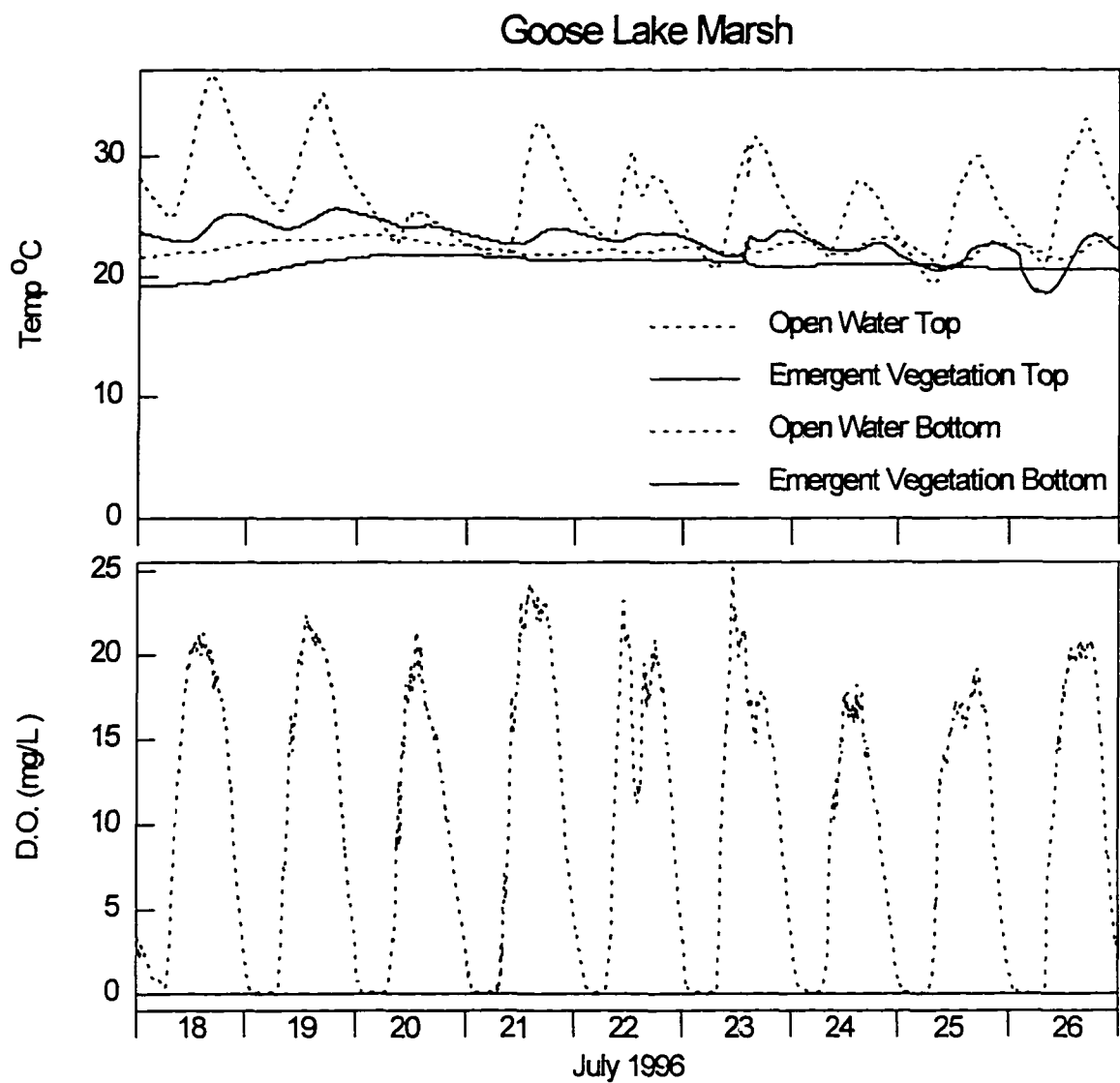


Fig. 10. Temperature and dissolved O_2 changes through time at the top and bottom of open water and emergent vegetation sites.

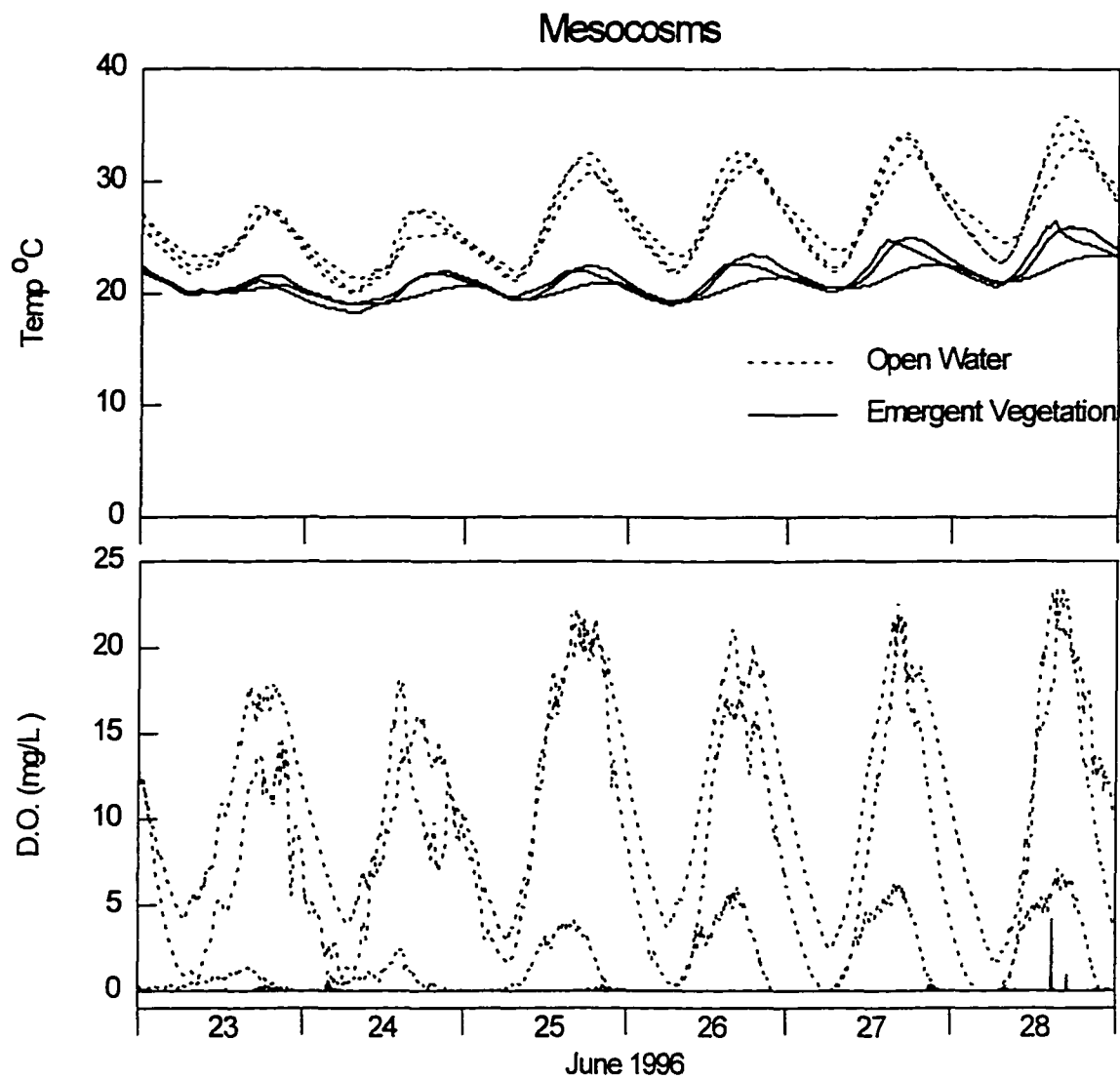


Fig. 11. Temperature and dissolved O₂ changes through time for three open water mesocosms and three normal (emergent vegetation) mesocosms.

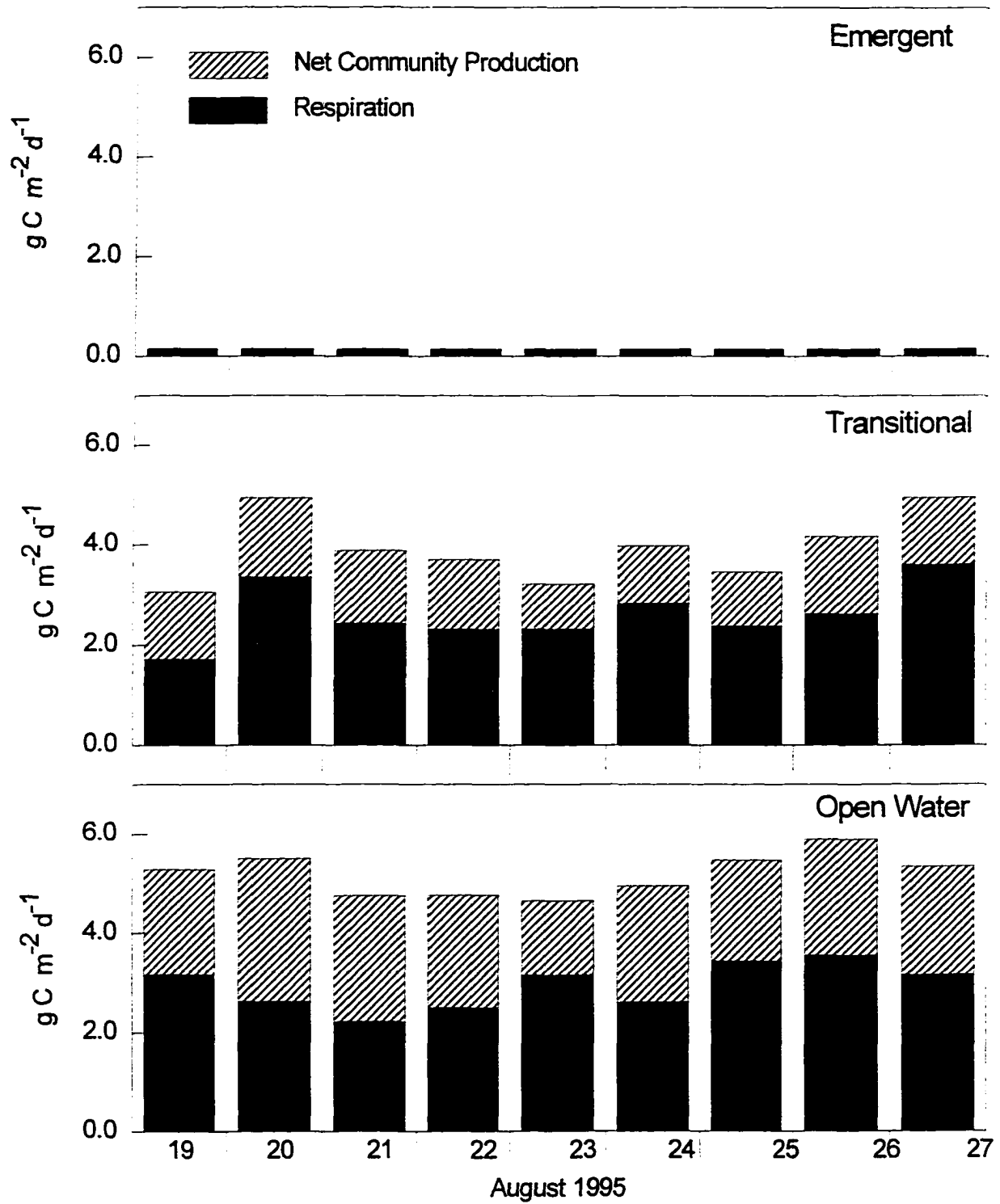


Fig. 12. Aerobic respiration parameters (derived from diurnal oxygen curve analyses) through time at sites 1 open water, 2 transitional, and 3 emergent vegetation sites.

CHAPTER 4. GENERAL SUMMARY

Wetland areas with varying amounts of emergent and free-floating vegetation potentially have very different pathways of carbon and energy flow. In Goose Lake Marsh, a natural prairie pothole wetland, synoptic surveys, continuous monitoring, and transect measurements were used to examine patterns light availability, temperature, dissolved O_2 concentrations, dissolved CH_4 concentrations, plant densities, litter densities, and CH_4 flux (due to diffusion and ebullition) within and outside emergent vegetation zones were used to determine differences in wetland microbial processes. Three habitat zones were identified based on the distribution of vegetation and dissolved oxygen: (1) a zone of dense emergent macrophytes providing significant submerged structure but with nearly or completely anoxic water, (2) a transition zone of sparse emergent macrophytes providing less structure but with more aerobic water, and (3) an open water zone with consistently aerobic water but with little submerged structure. Water column light availability was as low as 2% of ambient light in emergent vegetated due to canopy cover, small floating plants (lemnids), and plant litter. Water temperatures and dissolved oxygen concentrations were significantly lower and varied less diurnally in vegetated areas. Photosynthesis and aerobic respiration rates in the water column were much greater in open water than emergent vegetation zones. Methane concentrations in the water column were lower in open water than in emergent vegetation zones. The difference in dissolved O_2 , temperature, and methane concentration patterns between the vegetated and open water zones can be attributed to the physical effects of vegetation on O_2 supply. Despite differences in dissolved CH_4 concentrations, CH_4 fluxes generally did not differ significantly among zones due to increased plant cover and thicker stagnant boundary layers in the emergent zones which slow gas diffusion and possibly due to the quality of organic substrate. The results from the mesocosm experiments are in agreement with the patterns of dissolved O_2 , temperature, and diffusive CH_4 flux found in Goose Lake Marsh.

The papers presented here concern only small parts of the carbon cycle; however, large differences among carbon metabolic pathways were found in the wetland zones. It is reasonable to assume that processes linked to carbon cycling would also differ among zones. Some of the effects of the emergent vegetation/low dissolved O_2 relationship may have management implications at the watershed/landscape scale. Created and restored wetlands have been suggested as a method of reducing the nitrate concentration in waters that are used as sources for drinking water as well as nitrogen-limited coastal waters (Jansson et al. 1994). Wetlands are sinks for water-borne nitrate due to their potentially high rates of denitrification. The results presented here suggest that as plant communities develop in newly created or restored wetlands, the additional plant cover and litter results in the water column becoming increasingly anaerobic. One consequence can be increased nitrate removal rates (Stefan et al. 1994, Crumpton, et al. in prep). Other water quality parameters may also be effected, so there is a need for further research into these areas.

Through direct and indirect processes, the relationship between plant structure and O₂ distribution may influence many wetland functions including food web structure and bioenergetics, aerobic and anaerobic metabolism, nutrient cycling, and the fate and effects of chemical contaminants. Because of their annual and interannual changes in water levels and aquatic vegetation, prairie pothole wetlands may be very interesting systems in which to carry out further studies of these processes. If we are to understand functional processes of wetlands, we must recognize that they are complex spatial and temporal mosaics of habitats with distinctive structural and functional characteristics.

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