

ABSTRACT

The Effects of Inundation and Vegetation on
Microbial Metabolism of Dissolved Organic Carbon

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ABSTRACT

DOC concentration and microbial utilization of DOC from salt marsh sediment porewater was measured in four native vegetation zones, (tall *Spartina alterniflora* - TS, short *Spartina alterniflora* - SS, *Juncus roemerianus* - J, and *Spartina patens* - P) and four experimentally flooded and control plots of *J. roemerianus* and *S. patens* (JF, JC, PF, and PC). Suction lysimeters placed at 15 cm depth were used to sample porewater between August 1994 and October 1995. Porewater concentrations of DOC, NH_4^+ , PO_4^{3-} , and H_2S were measured. Filter-sterilized porewater ($0.2\ \mu\text{m}$) was inoculated with the microbial community from an adjacent tidal creek and incubated in the dark for 24 h under aerobic conditions. Bacterial utilization of DOC was measured as the difference between initial and final concentrations of DOC and changes in bacterial abundance. Bacterial incorporation of DOC was measured on one sampling date by estimating bacterial biomass production during the incubation. Bacterial mineralization of DOC was measured as the difference between initial and final CO_2 concentrations in sealed vials over 24 h.

DOC concentrations were almost always lower than DOC concentrations within the three interior sites. DOC concentrations were also found to be lowest in the experimentally Flooded plots when compared with the respective Control plot. Changes in bacterial abundances and apparent growth rate constants were

quite variable within the native zones. Changes in abundances and growth rate constants appeared to be somewhat depressed within the JF plots compared to JC. There were no apparent differences between PF and PC.

Bacterial incorporation into biomass of DOC associated with the native TS zone was much greater than the three interior sites. Evolution of CO₂ bioassays were problematic and revealed no noticeable differences between zones. The combination of CO₂ and biomass production, however, yielded differences in total carbon metabolized between sites; the greatest amount of DOC was metabolized within the native J zone. Biomass production was not measured within the experimentally flooded plots.

The results of the present research indicate a flooding effect on DOC quantity and a probable combined effect of plant and flooding on microbial utilization of porewater DOC.

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I want to thank my family, all of whom have been extremely supportive during the last 3 years. My father, to whom this thesis should be dedicated, has been my biggest emotional, spiritual and financial supporter, and has never let me lose sight of why I went to graduate school. Thanks go to mom, Brad, Jerica, Nicole, Audrey, Todd, and Mark for putting up with me and my graduate student mood swings and for your constant encouragement.

I have to thank my friends, far away and in Charlottesville. Thanks Elizabeth and Julie for commiserating about grad school. Thanks Leah, Stacey, Ben and Steve for giving me glimpses of what I was missing in the "real world". Thanks Heather and company for giving me reasons to go to the beach!

Huge thanks go to Pam, Vaughan, Tom and Ben for getting me through my first (and second) "R.E. Hennessey" year! Karen and Becky were my mentors and friends in and out of lab. Kristin, Christy and Andy helped break the monotony of work by keeping me company in the brew pubs and on the links! Alison, John, and Tashia managed to keep me sane during long hours in the lab and at the shore. Brian and Jill were the best field hands I could have ever asked for! Bill gave me advice and friendship in the crucial writing stages. Thanks also go to the women of Zeta Xi chapter for giving me a purpose outside of the department.

Finally, and most importantly, I have to thank God for giving me the courage and the capabilities to see this research and thesis through.

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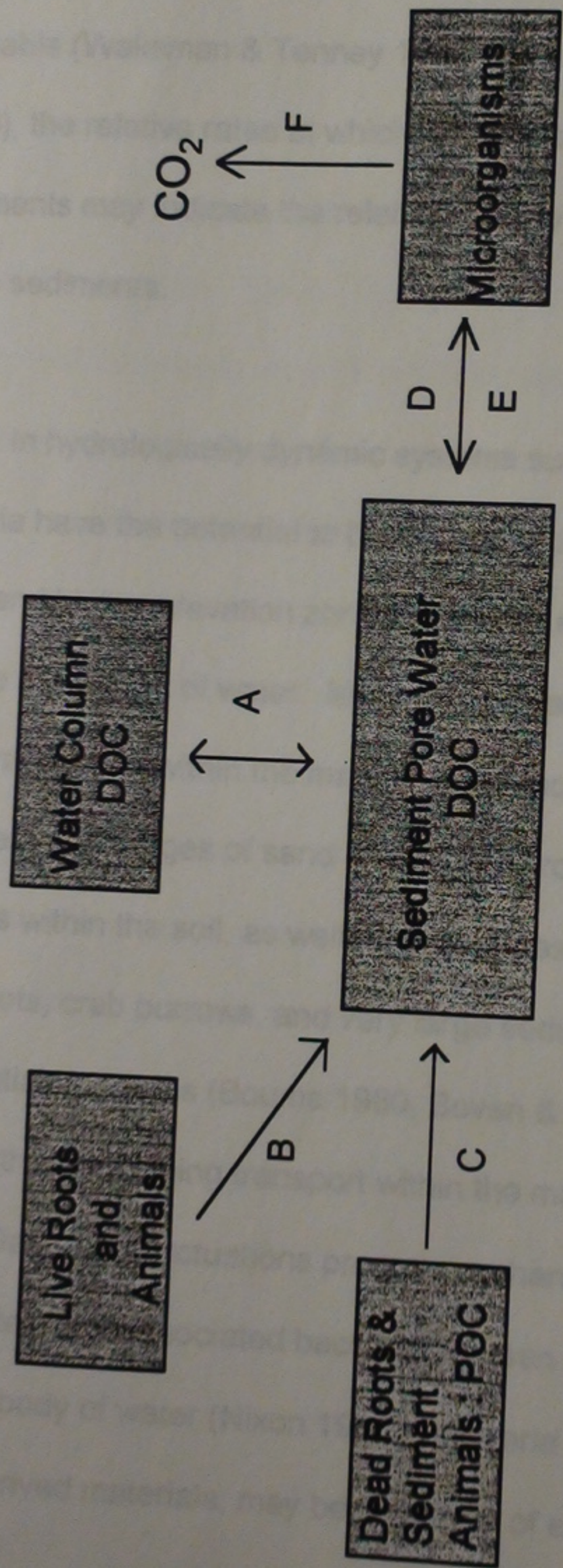
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INTRODUCTION

Carbon (C) is an element essential for basic life functions in all living things. The carbon cycle begins with primary producers converting radiant energy to chemical energy in the form of organic compounds (Atlas & Bartha 1993). Teal (1962) provided the first comprehensive overview of energy flows within a salt marsh system. He indicated that marsh macrophytes (primarily *Spartina* species) were the most important primary producers, providing food for marsh fauna while living, and supporting the detritus based food web after senescence and death. He also recognized that before *Spartina* could become widely available to most marsh and estuarine consumers, it must first be at least partially decomposed by fungi and bacteria. Macrophyte decomposition products represent a principle source of particulate and dissolved organic carbon within such a system. Additional sources and fates of DOC exist in a salt marsh ecosystem (Chart 1), yet, macrophyte primary production represents the dominant source.

One step in the decomposition of most plant materials involves the conversion of POC to DOC (Pomeroy *et al.* 1975). Due to membrane structure, bacteria can only assimilate dissolved materials. As a result bacteria are able to utilize dissolved constituents released upon plant senescence that higher organisms may not. Once DOC is incorporated into bacterial biomass, the

Sources and Fates of Salt Marsh DOC



- A = Import/Export during Tidal Exchange
- B = Root Exudates and Animal Excretions
- C = POC conversion to DOC Mediated by Microbial Decay Enzymes
- D = Microbial Uptake
- E = Microbial Cell Lysis
- F = Respiration

Chart 1. Primary sources and fates of dissolved organic carbon in a tidal salt marsh ecosystem.

associated energy is then transferable to higher trophic levels through consumption of bacterial cells (Azam, et al. 1983, Fenchel 1984, Pomeroy, et al. 1988, Day 1989). Since DOC derived from plant materials are not equally available (Waksman & Tenney 1928, de la Cruz & Gabriel 1974, Day et al. 1989), the relative rates at which bacteria can incorporate DOC from different sediments may indicate the relative "quality" of the organic matter specific to those sediments.

In hydrologically dynamic systems such as salt marshes, DOC and bacteria have the potential to be transported. Hydraulic gradients exist between lower and higher elevation zones within the marsh, causing subsurface and surface movement of water. More porous sediments also enhance water and solute movement within the marsh. Differences in soil porosity can be attributed to higher percentages of sand and lower percentages of silt and clay sized particles within the soil, as well as the shapes of individual grains (Fetter 1988). Plant roots, crab burrows, and very large sediment grains may create preferential flowpaths (Bouma 1980, Beven & Germann 1982) within salt marsh soils, further enhancing transport within the marsh (Harvey et al. 1987, Harvey 1993). Daily tidal fluctuations promote exchanges of DOC, nutrients, sediments, particulates, and associated bacteria between near-tidal creek soils and the adjacent body of water (Nixon 1980). Bacteria and DOC, as well as other marsh-derived materials, may become part of estuarine food webs and

biochemical processes, or may be further transported to near-shore or shelf environments.

DOC may also be removed from marsh sediments through several biogeochemical processes. Near-creek soils often experience periods of anoxia due to soil waterlogging alternating with periods of aeration when tidal waters recede (Naidoo *et al.* 1992). Under aerobic conditions, conversion of organic carbon to CO_2 and bacterial biomass is relatively simple (Good *et al.* 1982). Anaerobic metabolism of DOC is more complex, resulting in the production of biomass and the transfer of DOC derived energy to higher trophic levels via stored inorganic end products of reactions such as sulfate reduction. Such stored energy could support chemoautotrophs, resulting in the eventual conversion of reduced inorganic compounds into biomass. (Howarth & Teal 1979). Howarth & Hobbie (1982) also reported that lack of molecular oxygen limited the decomposition of certain plant structural components, like lignin, while accelerating the decomposition of others, such as cellulose. Therefore, in salt marsh sediments, biogeochemistry and decomposition processes govern both the quantity and quality of DOC available for transport and/or bacterial utilization.

PROJECT OBJECTIVES

The current research focused primarily on differences in quantity and susceptibility to microbial metabolism of DOC associated with distinct vegetative zones within a salt marsh. An emphasis was placed on relating differences to differences in dominant plant cover, differences in tidal inundation, or both. Two working hypotheses were established based on preliminary experiments in a mainland salt marsh on Virginia's Delmarva peninsula:

- 1) Porewater DOC concentration increases as flooding frequency decreases.
- 2) Microbial metabolism of porewater DOC increases as inundation frequency increases.

Studies of aquatic systems have quantitatively, as well as qualitatively, compared spatial variability of DOC between freshwater bays (Leff *et al.* 1991), along a single river (Leff & Meyer 1991), and between marine and freshwater systems (Benner *et al.* 1988, Baines & Pace 1991, Sondergaard & Middelboe 1995). Few studies have quantified DOC within marsh sediments (Sottile 1973, Yelverton & Hackney 1986). While the potential importance of salt marsh derived DOC to bacterial communities is generally accepted, few, if any, studies

have examined DOC quality and quantity associated with distinct vegetation zones across a marsh transect. Such a study could provide valuable information about potential changes in DOC availability for microbial utilization in the face of sea level rise or other salt marsh perturbations.

Coastal salt marshes like those on the Delmarva peninsula are geologically young formations and experience rapid change (Edmonds *et al.* 1986, Hayden *et al.* 1991). Changes in sea level trigger systematic hydrologic and ecological responses characterized by the migration of marsh zones coinciding with increased inundation (ASCE Task Comm. 1992). As areas of the marsh experience increased flooding, the vegetation characteristic of the low, mid, and high marsh zones also migrate in response to the change (Brinson *et al.* 1995).

Along with the obvious changes in plant species as marshland migrates into upland areas, less obvious changes in the organic matter content of sediments also occurs (Nyman & DeLaune 1991, Brinson *et al.* 1995). The low organic matter content upland soils give rise to high organic matter content high marsh sediments, which in turn give rise to low organic matter content low marsh sediments (Brinson *et al.* 1995). Such changes in sediment organic matter content may be directly attributed to altered patterns of tidal flooding frequency or may be related to differences in the susceptibility of each zone's characteristic vegetation to decay.

Salt marsh survival in the face of rising sea-level depend upon several factors. A balance between coastal submergence due to rising seas-level and increased inundation, and the rate at which mineral sediment and organic matter accumulates within the marsh is the most important determinant of marsh maintenance (Mitsch & Gosselink 1993). Blum (1993) attributed differences in organic matter accumulation in high and low marsh areas to differences in root production. However, many studies have indicated accumulation of organic matter may be a function of the decomposition of marsh plants, which in turn is a function of location (Kirby 1971, Blum & Christian 1993), structural composition of the plants (Waksman & Tenney 1928, Bell 1974, de la Cruz & Gabriel 1974, Good *et al.* 1982, Benner *et al.* 1991), and nutrient availability (Heywood 1977, Benner *et al.* 1988).

If different marsh zones and different plant species experience different rates of decomposition, the quality and quantity of DOC within sediment pore water may reflect the rate of organic matter accumulation or mineralization in the marsh. For example, low concentrations of labile DOC would suggest rapid turnover and mineralization of organic matter, while high concentrations of refractory DOC would indicate slower turnover, long residence times and the potential for organic matter accumulation.

Similar to vegetative cover and soil organic matter, soil chemistry also changes with increased inundation. Characteristics such as nutrient and toxin concentrations (Pulford & Tabatabai 1988, Koch *et al.* 1990), pH and Eh (Nyman & DeLaune 1991, Naidoo *et al.* 1992, Nyman *et al.* 1995), and salinity (Price *et al.* 1988, Naidoo *et al.* 1992) are all related to flooding frequency.

Quantifying DOC is straightforward. Porewater concentrations of DOC can be easily analyzed since distinction between individual compounds is not necessary. Identification and quantification of individual compounds composing the DOC pool from each vegetative zone is not possible given current methods and technical capabilities. Instead, microbial metabolism of each pool of DOC was approximated in order to estimate the relative quality associated with different DOC pools from different vegetative zones.

Two types of bioassays were used to estimate microbial metabolism of DOC. One assay measured changes in bacterial abundance and biomass associated with specific DOC. The other assay estimated the evolution of CO₂ associated with bacterial metabolism of the DOC. As discussed previously, many factors may affect the decomposition and metabolism of DOC. Likewise, many factors may affect a laboratory bioassay. Incubation time, nutrient limitations, microbial community structure, and sampling techniques may affect metabolism measurements, and had to be addressed individually for each bioassay.

The current research involved (i) initial experiments to select suitable sites, (ii) test of the bioassays, and (iii) characterization of DOC quantity and quality to test the hypotheses. The approach used was (i) to measure DOC quantity in four native vegetation zones and in experimentally flooded plots to determine the effect of inundation on DOC concentration, and (ii) to compare DOC quality among plant types and flooding conditions to determine if DOC concentration differences may be related to the susceptibility of the DOC to microbial metabolism.

SITE DESCRIPTION

The study area was located in the upper Phillips Creek research marsh in Nassawadox, Northampton County, on the Delmarva Peninsula, Virginia (Fig. 1a). This marsh area represents one of two primary mainland marsh sites within the Virginia Coast Reserve complex and is a part of the Long Term Ecological Research Program. Within the Phillips Creek marsh, four individual sites were selected for this study (Fig. 1b), each representing a different vegetation zone: tall *Spartina alterniflora* in the low marsh, short *Spartina alterniflora* in the low-to-mid marsh, *Juncus roemerianus* in the mid marsh, and *Spartina patens* in the mid-to-high marsh. The low marsh site (TS), located < 3 m from Phillips Creek (the salt water tidal creek that floods this marsh) is < 0.5 m above mean sea level (MSL) and is flooded twice daily. The low-to-mid marsh site (SS) is located approximately 14 m from the creek, is 2.63 m above MSL, and is flooded at least once daily, except during spring tides when it is flooded 2 times each day. The mid marsh site (J) is located approximately 33 m from the creek, is 2.67 m above MSL, and is usually flooded once daily except during the lowest tides. The mid-to-high marsh site (P) is located approximately 45 m from the creek, is 2.8 m above MSL, and is not flooded by regular tidal fluctuations.

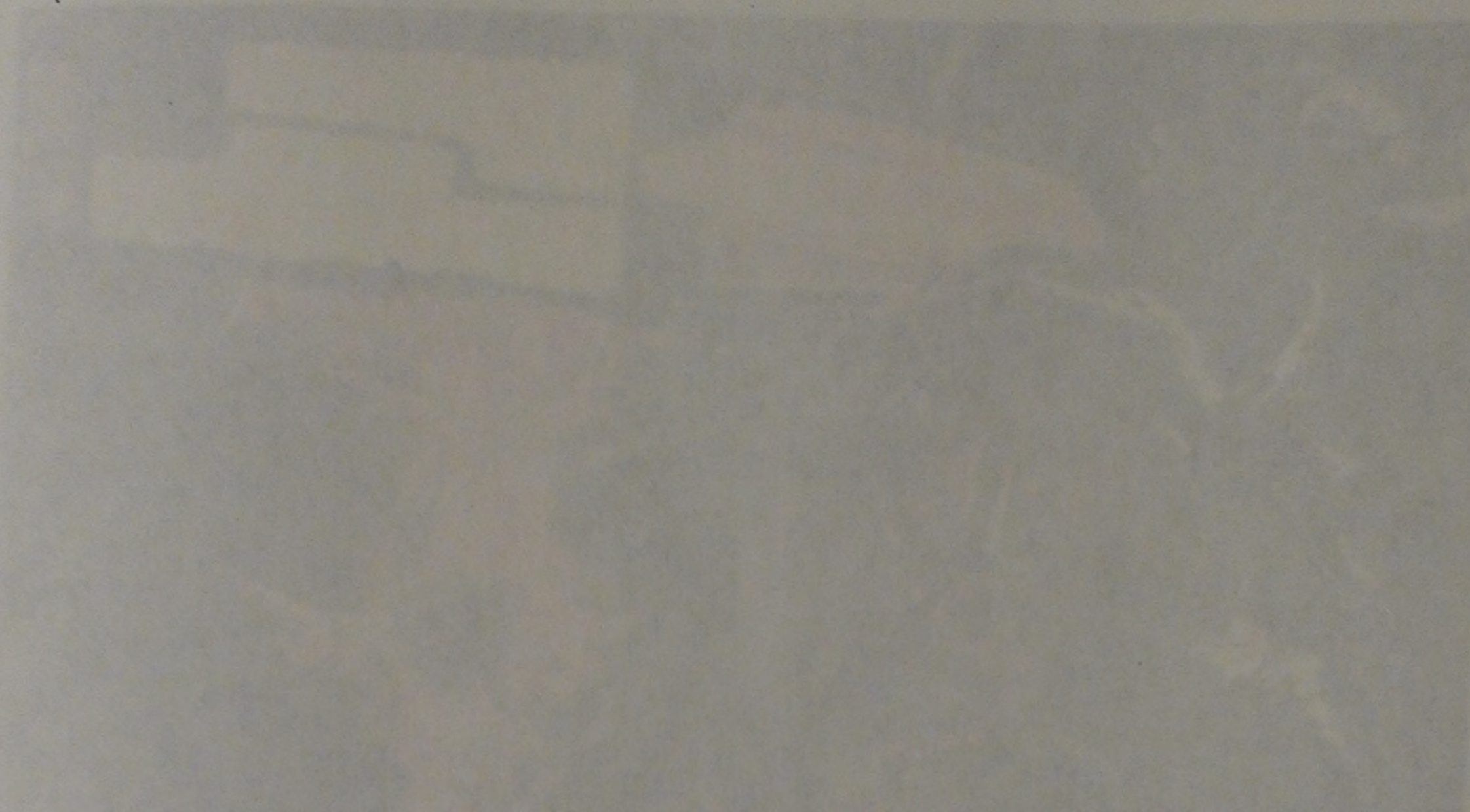


Fig. 1a. Location of the Phillips Creek research marsh on the seaside of the Delmarva Peninsula of Virginia.

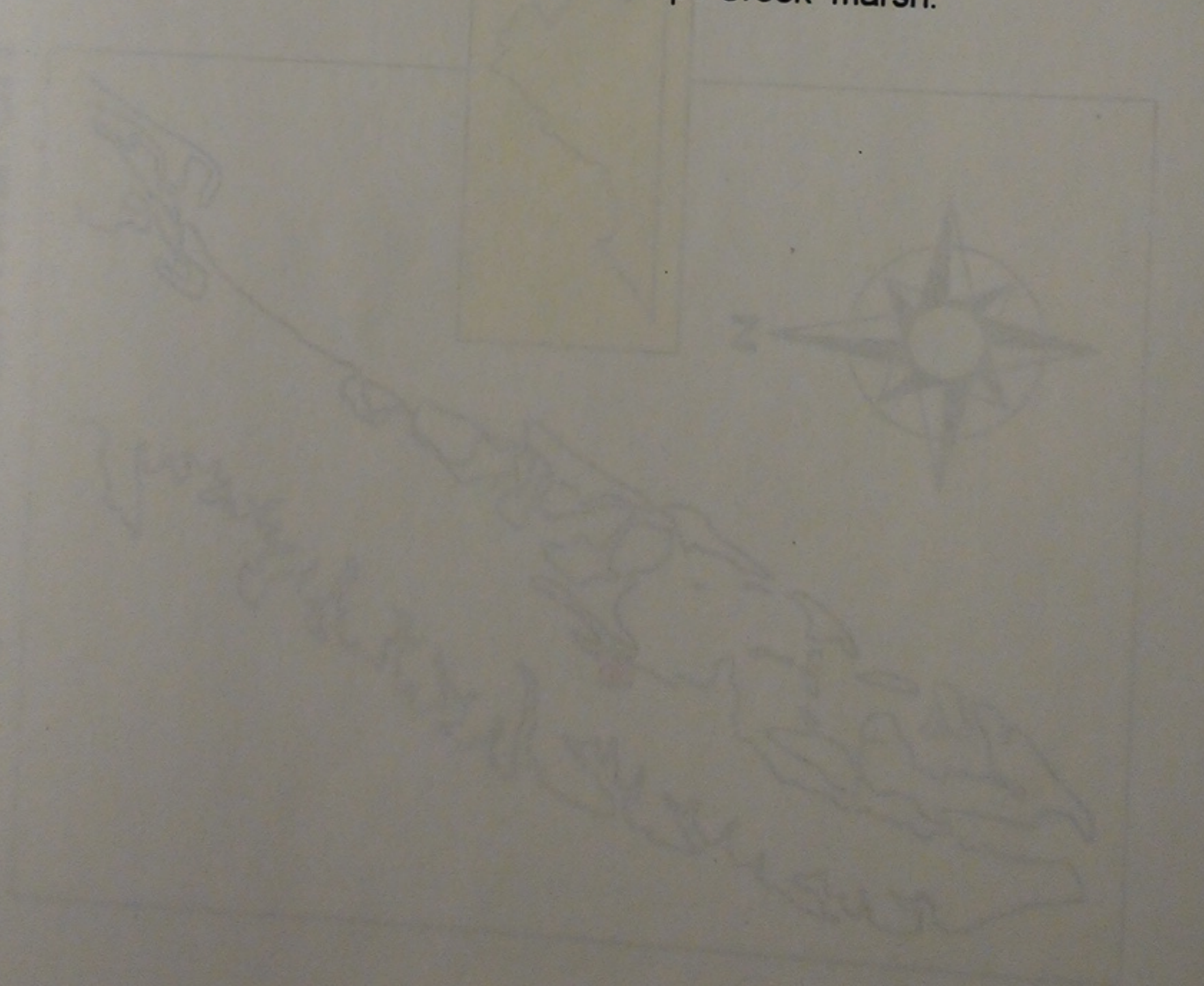


Fig. 1b. Approximate location of each Individual native vegetation zone and the experimentally flooded plots within the Phillips Creek marsh.

Phillips Creek Marsh





At three different times throughout the summer of 1995, measurements of water depth associated with tidal events were made within each of the four vegetation zones. During the June spring tide event on June 14 and 15, the July neap tide on July 26, and a mid-cycle tide on August 2, 1995, water depths at the base of each individual sipper within each site were measured. June measurements were made every hour for 12 hours between 7:00 a.m. and 7:00 p.m. for both days. July measurements were made at half hour intervals between 7:00 a.m. and 11:00 a.m. and again between 8:00 p.m. and 10:00 p.m. August measurements were initially made hourly beginning at 10:00 a.m., and then every half hour from 12:00 noon until 6:30 p.m. Measurements were concentrated around the high tides. Averages of water depths associated with each sampling site within a site were averaged and plotted in order to determine the relative flooding frequency and intensity for each site.

Experimentally flooded plots were also located within the Phillips Creek research marsh (Fig. 1b). An approximately elliptical area (Fig. 1c) was divided into rectangular plots. The center of the ellipse was located approximately 30 m from Phillips Creek. Half of each plot contained *Juncus roemerianus* (J), while the other half contained *Spartina patens* and *Distichlis spicata* (P). Each half was then divided into wrack-covered and non-wrack-covered halves. Only non-wrack halves were sampled for the purposes of this study. Under normal

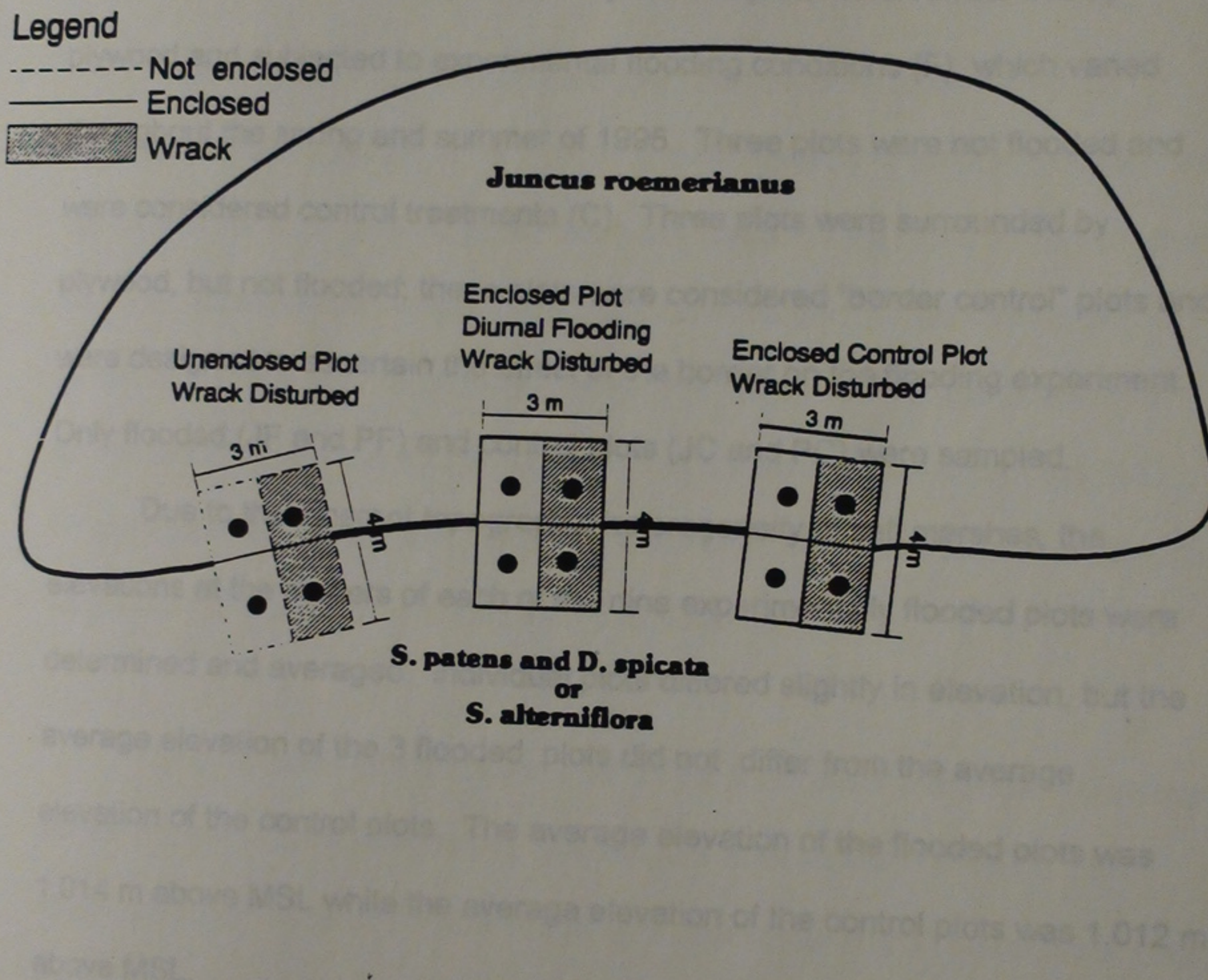


Fig. 1c. Schematic representation of the experimentally flooded plots design. Triplicates of each treatment (Unenclosed, Enclosed, and Enclosed Control) were established randomly within the ellipse. The unenclosed plot served as the control for this research, since the unenclosed control was not sampled. Only non-wrack-disturbed halves were sampled.

conditions, these plots were not subject to daily tidal fluctuations. Only extreme tidal events and large storms induced tidal flooding.

Pore Water Sampling

Three of the nine experimentally flooded plots were surrounded by plywood and subjected to experimental flooding conditions (F), which varied throughout the spring and summer of 1995. Three plots were not flooded and were considered control treatments (C). Three plots were surrounded by plywood, but not flooded; these plots were considered "border control" plots and were designed to ascertain the effect of the border on the flooding experiment. Only flooded (JF and PF) and control plots (JC and PC) were sampled.

Due to the inherent topographic heterogeneity of salt marshes, the elevations at the corners of each of the nine experimentally flooded plots were determined and averaged. Individual plots differed slightly in elevation, but the average elevation of the 3 flooded plots did not differ from the average elevation of the control plots. The average elevation of the flooded plots was 1.014 m above MSL while the average elevation of the control plots was 1.012 m above MSL.

METHODS

Pore Water Sampling

Twelve suction lysimeters, hereafter referred to as sippers (Fig. 3), described by Montgomery, et al. (1979) and modified by Chambers (1990) were constructed of 3.75 cm PVC pipe covered at one end by a piece of 0.45 μm pore diameter Scienceware polyethylene membrane (Baxter). Tygon tubing the length of the pipe was secured inside the tube just above the membrane and connected to a two-hole rubber stopper fitted on the opposite end of the PVC. Straight tube connectors and three-way luer-tipped stopcocks extended from the top of the stopper to provide sampling and evacuation ports.

Three sippers were placed at each of the four native plant/tidal inundation zones in the Phillips Creek marsh. Two sippers were located within the non-wrack covered halves of 3 experimentally flooded plots and 3 control plots, one sipper in each plant type (Fig. 1c). Prior to each sampling time, standing water was evacuated from each sipper by introducing nitrogen into the evacuation port. Suction lysimeters sample pore water by creating a negative pressure within the sampler and inducing flow from higher to lower (negative) pressure (Montgomery et al 1979). A negative pressure of 22 mm Hg was placed on each sipper with a hand held Nalgene pump to induce porewater flow into the

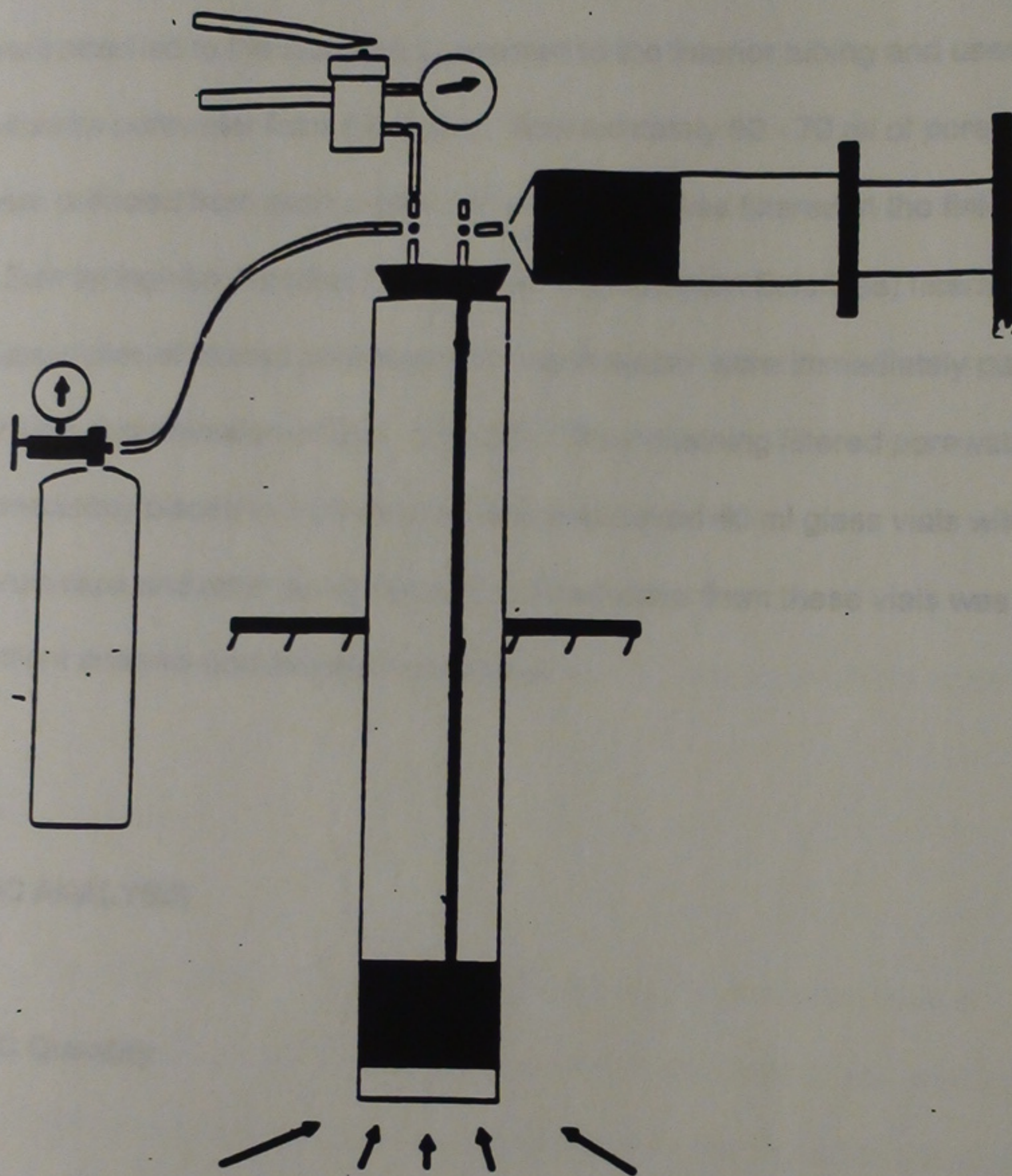


Fig. 2. Diagram of suction lysimeter (sipper), including the ports for evacuation and sampling. Three sippers used to sample sediment porewater within each native vegetation zone and experimentally flooded plot.

sippers for several hours prior to sampling. Sterile, disposable 60 ml syringes were attached to the stopcock connected to the interior tubing and used to withdraw porewater from the sipper. Approximately 60 - 70 ml of pore water were collected from each sipper. All pore water was filtered in the field using 0.2 μ m syringe-tip Acrodisc (25 mm diameter, Gelman Sciences) filters. Subsamples of filtered porewater from each sipper were immediately partitioned for later determination of DOC and H_2S . The remaining filtered porewater was immediately placed in acid-washed and autoclaved 40 ml glass vials with Teflon serum caps and returned to the lab. Filtered water from these vials was used for nutrient analysis and metabolism assays.

DOC ANALYSIS

DOC Quantity

Prior to each sampling time, 1 - 2 ml of 15% HNO_3 were placed in 20 ml scintillation vials. Upon sampling of each sipper, the HNO_3 was removed and 1 - 2 ml of filtered pore water was used to rinse the vial and cap. To preserve samples for determination of DOC concentrations in pore water, two drops of concentrated H_2SO_4 was added to 2-3 ml of filtered (0.2 μ m pore size) pore water. Samples were tightly capped and returned to the lab. The acidified

samples were kept cold until they were analyzed for DOC concentration by UV-assisted persulfate digestion in a Dohrmann TOC analyzer.

Six carbon standards ranging from 0 PPM C to 20 PPM C were analyzed prior to sample analysis. Sequential injection of 100 μ l of each standard yielded a standard curve. Each injection resulted in a response recorded as a peak on an integrator. Areas under each peak and the known standard concentration associated with each peak were regressed in order to obtain the equation for the line used to determine the relative sample DOC concentrations. Complete sets of standards were injected prior to running all samples and after all samples were completed and then averaged to account for analyzer drift over time.

DOC Metabolism

Because DOC may be either incorporated into microbial cells or mineralized (to CO_2), it was necessary to determine bacterial cell production and respiration. Two separate aerobic bioassays were performed to ascertain incorporation and respiration of pore water DOC. The microbial community used in the bioassays was that which occurs naturally in the Phillips Creek water column. Wu (1995) has shown that protozoa graze a significant portion of the microbial community in Phillips Creek. Therefore, Phillips Creek water was filtered through an 8.0 μ m pore size filter to minimize the number of grazers

within the community. This procedure reduced the impact of protozoan grazing on measurements of bacterial production.

Bacterial production was measured as the change in cell abundance in response to an incubation with sediment porewater DOC. Respiration was measured as the change in headspace CO_2 concentration in sealed vials when bacteria were incubated with sediment porewater DOC. To determine cell production and respiration, equal volumes of 0.2 μm and 8.0 μm pore size filtered Phillips Creek water were combined in 250 ml Erlenmeyer flasks covered with aluminum foil and allowed to incubate in the dark at room temperature for 24 h (August and October 1995 incubations were only 12 h). After combining the filtered waters, 2.0 ml of the combined water was added to 8.0 ml of 2% formaldehyde in artificial seawater for determination of bacterial abundance using the acridine orange direct count method (Hobbie et al., 1977). A subsample was also taken for determination of DOC concentration of the combined water. Additional subsamples were taken for determination of bacterial abundances and DOC concentrations throughout the incubation period after 6, 12, and 24 h. A single sterile, disposable syringe and 1.5 in detachable needle was used for each Erlenmeyer flask. At each sampling time, 2.0 ml of the incubating water were removed and prepared for bacterial enumeration as previously described. Another 3.0 ml were removed and passed through a 13 mm diameter 0.2 μm pore size Acrodisc syringe-tip filter (Gelman Sciences). A

small amount of filtered water was used to rinse residual 15% HNO_3 from a prepared scintillation vial. The DOC samples were preserved as previously described.

Apparent growth rate constants were calculated from changes in bacterial abundances. A linear regression was performed on the natural log of bacterial abundances versus time; the X - coefficient was taken as the growth rate constant and compared to the apparent growth rate constant obtained by equation (1):

$$(1) \quad \mu = (\ln X_1 - \ln X_0) / \text{time}$$

Both calculations yielded the same results. Calculated growth rate constants from each sipper were then averaged.

On the July 24 sampling date, photomicrographs (Ektachrome 200, 50-60 second exposure times) were taken of stained bacterial cells collected after 0 and 24 h of incubation for determination of changes in bacterial biovolume. Photographs were projected on a wall and bacterial cells were measured. A conversion factor to account for the magnification of the microscope, camera, and projector system was determined based on a projected photograph of a stage micrometer. Biovolume frequency distributions from replicate sippers

within each site were pooled so that at least 100 cells were measured for each site and incubation time. Biovolumes for each incubation time and site were calculated using Bjornsen's (1986) equation (2):

$$(2) \quad \text{Volume} = (\pi/4) * w^2 * (1 - (w/3))$$

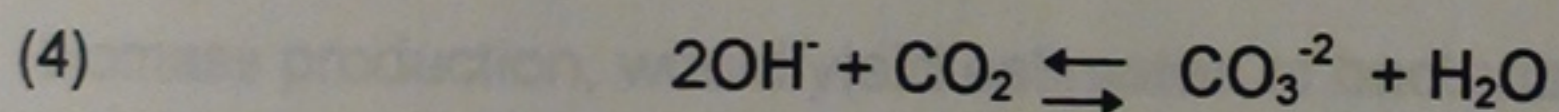
Bacterial biomass for each site and incubation time was calculated using equation (3):

$$(3) \quad \text{Biomass} = \text{Frequency} * \text{Abundance (cells/ml)} * \text{size class } (\mu^3/\text{cell}) * 0.354 \text{ pg C}\mu^{-3}$$

where $0.354 \text{ pg C}\mu^{-3}$ is the empirical conversion factor for calculations of biomass from biovolume measurements produced by Bjornsen (1986). Bacterial biomass at the beginning of the experiment was subtracted from bacterial biomass after 24 of incubation to determine the biomass produced within the incubation time.

For the respiration bioassay, 15.0 ml of the combined water (filtered pore water + filtered creek water) was placed in each of 2 sterile 50 ml glass bottles with serum caps. A plastic well containing a section of filter paper was inserted into the serum top. Immediately after vial preparation and water addition, all

vials were sealed. After sealing the vial, the filter paper within each well was saturated with 0.4 ml of 1.5 N NaOH to trap CO₂ respired over the course of the incubation. Following the addition of NaOH, the sample water in one vial was acidified with 2.0 ml of concentrated HNO₃ injected through the serum cap with a sterile disposable syringe and 1.5 inch needle, to serve as a "killed" (abiotic) control. The second vial was allowed to incubate in the dark at room temperature for 24 h before being acidified in the same manner. Addition of concentrated HNO₃ shifts the CO₂ - bicarbonate equilibrium towards CO₂, so that all CO₂ should be contained within the vial's head space and therefore trapped by the NaOH in the well. Carbon dioxide reacts with NaOH to form carbonate and water according to equation (4):



At least 12 h after the acidification of "live" (total) samples, individual filter papers (from total and abiotic vials) were placed in 25.0 ml of autoclaved DOC-free water in acid-washed 50 ml Erlenmeyer flasks and 1-2 drops of phenolphthalein indicator was added. The solution was titrated to equilibrium with 0.02N HCl. Carbon respired was calculated by equation (5):

$$(5) \quad ((X-Y)/2) * 12.01 \text{ mg C/meq} = \text{mg C in sample}$$

where $X = \text{Volume NaOH} * \text{Normality NaOH}$ and

and $Y = \text{Volume HCl titrated} * \text{Normality HCl}$.

Concentrations of CO_2 were converted to PPM C by accounting for the 15 ml sample size.

CO_2 contained in the "killed" control represents abiotic CO_2 present in each vial due to exposure to the atmosphere during preparation. CO_2 contained within the "live" vials represents total CO_2 due to abiotic inputs and aerobic microbial respiration over the incubation time. By subtracting the CO_2 within the abiotic control vials from the CO_2 within the "total" vials, an estimation of CO_2 mineralization due to microbial metabolism of the DOC source within each site may be made. Respiration estimates, coupled with measurements of bacterial biomass production, would yield estimates of bacterial utilization and carbon conversion efficiency for porewater DOC characteristic of different vegetation zones.

Nutrient Analysis

Porewater salinity, NH_4^+ , H_2S , and PO_4^{3-} were monitored within each vegetative zone. When sippers were sampled, 5.0 ml of 0.2 μm pore size filtered pore water was immediately added to 5.0 ml ZnAc in clean 20 ml

scintillation vials and kept cold for H_2S determination described by Cline (1969) and modified by Morris and Otte (1994). The modified method of sulfide determination involved dilution of prepared samples based on the relative amount of ZnS precipitate formed in the vial. Dilutions were made in new, clean scintillation vials and 0.4 ml N,N -dimethyl- p -phenylenediamine sulfate + ferric chloride dye was added to each. Samples incubated in the dark for at least 20 minutes before colometric determination was made at 670 nm wavelength.

Approximately 10-15 ml of the filtered pore water was returned to the lab for spectrophotometric determination of NH_4^+ and PO_4^{3-} as described in Grasshoff et al. (1983). Ammonium was determined by addition of 0.3 ml of tri-sodium citrate, phenol and hypochlorite reagents to 5.0 ml of filtered sample water and 5.0 ml of stock solution for standards. Phosphate was determined by the addition of a combined reagent composed of ammonium molybdate, sulfuric acid, ascorbic acid, and potassium antimonyl tartrate solutions to all samples and standards. All nutrients were determined colometrically at 630 and 885 nm wavelengths for NH_4^+ and PO_4^{3-} , respectively.

Pore water pH and platinum electrode potential were determined twice for unfiltered pore water and creek water. On July 25 and October 14, 1995, sippers were evacuated and prepared as described. Approximately 20 ml of pore water was removed, but not filtered. A reference electrode, calibrated with

pH buffer solutions at pH 4 and 7, and a platinum electrode were connected to a pH meter and submerged in the pore water from each sipper to measure pH and platinum electrode potential. The potential for the Ag/AgCl, saturated KCl reference electrode (+199) was added to each potential read from the meter (Caton 1977).

Sampling Schedule

All variables were not measured at every sampling time due to time constraints and/or limited porewater availability from individual sippers. Each measurement, except biomass measurements, was made at least twice for native vegetation zones. Most measurements were made twice within the experimentally flooded plots (Table 1).

Statistics

Correlation analysis and ANOVA were performed with SPSS 6.1.2 for Windows. Regression analysis and additional ANOVA were performed with statistical tools within Microsoft Excel 5.0 for Windows. Statistical significance was accepted when $p < .05$.

Table 1. Sampling schedule for all measured variables. AODC indicates measurement of cells production; μ indicates calculation of apparent growth rate constant. Resp. indicates the performance of the respiration bioassay. PEP represents the measurement of platinum electrode potential.

	Sampling Dates											
	8-8	10-17	2-4	3-5	3-26	4-21	5-24	6-7	6-21	7-8	7-24	7-25 10-14
<u>Native Plots</u>												
DOC	X	X	X	X	X	X		X	X	X	X	
AODC	X	X	X	X	X	X		X		X	X	
μ				X	X	X		X		X	X	
resp.								X		X	X	
biomass											X	
salinity		X			X			X	X		X	
NH ₄ ⁺	X	X	X		X	X	X	X	X	X	X	
PO ₄ ⁻³	X	X	X		X	X		X	X	X	X	
H ₂ S	X					X	X	X	X	X	X	
pH												X X
PEP												X X
<u>Experimentally Flooded Plots</u>												
DOC							X					X
AODC							X					X
μ							X					X
resp.												X
nutrients							X					X

RESULTS

Tidal Inundation Characteristics

There were visible differences between the 4 native vegetation sites in proximity to the tidal creek and extent of tidal flooding. In order to estimate the relative frequency and intensity of tidal flooding within each of the sites, water depths at the bases of each sipper within each site were measured over portions of multiple daily tidal cycles. During the spring tide event in June (Fig. 3a), the TS and SS sites were flooded twice, the J site was flooded once, and the P site was not flooded. Within the J site, standing water continued to cover the sediment surface even after the high tide had fallen. Hourly measurements indicate that the tide fell faster than it rose, and there is a marked difference in inundation depth between the sites.

Water depth measurements were made during a neap tide event in order to determine the extent of inundation when tidal amplitudes were expected to be the least. The irregular timing of measurements (Fig. 3b) was an effort to record water depth associated only with the high tides of the neap event. Only TS is flooded twice on neap tides. The SS site was flooded once, and neither the J nor P sites were affected by tidal action. Measurements were made at half-hour intervals on this date in an attempt to capture more detail, since the length of

time water covers the marsh is relatively short and changes rapidly. The third set of measurements (Fig. 3c) were made during the middle of a single tidal cycle to determine if there were differences in flooding between the J and SS sites. Unfortunately, due to the timing of the high tides, only one high tide was captured on this date. Fig. 3c, therefore, does not indicate that the SS site is flooded twice daily on all but the lowest tide events in a cycle. These measurements do, however, reiterate the relative differences in magnitude of flooding and water depth coverage between the sites.

Water depth measurements was not made within the experimentally flooded sites for two reasons. First, under normal flooding conditions, the plots are not subject to daily tidal action. Second, artificial flooding was sporadic for most of the artificial flooding experiment. Therefore, water depths measured at any given time may not have necessarily been indicative of water coverage over the course of the experiments.

Fig. 3. Water depth measurements made using an aluminum meter stick taped to the base of each sipper in each native vegetation zone. Water depth was recorded periodically throughout a) a spring tide event, b) a neap tide event, and c) a mid-tidal cycle high tide.

Water Depth Measurements in Native Plant Zones - Spring Tide

a)

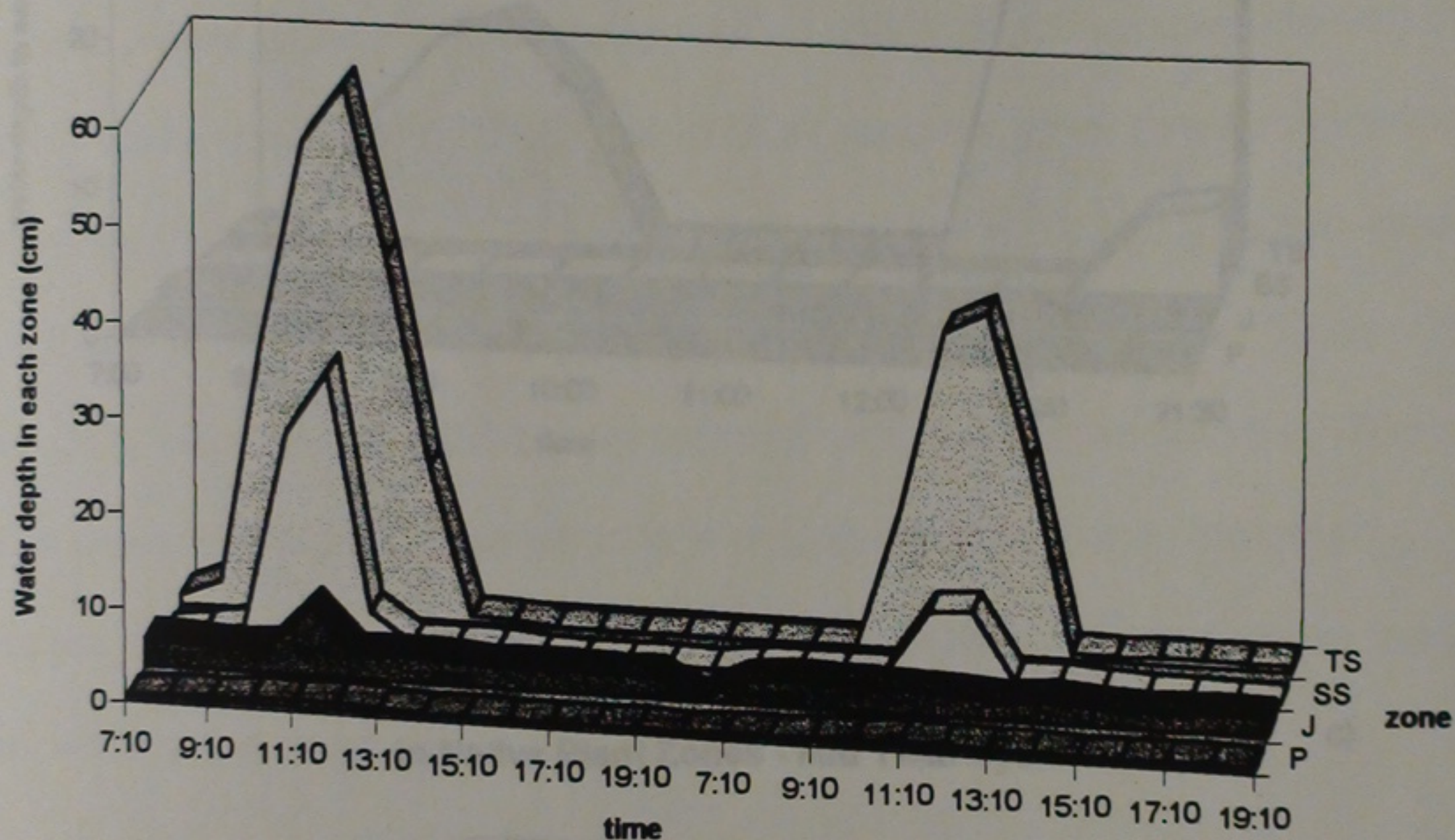
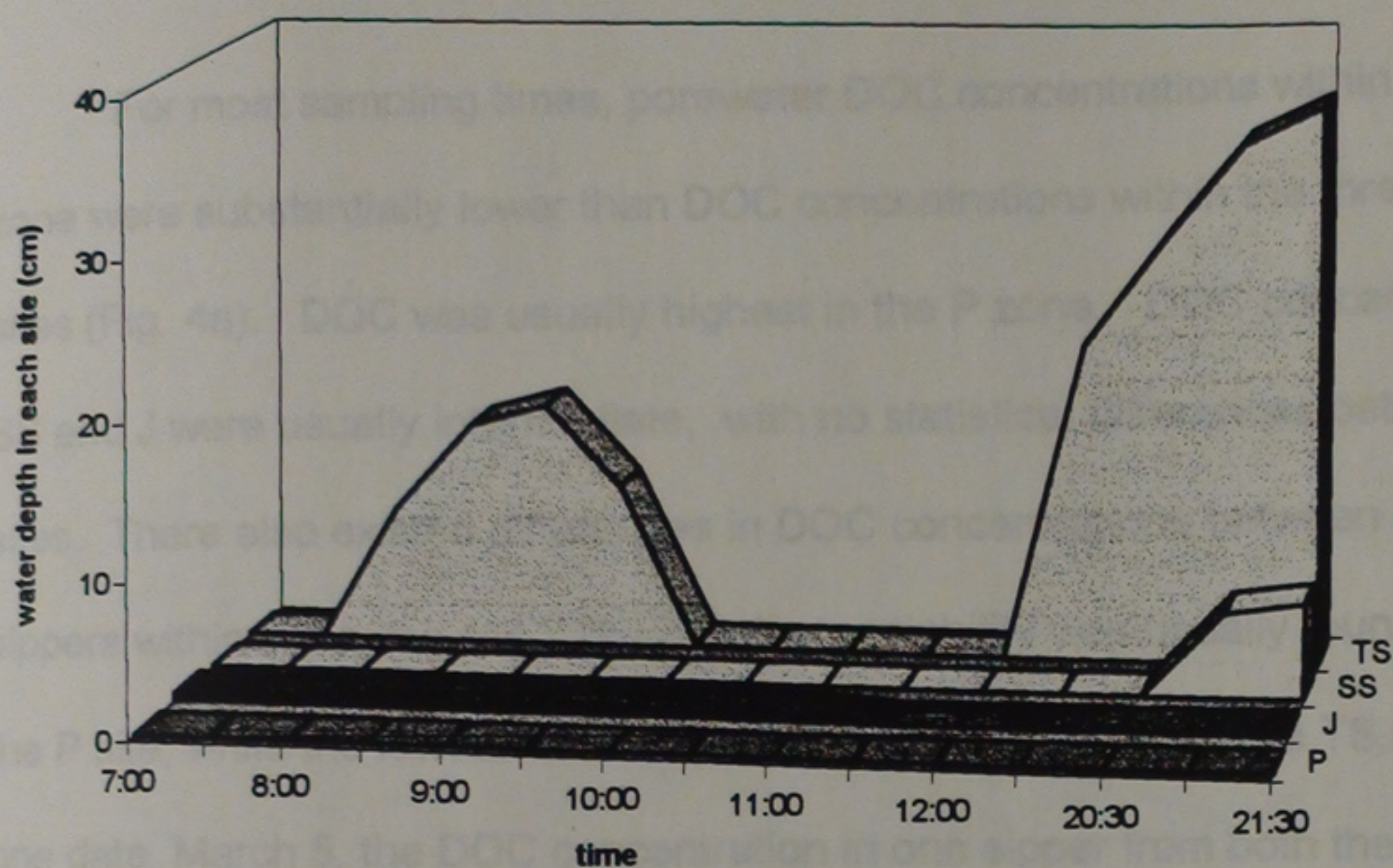


Fig. 3. Water depth measurements made using an aluminum meter stick taped to the base of each sipper in each native vegetation zone. Water depth was recorded periodically throughout a) a spring tide event, b) a neap tide event, and c) a mid-tidal cycle high tide.

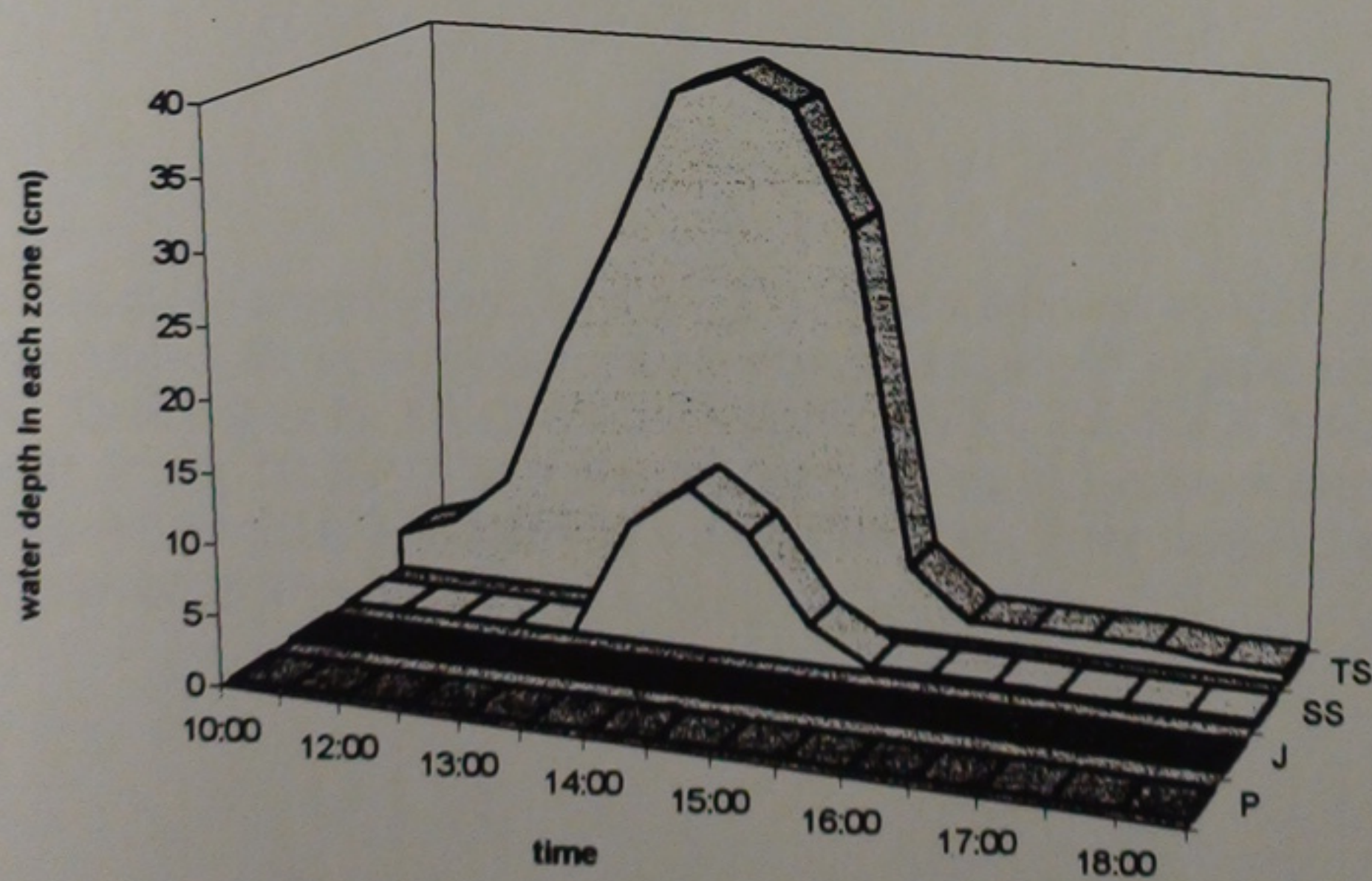
**Water Depth Measurements
in Native Plant Zones - Neap Tide**

b)



**Water Depth Measurements
in Native Plant Zones - Mid Tidal Cycle**

c)



DOC Quantity

DOC Concentrations

For most sampling times, porewater DOC concentrations within the TS zone were substantially lower than DOC concentrations within the three interior sites (Fig. 4a). DOC was usually highest in the P zone. DOC concentrations in SS and J were usually intermediate, with no statistical differences between the sites. There also existed differences in DOC concentrations between individual sippers within the same site. The greatest variability was usually found within the P site, while the lowest variability was usually found within the TS site. On one date, March 5, the DOC concentration in one sipper from both the TS and J sites was extremely high compared to the concentrations within the other sippers, resulting in extremely elevated average DOC concentrations for these two sites on this sampling date.

Fig. 4a. Dissolved organic carbon (mg C L^{-1}) concentrations at each native vegetation zone. All data points represent the average of 3 independent samples. Data points for TS 10-17, TS & J 2-4, TS & J 3-5, SS & P 4-21, TS 6-7, SS 6-21, P 7-8, TS & P 7-24 represent the average of 2 independent samples. The data point for SS 9-7 represents a single sample. Error bars represent one standard deviation from the mean.

DOC Concentrations

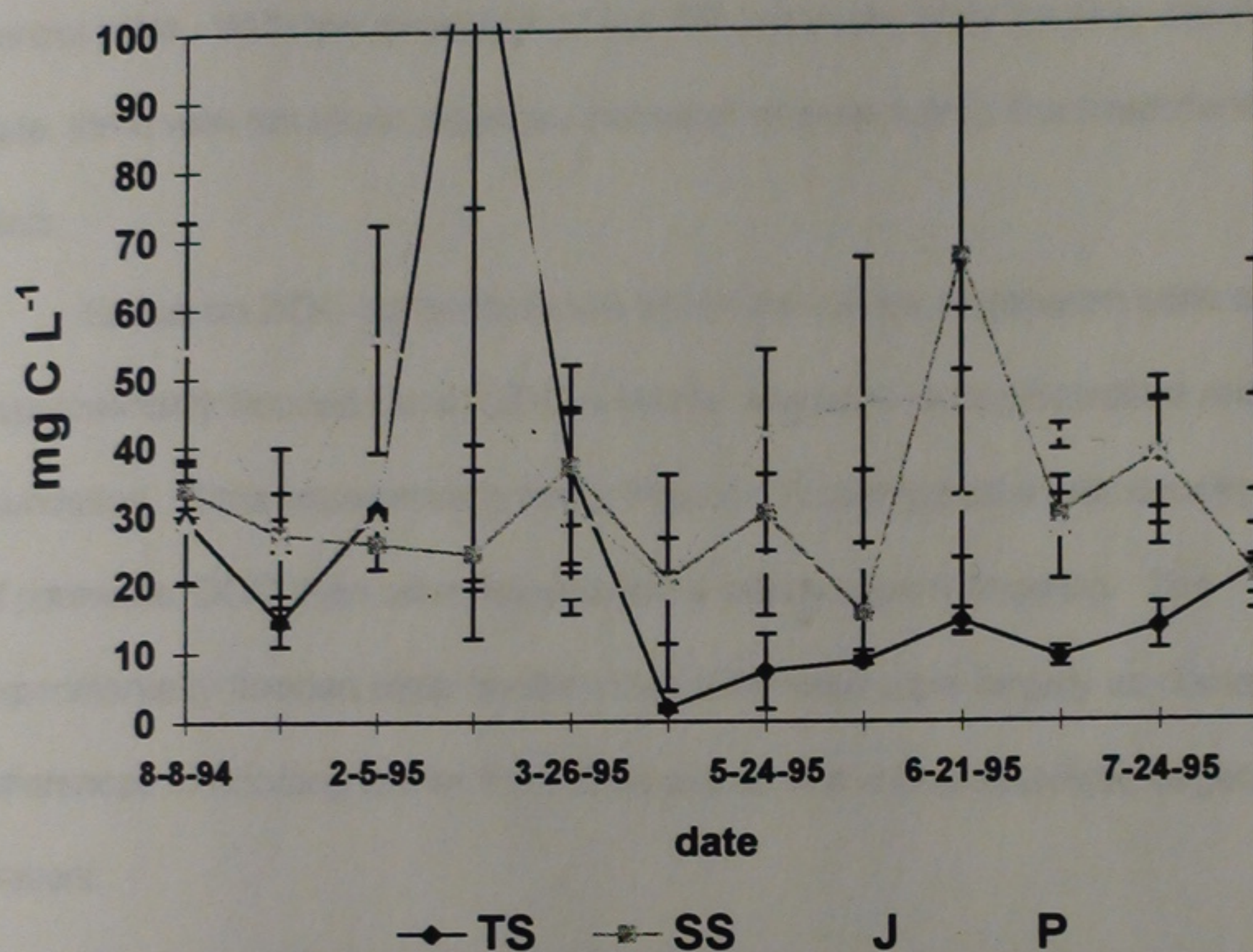


Fig. 4a. Dissolved organic carbon (mg C L^{-1}) concentrations at each native vegetation zone. All data points represent the average of 3 independent samples. Data points for TS 10-17, TS & J 2-4, TS & J 3-5, SS & P 4-21, TS 6-7, SS 6-21, P 7-8, TS & P 7-24 represent the average of 2 independent samples. The data point for SS 6-7 represents a single sample. Error bars represent one standard deviation from the mean.

inundation frequency for the plots. At the July 25 sampling date, there were substantial differences between DOC concentrations within the flooded and control plots. With the exception of the PF treatment from the May sampling date, there was not much variation between sippers within like treatments and plots.

Based on DOC concentrations within the native vegetation sites and the experimentally flooded plots, DOC quantity appears to be controlled primarily by inundation. Sites experiencing more frequent flooding had lower concentrations of porewater DOC than sites experiencing less frequent flooding. The experimentally flooded plots confirm that differences are largely attributable to differences in flooding rather than differences in the characteristic vegetation present.

Porewater DOC concentrations within the experimentally flooded plots were also found to be elevated in plots experiencing less frequent flooding (Fig. 4b). The May sampling was indicative of pre-flooding conditions. Up to this date, only 27369.3 liters of creek water had been pumped onto the plots over the course of almost 2 months. DOC concentrations within the F and C treatments were not different during May. However, the July sampling was indicative of increased flooding in these plots. A total of 72232.9 liters had been pumped up to this sampling date, on a more regular schedule, reflecting a true change in

DOC Concentrations Experimentally Flooded Plots

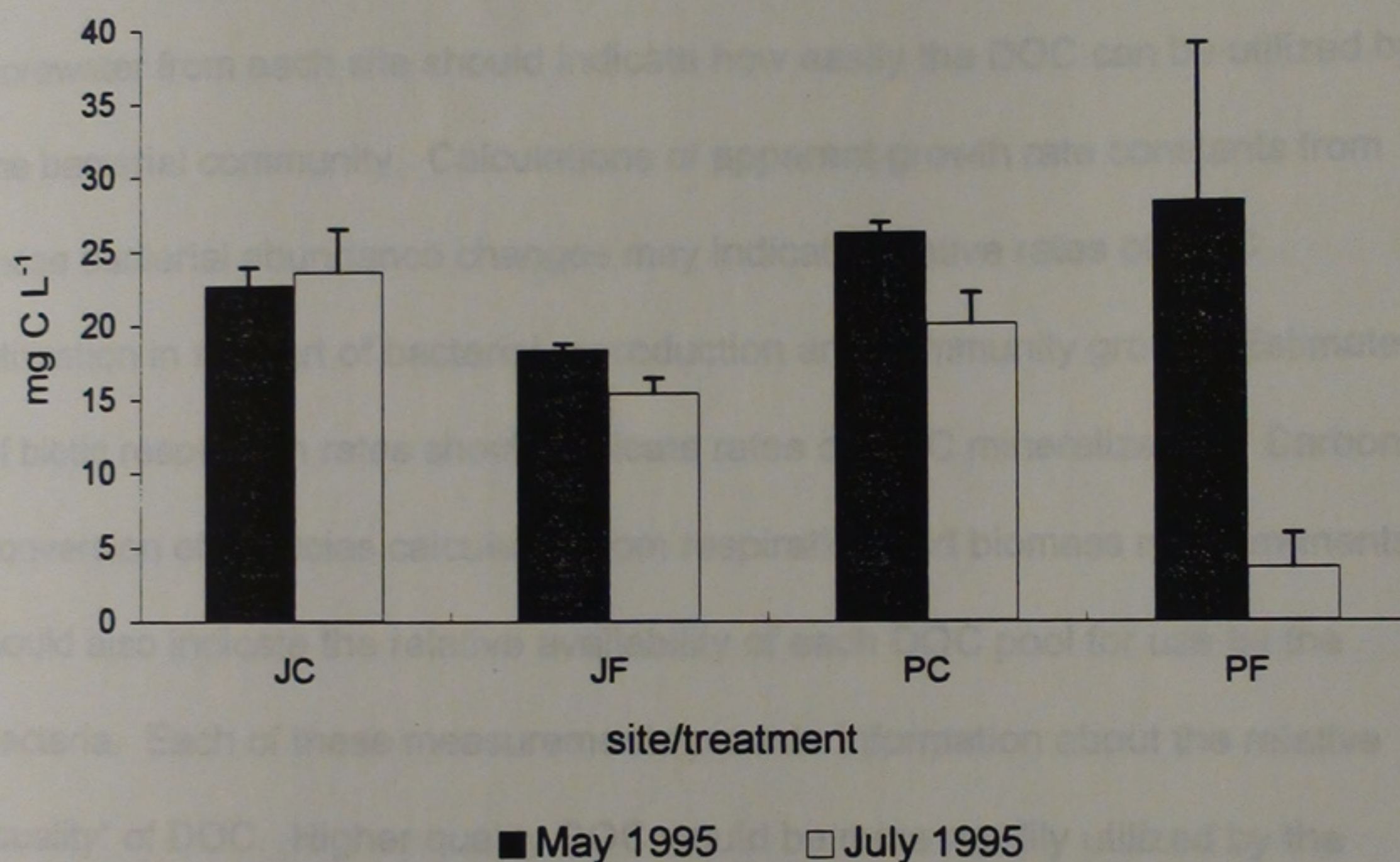


Fig. 4b. Dissolved organic carbon (mg C L^{-1}) concentrations within the experimentally flooded plots. All data bars represent the average of 3 independent samples within each treatment. Data bars for JF 5-24 and PF 7-25 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

DOC Availability

Bacterial Abundance

Several measures were used to ascertain the relative availability of DOC from different sites to bacteria from a common source. Changes in bacterial abundances (i.e. production) after a specific incubation period in filtered porewater from each site should indicate how easily the DOC can be utilized by the bacterial community. Calculations of apparent growth rate constants from these bacterial abundance changes may indicate relative rates of DOC utilization in support of bacterial reproduction and community growth. Estimates of biotic respiration rates should indicate rates of DOC mineralization. Carbon conversion efficiencies calculated from respiration and biomass measurements would also indicate the relative availability of each DOC pool for use by the bacteria. Each of these measurements provide information about the relative "quality" of DOC. Higher quality DOC would be more readily utilized by the bacterial community; changes in bacterial abundances, higher apparent growth rate constants, greater rates of biomass production and higher rates of respiration would be expected of bacteria growing on higher quality DOC.

values, negative and positive were used in calculations

Bacterial Abundance

Changes in bacterial abundance per hour (Fig. 5a) were significantly different between sampling dates, but not between sampling sites. Decreases in abundance over the incubation period (bacterial abundance at the end of the incubation lower than at the beginning) are represented by negative changes in abundance. Changes in bacterial abundance were strongly and negatively correlated with initial bacterial abundance ($r = -0.5709$) and total respiration measurements ($r = -0.4801$).

Changes in bacterial abundance within the experimentally flooded plots were not significantly different between sites or dates (Fig. 5b). There were differences in changes in abundance between flooded and control treatments within the J plots but not in the P plots. The large error associated with the July JF treatment is due to negative changes in bacterial abundance caused by subtracting a larger initial abundance from a smaller final abundance. All values, negative and positive were used in calculations.

Change in Abundance per Hour

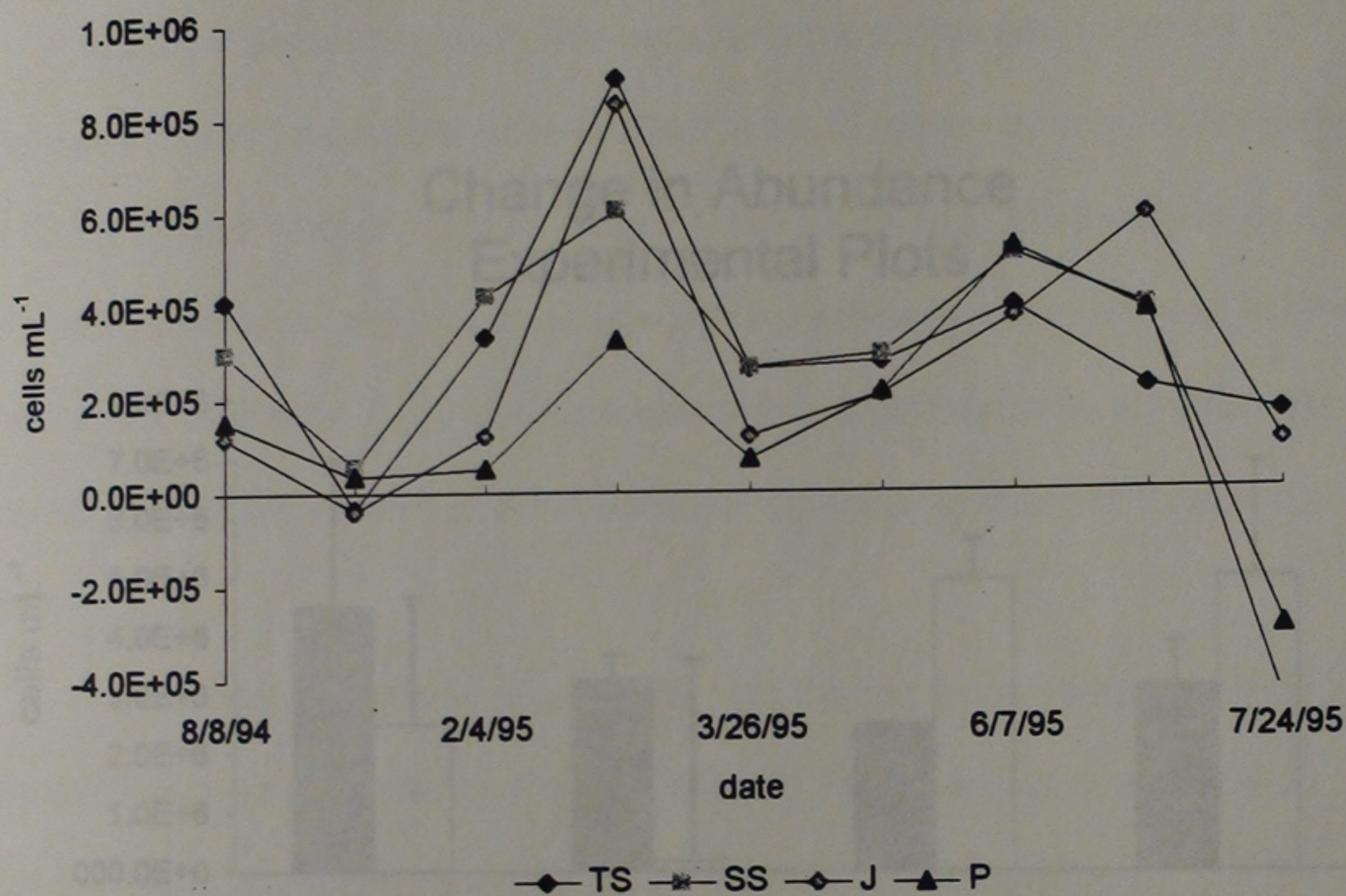


Fig 5a. Changes in bacterial abundance in each native vegetation zone. Change in abundance equals final abundance (after 24 h) minus initial abundance. Each data point represents the average of 3 independent samples. Data points for TS 10-17, SS & J 2-4, TS & J 3-5, J 3-26, SS 4-21, TS 6-7, P 7-8, TS, SS & P 7-24 represent the averages of 2 independent samples. The data points for TS 2-4, TS 3-26, and SS 6-7 represent a single sample. Standard deviations for data points were large and variable, and therefore excluded.

Apparent Bacterial Growth Rate Constants

Apparent bacterial growth rate constants were calculated from the changes in bacterial abundance measured in the bioassay to determine relative DOC quality from March 5 and July 25. On these dates a 24 hour incubation bioassay was done in which substrates were removed at times 0, 5, 12, and 24 hours. For these sampling dates, initial bacterial abundance was determined from the 0 hour time point. Bacterial abundance was determined from the 24 hour time point. For these sampling dates, initial bacterial abundance was determined from the 0 hour time point. Bacterial abundance was determined from the 24 hour time point.

Change in Abundance Experimental Plots

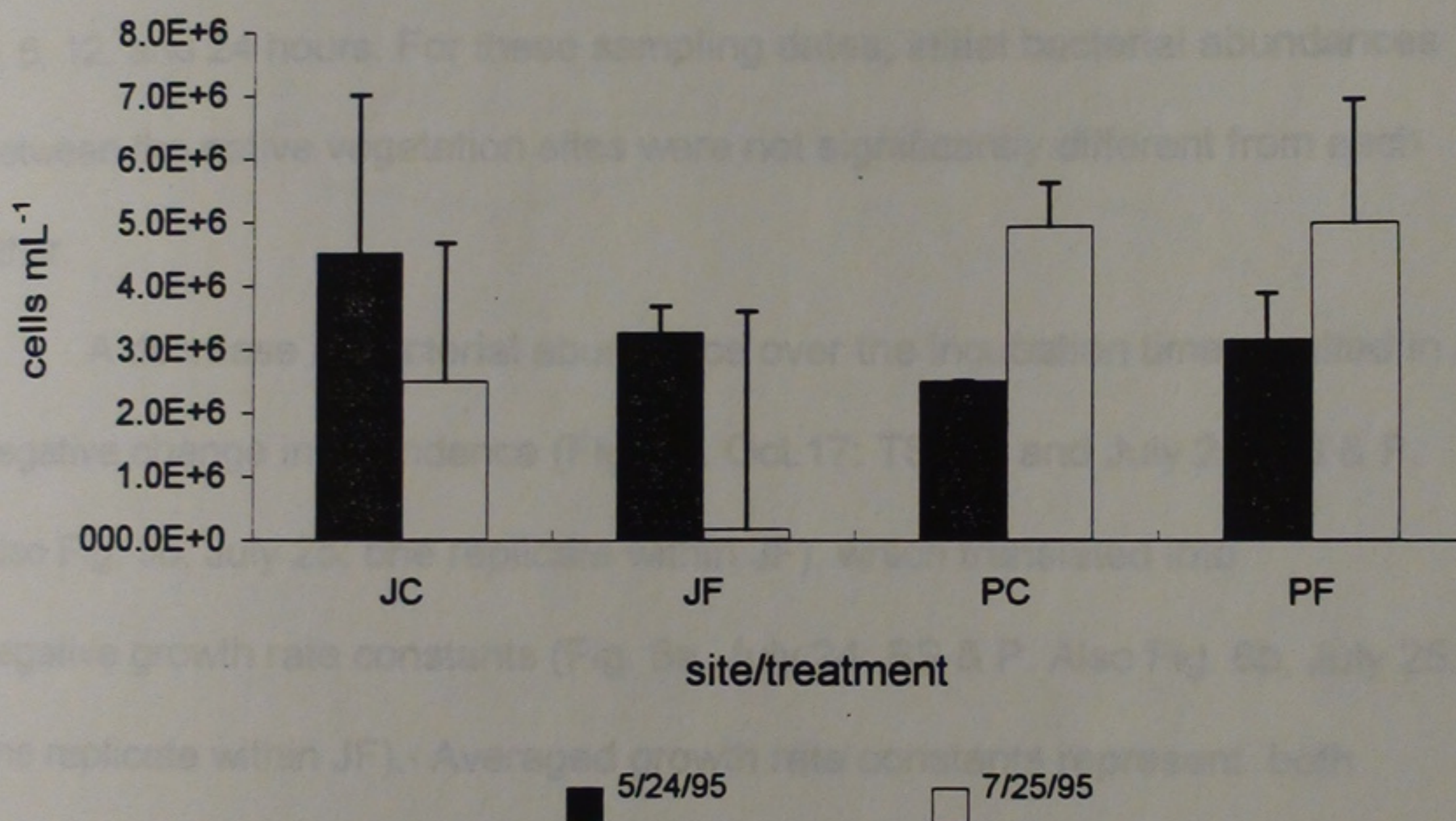


Fig. 5b. Changes in bacterial abundances in the experimentally flooded plots. Change in abundance equals final abundance (after 24 h) minus initial abundance. Each data point represents the average of 3 independent samples. JC, JF, & PC 5-24 and PF 7-25 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

Apparent Bacterial Growth Rate Constants

Apparent bacterial growth rate constants were calculated from the changes in bacterial abundance measured in the bioassay to determine relative DOC quality from March 5 through July 24, 1995 (Fig. 6a). On these dates a 24 hour incubation bioassay was done in which subsamples were removed at times 0, 6, 12, and 24 hours. For these sampling dates, initial bacterial abundances between the native vegetation sites were not significantly different from each other.

A decrease in bacterial abundance over the incubation time resulted in a negative change in abundance (Fig. 5a, Oct.17: TS & J and July 24: SS & P. Also Fig. 5b, July 25: one replicate within JF), which translated into negative growth rate constants (Fig. 6a, July 24: SS & P. Also Fig. 6b, July 25: one replicate within JF). Averaged growth rate constants represent both positive and negative values. Growth rate constants were not significantly different between sites or dates. However, growth rate constants were negatively correlated with salinity ($r = -0.4849$), H_2S concentration ($r = -0.4594$), Total respiration measurements ($r = -0.4931$), and with initial bacterial abundance ($r = -0.7649$).

Similar to data for bacterial growth on DOC from the 4 native vegetation zones, no statistical differences were found between apparent growth rate.

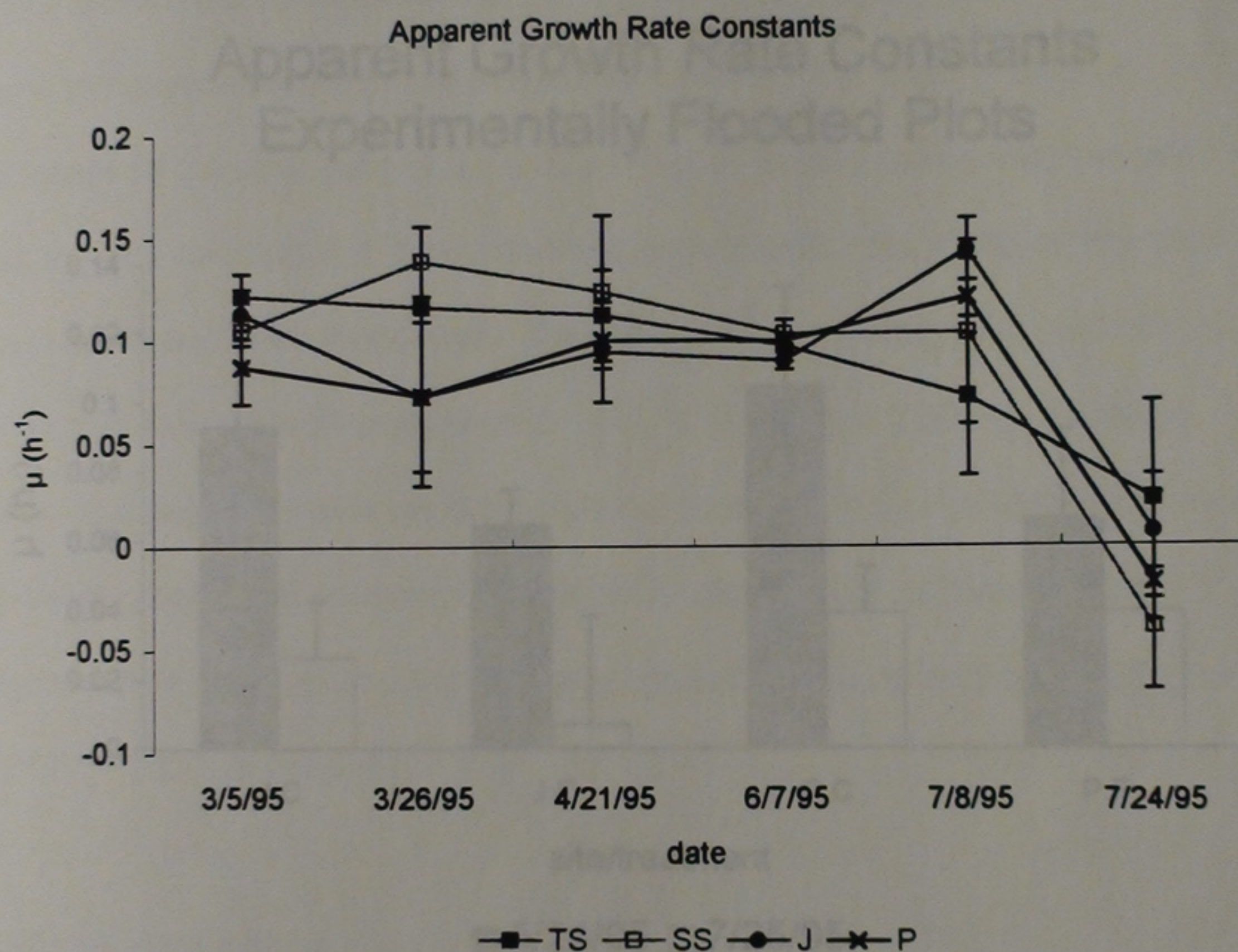


Fig. 6a. Apparent growth rate constants for each native vegetation zone calculated from changes in bacterial abundances. Data points represent the average of 3 independent samples. Data points for TS, SS, & J 3-5, J 3-26, TS 6-7, P 7-8, and TS & P 7-24 represent the average of 2 independent samples. The data points for TS 3-26 and SS 6-7 represent a single sample. Error bars represent one standard deviation from the mean.

Apparent Growth Rate Constants Experimentally Flooded Plots

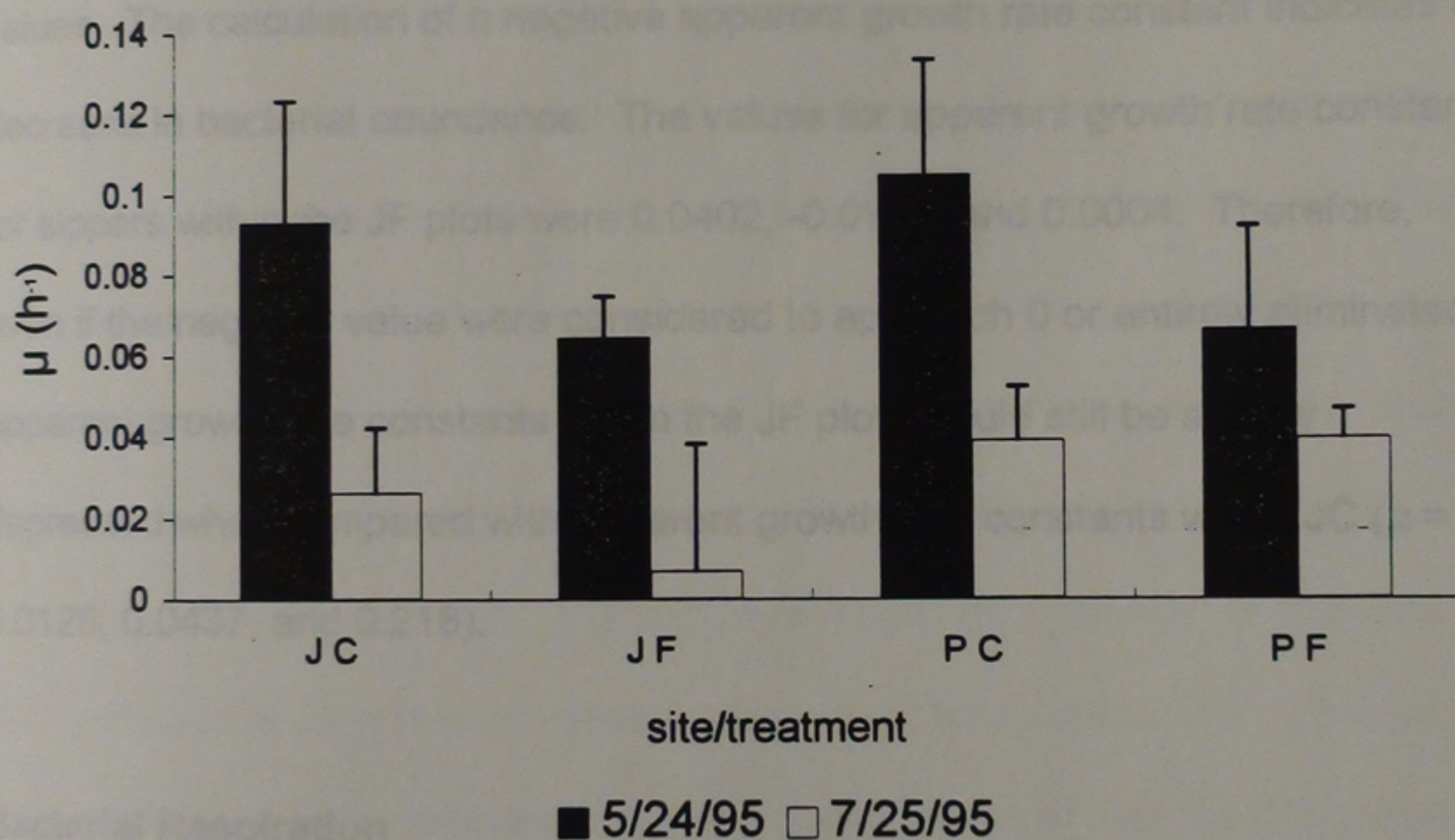


Fig. 6b. Apparent growth rate constants for the experimentally flooded plots calculated from changes in bacterial abundances. Each data bar represents the average of 3 independent samples. Data points for JC, JF, & PC 5-24 and JF 7-25 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

constants within control and flooded treatments for either sampling date (Fig. 6b) in the experimentally flooded plots. However, there was a depression of growth rate constants within the JF treatment (control $\mu = 0.0261$, flooded $\mu = 0.007$) in July compared to the PF treatment (control $\mu = 0.0386$, flooded $\mu = 0.0388$). Since growth rate constants were calculated from changes in abundance, the large standard deviation in the JF treatment in July (Fig. 6b) can also be explained by the averaging of a negative change in abundance with two positive values. The calculation of a negative apparent growth rate constant indicates a decrease in bacterial abundance. The values for apparent growth rate constants for sippers within the JF plots were 0.0402, -0.0197, and 0.0004. Therefore, even if the negative value were considered to approach 0 or entirely eliminated, apparent growth rate constants within the JF plots would still be slightly depressed when compared with apparent growth rate constants within JC ($\mu = 0.0129$, 0.0437, and 0.218).

Bacterial Respiration

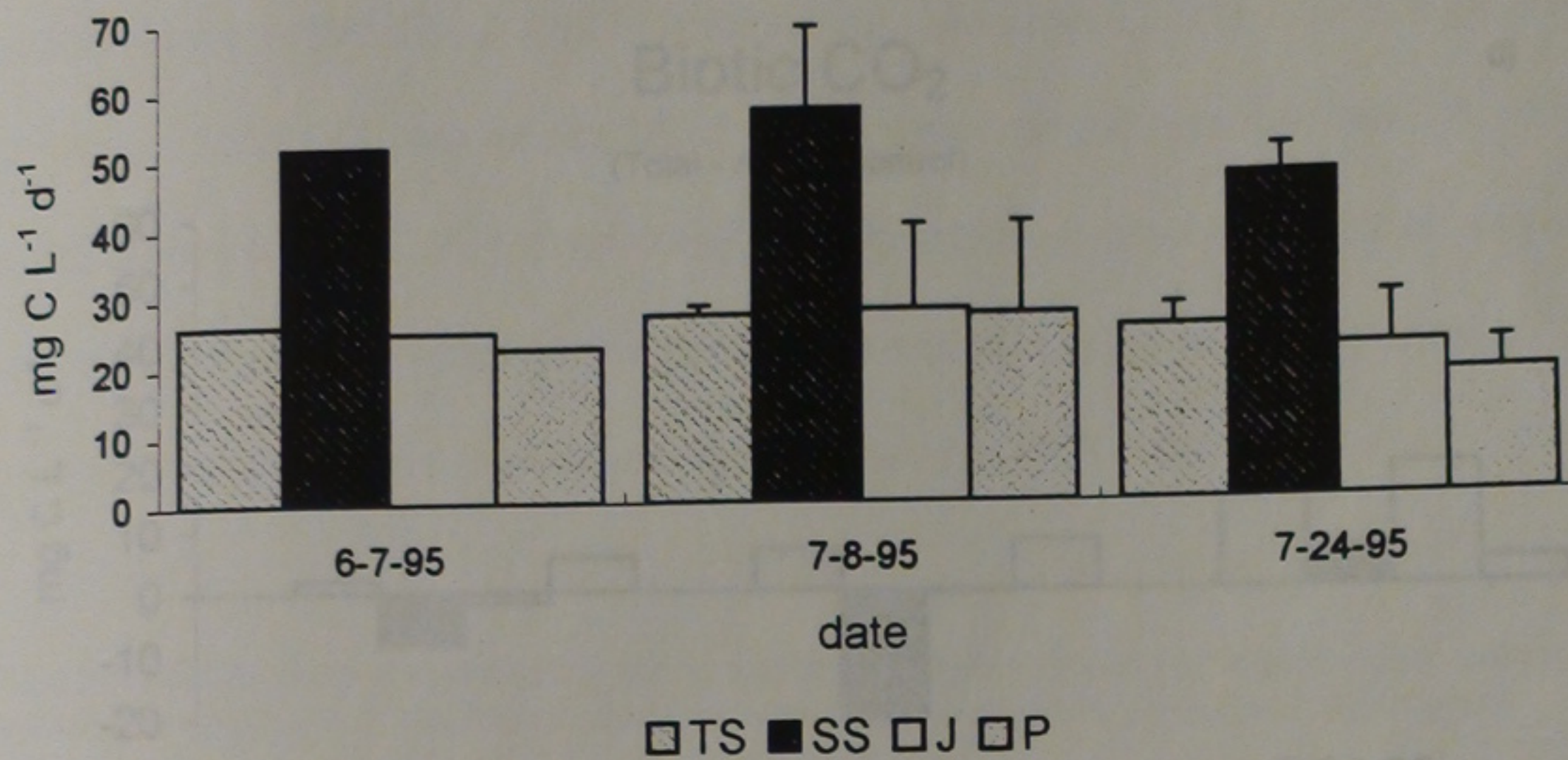
Total CO₂ data (Fig. 7a) represent the CO₂ titrated from vials allowed to incubate for 24 hours before acidification. They include CO₂ from abiotic and biotic sources. The abiotic control CO₂ data (Fig. 7b) represent CO₂ titrated from the vials which were acidified prior to incubation. These data represent CO₂ from abiotic sources only and was treated as the bioassay control. The

biotic CO_2 data (Fig. 7c) represent the difference between the abiotic control the total CO_2 . Negative biotic CO_2 values (Fig. 7c: June 7 and July 8 SS & J) represent samples where the abiotic control contained more trapped carbon dioxide than the total CO_2 vials.

Abiotic CO_2 values from the June 7 experiment were erroneous due to the addition of formaldehyde to inhibit microbial activity within the vials. Formaldehyde, HCHO , is a carbon-based compound. Its use in the inhibition of microbial activity may have provided an additional carbon source for reaction with the NaOH within each well. The acid-base titration used to determine CO_2 evolved was a simple acid-base titration; HCl was added to the NaOH soaked filter paper in water in order to determine the amount of NaOH remained. Based on the amount of NaOH remaining, a calculation determines how much CO_2 must have been present within the vial for reaction. If formaldehyde provided another reactive carbon source, less NaOH would have remained in the well. This would have been reflected in elevated calculations of evolved CO_2 within the abiotic vials. Due to the probability that additional reactions may have occurred within the abiotic vials on this date, the abiotic control values (Fig. 7b) for June 7 were calculated as the mean of the abiotic control values from the July 8 and July 24 sampling dates.

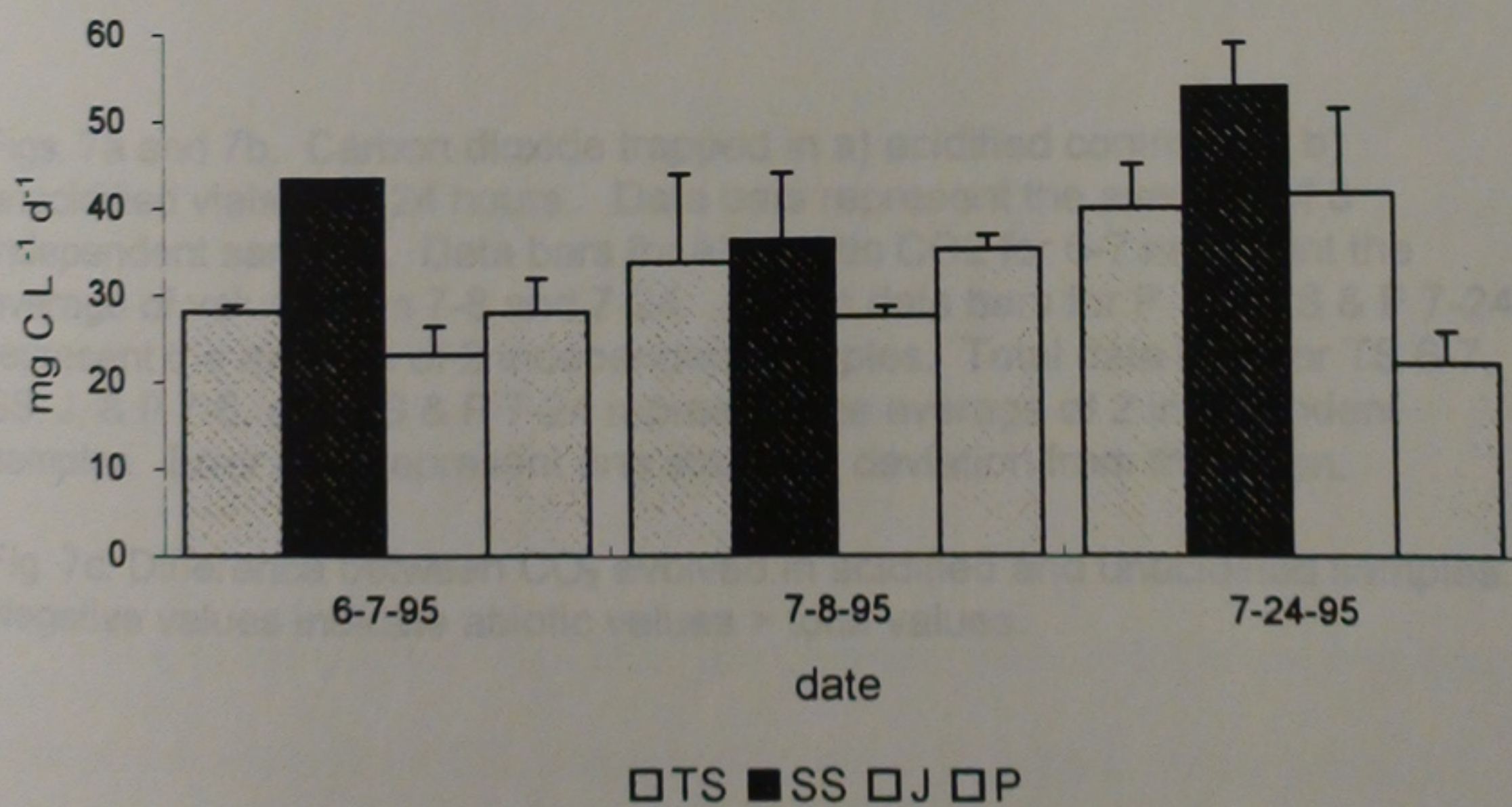
Abiotic control CO₂ (acidified incubations)

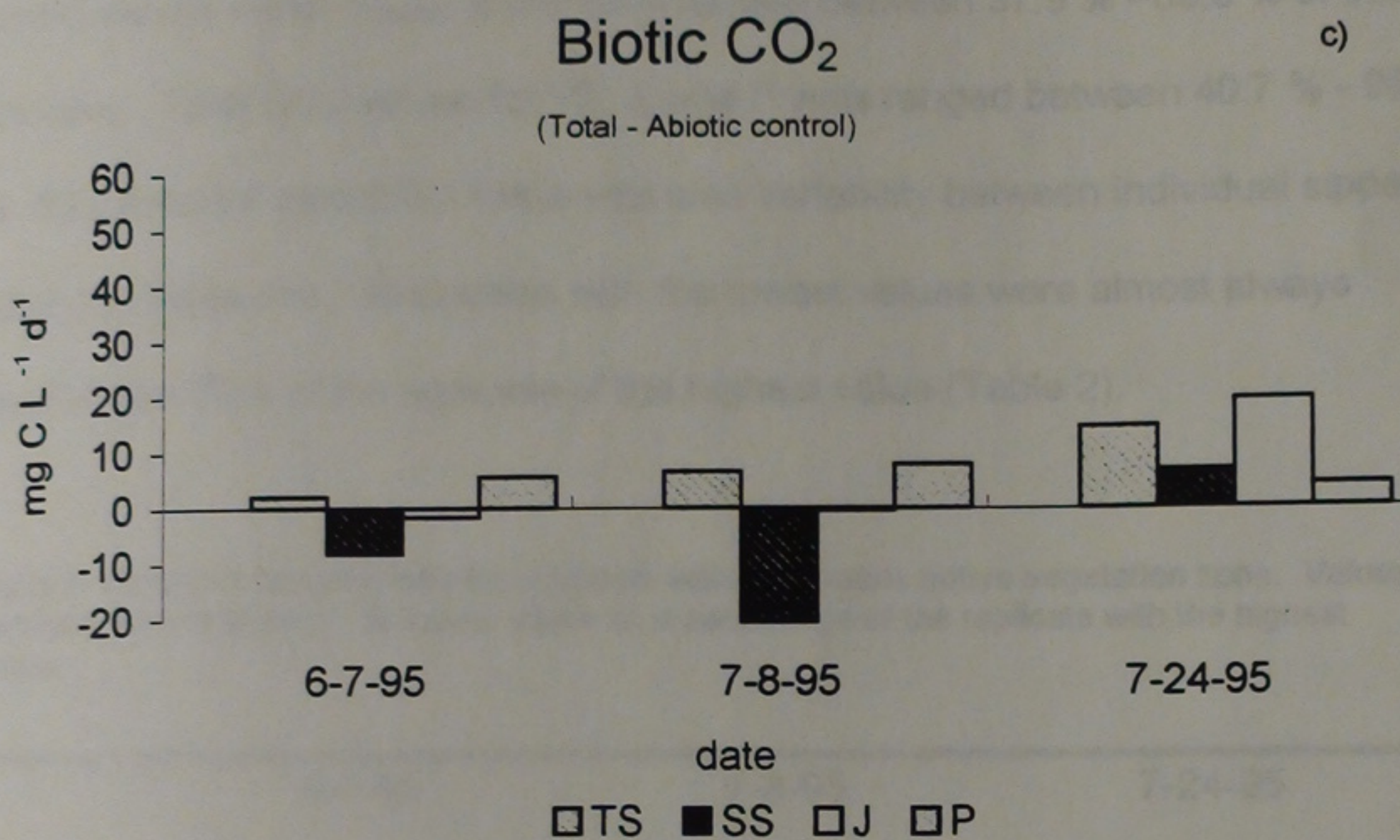
a)



Total CO₂ (unacidified incubations)

b)





Figs. 7a and 7b. Carbon dioxide trapped in a) acidified control and b) unacidified vials over 24 hours. Data bars represent the average of 3 independent samples. Data bars for all abiotic CO₂ for 6-7 represent the average of values from 7-8 and 7-24. Abiotic data bars for P 7-8, TS & P 7-24 represent the average of 2 independent samples. Total data bars for TS 6-7, SS, J, & P 7-8, and TS & P 7-24 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

Fig. 7c. Difference between CO₂ evolved in acidified and unacidified samples. Negative values indicate abiotic values > total values.

The largest respiration measurements within both the abiotic control and total CO₂ vials occurred within the SS site. For all three bioassay dates, abiotic control values within TS, J, and P vials ranged between 37.9 % - 53.8 % of the SS value. Total CO₂ values for TS, J, and P vials ranged between 40.7 % - 96.7 % SS values for total CO₂. There was also variability between individual sippers within the same site. Replicates with the lowest values were almost always greater than 50% of the replicate of the highest value (Table 2).

Table 2. Variability between individual sippers within the same native vegetation zone. Values represent the replicate of the lowest value as a percentage of the replicate with the highest value.

site	6-7-95		7-8-95		7-24-95	
	abiotic	total	abiotic	total	abiotic	total
TS		94.4	88.9	45.0	78.6	77.5
SS			63.4	91.5	84.5	89.4
J		70.6	29.2	94.3	50.0	56.7
P		71.2	35.0	64.1	60.0	71.5

Due to the unclear respiration data, several tests of statistical significance were performed on total CO₂ alone and on biotic CO₂ data. While biotic CO₂ data were not correlated with any other measurements, total CO₂ data alone were negatively correlated with soil PEP ($r = -0.8801$), changes in abundance

($r = -0.4801$) and growth rate constant ($r = -0.4931$), and positively correlated with H_2S and PO_4^{3-} concentrations ($r = 0.5614$) and ($r = 0.5244$), respectively.

Respiration measurements were only made on July 25 within the experimentally flooded plots. Biotic CO_2 estimates (Fig. 8) within the experimental plots were slightly elevated in the flooded treatments compared to the control treatments for both plant species (6.61, 10.94, 2.0, and 5.2 mg C l^{-1} for JC, JF, PC, and PF, respectively). Negative values representing abiotic CO_2 fixation were measured within at least one abiotic control vial from each site and treatment. Calculations of biotic CO_2 did not include these negative values, due to the uncertainty of their origin. There was also variability associated with individual sippers within the same treatment. Total CO_2 variability (lowest value replicate expressed as a percentage of the highest value replicate) ranged between 17.1 % - 58.5 %. Variability for JF and PC abiotic control vials were 46.7 % and 35.7 %. Due to negative replicates within JC and PF, no calculation may be made. Such variability may render respiration estimates from the experimentally flooded plots inutile.

July Biotic CO₂ Measurements Experimentally Flooded Plots

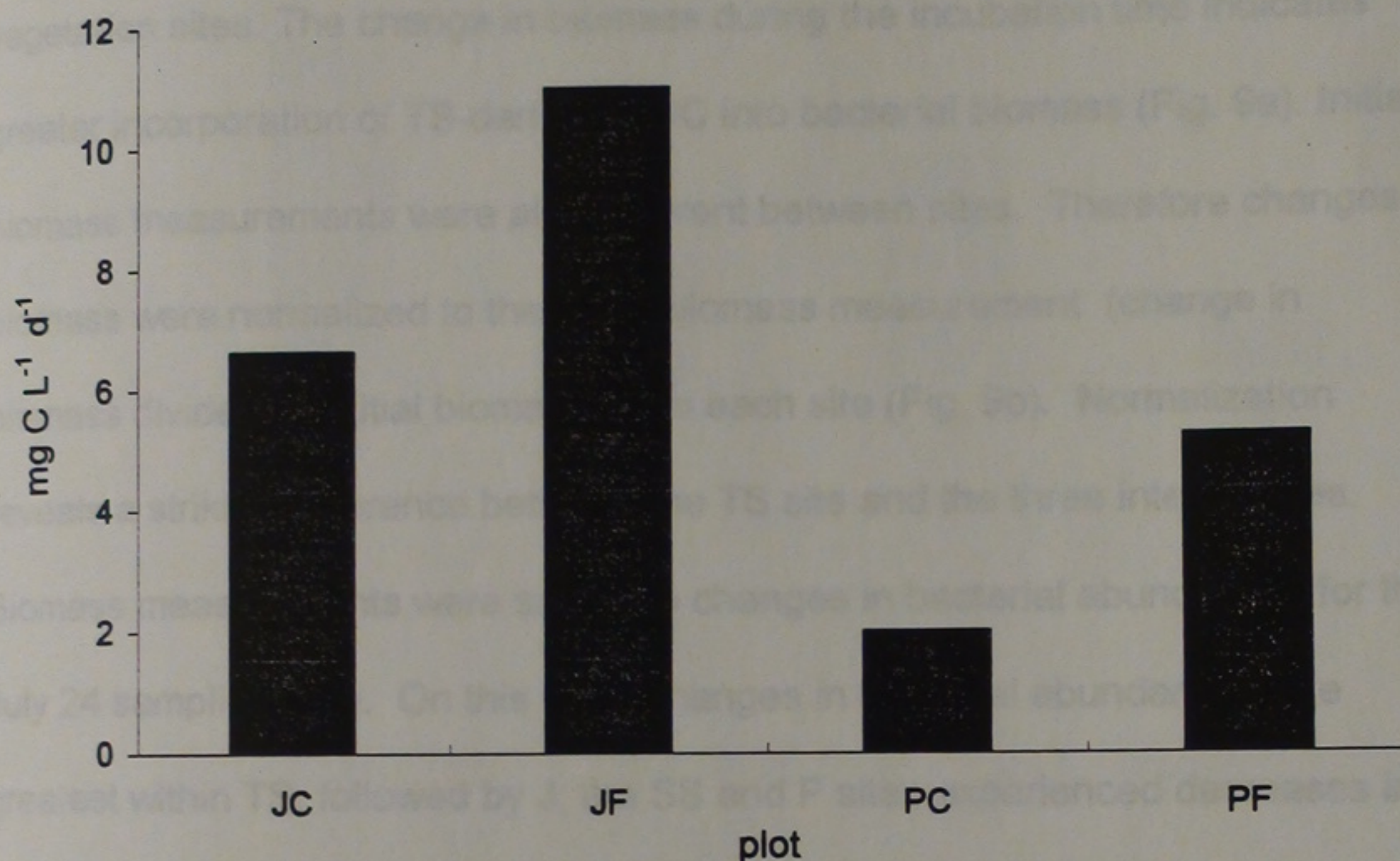


Fig. 8. Carbon dioxide evolved over 24 h incubation within sealed vials from the experimentally flooded plots. Data bars represent CO₂ evolved within acidified (abiotic control) vials subtracted from CO₂ evolved within unacidified (total CO₂) vials. Each data bar represents the average of 3 (JF, JC, & PF represent the average of 2) independent acidified samples subtracted from 3 (JC & PF represent the average of 2) independent unacidified samples.

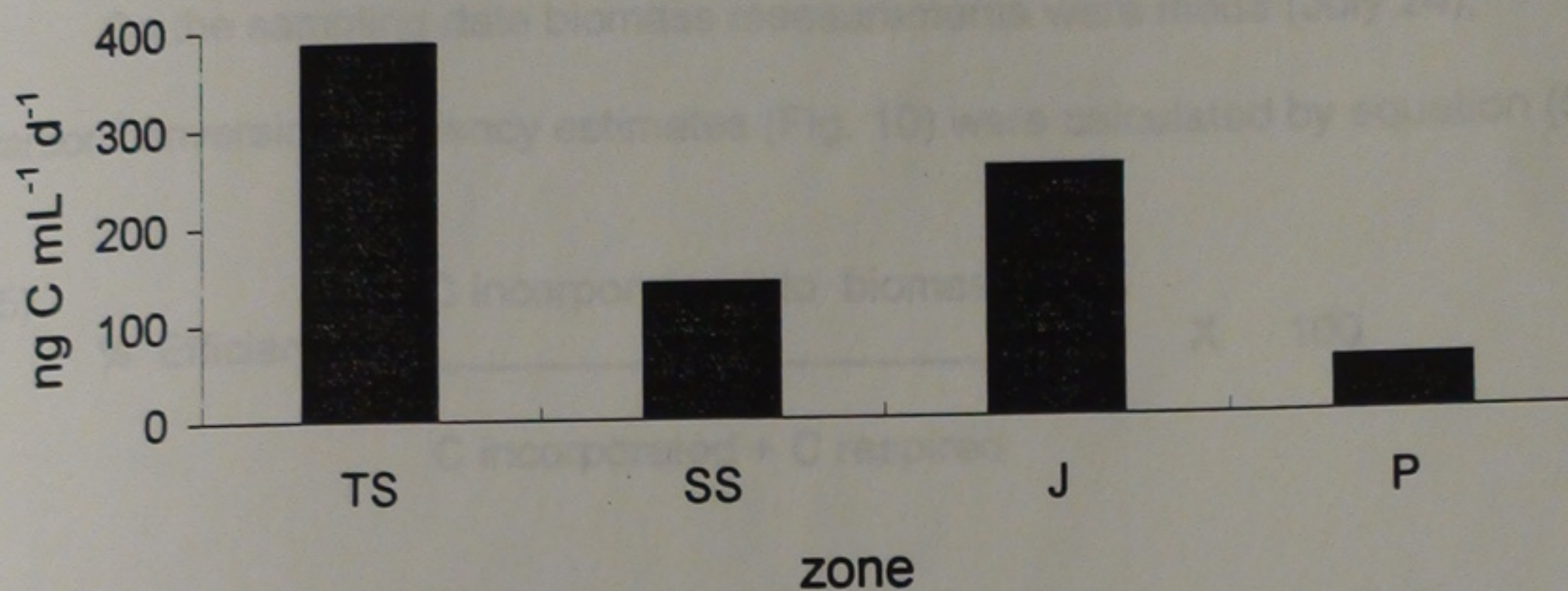
Bacterial Biomass

Bacterial biomass was determined only on July 24 for the 4 native vegetation sites. The change in biomass during the incubation time indicates greater incorporation of TS-derived DOC into bacterial biomass (Fig. 9a). Initial biomass measurements were also different between sites. Therefore changes in biomass were normalized to the initial biomass measurement (change in biomass divided by initial biomass) from each site (Fig. 9b). Normalization reveals a striking difference between the TS site and the three interior sites. Biomass measurements were similar to changes in bacterial abundances for the July 24 sampling date. On this date, changes in bacterial abundance were greatest within TS, followed by J; the SS and P sites experienced decreases in bacterial abundance over the incubation (Fig. 5a). Similarly, changes in bacterial biomass, and normalized changes in biomass, were greatest in TS, followed by J, SS, and P, respectively.

Fig. 9. Bacterial biomass production shows 24 h incubation time and normalized to initial biomass measurement. Change in biomass equals initial biomass subtracted from final biomass.

Bacterial Biomass Production 7/24/95

a)



Normalized Changes in Biomass 7/24/95

b)

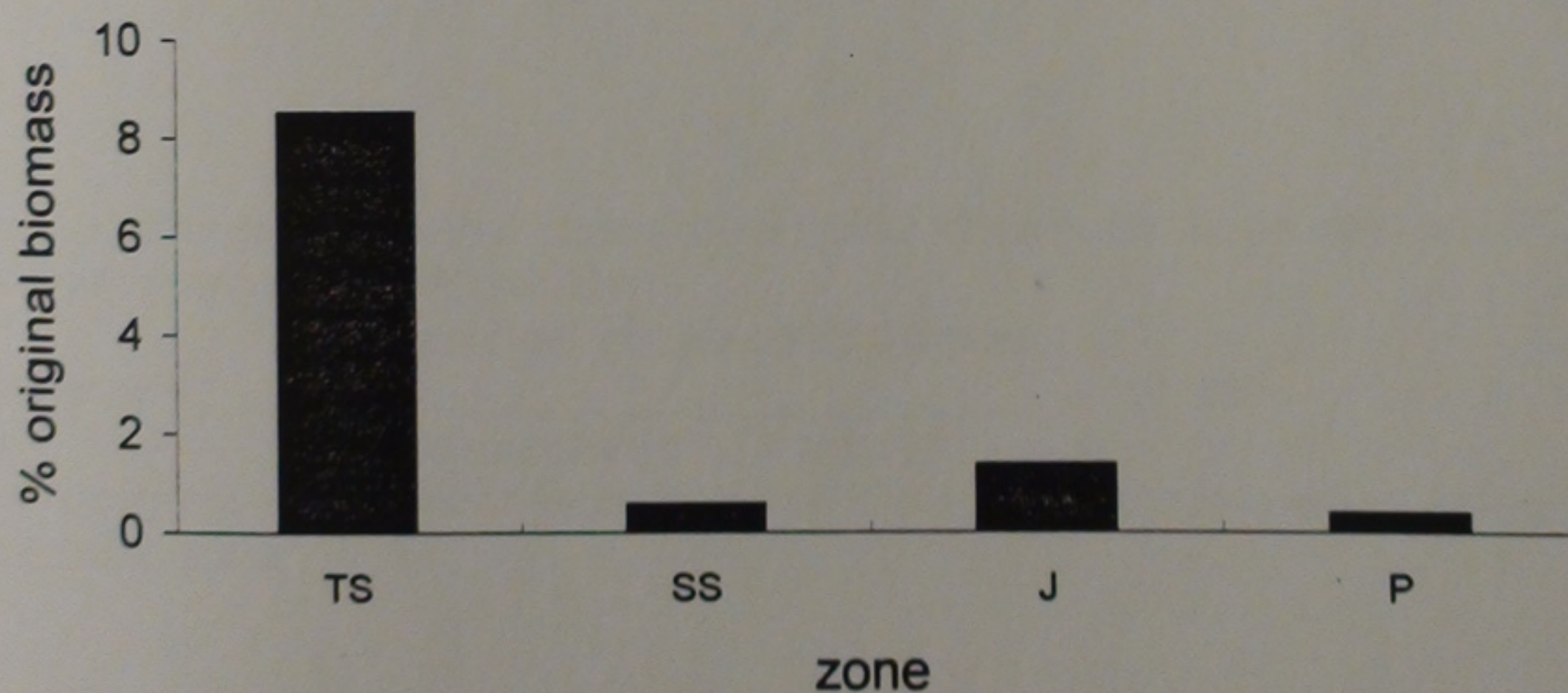


Fig. 9. Bacterial biomass production a) over 24 h incubation time and b) normalized to initial biomass measurement. Change in biomass equals initial biomass subtracted from final biomass.

Bacterial Carbon Conversion Efficiency

On the sampling date biomass measurements were made (July 24), carbon conversion efficiency estimates (Fig. 10) were calculated by equation (5):

$$(5) \quad \% \text{ Efficiency} = \frac{\text{C incorporated into biomass}}{\text{C incorporated} + \text{C respired}} \times 100$$

There were no substantial differences between the sites.

Fig. 10. Estimated bacterial carbon conversion efficiencies for growth on DOC from each native vegetation zone.

Efficiency = $\frac{\text{C incorporated into bacterial biomass}}{\text{C incorporated} + \text{C respired}} \times 100$
 Percentage above each bar represents the efficiency for the respective native vegetation zone.

Bacterial Efficiencies 7/24/95

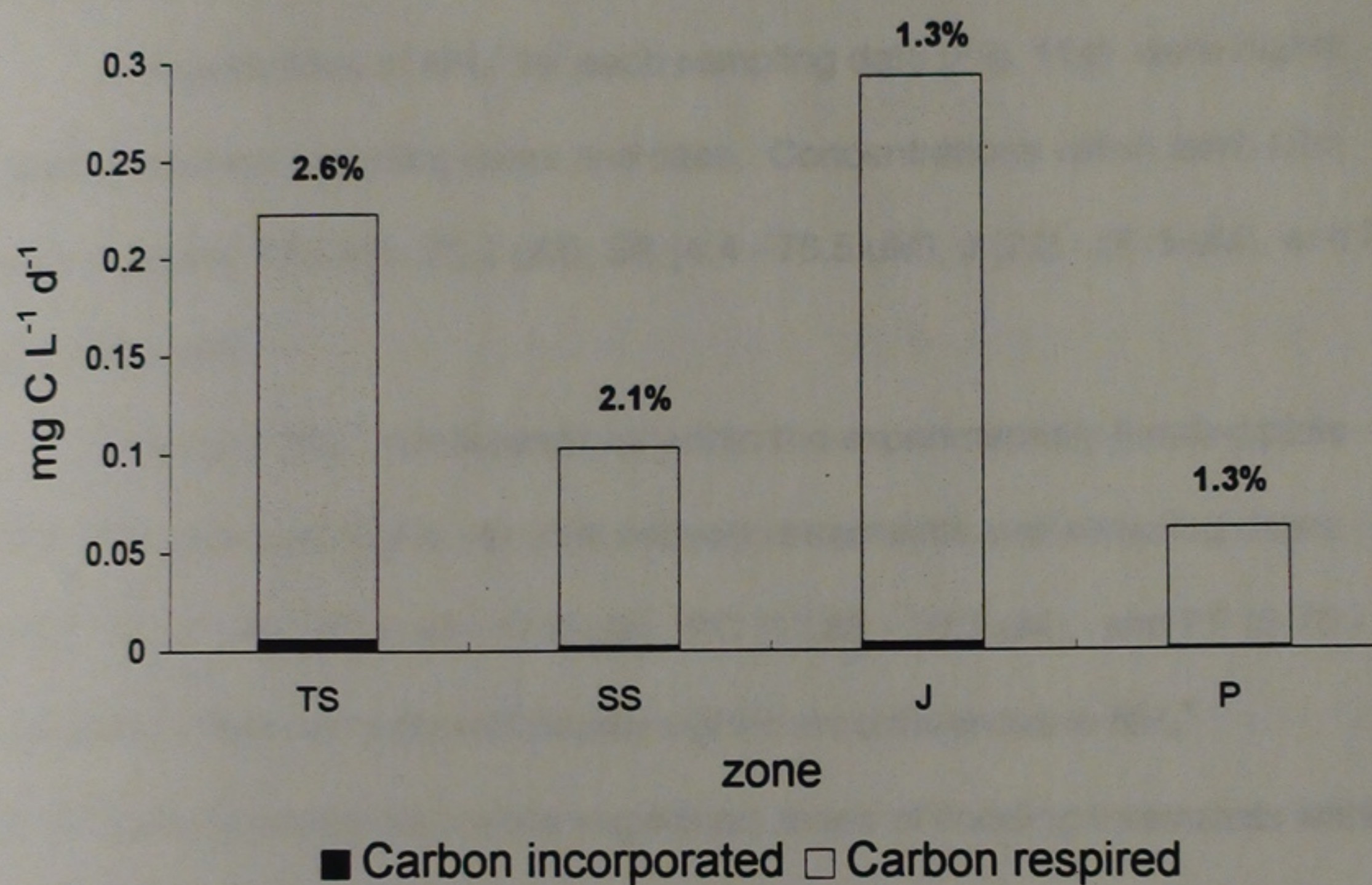


Fig. 10. Estimated bacterial carbon conversion efficiencies for growth on DOC from each native vegetation zone.

$$\text{Efficiency} = \frac{\text{C incorporated into bacterial biomass}}{\text{C incorporated} + \text{C respired}} \times 100$$

Percentage above each bar represents the efficiency for the respective native vegetation zone.

Nutrients

Ammonium

Concentrations of NH_4^+ for each sampling date (Fig. 11a) were highly variable between sampling dates and sites. Concentrations within each site ranged greatly: TS (3.9 - 70.2 μM), SS (4.4 - 76.5 μM), J (2.2 - 50.5 μM), and P (6.5 - 68.1 μM).

Averaged NH_4^+ concentrations within the experimentally flooded plots (Fig. 11b) were also highly variable between treatments and sampling dates: JC (3.47 - 31.37 μM), JF (4.49 - 17.0 μM), PC (12.86 - 19.3 μM), and PF (6.78 - 15.33 μM). There were no statistically significant differences in NH_4^+ concentrations among the native vegetation zones of flooding treatments within the experimentally flooded plots.

Phosphate

Concentrations of PO_4^{3-} were significantly higher in the TS and SS zones than the P and J zones for each sampling date (Fig. 12a). Phosphate was negatively correlated with platinum electrode potential ($r = -0.8535$) and positively correlated with salinity ($r = 0.8521$).

Phosphate concentrations within the experimentally flooded plots were variable and not statistically significantly different (Fig. 12b). Phosphate was

not measured during the May sampling due to the low volume of water removed from the sippers. The July concentrations appear to be slightly lower in flooded treatments. However, there was one extremely high measurement within each of the flooded sites which cause the averaged concentrations to be much higher.

Sulfide

For all dates, except the two July 1995 sampling dates, H_2S concentrations were significantly higher in the TS site than the three interior sites (Fig. 13a). In July 1995, SS H_2S concentrations were slightly higher than TS. The J and P sites rarely contained detectable concentrations of H_2S , and often negative values were found.

Hydrogen sulfide concentrations within the experimentally flooded plots (Fig. 13b) were variable between treatments and sampling dates. During the May sampling, only PC contained detectable concentrations of H_2S . In the July sampling, however, all treatments contained detectable H_2S concentrations. During this sampling date, H_2S appears to be slightly lower in flooded treatments.

**Porewater Ammonium Concentrations
Native Plant Zones & Tidal Creek**

a)

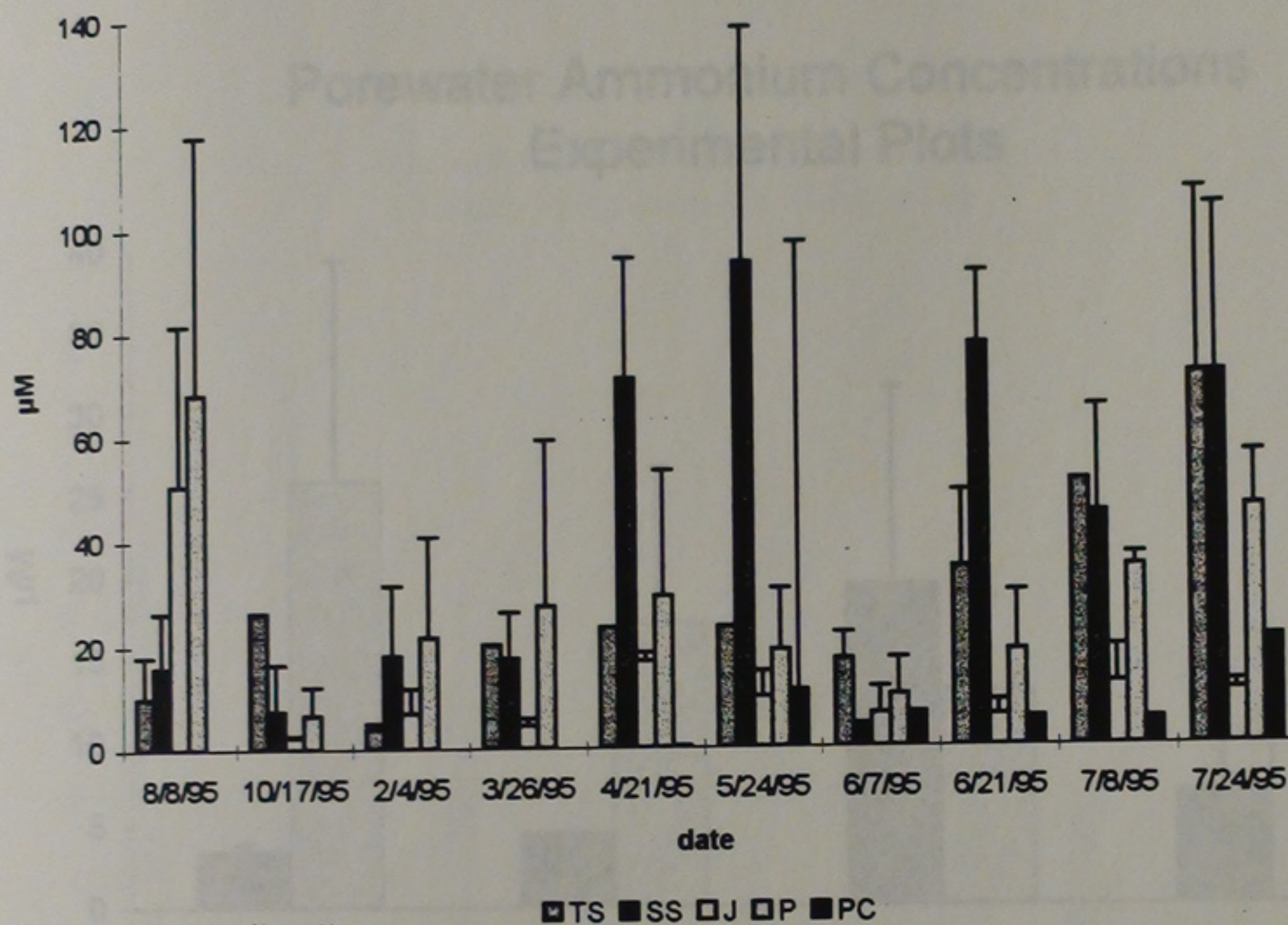


Fig. 11a. Ammonium concentrations within each native vegetation zone. All data bars represent the average of 3 independent samples. Data bars for TS 10-17, TS & J 2-4, SS 3-26, TS 4-21, P 5-24, TS 6-7, SS & P 7-8, and TS, SS, & P 7-24 represent the average of 2 independent samples. Data bars for TS 3-26, TS 5-24, SS 6-7, and TS 7-8 represent a single sample. Error bars represent one standard deviation from the mean.

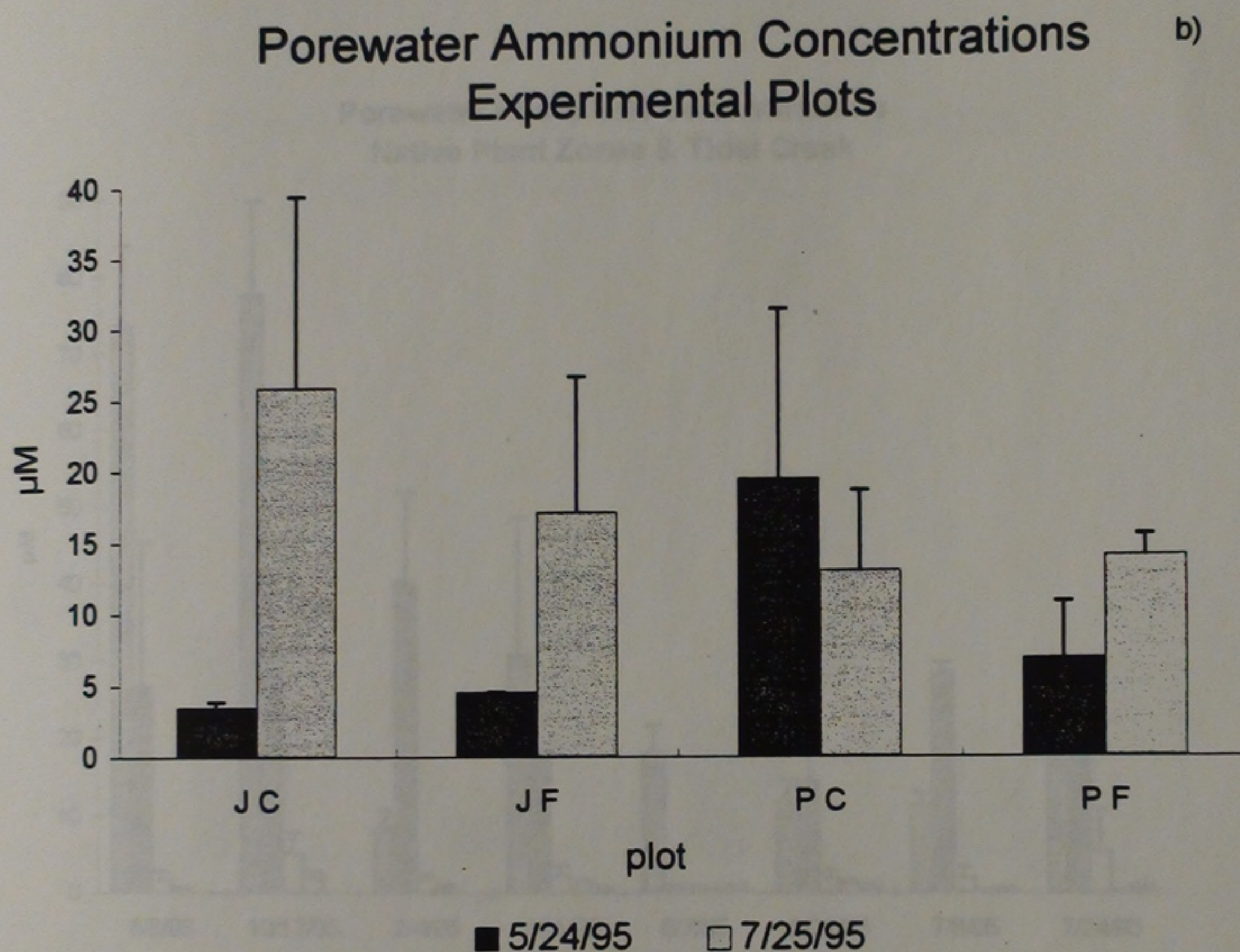


Fig. 11b. Ammonium concentrations within the experimentally flooded plots. Data bars represent the average of 3 independent samples. Data bars for JC & PF 5-24, and PF 7-25 represent the average of 2 independent samples. The data bar for JF 5-24 represents a single sample. Error bars represent one standard deviation from the mean.

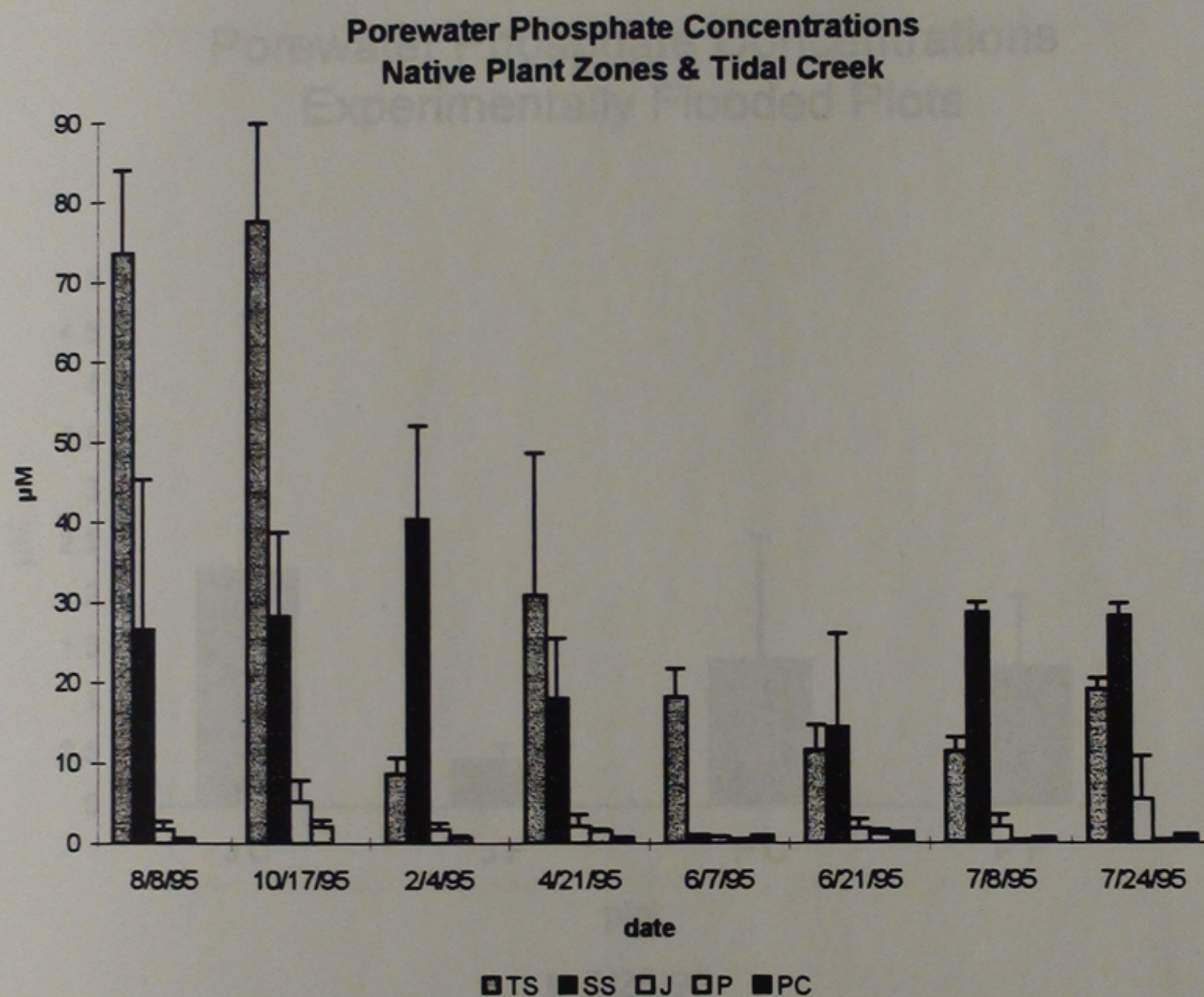


Fig. 12a. Phosphate concentrations in each native vegetation zone. Each data bar represents the average of 3 independent samples. Data bars for TS 10-17, TS 2-4, TS 4-21, TS 6-7, TS & SS 6-21, SS & P 7-8, TS, SS & P 7-24 represent the average of 2 independent samples. Data bars for TS 5-24, SS 6-7 represent a single sample. Error bars represent one standard deviation from the mean.

Porewater Phosphate Concentrations Experimentally Flooded Plots

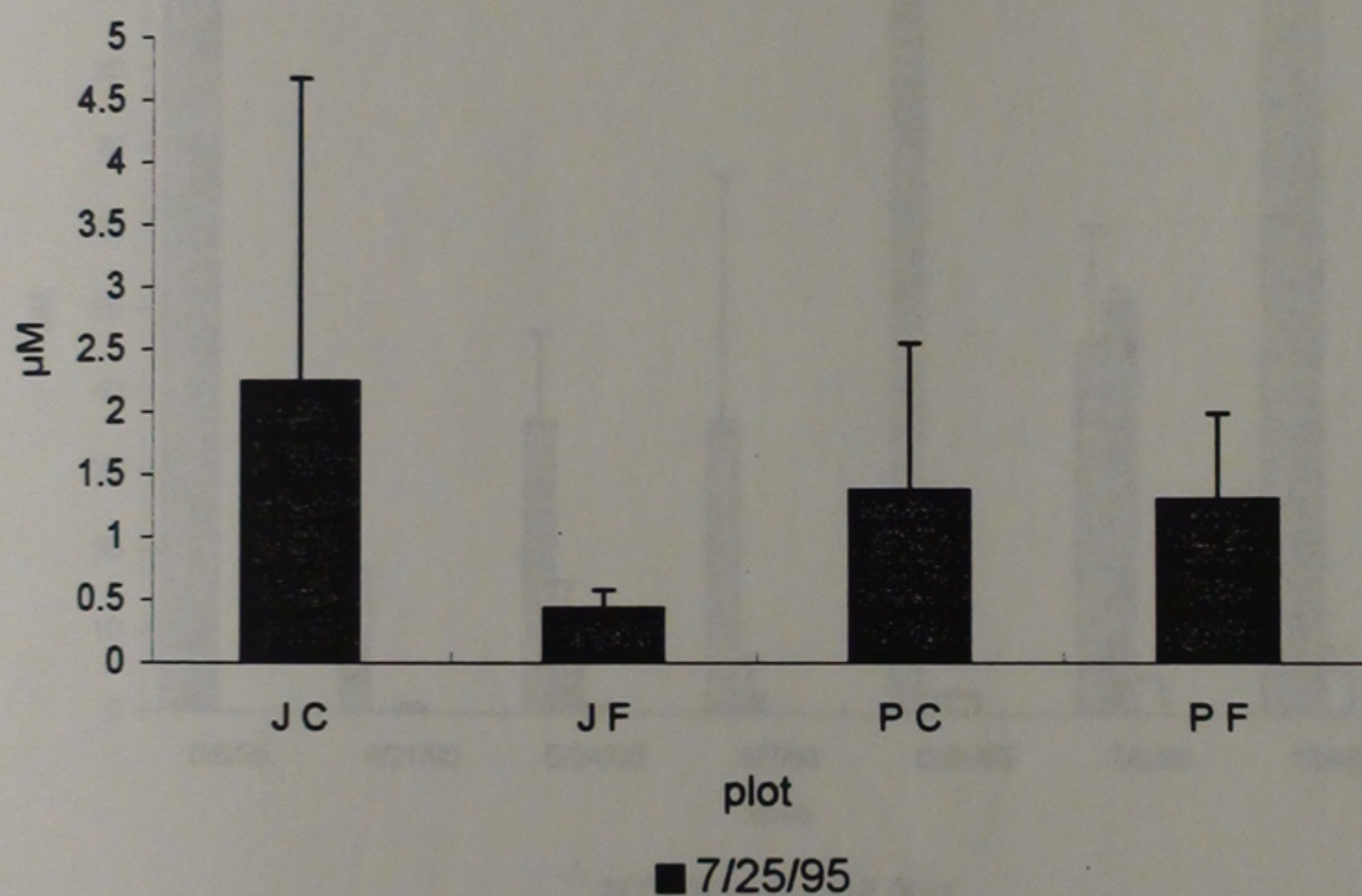


Fig. 12b. Phosphate concentrations within the experimentally flooded plots. Data bars represent the average of 3 independent samples. The data bar for PF represents the average of 2 independent samples. Error bars represent one standard deviation from the mean.

Porewater Hydrogen Sulfide Concentrations Native Plant Zones & Tidal Creek

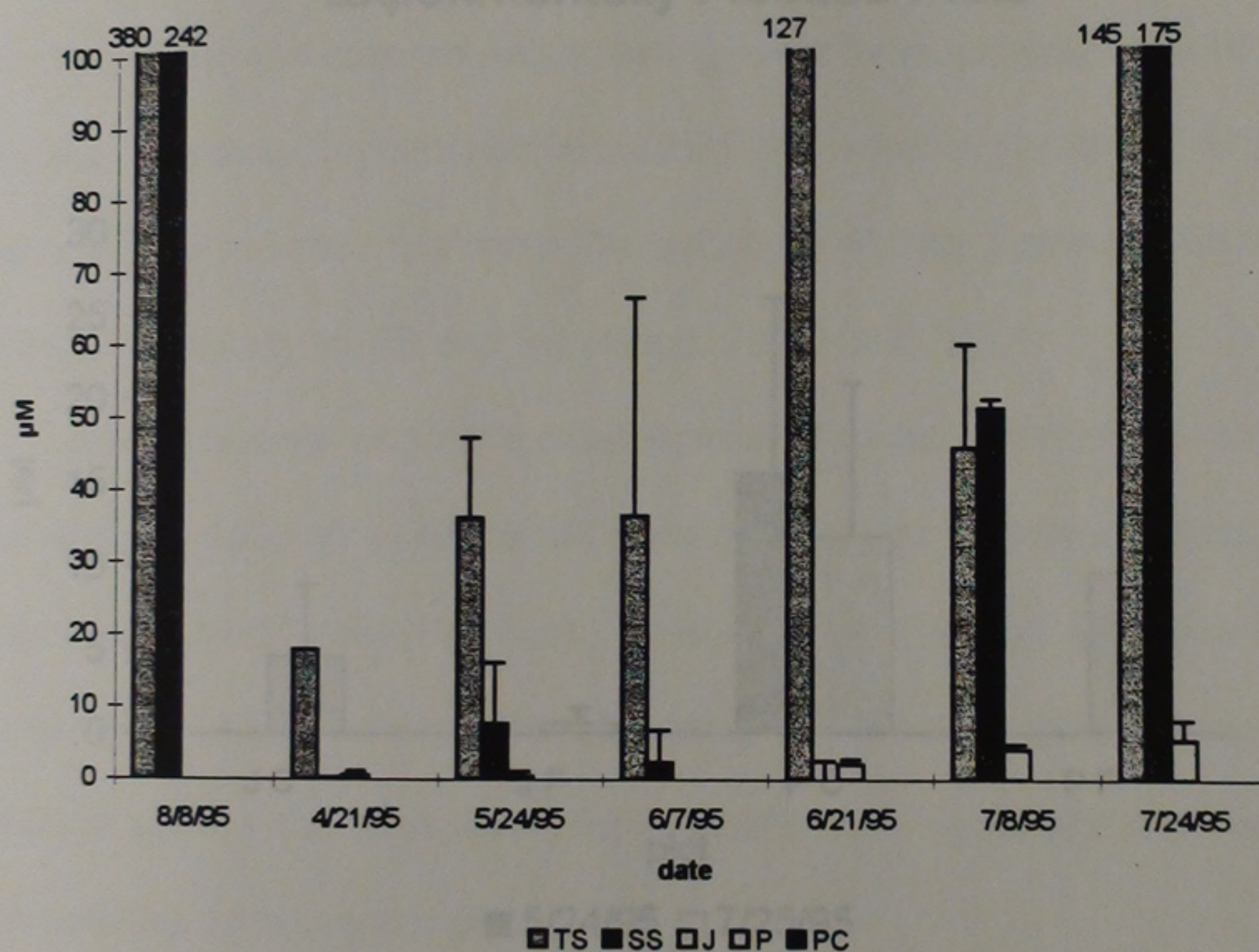


Fig. 13a. Hydrogen sulfide concentrations in each native vegetation zone. Each data bar represents the average of 3 independent samples. Data bars for SS 4-21, SS 6-7, SS 6-21, SS & P 7-8, TS SS, & P 7-24 represent the average of 2 independent samples. The data bars for TS 4-21 represents a single sample. Error bars represent one standard deviation from the mean.

Porewater Sulfide Concentrations Experimentally Flooded Plots

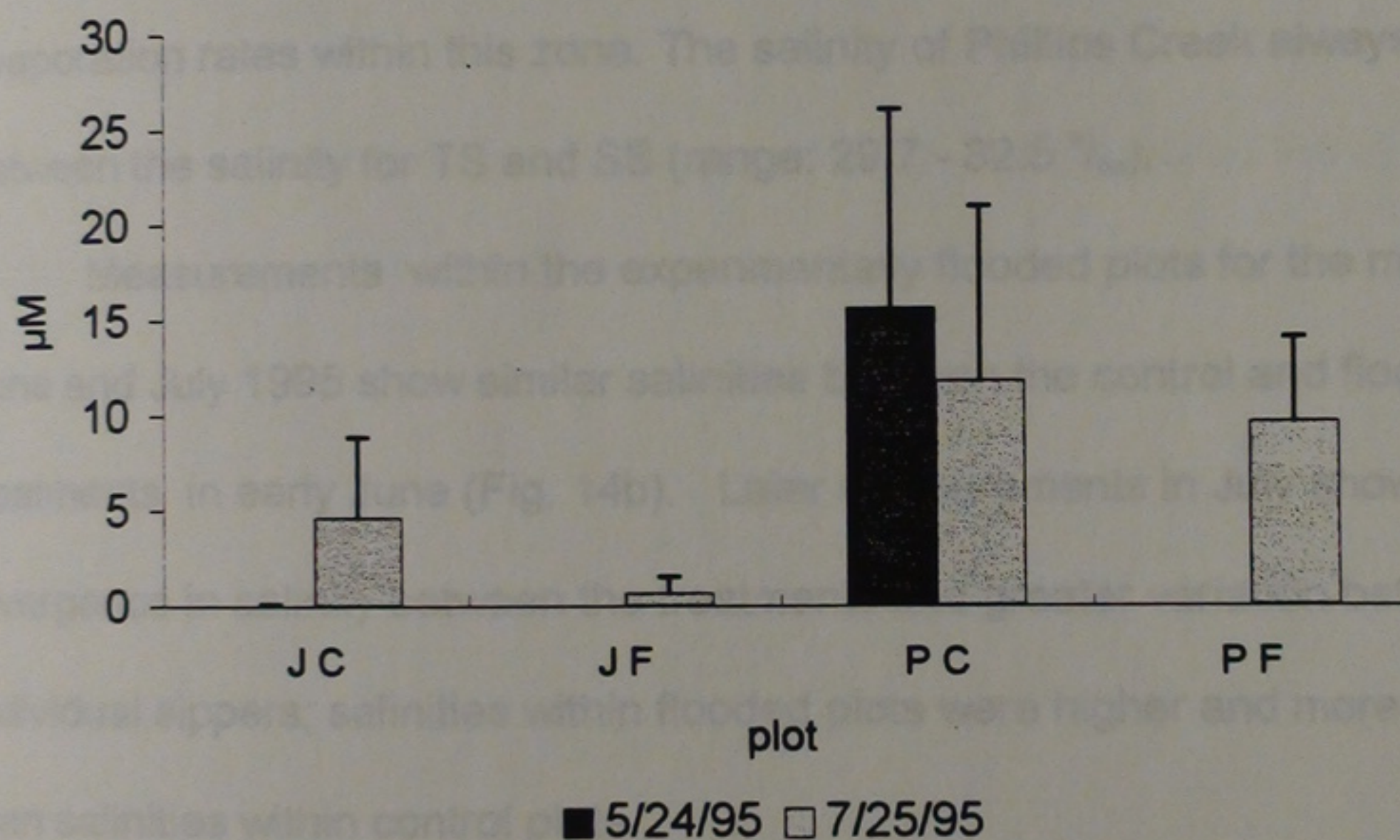


Fig 13b. Hydrogen sulfide concentrations within the experimentally flooded plots. Data bars represent the average of 3 independent samples. Data bars for PC 5-24 and PF 7-25 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

Salinity

Salinity (Fig. 14a), was always highest in the SS site. Salinity ranged between (25 - 35 ‰), (34.3 - 41.5 ‰), (22.7 - 35 ‰), and (19.7 - 37 ‰) for the TS, SS, J, and P sites respectively. Lower salinities within the J and P sites correspond with lower frequency of inundation. However, TS was inundated most frequently, and covered with standing water for much longer periods of time than SS. Therefore, higher salinities within SS are probably related to higher evaporation rates within this zone. The salinity of Phillips Creek always fell between the salinity for TS and SS (range: 29.7 - 32.5 ‰).

Measurements within the experimentally flooded plots for the months of June and July 1995 show similar salinities between the control and flooded treatments in early June (Fig. 14b). Later measurements in July show a divergence in salinity between the treatments and greater variation between individual sippers; salinities within flooded plots were higher and more variable than salinities within control plots.

Platinum Electrode Potential and pH

Platinum electrode potentials (Fig. 15) were lowest in the TS and SS sites and highest in the P site. These differences were statistically significant. Such differences can also be related to flooding frequency: highest potentials were found in zones with lower inundation frequencies, and lowest potentials were

found in zones more frequently flooded. Furthermore, platinum electrode potential was negatively correlated with total CO_2 ($r = 0.8801$), PO_4^{3-} ($r = 0.8535$), and H_2S ($r = 0.8250$).

Measurements of porewater pH were very similar between sites, and always less than 7.0 (Fig. 16). July 1995 values were 6.72, 6.97, 6.51, and 6.48 for TS, SS, J, and P, respectively. Phillips Creek water had a pH of 7.3. In October 1995, pH values were 6.76, 6.77, 6.53, and 6.55 for TS, SS, J, and P, respectively.

Platinum electrode potentials and pH were not measured within the experimentally flooded plots.

Fig. 14a. Salinity in parts per thousand in each native vegetation zone. Each data point represents the average of 3 independent samples. Data points for TS 10-17, SS 6-21, TS, SS, & P 7-24 represent the average of 2 independent samples. The data point for SS 6-7 represents a single sample. Error bars represent one standard deviation from the mean.

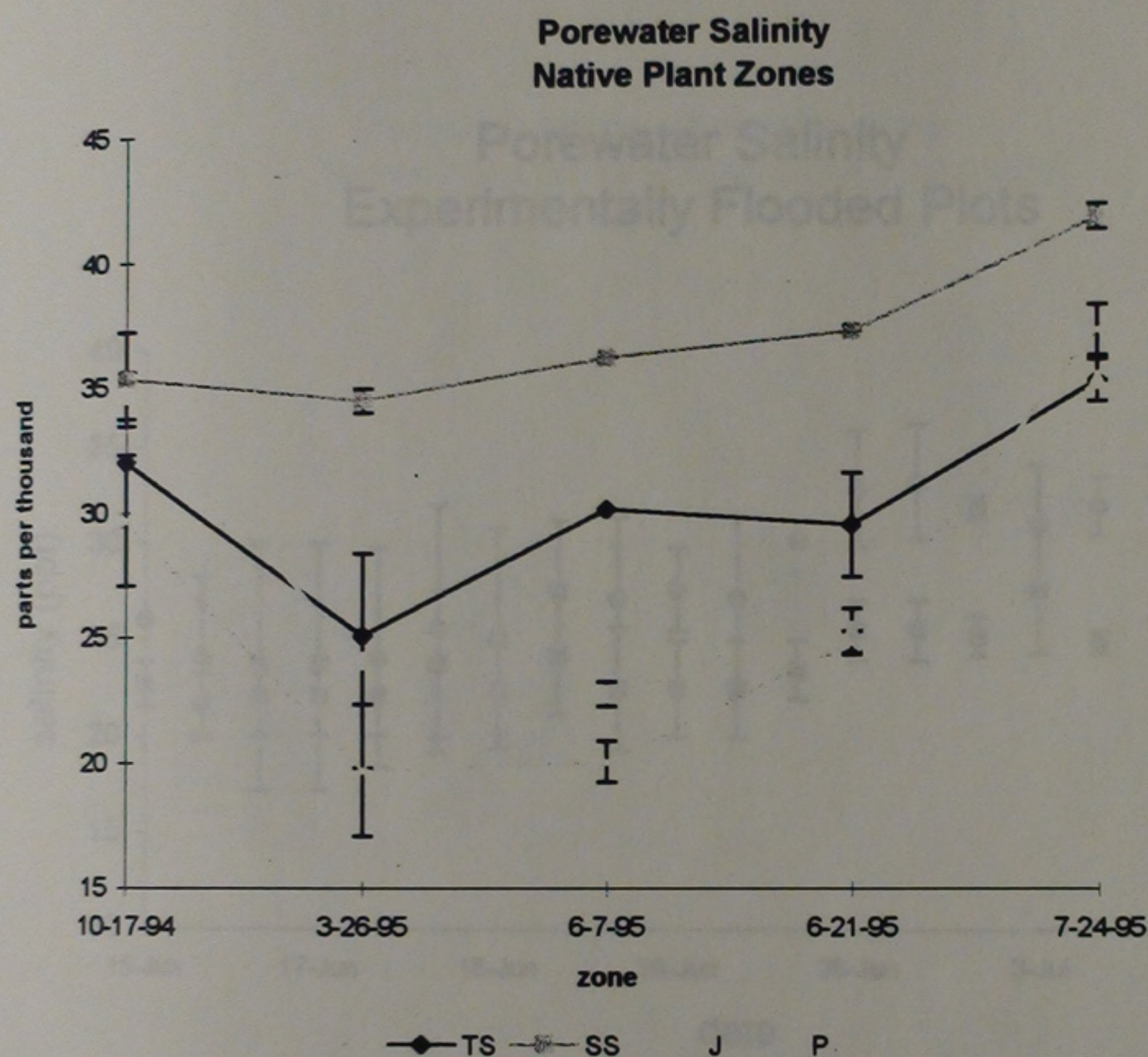


Fig. 14a. Salinity in parts per thousand in each native vegetation zone. Each data point represents the average of 3 independent samples. Data points for TS 10-17, SS 6-21, TS, SS, & P 7-24 represent the average of 2 independent samples. The data point for SS 6-7 represents a single sample. Error bars represent one standard deviation from the mean.

Porewater Salinity Experimentally Flooded Plots

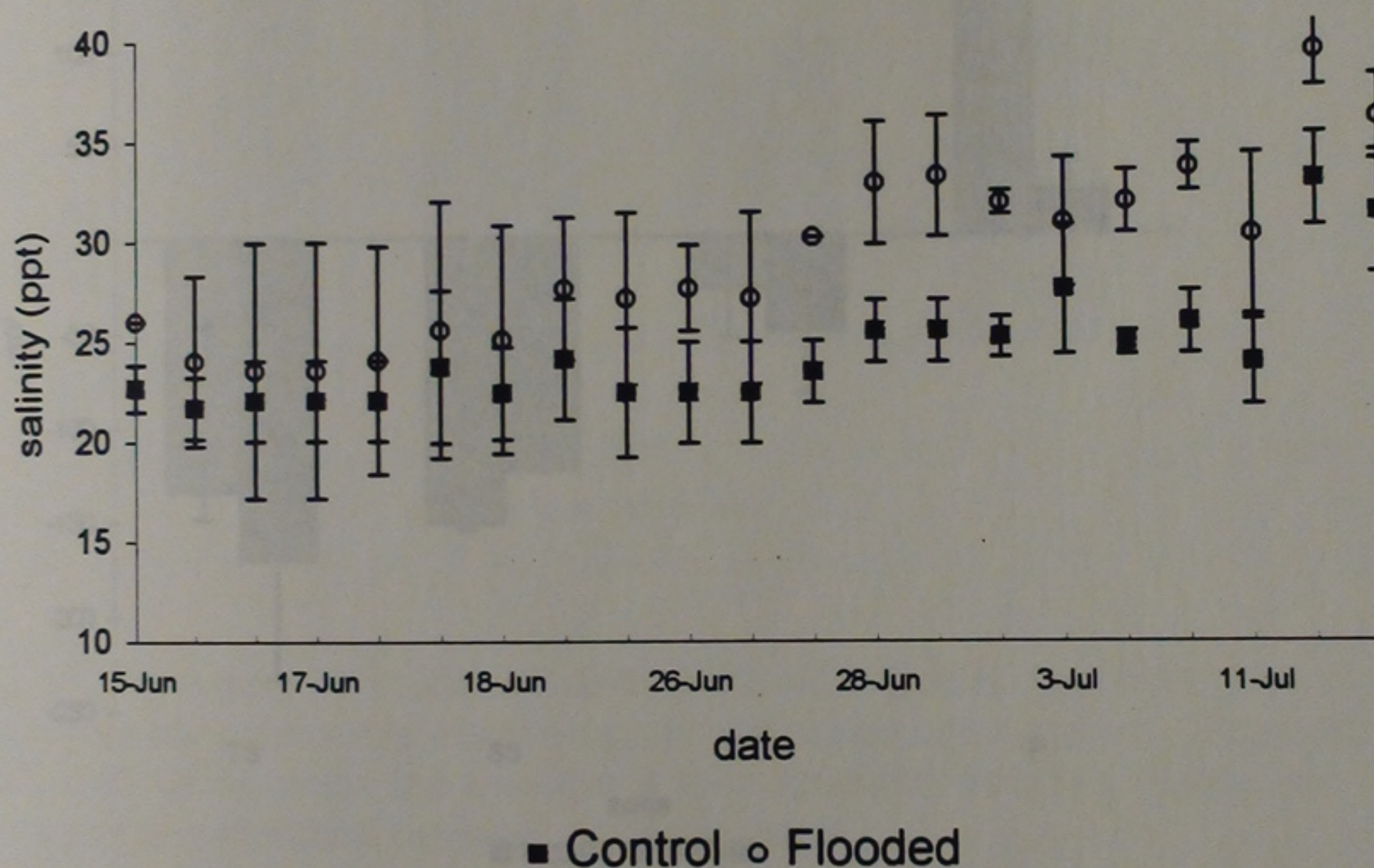


Fig. 14b. Salinity in parts per thousand within the experimentally flooded plots. Each data point represents the average of 3 independent samples. Data points for the Flooded plots for June 12 - June 27 represent the average of 2 independent samples. The data point for June 15 Flooded represents a single sample. Error bars represent one standard deviation from the mean.

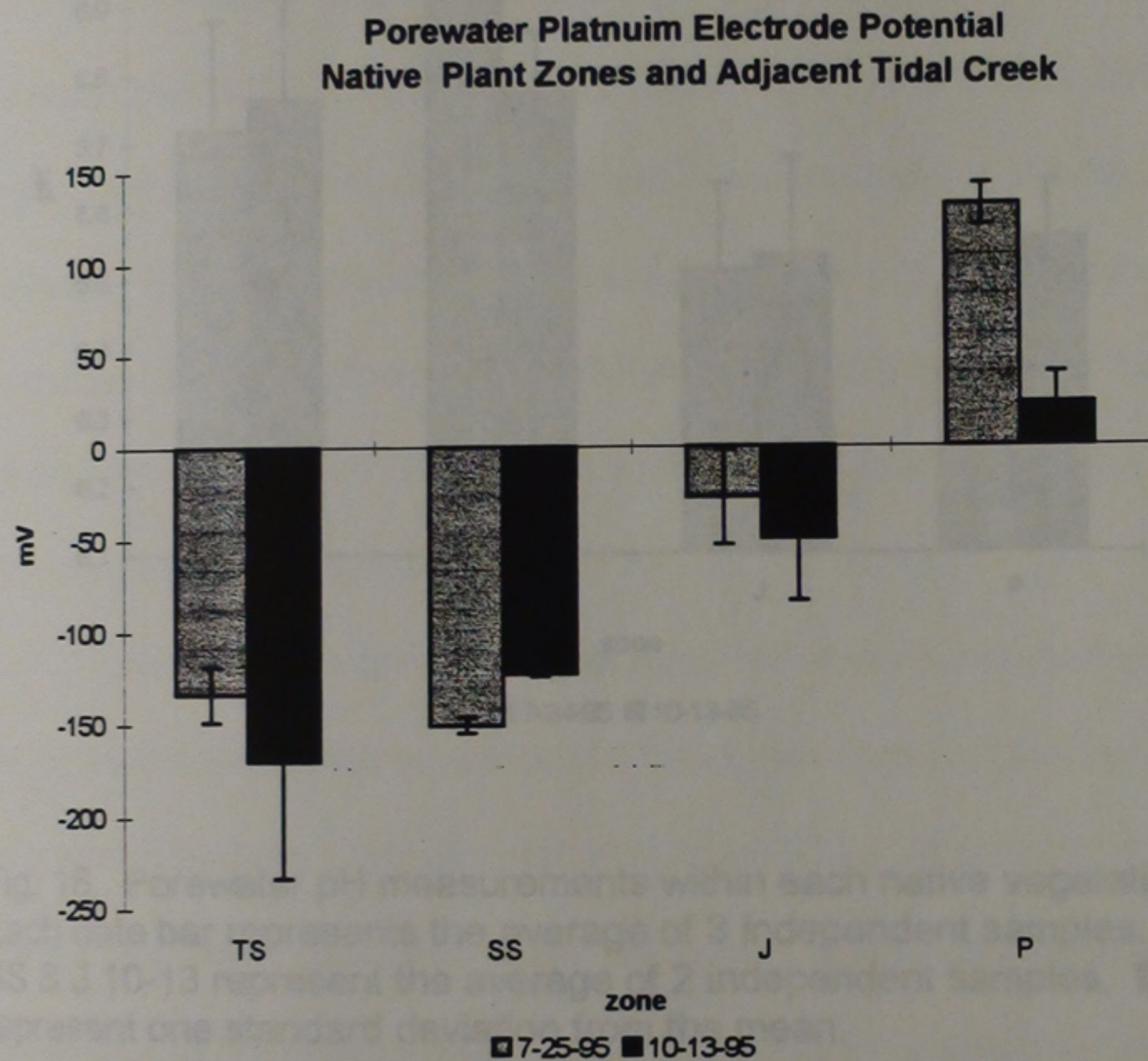


Fig. 15. Platinum electrode potential (PEP) measured in mV within each native vegetation zone. Each data bar represents the average of 2 independent samples. Data bars for SS & J 10-13 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

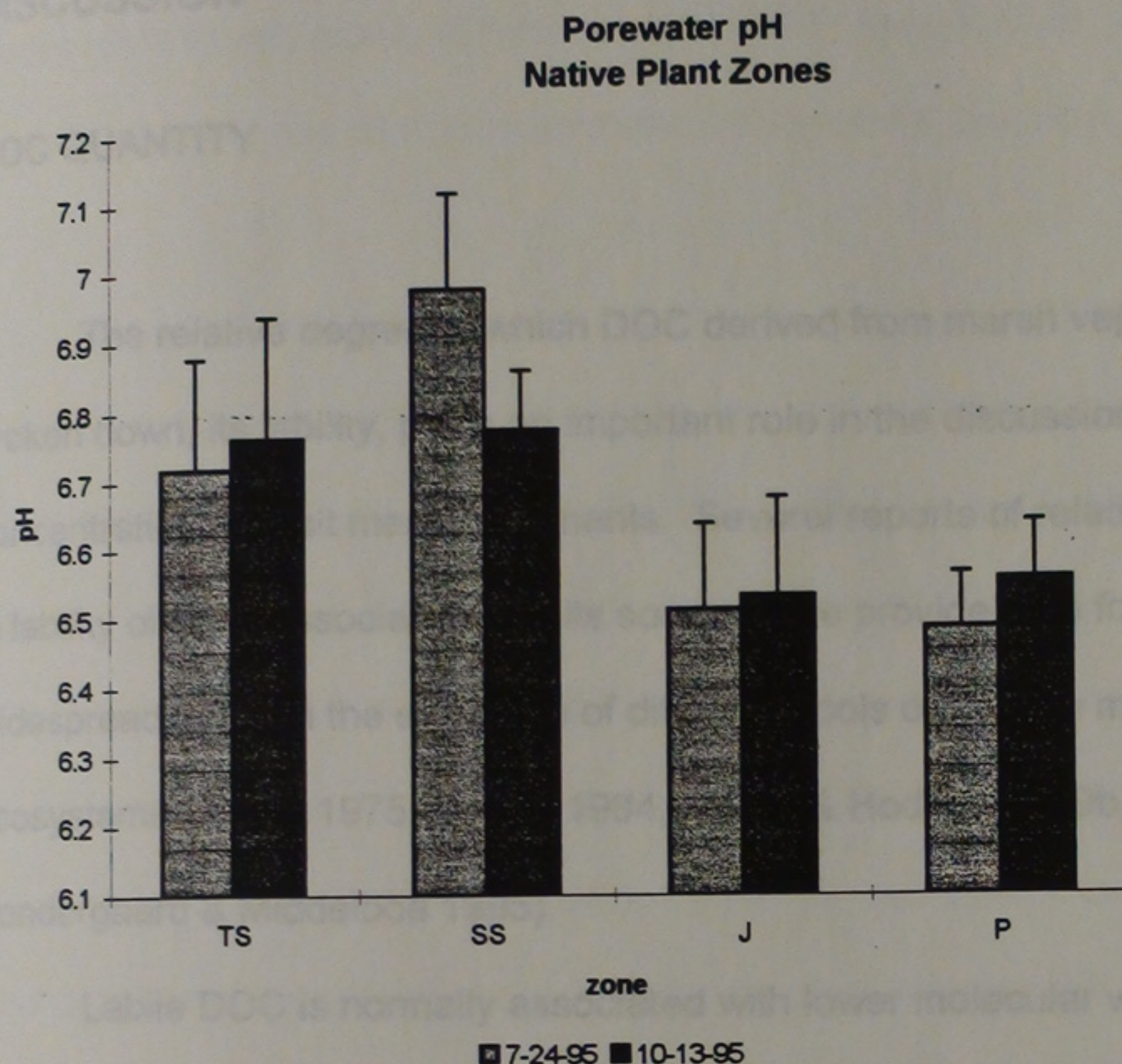


Fig. 16. Porewater pH measurements within each native vegetation zones. Each data bar represents the average of 3 independent samples. Data bars for SS & J 10-13 represent the average of 2 independent samples. Error bars represent one standard deviation from the mean.

DISCUSSION

DOC QUANTITY

The relative degree to which DOC derived from marsh vegetation can be broken down, its lability, plays an important role in the discussion of DOC concentrations in salt marsh sediments. Several reports of relative differences in lability of DOC associated with its source have provided the foundation for a widespread belief in the existence of different pools of DOC in many aquatic ecosystems (Ogura 1975, Wright 1984, Moran & Hodson 1989b, 1990, Sondergaard & Middelboe 1995).

Labile DOC is normally associated with lower molecular weight and non-humic substances (Moran & Hodson 1990), exudates of photosynthetic organisms such as phytoplankton and algae (Cole, et al. 1982, Kirchman, et al. 1991), live roots (Gallagher, et al. 1976), and submerged macrophyte exudates (Brylinsky 1977). Labile DOC usually accounts for a smaller percentage of the total DOC pool (Sondergaard, et al. 1995, Sondergaard & Middelboe 1995), turns over relatively rapidly (Blum & Mills 1991, Kirchman 1991, Sundh 1992), and is considered more easily assimilated by bacterial communities.

Alternatively, refractory DOC is most often associated with higher molecular weight compounds (Sundh 1992), humic substances (Moran & Hodson 1990), and many plant structural materials (Waksman & Tenney 1928).

Refractory DOC usually constitutes a larger percentage of the total DOC pool, turns over relatively slowly (Christian, et al. 1978, Blum & Mills 1991), and is considered to be less easily incorporated into bacterial biomass.

Many studies have documented the sequential decomposition of materials containing both labile and refractory components (Waksman & Tenney 1928, de la Cruz & Gabriel 1974, Ogura 1975, Benner, et al. 1991, and Blum & Mills 1991). However, it has become widely accepted (Christian, et al. 1978, Wright 1984, Moran & Hodson 1989b, 1990) that degrading structural components of salt marsh macrophytes are predominantly refractory sources of dissolved organic matter (DOM). Although it has also been shown that initial leachates from newly dead and decomposing plant material (Blum & Mills 1991) and exudates from submerged roots (Gallagher, et al. 1976) can be extremely labile and readily taken up by bacteria, labile DOC is likely to constitute a small portion of the total DOC associated with marsh plants.

Therefore, for the purposes of this research, it has been assumed that DOC from salt marsh sediment pore water is refractory in nature, and it is this refractory nature that will be partly responsible for accumulation of DOM within the marsh sites. Christian, et al. (1978) attributed the lack of bacterial response to marsh plant perturbations to the refractory nature of marsh organic matter. They suggested that salt marsh soil OM degrades so slowly that removal of aboveground and/or belowground plant biomass had no immediate effect on the

OM already available to the soil microbes. Only after 18 months were changes detected in soil OM due to initial perturbations. Therefore, natural changes in aboveground and belowground marsh macrophyte production due to flowering, death, and senescence, would not be expected to be reflected in porewater DOM. The lack of temporal variation in DOC concentrations within each of the 4 native vegetative zones in this study (Fig. 4a) indicates the probable predominance of marsh macrophyte derived DOC within the total pore water DOC pool in each site. If porewater DOC within the 4 native plant zones exhibited distinct temporal variations, it may indicate the presence of another dominant source of DOC, like phytoplankton or macroalgae, which experience definite blooms in warmer months (Kirchman, et al. 1991, Sondergaard, et al 1995).

My first hypothesis suggests that DOC concentrations would be higher in vegetative sites that were subject to infrequent tidal inundation than sites that were frequently inundated. Inherent in this hypothesis are the relative differences in proximity to the tidal creek, elevation, and hydrologic gradient between these sites. Each of the 4 native vegetation zones occupies a characteristic area of the marsh. As distance increases from the tidal creek, tidal inundation decreases and topographic elevation increases.

The DOC data collected over 11 sampling dates (Fig. 4a) indicate that DOC concentrations were usually highest in the P zone, which was farthest from

the creek and experienced no surface water inputs due to normal daily tidal action. The data also indicate that DOC concentrations were usually lowest within the TS zone, which was very close to the tidal creek and experienced substantial flooding twice daily due to normal tidal action. These data correspond well with DOC concentrations measured within a Georgia salt marsh and adjacent estuary and shelf (Sottile 1974); concentrations of interstitial DOC were found to increase inland from the levee.

To differentiate between the covarying effects of flooding frequency and plant type, the experimentally flooded plots containing the same vegetation types as 2 of the native vegetation zones were also sampled for DOC quantity. Data from these plots indicate that DOC concentrations within a particular site were affected more by flooding than by the plant type within that site. The relative proximity of each plot within the elliptical area to the tidal creek was not different, but the flooding frequency was different between the flooded and control treatments. Therefore, it appears that DOC quantity within the salt marsh is directly related to inundation frequency.

Several processes may be responsible for the inverse relationship between flooding frequency and DOC concentration. First and most important, is the general hydrologic differences between sites which experience different flooding patterns. Relative elevations were measured within each of the four

vegetative zones. The TS zone was more than 2 m lower in elevation than the three interior sites and greater than 10, 20 and 30 m closer to the creek than the SS, J, and P zones, respectively. Without taking into consideration differences in porosity and soil grain size differences, simple qualitative estimates of fluxes based on inherent hydrologic differences alone would suggest increased flow in the area near the tall *Spartina* zone (Osgood, et al. 1995) compared to the marsh interior. Yelverton & Hackney (1986), Nuttle & Hemmond (1988), and Williams, et al. (1992) found substantially greater removal of dissolved and particulate carbon and nutrients closest to the creek, where seepage during the periods of low water played an important role in solute export. The exact area contributing to this seepage differed for each study, from 2 m (Yelverton & Hackney 1986) to between 10 and 15 m (Nuttle & Hemmond) from the creek. Yet these studies indicated that removal of organic matter was limited to a relatively narrow band of marsh bordering the tidal creek. Williams, et al (1992) suggested that leaching from submerged *Spartina* and/or diffusion of DOC from sediments into overlying water during high water were possible substantial DOC removal mechanisms.

It may have been hydrologic implications such as these which fueled the hypothesis that significant portions of marsh primary production were exported annually from many salt marshes (Teal 1962, Kirby & Gosselink 1976, Valiela 1978, Odum 1980, and Dame 1986) and were responsible for supporting estuarine and near-coastal secondary production (Heinle 1977, Nixon 1980,

Odum 1980). However, as Taylor and Allanson (1995) noted, most studies which found significant export of DOC were performed in low elevation, primarily *S. alterniflora*, marshes. These authors suggested that organic carbon fluxes were much lower in higher elevation marsh sites, due to larger percentages of primary production being respired or buried instead of being exported. Higher concentrations of porewater DOC found within the P zone throughout the present study support these conclusions. Additional studies conducted at various elevations and within different vegetation zones have also suggested higher percentages of marsh primary production are respired or buried rather than exported (Newell, et al. 1983, Dankers, et al. 1984, Howes, et al. 1985, Biddanda, et al. 1994 and Taylor & Allanson 1995).

An apparent lack of subsurface transport of DOC from the interior sites suggests that removal of sediment DOC must occur by other means. Borey, et al. (1983) explained removal of organic carbon from an irregularly flooded brackish marsh in Texas as a combination of rainfall, vegetative structure, microtopographic variations and decomposition. Maintaining the assumption that most plant material is relatively refractory and more slowly degraded by microbial communities, it appears that much of the DOC derived from the short *S. alterniflora*, *S. patens* and *J. roemerianus* plants may remain for long periods of time within the sediments, resulting in the consistently elevated concentrations found within these zones throughout the present study.

Another potential explanation, of low DOC concentrations in near creek marsh sites is the utilization of pore water DOC as a carbon source during the reduction of sulfate. Dissimilatory sulfate reduction is carried out primarily by obligate anaerobes and results in the production of hydrogen sulfide (H_2S). Dissimilatory SO_4^{2-} reduction can occur over a range of pH, temperature, and salinity (Atlas & Bartha 1993). There were consistently high concentrations of H_2S within the TS zone and on occasion, elevated levels of H_2S in the SS zone. These two sites also had the lowest platinum electrode potentials in July and October (-133.8 & -169.6 mV) and (-150.3 & -122.7 mV) TS and SS sites, respectively. Both the TS and SS zones contained soils which were very dark in color, and were covered with water for several hours each day, indicating highly reduced conditions. Dissimilatory SO_4^{2-} reduction, therefore, may be a mechanism for utilization and removal of dissolved organic carbon from the TS zone. Howarth & Teal (1979) estimated that SO_4^{2-} reduction in a New England salt marsh accounted for the consumption of a substantial percentage of marsh macrophyte primary production.

Based on data from the 4 native vegetation plots and the experimentally flooded plots within the Phillips Creek marsh, it appears that porewater DOC quantity is controlled primarily by inundation frequency. The presence of removal mechanisms, such as steep hydrological gradients and dissimilatory SO_4^{2-} reduction, effectively reduce porewater concentrations within vegetation

zones closest to the tidal creek. Alternatively, relatively small hydrological gradients and less frequent tidal inundation promote the accumulation of higher concentrations of DOC within the porewater of vegetation zones farther from the tidal creek.

DOC METABOLISM

Throughout the course of the present study, nutrients were monitored within each vegetative zone and within the experimental plots in order to ensure that nutrient limitations on microbial metabolism of DOC did not exist. Nutrient concentrations may also serve an indicator of tidal inundation frequency and general vegetation health. Porewater concentrations of both NH_4^+ and PO_4^{3-} fall within the range of reported values for other estuarine systems along the East and Gulf Coasts of the United States (Table 3). Numerous studies have shown that amendments of nutrients enhance decomposition and microbial metabolism of DOC (Marinucci, et al. 1983, Heywood 1977, Newell, et al. 1983, Moran & Hodson 1990, Zweifel, et al. 1993, Zweifel, et al 1995). Likewise, many studies have indicated that often PO_4^{3-} and sometimes NH_4^+ are present in limiting quantities in many estuarine and salt marsh systems (Zweifel, et al. 1993, Zweifel, et al. 1995). However, the concentrations found in these sites do not appear to be limiting, and were therefore, not considered in the discussion of differences in microbial utilization of DOC.

Table 3. Nutrient concentrations from previous studies of East and Gulf Coast salt marshes and estuaries and concentrations from the present study.

Study	site	NH ₄ ⁺ (μM N)	PO ₄ ⁻³ (μM P)
this study	15 cm		
	tall <i>S. alterniflora</i>	3.9 - 70.2	8.5 - 77.2
	short <i>S. alterniflora</i>	4.4 - 92.4	1.1 - 40.1
	<i>J. roemerianus</i>	2.2 - 50.5	0.8 - 5.5
	<i>S. patens</i>	6.5 - 68.1	0.3 - 2.1
Jordan & Correll 1985 (Rhode River Estuary)	10 - 60 cm creekbank	1.0 - 1.36	0.39 - 0.81
Osgood & Zieman 1995 (Hog Island, VA)	10 cm		
	low elev. (tall <i>S. alterniflora</i>)	20.5 - 36.1	21.9 - 29.9
	mid elev. (short <i>S. alterniflora</i>)	3.2 - 4.2	6.8 - 13.0
	high elev. (<i>L. carolinum</i> , <i>S. patens</i> <i>S. carolinum</i> , <i>D. spicata</i>)	3.8 - 6.4	0.6 - 1.2
Kaye & Blum 1992 (Nassawadox, VA) (unpublished data)	15 cm		
	low marsh <i>S. alterniflora</i>	~5 - ~45	~42 - ~107
	mid marsh <i>S. alterniflora</i>	~45 - ~160	~9 - ~31
	<i>J. roemerianus</i>	~3 - ~27	~0 - ~3.5
	<i>S. patens</i>	~40 - ~125	~0 - ~13
Agosta 1985 (North Inlet, SC)	20 cm creekbank	~0 - 200	
Gardner 1975 (North Inlet, SC)	creekbank		1.61 - 129.1
Montgomery, et al. 1979 (Indian River, FL)	mudflat	6.6 - 7.8	
this study	Phillips Creek	0.36 - 20.2	0.7 - 1.4
Imberger, et al. 1983 (Sapelo Island, GA)	H ₂ O column	0.03 - 0.36	
Pomeroy & Wiegert 1981 (Sapelo Island, GA)	H ₂ O column		0.97 - 2.91
Biddanda, et al 1994 (Louisiana)	cont. shelf	0.42 - 0.44	0.45 - 0.35
	slope	1.26 - 1.96	0.03 - 0.19

Gardner, et al. (1994) explained reductions in bacterial growth, growth rates and efficiencies over time by changes in DOC quality over time. They contend that quality as well as quantity changed over time and were coupled. Therefore, changes in variables such as growth rate constant and change in abundance could be indicative of a similar change in the relative quality of the DOC. Such changes in relative DOC quality may be attributed to the chemical, physical, and biological alterations in soil and vegetation functions within salt stressed areas of the marsh.

Preliminary experiments (August 8, 1994 - March 5, 1995) indicated differences in porewater DOC concentrations and changes in bacterial abundances over an incubation period. Beginning with the March 26, 1995 sampling date, subsamples were taken for DOC concentration and bacterial abundance from each incubating flask at specific time intervals (after 0, 6, 12, and 24 h) to monitor substrate depletion and plot bacterial growth rate curves. Over 24 hour incubations, DOC concentrations were expected to decrease, while bacterial abundances were expected to increase. DOC concentrations (Fig. 17 a,b,c, and d) were variable over the incubation time for each sampling date. End DOC concentrations were not always smaller than starting concentrations, and often, highest values were found mid-incubation. Other

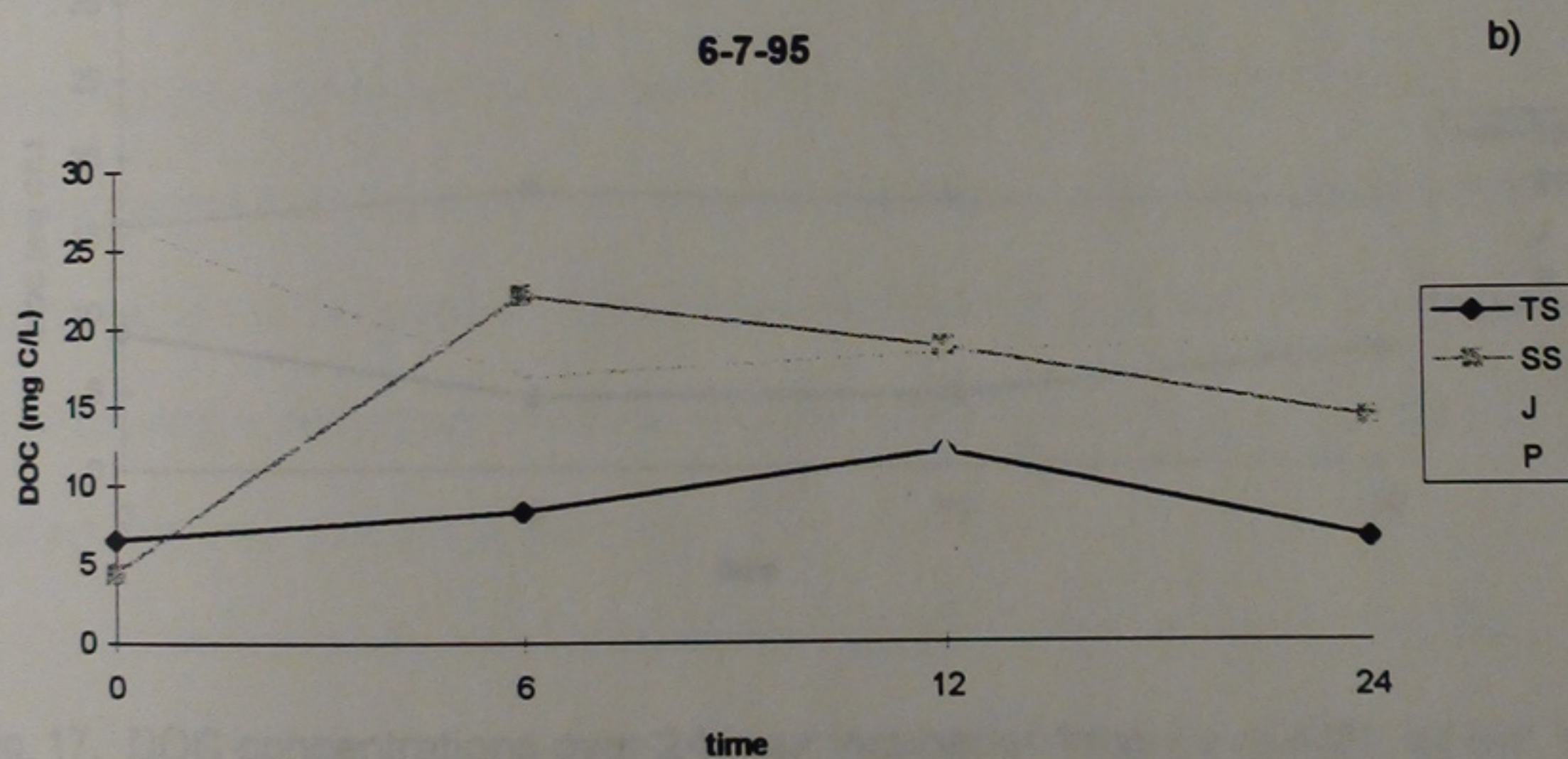
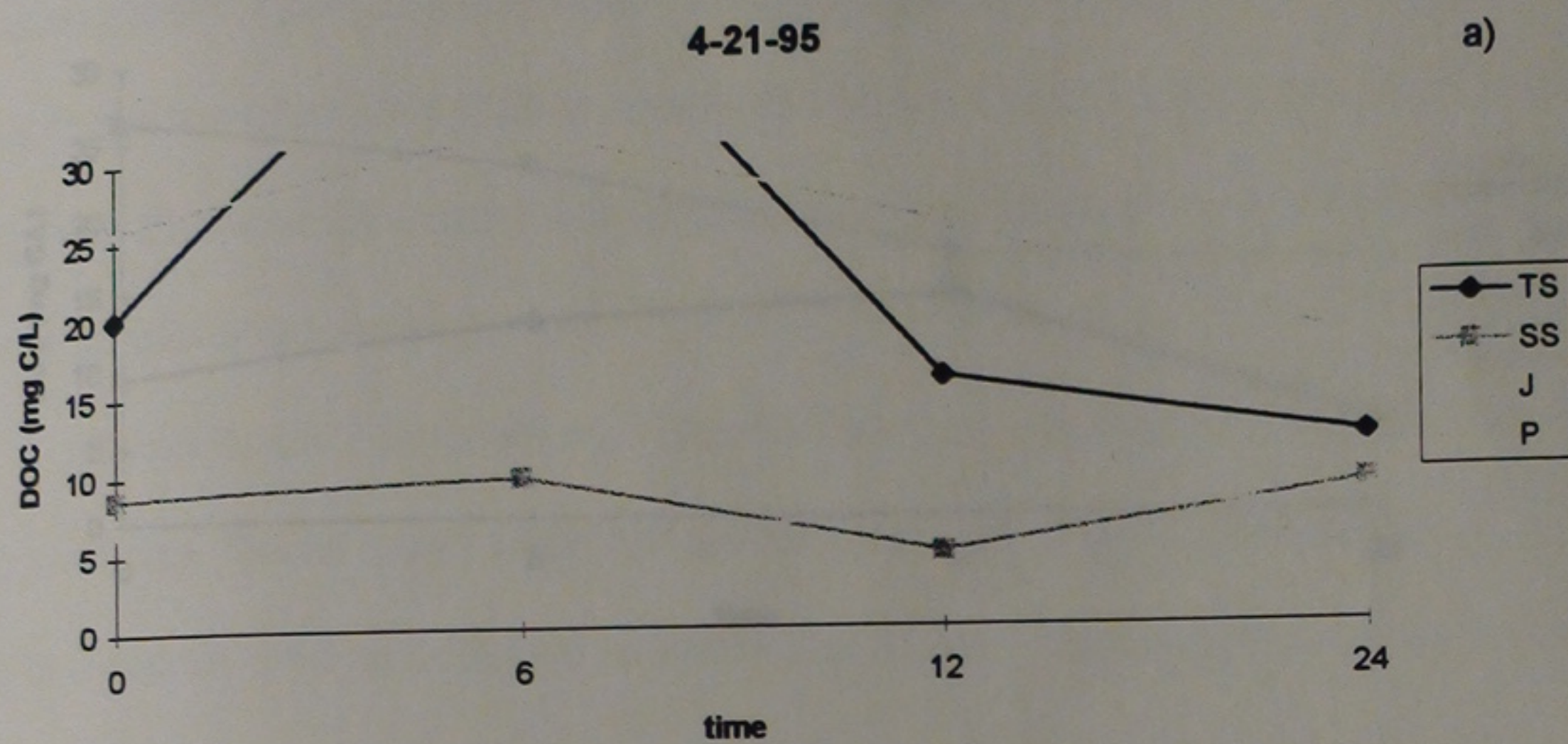


Fig. 17. DOC concentrations over time for samples TS, SS, J, and P on 4-21-95 and 6-7-95. All data points represent the mean of 3 replicates. Error bars represent standard deviation. Data for J and P are from independent samples. Data for TS and SS are from the same sample.

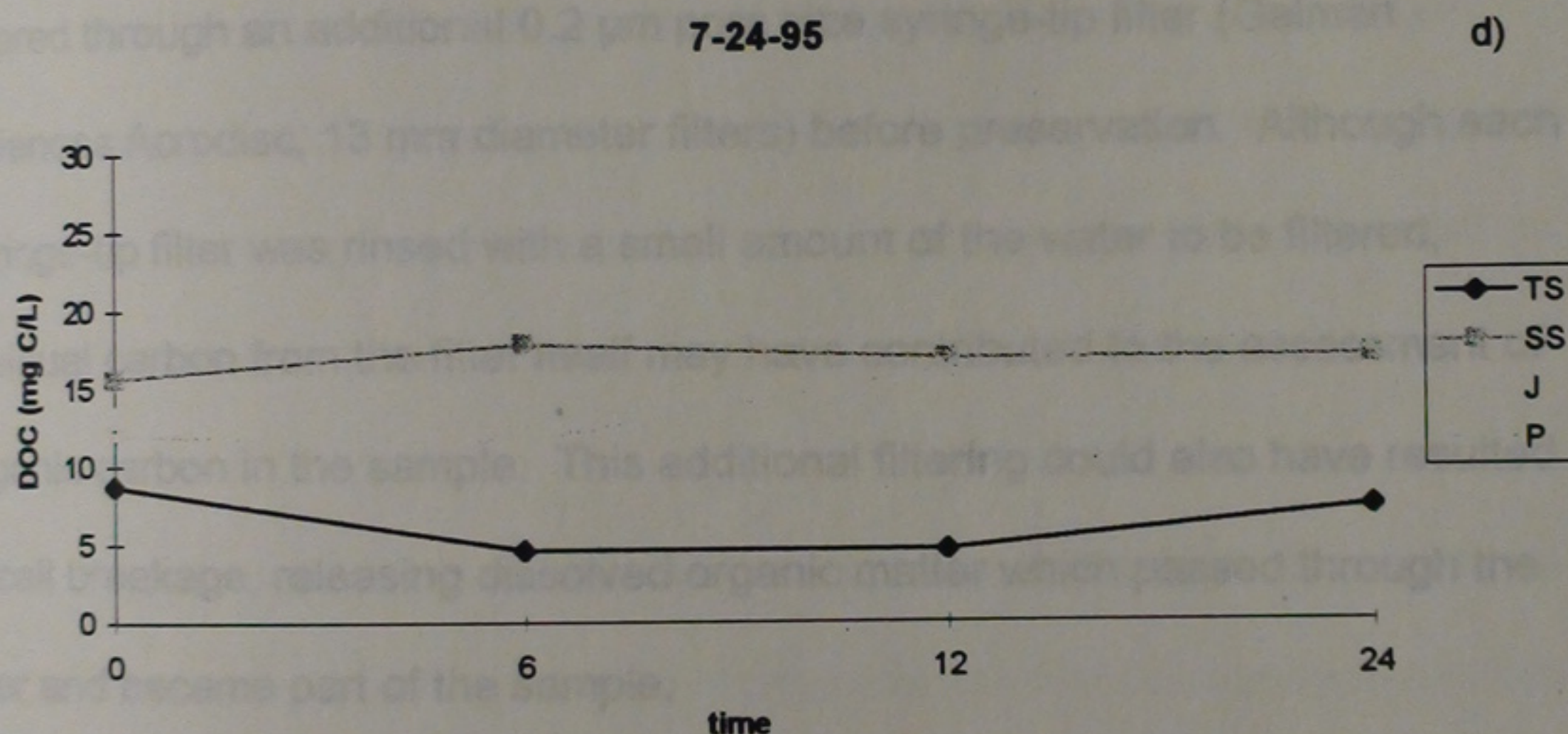
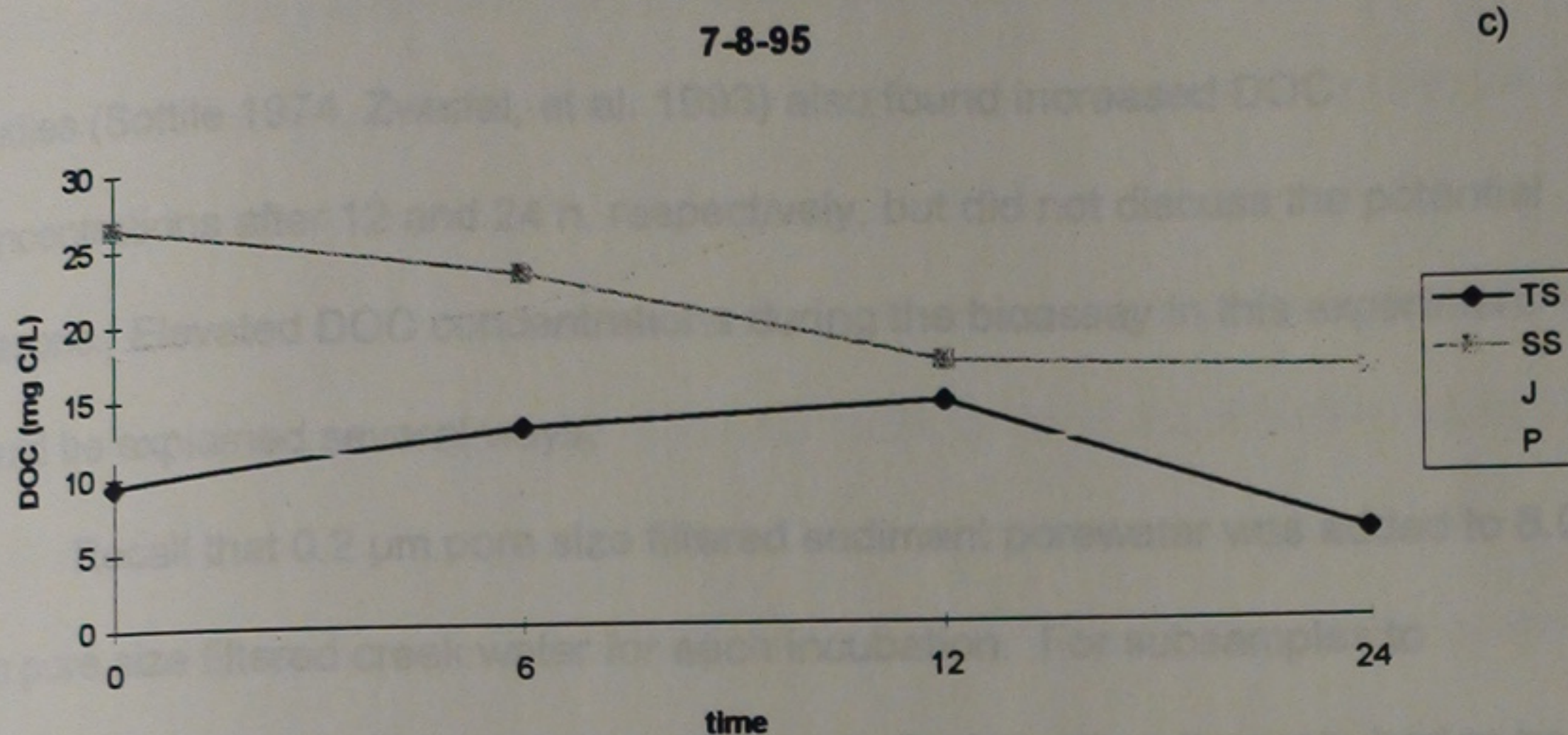


Fig. 17. DOC concentrations over 24 hour incubation time for a) 4-21, b) 6-7, c) 7-8, and d) 7-24. All data points represent the average of 3 independent samples (J t=6 4-21, TS t=0,6,12,24 6-7, SS t=6 & P t=0,6,12,24 7-8, TS t=0,6,12,24, SS t=0, & P t=0,6,12,24 7-24 represent the average of 2 independent samples. Data points for SS t=0,6,12,24 6-7 & P t=6 7-8 represent a single sample.

studies (Sottile 1974, Zweifel, et al. 1993) also found increased DOC concentrations after 12 and 24 h, respectively, but did not discuss the potential reasons. Elevated DOC concentrations during the bioassay in this experiment could be explained several ways.

Recall that 0.2 μm pore size filtered sediment porewater was added to 8.0 μm pore size filtered creek water for each incubation. For subsamples to represent dissolved organic matter within each flask, each subsample had to be filtered through an additional 0.2 μm pore size syringe-tip filter (Gelman Sciences Acrodisc, 13 mm diameter filters) before preservation. Although each syringe-tip filter was rinsed with a small amount of the water to be filtered, residual carbon from the filter itself may have contributed to the assessment of organic carbon in the sample. This additional filtering could also have resulted in cell breakage, releasing dissolved organic matter which passed through the filter and became part of the sample.

Another possible explanation of the variability of DOC concentrations over time could be the method of analysis itself. Ultra-violet assisted persulfate oxidation of organic carbon was achieved by using a Dohrmann Total Carbon analyzer. Sugimura & Suzuki (1988) compared the results of DOC determinations of several studies and the methods used to obtain the data. Based on their findings, they reported that discrepancies existed between the two primary methods, persulfate oxidation and high-temperature catalytic

oxidation, with the persulfate method resulting in under-estimates of DOC concentration based on its inefficient oxidation of high molecular weight organic carbon from saline waters. Although later reports (Benner & Hedges 1993) indicated that both methods produce relatively indistinguishable results (in fresh water samples), and many believe this also holds for samples of higher salinities (R.R. Christian, pers. comm.), the issue of high salinities and potentially high molecular weight compounds with longer oxidation times may account for some of the variability found in DOC concentrations over the incubation period.

The possible impacts of additional filtration and/or persulfate oxidation determination on DOC fluctuations over the incubation are probably negligible. If present, such discrepancies would represent a relatively uniform error since all samples were collected, filtered, and analyzed identically.

Therefore, another more probable factor accounting for these variations in DOC concentrations is the presence of phytoplankton and bacteriovores within the incubation flasks. Phytoplankton production was minimized by covering all incubation flasks with thick aluminum foil to eliminate light penetration. However, when cotton plugs were removed from the flask mouths for sampling purposes, light did enter the bottles. Although it may not have been enough light to foster phytoplankton production, it must be remembered that total light exclusion was not fully achieved for the entire 24 hour incubation.

More importantly is the inclusion of bacteriovores. Kirchman, et al. (1991) implicated bacterial grazers in lowering bacterial abundances and releasing DOC, thereby slowing the rate of DOC depletion. Prior to the February 1995 sampling date, a filtration experiment was conducted in the lab with water from a drainage ditch in Charlottesville. The only criteria for selecting the source of the water was the probability for containing high numbers of bacteria. The drainage water was then filtered through several different pore size filters and stained for microbial enumeration to determine relative abundances of microbes passing through each filter. Unfiltered water was also stained. It was this simple filtration experiment that resulted in the selection of a 8.0 μm pore size filter to remove most of the bacteriovores. Filters with smaller pore sizes yielded substantially lower numbers of cells and enumeration was extremely difficult. When temperatures were low, it was assumed that maximal bacterial cells would be needed for the incubation experiment. As temperatures increased, the use of 8.0 μm pore size filters was maintained in order to minimize heterogeneity within the experimental design between sampling dates. Wu (1995) described substantial bacterial grazing by nanoflagellates (2 - 20 μm protozoa) in seaside tidal creeks on the Delmarva Peninsula, Virginia. Therefore, the probability that bacteriovores were included in incubations is relatively great.

In the early incubations (spring and early summer), when temperatures were rising and initial bacterial abundances were similar, bacterivory may not have been very important. However, for the last July sampling, when

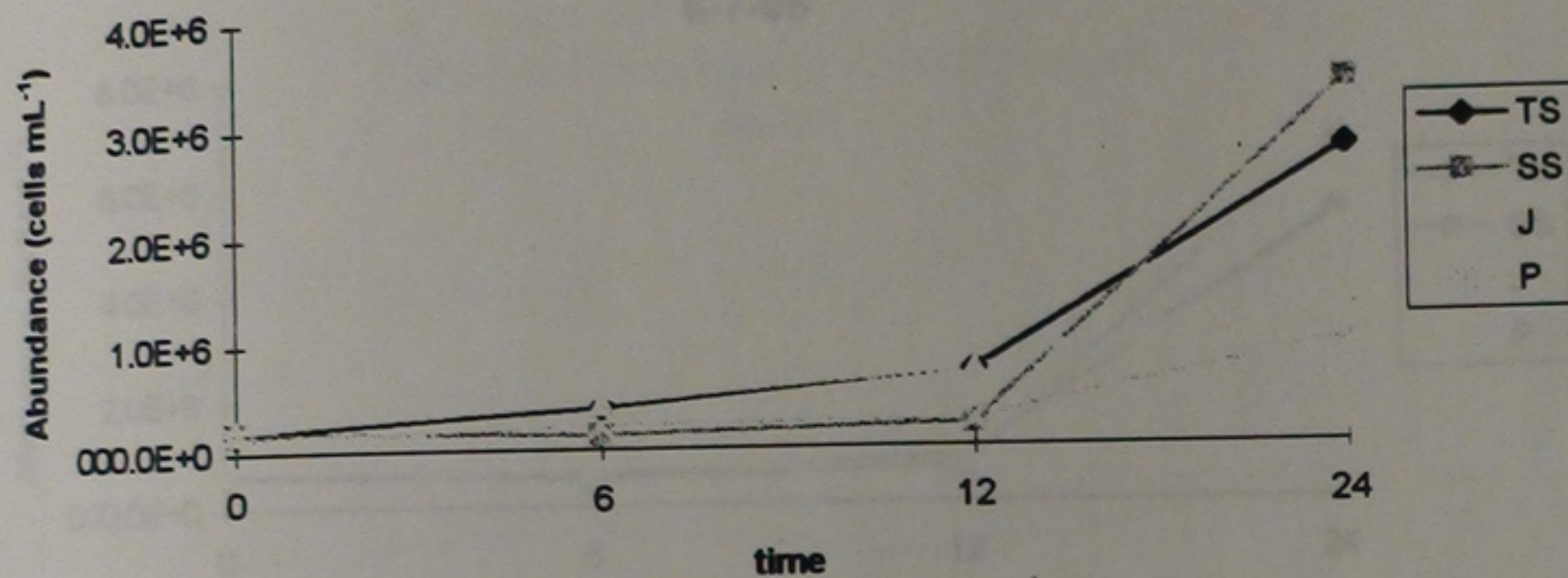
temperatures and initial bacterial abundances were highest, bacterivory may have contributed to increased DOC concentrations within the 24 h incubations.

Bacterivory would also explain the variability in changes in abundances over the incubations (Kirchman, et al 1991). Bacterial growth over 24 h showed clear exponential growth preceded by an initial lag phase, usually within the first 6 to 12 h (Fig. 18 a,b,c, and d). Apparent exponential growth occurred between 12 and 24 h. Pomeroy, et al. (1994) also found exponential growth between 12 and 24 h, followed by near steady-state conditions or decreases in bacterial numbers. This pattern obviously breaks down during the July 24 sampling date (Figure 18e). Initial bacterial numbers were highest at this date, and apparently very different (though not statistically different).

Shiah and Ducklow (1995) suggested that when substrate availability and supply exceed bacterial demand, temperature determines bacterial growth rates. However, when bacterial demand exceeds substrate supply and availability, it is the supply and availability that limit bacterial growth. MacMillin (1993) suggested that substrate quality may limit bacterial productivity in Phillips Creeks. If bacteria were limited by substrate during the July 24 sampling, bacterial growth may not have been able to keep up with grazing pressure, resulting in decreases in bacterial abundances rather than exponential growth in the first 12 - 24 h. However, DOC concentrations within each site were

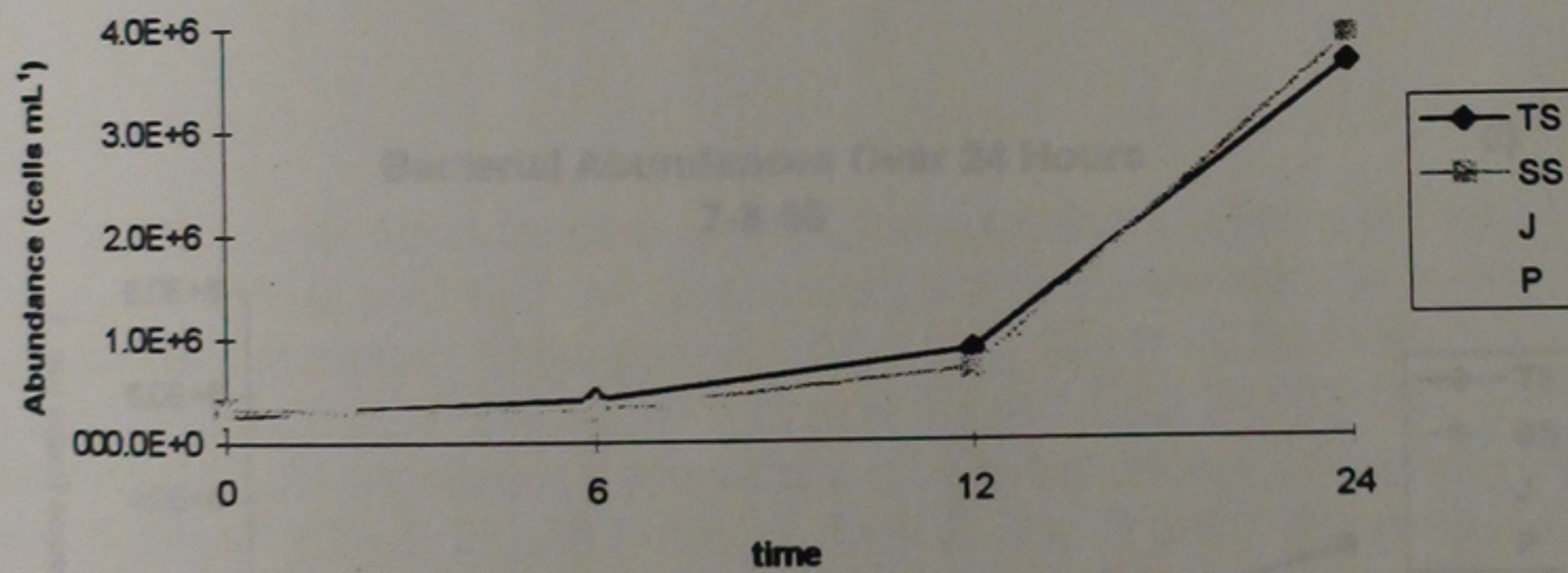
Bacterial Abundances Over 24 Hours
3-26-95

a)



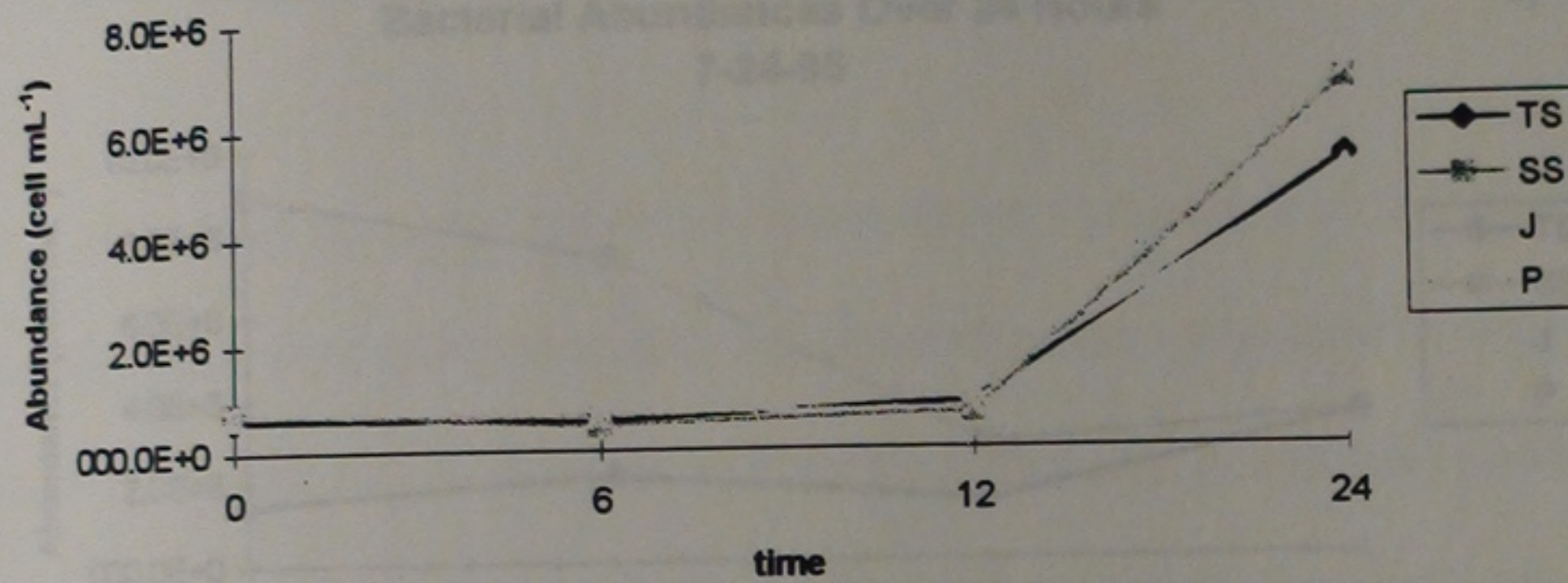
Bacterial Abundances Over 24 Hours
4-21-95

b)



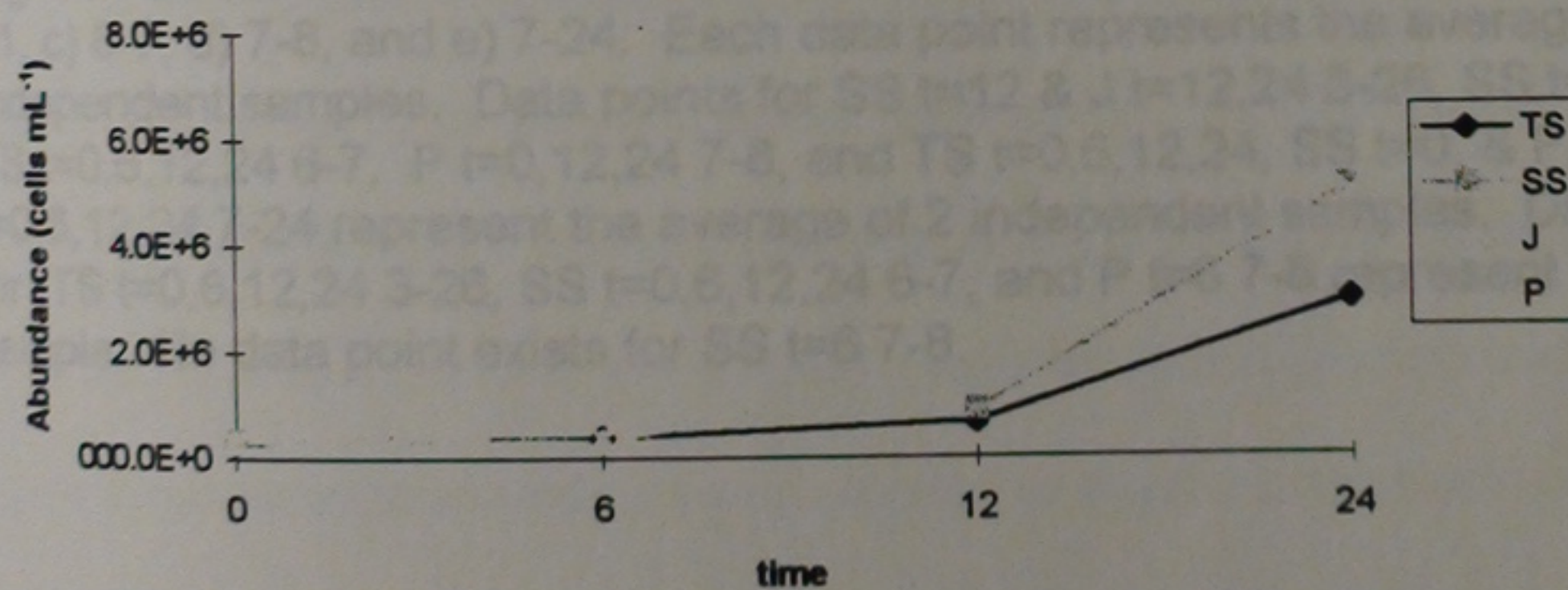
Bacterial Abundances Over 24 Hours
6-7-95

c)



Bacterial Abundances Over 24 Hours
7-8-95

d)



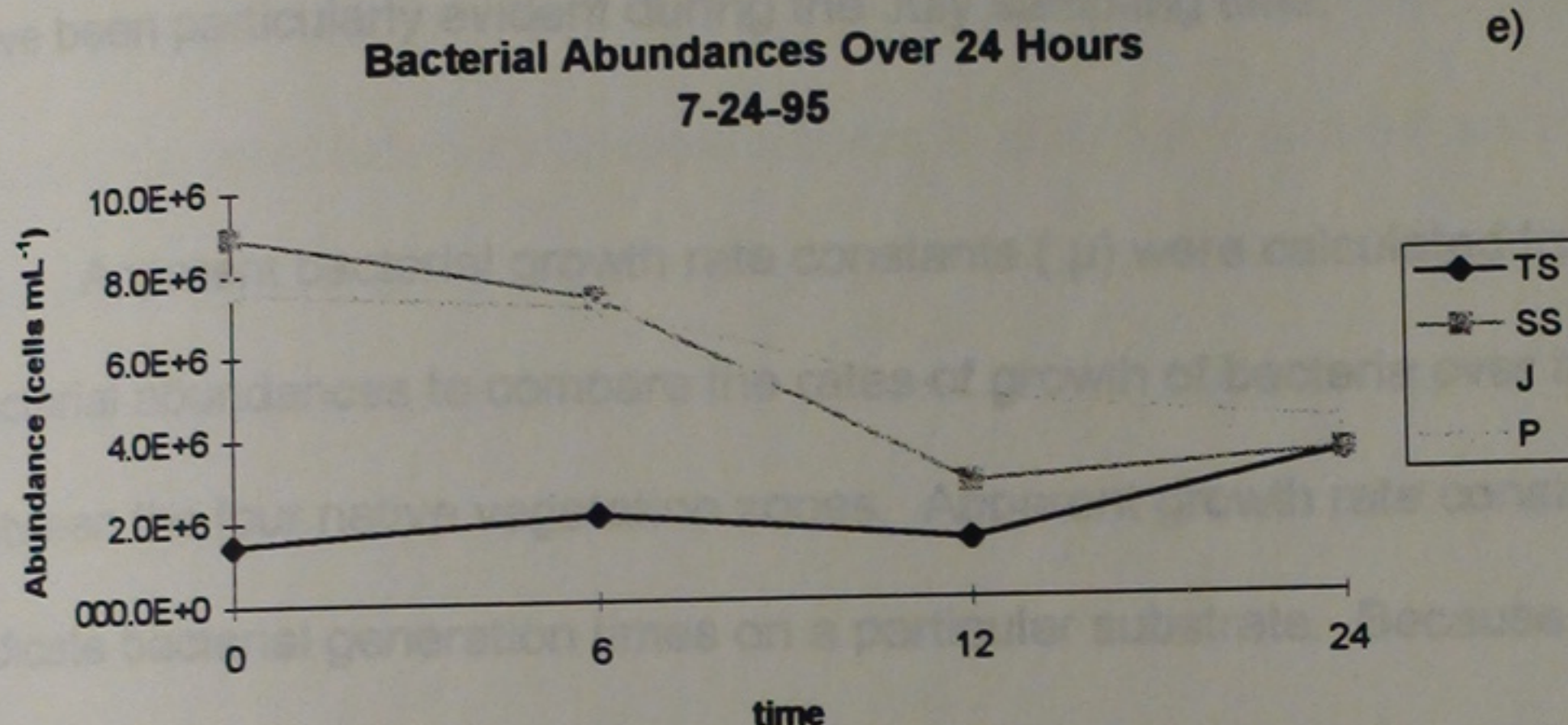


Fig. 18. Bacterial abundances over 24 hour incubation times for a) 3-26, b) 4-21, c) 6-7, d) 7-8, and e) 7-24. Each data point represents the average of 3 independent samples. Data points for SS t=12 & J t=12,24 3-26, SS t=0 4-21, TS t=0,6,12,24 6-7, P t=0,12,24 7-8, and TS t=0,6,12,24, SS t=0, & P t=0,6,12,24 7-24 represent the average of 2 independent samples. Data points for TS t=0,6,12,24 3-26, SS t=0,6,12,24 6-7, and P t=6 7-8 represent a single sample. No data point exists for SS t=6 7-8.

comparable between all sampling dates (except March 5); therefore, large differences in bacterial response to the DOC present at each site may indicate differences in the DOC quality between sites and within each site which may have been particularly evident during the July sampling time.

Apparent bacterial growth rate constants (μ) were calculated from bacterial abundances to compare the rates of growth of bacteria over time between the four native vegetation zones. Apparent growth rate constants also indicate bacterial generation times on a particular substrate. Because each μ was calculated from changes in bacterial abundances, it must be assumed that they were also affected by the inclusion of bacteriovores. However, because all samples were treated the same, apparent growth rate constants can still be used comparatively to yield information about the relative utilization of DOC from the 4 native plant zones by the same bacterial community.

The negative correlation between apparent growth rate constants and initial bacterial abundances ($r = 0.7649$) may also reflect grazing pressures. If higher initial bacterial abundances are related to smaller changes in bacterial abundances over a specific time, grazing could be effectively reducing bacterial growth. Grazing pressure can be related to bacterial abundance; higher prey abundance increases the probability of a bacteriovore contacting and subsequently ingesting a cell in the water column (Kennish 1986), which could

be particularly useful when explaining the drastic decline in growth rate constants found for the last July sampling date. On this date, initial bacterial abundances were higher than on previous sampling dates. Yet, changes in abundance and apparent growth rate constants were lowest. In fact, bacterial abundance decreased during the incubation, resulting in negative apparent growth rate constants for individual sippers in both the P and SS zones. Therefore, when grazing pressures apparently played a large role in the regulation of bacterial numbers (July 24 sampling), DOC from the TS zone was able to support greater bacterial production than DOC from the 3 interior sites..

Changes in bacterial abundances, changes in DOC, and estimates of apparent growth rate constants within the four native vegetative zones did not offer any definitive indication of relative DOC quality. However, the results of the bioassays conducted within the experimentally flooded plots did offer some insight; the response of the bacterial community to increased flooding frequency appears to be related to the dominant plant community within each plot. An apparent depression of changes in abundance and apparent growth rate constants were found within the JF plots but not in the PF plots (Fig. 5b and 6b). Although changes in bacterial abundances and μ were not different between the PC and PF plots, aboveground biomass was significantly lowered in the PF plots, relative to the PC. Differences in aboveground biomass were not found in the JC and JF treatments. (P. Tolley, pers. comm.). Perhaps increased flooding

affects *J. roemerianus* and *S. patens* plants differently. Regression analysis of bacterial growth rate constants and salinity from the native *J. roemerianus* zone (Fig. 19) revealed a negative relationship ($r = 0.88$) between the two variables; as salinity increased, bacterial growth rate constant decreased. A similar relationship was found between bacterial growth rate constants and salinity (Fig. 20) in the three other native vegetative zones ($r = 0.51$). Plant biomass was not measured within the native plant zones, so comparisons may not be made with the plant biomass within the experimental plots. The microbial and plant biomass data that is available from the experimentally flooded plots suggest that increased flooding frequency affects both *J. roemerianus* and *S. patens*, although initial plant responses to flooding appear to differ between the 2 species.

Extensive studies of the effect of different salinity regimes on *Juncus roemerianus* (Eleuterius 1989 a,b) have indicated that *J. roemerianus* is highly sensitive to even minor differences in salinity. Studying *J. roemerianus* *in situ*, Eleuterius (1989 a, b) found differences in growth patterns including leaf length, leaf diameter, and rhizome diameter, amino-acid composition, silica content, seed germination, and flowering period due to differences in salinities. Physiological changes and alterations of plant chemistry could affect decomposition processes and alter the relative quality of the DOC available to microbial communities.

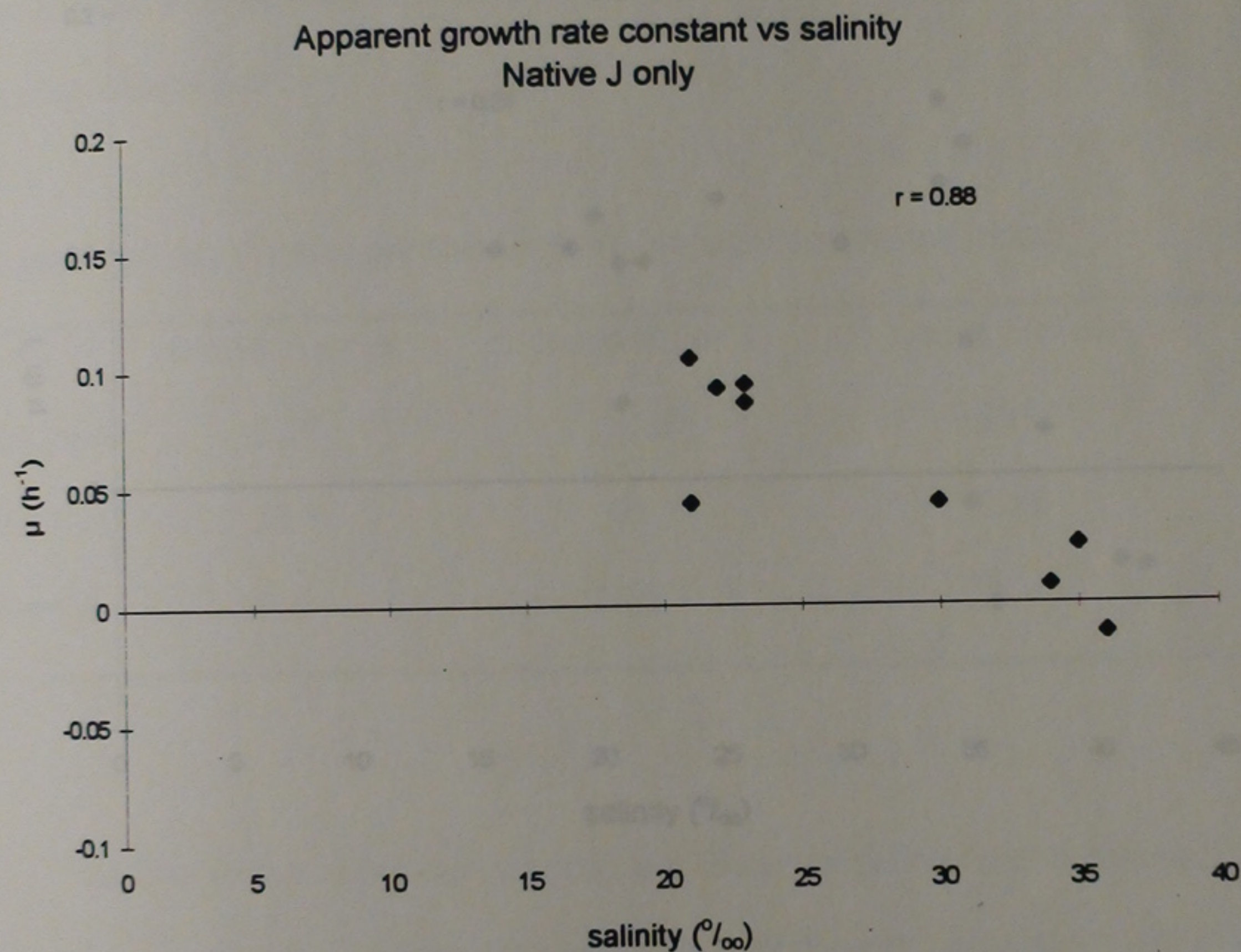


Fig. 19. Correlation between apparent growth rate constant (μ) and salinity within the native *Juncus roemerianus* zone. Data points represent each of 3 independent samples taken on 3-26, 6-7, or 7-24.

Apparent growth rate constant vs salinity Native TS, SS, & P

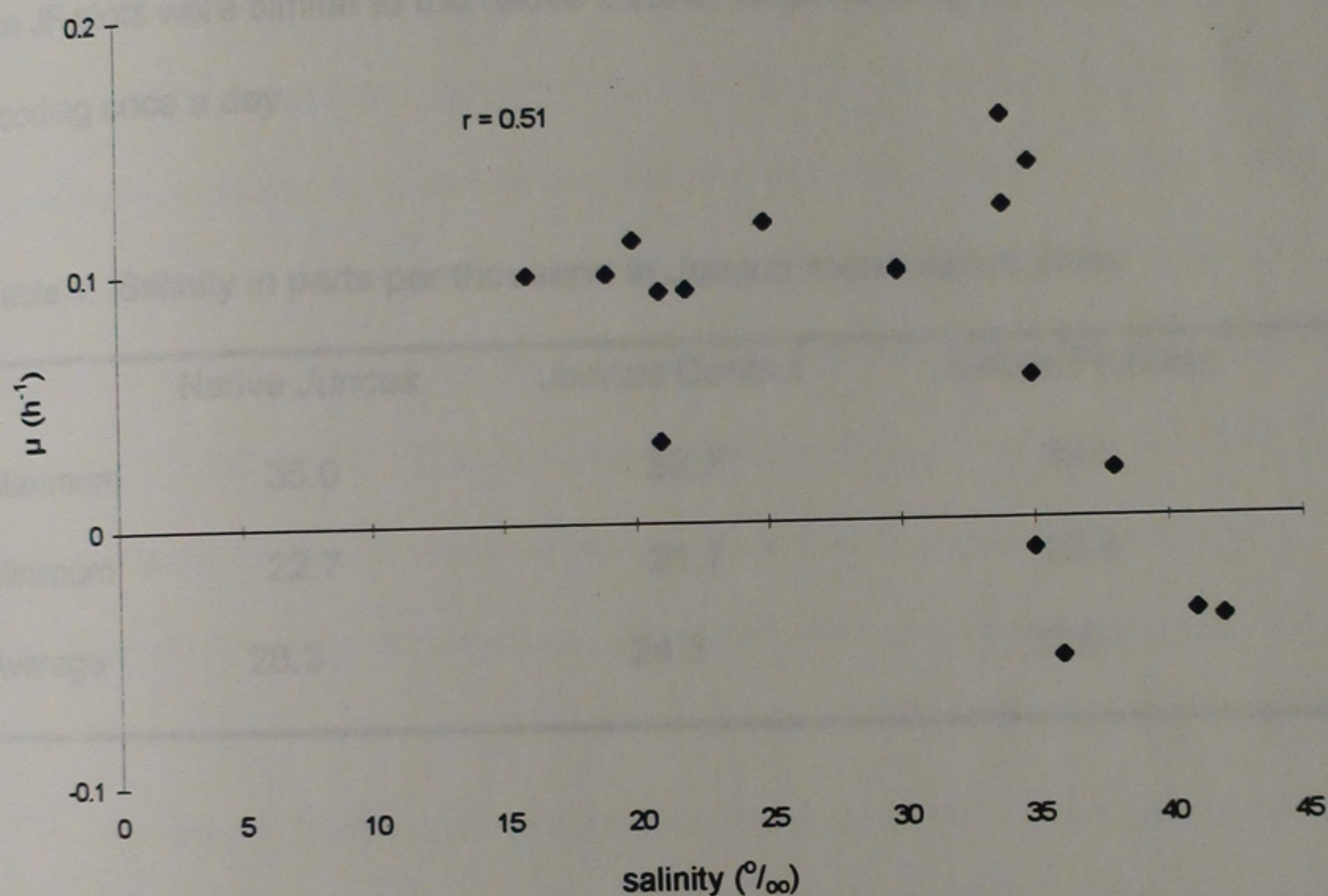


Fig. 20. Correlation between apparent growth rate (μ) and salinity in the native tall *Spartina alterniflora*, short *Spartina alterniflora*, and *Spartina patens* zones. Data points represent an independent sample taken on 3-26, 6-7, or 7-24.

Salinities within the experimental plots were closely monitored throughout June and July 1995. Table 3 contains maximum, minimum, and average salinities for the native and experimental *J. roemerianus* plots. Salinities within the JF plots were similar to the native J zone, which usually receives tidal flooding once a day.

Table 4. Salinity in parts per thousand in *Juncus roemerianus* plots.

	Native <i>Juncus</i>	<i>Juncus</i> Control	<i>Juncus</i> Flooded
Maximum	35.0	32.7	39.0
Minimum	22.7	21.7	23.5
Average	28.3	24.3	27.6

Several studies have documented the effects of salinity and increased flooding frequency on vegetation (Phleger 1971, Pulford & Tabatabai 1988, Pezeshki, et al. 1990, Nyman & DeLaune 1991, Naidoo, et al. 1992, and Nyman, et al. 1995). Pezeshki, et al. (1990) summarized such effects as alterations in normal chemical, physical and biological functions of soil and vegetation. Increased proline (Naidoo, et al 1992) and decreased protein and lipid content (Phleger 1971) in different *Spartina* species attributed to increased salinity, higher respiration rates within sites of higher salinities (Nyman & DeLaune 1991,

Nyman, et al 1995), changes in reaction rates of several enzymes associated with nutrient cycling due to waterlogging (Pulford & Tabatabai 1988), and reductions in photosynthetic rate, carbon assimilation and total leaf area in coastal tree species (Pezeshki, et al 1990) have been recently reported.

In all four native vegetative zones, there appears to be no relationship between DOC quantity and salinity (Fig. 21a and b). DOC quantity appears to be similarly unrelated to microbial respiration rates within the four native zones (Fig. 22). However, there does appear to be a relationship between biotic CO_2 production and salinity (during the July 24 sampling date) (Fig. 23, $r = 0.78$) within the TS, SS, and P sites only. When biotic CO_2 production is correlated with salinity within the J plot alone, the significance disappears; when J is combined with the other three zones, the relationship further deteriorates.

The results from the respiration bioassays must be interpreted cautiously, however. Measurements of CO_2 evolution over a 24 h incubation period were attempted on three occasions. During the first bioassay, (June 7), abiotic control samples were treated with formaldehyde to inhibit bacterial activity. Due to an apparent unforeseen reaction, all abiotic control vials contained greater amounts of CO_2 than the corresponding total CO_2 vials. During the second attempt, although abiotic control vials were injected with concentrated HNO_3 to inhibit microbial activity, several abiotic control vials apparently contained more CO_2 than the corresponding total CO_2 vials, resulting in negative biotic CO_2

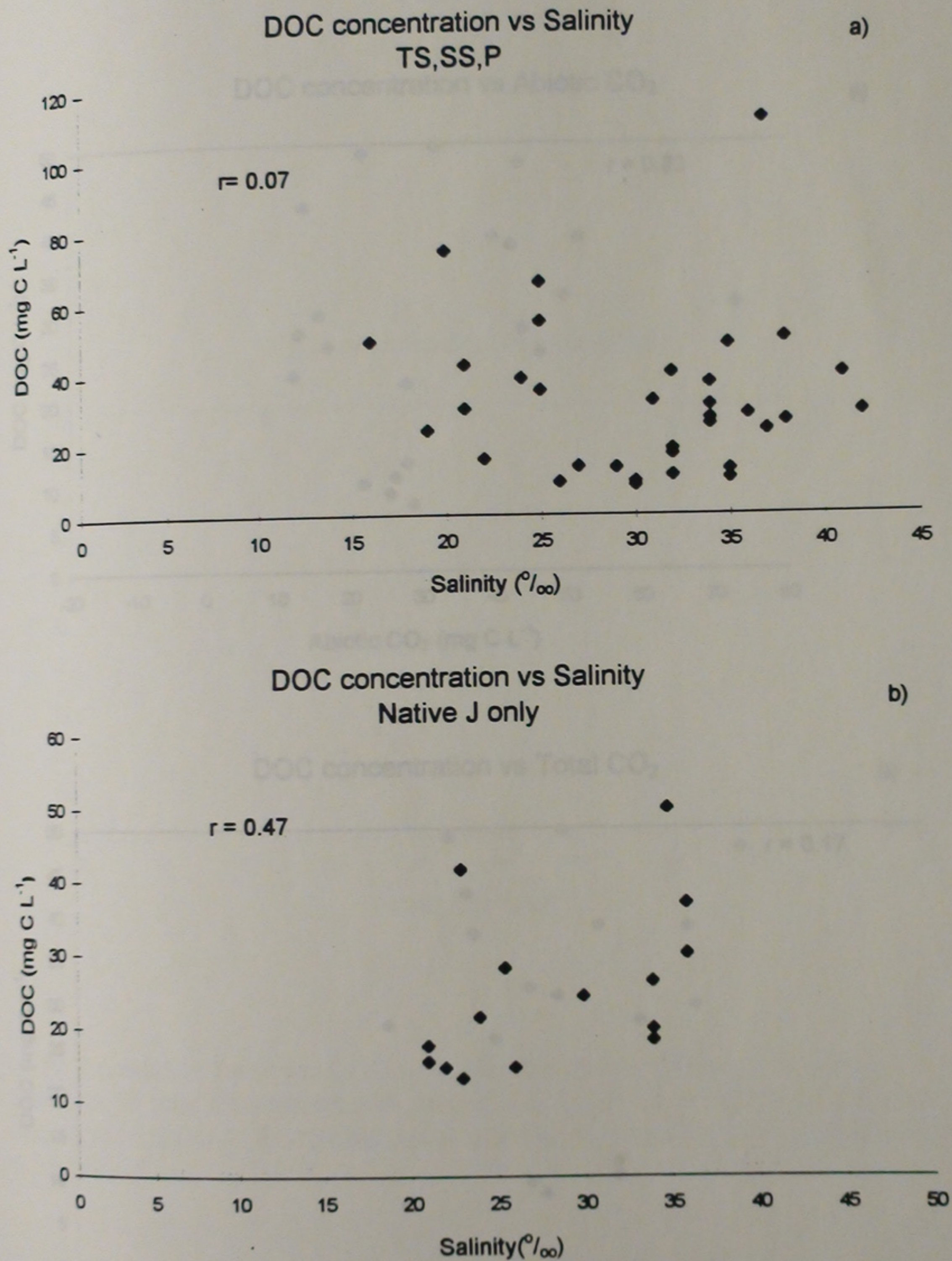
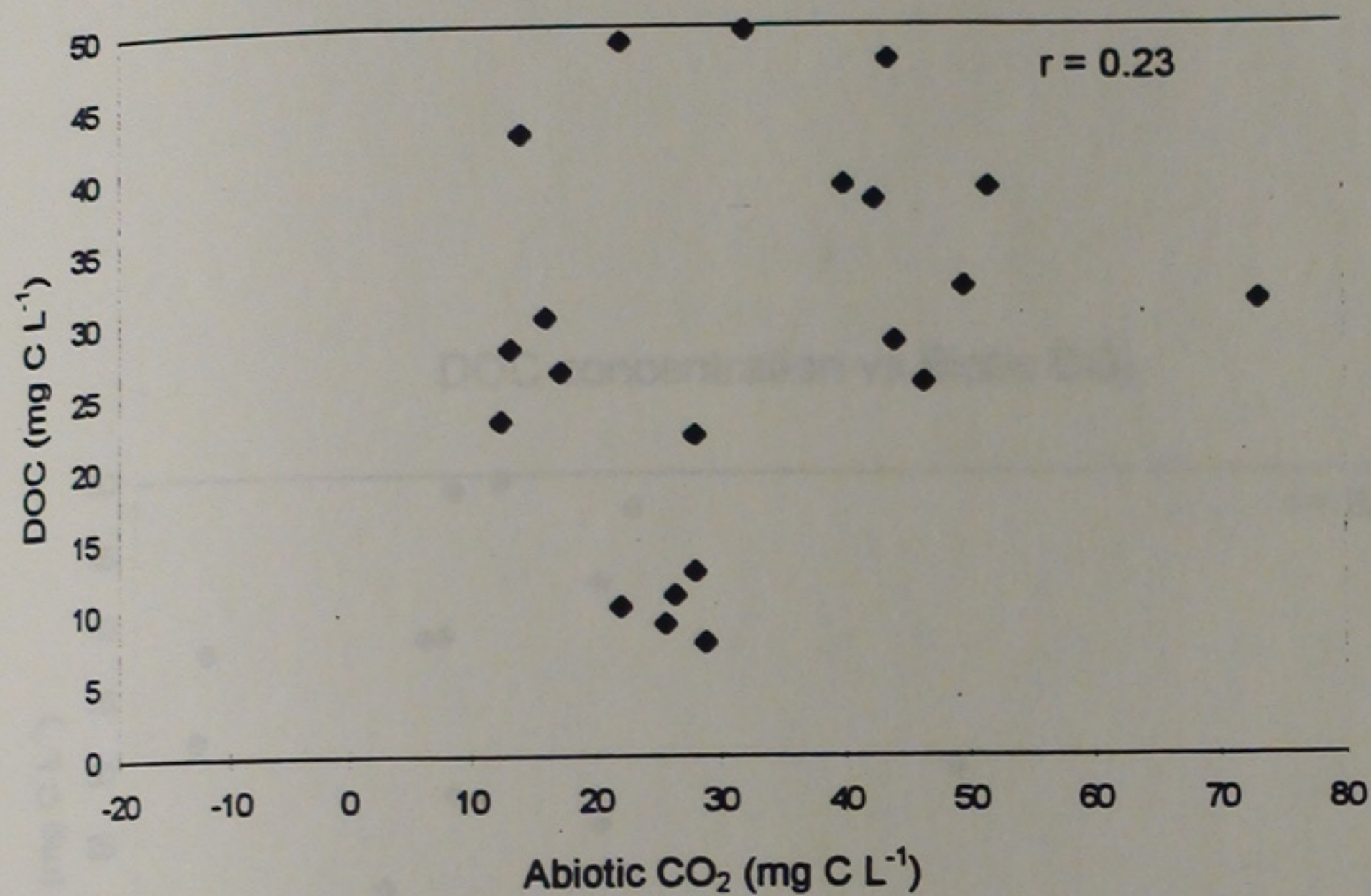


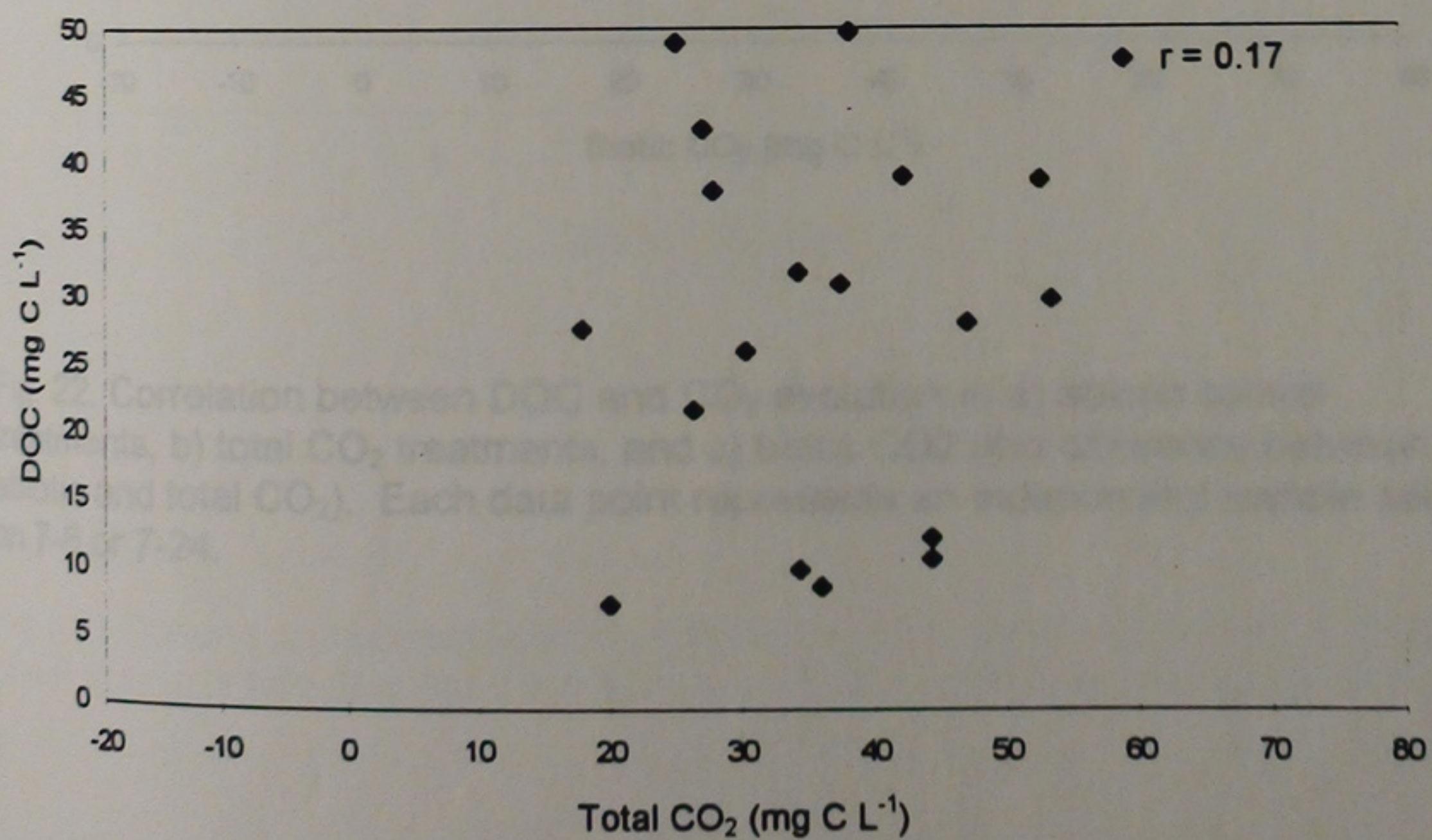
Fig. 21. Correlation between DOC and salinity in a) native TS, SS, and P zones and b) native J zone. Each data point represents an independent sample taken on 10-17, 3-26, 6-7, 6-21, or 7-24.

DOC concentration vs Abiotic CO_2

a)

DOC concentration vs Total CO_2

b)



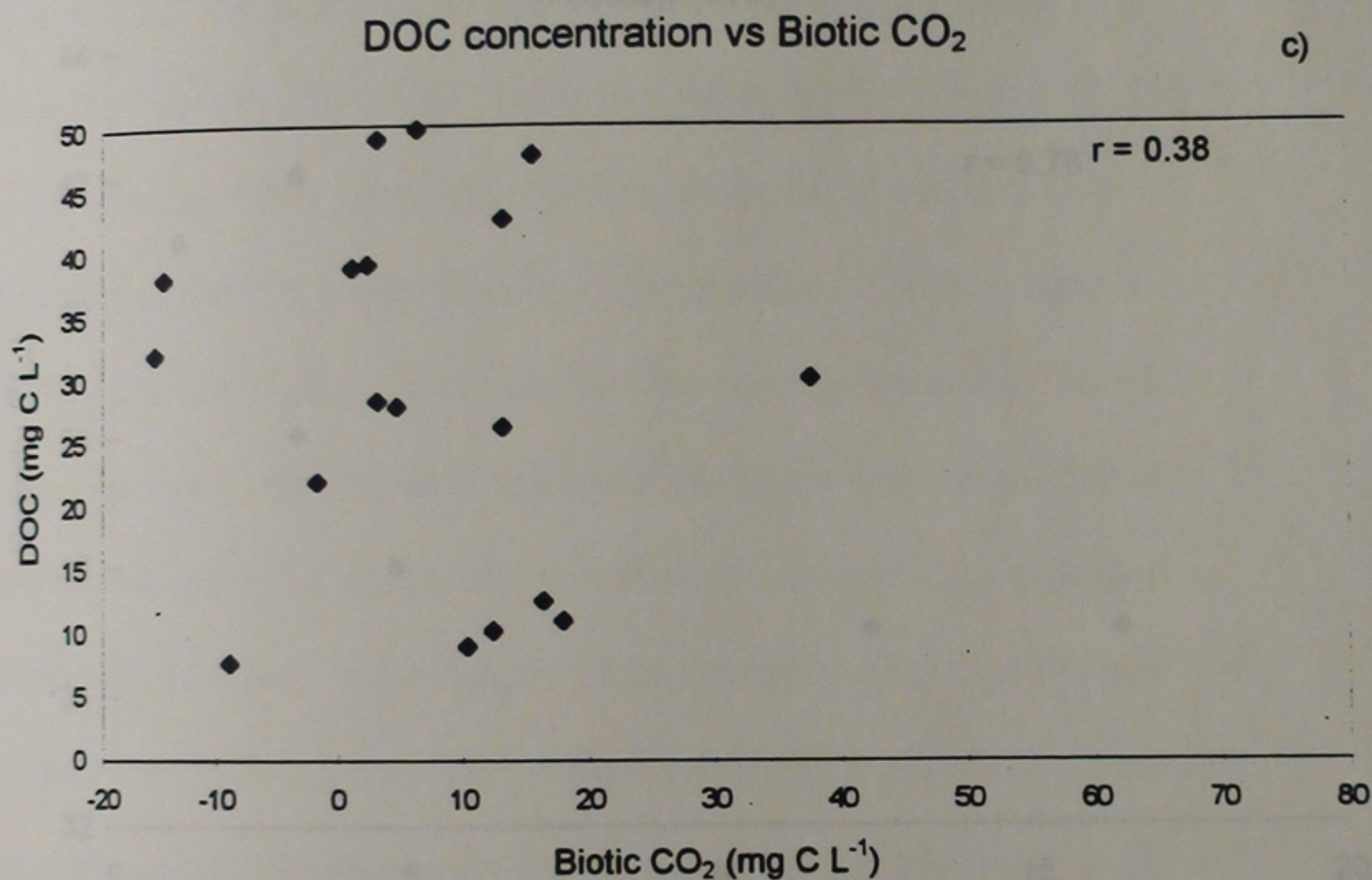


Fig. 22. Correlation between DOC and CO₂ evolution in a) abiotic control treatments, b) total CO₂ treatments, and c) biotic CO₂ (the difference between abiotic and total CO₂). Each data point represents an independent sample taken on 7-8 or 7-24.

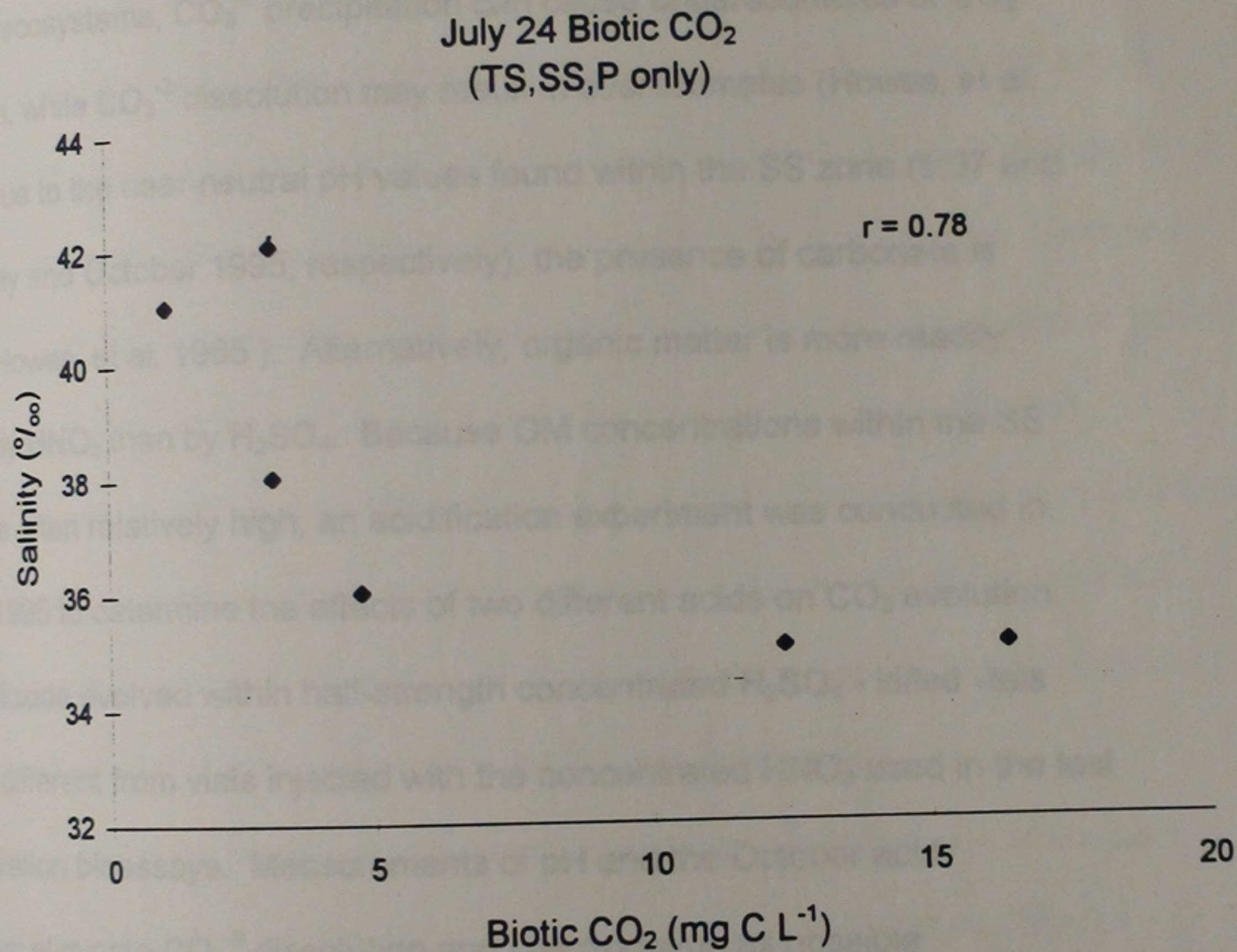


Fig. 23. Correlation between salinity and biotic CO₂ within the native TS, SS, and P zones. Each data point represents an independent sample taken on 7-24.

measurements over the incubation time. Only during the third and final attempt

did all CO_2 evolution calculations result in positive respiration values.

Another point worth discussing is the unusually, though consistent, high

CO_2 values found within the SS zone, in both abiotic control and total CO_2 vials.

In marine ecosystems, CO_3^{2-} precipitation can cause underestimates of CO_2

production, while CO_3^{2-} dissolution may result in overestimates (Howes, et al.

1985). Due to the near-neutral pH values found within the SS zone (6.97 and

6.77 in July and October 1995, respectively), the presence of carbonate is

unlikely (Howes, et al. 1985). Alternatively, organic matter is more readily

oxidized by HNO_3 than by H_2SO_4 . Because OM concentrations within the SS

zone were often relatively high, an acidification experiment was conducted in

October 1995 to determine the effects of two different acids on CO_2 evolution.

Carbon dioxide evolved within half-strength concentrated H_2SO_4 - killed vials

were not different from vials injected with the concentrated HNO_3 used in the last

two respiration bioassays. Measurements of pH and the October acid

experiment eliminate CO_3^{2-} dissolution and OM oxidation as possible

explanations of elevated CO_2 measurements within the SS zone. Therefore,

elevated CO_2 measurements found within this zone must be attributable to other

factors, and though not necessarily erroneous, must be interpreted cautiously.

Keeping in mind these uncertainties and the relative nature of the

respiration measurements, biotic CO_2 measurements from the July 24 sampling

date were combined with biomass measurements from the same date in order to

estimate bacterial carbon conversion efficiencies. Since biomass measurements were made only for the July 24 sampling date it is impossible to make comparisons between dates. However, these measurements may still be extremely useful. On the July 24 sampling date, changes in abundance and apparent growth rate constants were lowest for all four native zones, yet biomass increased over 24 hours. Sondergaard, et al. (1995) found similar results: high bacterial biomass and low bacterial growth rates, and suggested such results indicate utilization of organic carbon for maintenance of biomass instead of cell production. Changes in biomass over the 24 h incubation period were greater within the TS site than in the three interior sites (Fig. 9a). However, initial biomass measurements from each site were also very different. Therefore, biomass production measurements were normalized to the initial biomass for each site (Fig. 9b). Normalized biomass measurements suggest a much greater difference between the TS and interior sites.

Although there were apparent differences in respiration and biomass individually, when combined for efficiency estimations, there was little or no difference between any of the sites. However, estimated efficiencies may still be useful. The rather low efficiencies (1.3 - 2.6%) may actually strengthen the argument that bacteriovores were present and affected bacterial abundances within incubation vials. Benner, et al. (1988) discussed the effects of grazers on biomass measurements and bacterial efficiencies; they found that active bacteriovores decreased bacterial biomass present at the end of the incubation

and consequently reduced efficiency estimates. However, these calculated efficiencies were not dissimilar from calculated carbon conversion efficiencies for estuarine macrophytes from other studies. Newell, et al. (1983) found carbon conversion efficiencies for bacteria growing on *Juncus roemerianus* DOC to be as low as 2.5% at 10° C. Blum and Mills (1991) found efficiencies ranging between 2 - 20% for bacteria associated with *Zostera marina* detritus. Unfortunately, photomicrographs of stained bacterial samples from the experimentally flooded sites did not develop, and therefore, comments may not be made as to the relationship between flooding and carbon conversion efficiency.

Total carbon metabolism (Fig. 10) measurements may be more useful than estimated carbon conversion efficiencies. Although DOC from the TS zone supported the greatest biomass production (Fig. 9a and 9b) and bacterial cell growth (Fig. 5a) during the July 24 sampling, DOC from the J zone actually supported the greatest metabolism (biomass + respiration) of carbon on the same date (Fig. 10). It may be postulated then, that the native TS and J zones are more similar than originally presumed. These 2 sites may represent areas experiencing initial perturbation related to marsh transition (Brinson, et al. 1995). Brinson, et al. (1995) describe the serial changes which occur due to increases in tidal inundation across a typical east coast salt marsh. Increased inundation causes transition from low marsh tall *S. alterniflora* - dominated areas into zones of submerged aquatic vegetation (SAVs). Likewise, transitions from dominant

high marsh species, such as *J. roemerianus* to short form *S. alterniflora*, which withstands greater physiochemical stresses associated with more frequent flooding, also occurs. The distinctly higher rates of microbial metabolism associated with both the native TS and J zones may be indicative of initial changes occurring within this marsh.

The general suggestion may be made that DOC quality is determined by both plant and flooding frequency. Since decomposition involves the conversion of particulate organic material to dissolved organic material, factors controlling decomposition in the salt marsh will ultimately affect the DOC (quantity and quality) available for microbial utilization. Decomposition of organic material from each plant zone was not monitored in this study. Litter bag studies within Phillips Creek marsh (Blum 1993) suggest that decomposition is dependent upon location in the marsh, and therefore flooding frequency, and the composition and density of the material being degraded. Since both above and belowground plant biomass can be affected by increased flooding and salinity (Good 1982, Webb 1983, Christian, et al. 1990, Blum 1993, Nyman, et al. 1995, P. Tolley, pers. comm.), the relative quality of the dissolved organic matter available for microbial metabolism will probably also be affected by both plant type and flooding frequency and intensity.

CONCLUSIONS

For most months, pore water DOC concentrations within the TS zone were substantially different from DOC concentrations within the three interior sites. A general trend was found, in which the P zone usually contained the highest DOC concentrations; SS and J DOC concentrations were usually intermediate. In experimentally flooded plots, DOC concentrations were also found to be depressed within the flooded plots. These data suggest an inundation effect on DOC quantity between vegetation zones; DOC concentrations appear to increase with decreased inundation.

Data addressing microbial metabolism were less clear. Bacterial utilization of DOC depends primarily on DOC quality. Several measures of relative DOC quality were used including changes in bacterial abundance, calculation of apparent growth rate constants, and estimation of bacterial efficiencies based on respiration and biomass production measurements. There were no apparent differences in bacterial abundances, apparent growth rate constants, or carbon conversion efficiencies between the native vegetation zones. However, biomass production and total carbon metabolized were different between native plant zones. Additionally, bacterial abundances and apparent growth rate constants appeared to decrease within JF and PF when compared to JC and PC in the experimentally flooded plots. These results

indicate that microbial metabolism of pore water DOC may be a combination of vegetation type and inundation frequency and intensity.

In this Virginia salt marsh, the native TS and J vegetation zones may represent areas of transition between characteristic marsh zones similar to those described by Brinson, et al. (1995). This TS zone exists very close to the tidal creek (<3 m), experiences tidal flooding twice daily and can be covered with as much as 35 - 60 cm of water for 2 - 8 h each high tide. Even slight increases in sea level or tidal inundation could result in this low marsh site converting to a submerged zone. Similarly, the native J zone appears to occupy an area in transition. Data from the experimentally flooded sites suggest the JF site may be more similar to the native J zone than the JC site. Both the native J and JF sites experienced flooding at least once a day during June and July 1995 and average salinities within JF were similar to average salinities within the native J zone. As previously discussed, continued inundation of the JF sites may result in additional similarities between the native J and JF plots.

If the native TS and J zones are currently experiencing changes, the microbial community used in the bioassays may have been able to detect initial physiochemical changes due to increased inundation. The native TS and J zones represent the communities most likely to experience initial changes associated with marsh transition. Porewater DOC concentrations and microbial

metabolism may be indicative of initial physiochemical changes characteristic of marsh transition. Salt marsh DOC quantity and quality, therefore, may play an important role as indicators of state change.

On the Eastern US coast, where sea level is rising, and storm frequency and intensity appears to be increasing, increased inundation of many coastal marshes is probable. The effects of such inundation on plant zonation and microbial mediated processes involved in organic matter decomposition are not fully understood. Physiochemical differences between sites, due in large part to inundation differences, may be responsible for changes in the characteristic vegetation, which in turn affects OM quantity and quality. Maintenance of coastal marshes in the face of potential increases in inundation will therefore rely on rates of organic matter accumulation or mineralization within the marsh soils themselves. Monitoring changes in porewater DOC may provide information on initial perturbations and potential changes in salt marsh vegetative cover.

LITERATURE CITED

- Agosta, K. 1985. The effect of tidally induced changes in the creekbank water table on pore water chemistry. *Est. Coast. Shelf Sci.* 21:389-400.
- ASCE Task Committee on Sea-Level Rise and Its Effects on Bays and Estuaries. 1992. Effects of sea-level rise on bays and estuaries. *J. Hydraulic Engineering.* 118(1):1-10.
- Atlas, R.M. and R. Bartha. 1993. *Microbial Ecology Fundamentals and Applications*. The Benjamin/Cummings Publishing Co., Inc. CA. pp. 563.
- Baines, S.B. and M.L. Pace. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. *Limnol. Oceanogr.* 36(6):1078-1090.
- Benner, R., J. Lay, E. K'nees, and R.E. Hodson. 1988. Carbon conversion efficiency for bacterial growth on lignocellulose: Implications for detritus-based food webs. *Limnol. Oceanogr.* 33(6):1514-1526.
- Benner, R., M.L. Fogel, and E.K. Sprague. 1991. Diagenesis of belowground biomass of *Spartina alterniflora* in salt-marsh sediments. *Limnol. Oceanogr.* 36(7):1358-1374.
- Benner, R. and J.I. Hedges. 1993. A test of the accuracy of freshwater DOC measurements by high temperature catalytic oxidation and UV-promoted persulfate oxidation. *Mar. Chem.* 41:161-165.
- Beven, K. and P. Germann. 1982. Macropores and water flow in soils. *Water Res. Res.* 18(5):1311-1325.
- Biddanda, B., S. Opsahl, and R. Benner. 1994. Plankton respiration and carbon flux through bacterioplankton on the Louisiana shelf. *Limnol. Oceanogr.* 39(6):1259-1275.
- Bjornsen, P.K. 1986. Automatic determination of bacterioplankton biomass by image analysis. *Appl. Environ. Microbiol.* 51(6):1199-1204.
- Blum, L.K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. *Mar.*

Ecol. Prog. Ser. 102:169-178.

Blum, L.K. and R.R. Christian. 1997. Belowground production and decay along a tidal/elevational gradient. Poster.

Blum, L.K. and A.L. Mills. 1991. Microbial growth and activity during the initial stages of seagrass decomposition. *Mar. Ecol. Prog. Ser.* 70:73-82.

Borey, R.B., P.A. Harcombe, and F.M. Fisher. 1983. Water and organic carbon fluxes from an irregularly flooded brackish marsh on the upper Texas coast, USA. *Est. Coast. Shelf Sci.* 16:379-402.

Bouma, J. 1980. Soil morphology and preferential flow along macropores. *Ag. Water Mgt.* 3:235-250.

Brylinsky, M. 1977. Release of dissolved organic matter by some marine macrophytes. *Mar. Biol.* 39:213-220.

Brinson, M.M., R.R. Christian, and L.K. Blum. 1995. Multiple states in the sea-level induced transition from terrestrial forest to estuary. *Estuaries* 18(4):648-659.

Chambers, R.M. 1990. Nitrogen and phosphorus dynamics in tidal fresh water marshes. PhD Dissertation. University of Virginia. Charlottesville.

Chambers, R.M. and W.E. Odum. 1990. Pore water oxidation, dissolved phosphate and the iron curtain. Iron-phosphorus relations in tidal freshwater marshes. *Biogeochem.* 10:37-52.

Christian, R.R., K. Bancroft, and W.J. Wiebe. 1978. Resistance of the microbial community within salt marsh soils to selected perturbations. *Ecology* 59(6):1200-1210.

Christian, R.R., W.L. Bryant, and M.M. Brinson. 1990. *Juncus roemerianus* production and decomposition along gradients of salinity and hydroperiod. *Mar. Ecol. Prog. Ser.* 68:137-145.

Cline, J. 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. *Limnol. Oceanogr.* 4:454-458.

Cole, J.J., G.E. Likens, and D.L. Strayer. 1982. Photosynthetically produced dissolved organic carbon: An important carbon source for planktonic bacteria. *Limnol. Oceanogr.* 27(6):1080-1090.

- Dame, R., T. Chrzanowski, K. Bildstein, B. Kjerfve, H. McKellar, D. Nelson, J. Spurrier, S. Stancyk, H. Stevenson, J. Vernberg, and R. Zingmark. 1986. The outwelling hypothesis and North Inlet, South Carolina. *Mar. Ecol. Prog. Ser.* 33:217-229.
- Dankers, N., M. Binsberger, K. Zegers, R. Laane, and M.R. van de Loeff. 1984. Transportation of water, particulate and dissolved organic and inorganic matter between a salt marsh and the Ems-Dollard Estuary, The Netherlands. *Est. Coast. Shelf Sci.* 19:143-165.
- Day, J.W., Jr., C.A.S. Hall, W.M. Kemp, and A. Yanez-Arancibia. 1989. *Estuarine Ecology*. John Wiley & Sons. New York. pp.558
- de la Cruz, A.A. and B.C. Gabriel. 1974. Caloric, elemental, and nutritive changes in decomposing *Juncus roemerianus* leaves. *Ecology*. 55:882-886.
- Edmonds, W.J., P.R. Cobb, and C.D. Peacock. 1986. Characterization and classification of seaside salt marsh soils on Virginia's Eastern Shore. *Soil Sci. Soc Am. J.* 50:672-678.
- Eleuterius, L.N. 1989 a. Natural selection and genetic adaptation to hypersalinity in *Juncus roemerianus* Scheele. *Aquatic Bot.* 36:45-53.
- Eleuterius, L.N. 1989 b. Taximetric analysis of female and hermaphroditic plants among populations of *Juncus roemerianus* under different salinity regimes *J. Coast. Res.* 5(1):29-35.
- Fenchel, T. 1984. Suspended marine bacteria as a food source. In *Flows of energy and materials in marine ecosystems*. (Fasham, M.J. R., ed). Plenum Press. New York. pp. 301-315.
- Fetter, C.W. 1988. *Applied Hydrogeology*. Merrill Publishing Co. Columbus. pp. 592.
- Gallagher, J.L., W.J. Pfeiffer, and L.R. Pomeroy. 1976. Leaching and microbial utilization of dissolved organic carbon from leaves of *Spartina alterniflora*. *Est. Coast. Mar. Sci.* 4:467-471.
- Gardner, L.R. 1975. Runoff from an intertidal marsh during tidal exposure - recession curves and chemical characteristics. *Limnol. Oceanogr.* 20(1):81-89.
- Gardner, W.S., R. Benner, G. Chin-Leo, J.B. Cotner, Jr., B.J. Cavaletto. and

- M.B. Lansing. 1994. Mineralization of organic matter and bacterial dynamics in Mississippi River plume water. *Estuaries*. 17(4):816-828.
- Good, R.E., N.F. Good, and B.R. Frasco. 1982. A review of primary production and decomposition dynamics of the belowground marsh component. In *Estuarine Comparisons*. (V.S. Kennedy, ed.). Academic Press. New York. pp. 139-157.
- Grasshoff, K., M. Ehrhardt, and K. Kremling (eds.). 1983. *Methods of Seawater Analysis*. Verlag Chemie. Weinheim.
- Griffith, P.C. and L.R. Pomeroy. 1995. Seasonal and spatial variations in pelagic community respiration on the southeastern U.S. continental shelf. *Cont. Shelf Res.* 15(7):815-825.
- Hackney, C.T. 1987. Factors affecting accumulation or loss of macroorganic matter in marsh sediments. *Ecology*. 68(4):1109-1113.
- Harvey, J.W. 1993. Measurement of variation in soil solute tracer concentration across a range of effective pore sizes. *Water Res. Res.* 29(6):1831-1837.
- Harvey, J.W., P.F. Germann, and W.E. Odum. 1987. Geomorphological control of subsurface hydrology in the creekbank zone of tidal marshes. *Est. Coast. Shelf Sci.* 25:677-691.
- Hayden, B.P., R.D. Duesler, J.T. Callahan, and H.H. Shugart. 1991. Long-term ecological research at the Virginia Coastal Reserve. *Bioscience*. 41:314-322.
- Heinle, D.R., D.A. Flemer, and J.F. Ustach. 1975. Contribution of tidal marshlands to Mid-Atlantic estuarine food chains. In *Estuarine Processes*. (M. Wiley, ed). Academic Press, New York. pp. 309-320.
- Heywood, M.A. 1977. The effects of nutrient enrichment on the decomposition of *Spartina cynosuroides* and *Peltandra virginica*. Masters Thesis. University of Virginia.
- Hobbie, J.E., R.J. Daley, and S. Jasper. 1977. Use of nucleopore filters for counting bacteria by fluorescence microscopy. *Appl. Environ. Microbiol.* 33(5):1225-1228.
- Howarth, R.W. and J.E. Hobbie. 1982. The regulation of decomposition and heterotrophic microbial activity in salt marsh soils: a review. In *Estuarine*

- Processes (V.S. Kennedy, ed.). Academic Press. New York. pp. 183-207.
- Howarth, R.W. and J.M. Teal. 1979. Sulfate reduction in a New England salt marsh. *Limnol. Oceanogr.* 24(6):999-1013.
- Howes, B.L., J.W.H. Dacey, and J.M. Teal. 1985. Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. *Ecology*. 66(2):595-605.
- Jordan, T.E. and D.L. Correll. 1985. Nutrient chemistry and hydrology of interstitial water in brackish tidal marshes of Chesapeake Bay. *Est. Coast. Shelf Sci.* 21:45-55.
- Kennish, M.J. 1986. *Ecology of Estuaries vol. II. Biological Aspects*. CRC Press. Boca Raton. pp.391.
- Kirby, C.J. 1971. The annual net primary production and decomposition of the salt marsh grass *Spartina alterniflora* Loisel in the Barataria Bay Estuary of Louisiana. PhD Dissertation. Louisiana State University.
- Kirby, C.J. and J.G. Gosselink. 1976. Primary production in a Louisiana Gulf Coast *Spartina alterniflora* marsh. *Ecology*. 57:1052-1059.
- Kirchman, D.L., Y. Suzuki, C. Garside, and H.W. Ducklow. 1991. High turnover rates of dissolved organic carbon during a spring phytoplankton bloom. *Nature*. 352:612-614.
- Koch, M.S., I.A. Mendelssohn, K.L. McKee. 1990. Mechanism for the hydrogen sulfide-induced growth limitation in wetland macrophytes. *Limnol. Oceanogr.* 35(2):399-408.
- Leff, L.G., J.L. Burch, and J.V. McArthur. 1991. Bacterial use of dissolved organic carbon from Carolina Bays. *Amer. Mid. Nat.* 126:308-316.
- Leff, L.G. and J.L. Meyer. 1991. Biological availability of dissolved organic carbon along the Ogeechee River. *Limnol. Oceanogr.* 36(2):315-323.
- MacMillin, K. M. 1993. Bacteria dynamics in tidal creeks of the Eastern Shore of Virginia. M.S. Thesis. University of Virginia. Charlottesville.
- Marinucci, A.C., J.E. Hobbie, and J.V.K. Helfrich. 1983. Effect of litter nitrogen on decomposition and microbial biomass in *Spartina alterniflora*. *Micro. Ecol.* 9:27-40.

- Mitsch, W.J. and J.G. Gosselink. 1993. *Wetlands*. Van Nostrand Reinhold. New York. pp. 722.
- Montgomery, J.R., C.F. Zimmerman, and M.T. Price. 1979. The collection, analysis, and variation of nutrients in estuarine porewater. *Est. Coast. Mar. Sci.* 9:203-214.
- Moran, M.A. and R.E. Hodson. 1989a. Bacterial secondary production on vascular plant detritus: relationships to detritus composition and degradation rate. *Appl. Envi. Micro.* 55(9):2178-2189.
- Moran, M.A. and R.E. Hodson. 1989b. Formation and utilization of dissolved organic carbon derived from detrital lignocellulose. *Limnol. Oceanogr.* 34(6):1034-1047.
- Moran, M.A. and R.E. Hodson. 1990. Bacterial production on humic and nonhumic components of dissolved organic carbon. *Limnol. Oceanogr.* 35(8):1744-1756.
- Naidoo, G., K.L. McKee, and I.A. Mendelssohn. 1992. Anatomical and metabolic responses to waterlogging and salinity in *Spartina alterniflora* and *S. Patens* (Poaceae). *Am. J. Bot.* 79(7):765-770.
- Newell, R.C., E.A.S. Linley, and M.I. Lucas. 1983. Bacterial production and carbon conversion based on salt marsh plant debris. *Est. Coast Shelf Sci.* 17:405-419.
- Nixon, S.W. 1980. Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In *Estuarine Processes* (P. Hamilton and K. MacDonald, eds.). Plenum Press. New York. pp. 438-525.
- Nuttle, W.K. and H.F. Hemond. 1988. Salt marsh hydrology: implications for biogeochemical fluxes to the atmosphere and estuaries. *Global Biogeochem. Cycles.* 2(2):91-114.
- Nyman, J.A., and R.D. DeLaune. 1991. CO₂ emission and soil Eh responses to different hydrological conditions in fresh, brackish, and saline marsh soils. *Limnol Oceanogr.* 36(7):1406-1414.
- Nyman, J.A., R.D. DeLaune, S.R. Pezeshki, W.H. Patrick, Jr. 1995. Organic matter fluxes and marsh stability in a rapidly submerging estuarine marsh. *Estuaries.* 18(1B):207-218.

- Odum, E.P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling, and detritus-based food chains. In *Estuarine Perspectives* (V.S. Kennedy, ed). Academic Press. New York. pp.485-495.
- Ogura, N. 1975. Further studies on decomposition of dissolved organic matter in coastal seawater. *Marine Biology*. 31:101-111.
- Osgood, D.T. and J.C. Zieman. 1993. Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. *Estuaries*. 16(4):815-826.
- Osgood, D.T., M.C.F.V. Santos, and J.C. Zieman. 1995. Sediment physico-chemistry associated with natural marsh development on a storm-deposited sand flat. *Mar. Ecol. Prog. Ser.* 120:271-283.
- Otte, M.L. and J.T. Morris. 1994. Dimethylsulphoniopropionate (DMSP) in *Spartina alterniflora* Loisel. *Aquatic Botany*. 48:239-259.
- Pezeshki, S.R., R.D. DeLaune, and W.H. Patrick, Jr. 1990. Flooding and saltwater intrusion: Potential effects on survival and productivity of wetland forests along the U.S. Gulf Coast. *For. Ecol. Manage.* 33/34:287-301.
- Phleger, C.F. 1971. Effect of salinity on growth of a salt marsh grass. *Ecology*. 52(5):908-911.
- Pomeroy, L.R., K. Bancroft, J. Breed, R.R. Christian, D. Frankenberg, J.R. Hall, L.G. Maurer, W.J. Wiebe, R.G. Weigert, and R.L. Wetzel. 1975. Flux of organic matter through a salt marsh. In *Estuarine Processes (Vol. 2) Circulation, Sediments, and Transfer of Material in the Estuary*. (M. Wiley, ed). Academic Press, New York. pp.270-279.
- Pomeroy, L.R., J.E. Sheldon, and W.M. Sheldon, Jr. 1994. Changes in bacterial numbers and leucine assimilation during estimations of microbial respiratory rates in seawater by the Precision Winkler method. *Appl. Envi. Micro.* 60(1):328-332.
- Pomeroy, L.R. and W.J. Wiebe. 1988. Energetics of microbial food webs. *Hydrobiologia*. 159:7-18.
- Price, J.S., K. Ewing, M. Woo, and K.A. Kershaw. 1988. Vegetation patterns in James Bay coastal marshes. II. Effects of hydrology on salinity and

- vegetation. *Can. J. Bot.* 66:2586-2594.
- Pulford, I.D. and M.A. Tabatabai. 1988. Effect of waterlogging on enzyme activities in soils. *Soil Biol. Biochem.* 20(2):215-219.
- Shiah, F. and H.W. Ducklow. 1995. Multiscale variability in bacterioplankton abundance, production, and specific growth rate in a temperate salt marsh tidal creek. *Limnol. Oceanogr.* 40(1):55-66.
- Sondergaard, M., B. Hanson, and S. Markager. 1995. Dynamics of dissolved carbon lability in a eutrophic lake. *Limnol. Oceanogr.* 40(1):46-54.
- Sondergaard, M. and M. Middelboe. 1995. A cross system analysis of labile dissolved organic carbon. *Mar. Ecol. Prog. Ser.* 118:283-294.
- Sottile, W.S., Jr. 1974. Studies of microbial production and utilization of dissolved organic carbon in a Georgia salt marsh - estuarine system. Ph.D. Dissertation. University of Georgia. pp.153.
- Sugimura, Y. and Y. Suzuki. 1988. A high-temperature catalytic oxidation method for the determination of non-volatile dissolved organic carbon in seawater by direct injection of a liquid sample. *Mar. Chem.* 24:105-131.
- Sundh, I. 1992. Biochemical composition of dissolved organic carbon derived from phytoplankton and used by heterotrophic bacteria. *Appl. Environ. Micro.* 58(9):2938-2947.
- Taylor, D.I. and B.R. Allanson. 1995. Organic carbon fluxes between a high marsh and estuary and the inapplicability of the Outwelling Hypothesis. *Mar. Ecol. Prog. Ser.* 120:263-270.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology.* 43(4):614-624.
- Titus, J.G. 1987. The greenhouse effect, rising sea level and coastal wetlands. EPA-230-05-86-013. Office of Policy, Planning and Evaluation, Environmental Protection Agency, Washington, D.C.
- Valiela, I., J.M. Teal, S. Volkmann, D. Shafer, and E.J. Carpenter. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: tidal exchanges and inputs by precipitation and groundwater. *Limnol. Oceanogr.* 23(4):798-812.

- Waksman, S.S. and F.G. Tenney. 1928. Composition of natural organic materials and their decomposition in the soil: III. The influence of nature of plant upon the rapidity of its decomposition. *Soil Sci.* 26:155-171.
- Webb, J.W. 1983. Soil water salinity variations and their effects on *Spartina alterniflora*. *Contributions in Mar. Sci.* 26:1-13.
- Williams, T.M., T.G. Wolaver, R.F. Dame, and J.D. Spurrier. 1992. The Bly Creek ecosystem study - organic carbon transport within a euhaline salt marsh basin, North Inlet, South Carolina. *J. Exp. Mar. Biol. Ecol.* 163:125-139.
- Wright, R.T. 1984. Dynamics of pools of dissolved organic carbon. In *Heterotrophic Activity in the Sea*. (J.E. Hobbie & P.L. Williams, eds.). Plenum Press. pp. 121-154.
- Wu, K. 1995. Protozoan grazing effects on bacterial dynamics in estuarine tidal marsh creeks. Masters Thesis. University of Virginia.
- Yelverton, G.F. and C.T. Hackney. 1986. Flux of dissolved organic carbon and pore water through the substrate of a *Spartina alterniflora* marsh in North Carolina. *Est. Coast. Shelf Sci.* 22:255-267.
- Zweifel, U.L., B. Norrman, and A. Hagstrom. 1993. Consumption of dissolved organic carbon by marine bacteria and demand for inorganic nutrients. *Mar. Ecol. Prog. Ser.* 101:23-32.
- Zweifel, U.L., J. Wikner, and A. Hagstrom. 1995. Dynamics of dissolved organic carbon in a coastal ecosystem. *Limnol. Oceanogr.* 40(2):299-305.

Appendix I a - Bacterial abundances for individual sippers within each vegetation zone for each sampling date and each subsampling time.

t=0	t=6	t=12	t=24	t=0	t=6	t=12	t=24
cells/mL	cells/mL	cells/mL	cells/mL	cells/mL	cells/mL	cells/mL	cells/mL
8/8/1994				10/17/1994			
TS1	5.84E+06	4.17E+06		TS1	2.08E+06	1.54E+06	
TS2	1.61E+06	8.03E+06		TS2	1.87E+06	1.61E+06	
TS3	1.92E+06	1.19E+07		TS3			
SS1	1.25E+07	1.59E+07		SS1	1.54E+06	2.89E+06	
SS2	1.35E+07	1.73E+07		SS2	2.25E+06	2.93E+06	
SS3	1.10E+07	1.45E+07		SS3	1.76E+06	1.78E+06	
J1	1.74E+07	1.50E+07		J1	2.12E+06	1.53E+06	
J2	5.41E+06	9.27E+06		J2	2.56E+06	2.59E+06	
J3	4.99E+06	7.81E+06		J3	2.24E+06	1.45E+06	
P1	5.62E+05	3.71E+06		P1	2.17E+06	2.77E+06	
P2	2.28E+06	4.43E+06		P2	2.36E+06	2.75E+06	
P3	3.58E+06	3.82E+06		P3	2.95E+06	3.26E+06	
PC1				PC1			
PC2				PC2			
PC3				PC3			
2/4/1995				3/5/1995			
TS1		2.31E+06		TS1	5.87E+05	8.10E+05	1.00E+06
TS2				TS2			
TS3	1.07E+06	7.80E+06		TS3	4.33E+05	1.08E+06	1.64E+06
SS1		5.46E+06		SS1	4.75E+05	8.18E+05	9.95E+06
SS2	8.85E+05	8.91E+06		SS2			9.98E+06
SS3	1.03E+06	4.07E+06		SS3	9.64E+05	8.62E+05	7.67E+06
J1	8.18E+05	2.09E+06		J1	6.53E+05	1.12E+06	2.32E+06
J2				J2	1.06E+06	7.65E+05	2.14E+06
J3	8.66E+05	2.54E+06		J3			
P1	9.45E+05	1.22E+06		P1		5.06E+05	6.36E+05
P2	7.58E+05	2.20E+06		P2	1.07E+06	1.04E+06	2.02E+06
P3	9.02E+05	1.05E+06		P3	7.68E+05	5.76E+05	7.37E+05
PC1	1.52E+06	2.34E+06		PC1	1.06E+06	8.90E+05	2.09E+06
PC2	1.75E+06	2.60E+06		PC2	9.06E+05	1.49E+06	2.35E+06
PC3				PC3	9.13E+05	1.38E+06	3.74E+05

Appendix I a - Continued

	t=0 cells/mL	t=6 cells/mL	t=12 cells/mL	t=24 cells/mL
3/26/1995				
TS1				
TS2				
TS3	1.65E+05	3.82E+05	7.16E+05	2.77E+06
SS1	7.92E+04	1.31E+05	1.57E+05	3.29E+06
SS2	1.20E+05	1.39E+05	2.59E+05	2.85E+06
SS3	3.71E+05	1.22E+05		4.02E+06
J1	2.45E+05	3.38E+05	6.79E+05	2.70E+06
J2	1.39E+05	6.15E+05		
J3	2.10E+05	2.93E+05	7.39E+05	5.48E+05
P1	1.10E+05	2.18E+05	2.16E+05	2.68E+05
P2	1.33E+05	1.90E+05	2.61E+05	1.32E+06
P3	1.47E+05	2.45E+05	2.63E+05	1.34E+06
PC1	2.41E+05	4.35E+05	3.84E+05	3.42E+06
PC2	2.03E+05	3.29E+05	1.74E+05	4.14E+06
PC3	2.98E+05	2.99E+05	2.53E+05	2.25E+06

6/7/95

TS1				
TS2	7.09E+05	6.24E+05	8.06E+05	6.42E+06
TS3	5.13E+05	4.27E+05	8.73E+05	4.28E+06
SS1	7.27E+05	4.47E+05	6.42E+05	6.78E+06
SS2				
SS3				
J1	7.19E+05	6.21E+05	1.03E+06	5.45E+06
J2	6.44E+05	7.09E+05	1.01E+06	5.42E+06
J3	6.29E+05	7.56E+05	1.08E+06	4.51E+06
P1	7.19E+05	6.37E+05	9.12E+05	8.69E+06
P2	5.27E+05	6.28E+05	7.37E+05	4.37E+06
P3	8.80E+05	6.26E+05	5.99E+05	7.80E+06
PC1	3.18E+05	8.31E+05	1.35E+06	3.96E+06
PC2	2.75E+05	7.48E+05	1.25E+06	3.48E+06
PC3	3.66E+05	8.31E+05	1.10E+06	3.02E+06

t=0	t=6	t=12	t=24
cells/mL	cells/mL	cells/mL	cells/mL

4/21/1995

TS1	3.24E+05	3.97E+05	8.41E+05	2.47E+06
TS2	2.96E+05	4.56E+05	1.28E+06	4.06E+06
TS3	1.65E+05	3.64E+05	4.39E+05	4.19E+06
SS1	2.57E+05	3.55E+05	3.58E+05	2.34E+06
SS2	3.82E+05	2.92E+05	1.05E+06	4.29E+06
SS3		2.63E+05	6.30E+05	4.87E+06
J1	3.18E+05	4.33E+05	5.28E+05	1.80E+06
J2	2.70E+05	3.60E+05	5.14E+05	4.55E+06
J3	2.54E+05	2.81E+05	3.94E+05	1.96E+06
P1	2.71E+05	1.84E+05	3.61E+05	3.07E+06
P2	2.78E+05	3.98E+05	3.46E+05	2.63E+06
P3	3.17E+05	3.23E+05	4.87E+05	2.80E+06
PC1	3.18E+05	3.86E+05	8.45E+05	3.27E+06
PC2	2.75E+05	4.23E+05	1.13E+06	3.82E+06
PC3	3.66E+05	5.54E+05	9.29E+05	4.28E+06

7/8/95

TS1	2.61E+05	3.51E+05	4.31E+05	9.45E+05
TS2	2.09E+05	2.88E+05	6.09E+05	6.12E+05
TS3	3.49E+05	4.71E+05	7.23E+05	5.19E+06
SS1	3.23E+05		8.90E+05	1.11E+06
SS2	3.20E+05		1.08E+06	7.76E+06
SS3	3.28E+05		6.49E+05	6.14E+06
J1	3.11E+05	4.03E+05	9.83E+05	6.05E+06
J2	2.86E+05	2.99E+05	2.26E+06	9.37E+06
J3	3.00E+05	2.75E+05	9.50E+05	6.47E+06
P1				
P2	2.96E+05		1.87E+06	3.85E+06
P3	3.00E+05	3.61E+05	1.34E+06	5.86E+06
PC1	3.84E+05	6.92E+05	1.82E+06	3.73E+06
PC2	5.01E+05		1.20E+06	2.41E+06
PC3		6.30E+05	1.15E+06	4.10E+06

Appendix I a - Continued

	t=0 cells/mL	t=6 cells/mL	t=12 cells/mL	t=24 cells/mL
7/24/95				
TS1				
TS2	1.69E+06	1.98E+06	1.76E+06	1.35E+06
TS3	1.22E+06	2.16E+06	1.04E+06	5.43E+06
SS1		7.29E+06	2.57E+06	3.09E+06
SS2	1.22E+07	4.38E+06	2.82E+06	3.88E+06
SS3	5.63E+06	1.01E+07	2.82E+06	3.17E+06
J1	1.05E+07	8.05E+06	3.41E+06	8.15E+06
J2	7.83E+06	7.97E+06	3.30E+06	1.03E+07
J3	4.99E+06	4.08E+06	3.80E+06	8.45E+06
P1	1.26E+07	8.16E+06	4.45E+06	3.53E+06
P2				
P3	2.50E+06	5.94E+06	5.17E+06	4.73E+06
PC1	3.53E+06	6.82E+06	3.38E+06	1.20E+07
PC2	1.84E+06	3.01E+06	2.07E+06	8.20E+06
PC3				

Appendix I b - Bacterial abundances for individual sippers within experimentally flooded plots for each sampling date and each subsampling time.

	t=0 cells/mL	t=6 cells/mL	t=12 cells/mL	t=24 cells/mL		t=0 cells/mL	t=6 cells/mL	t=12 cells/mL	t=24 cells/mL
5/24/95					7/25/95				
J1	3.96E+05	8.45E+05	9.64E+05	6.67E+06	J1	4.37E+06	2.55E+06	1.86E+06	5.42E+06
J6					J6	3.08E+06	1.82E+06	1.07E+06	8.06E+06
J8	4.89E+05	1.08E+06	7.19E+05	3.23E+06	J8	1.79E+06	2.63E+06		3.25E+06
J2					J2	2.85E+06	1.75E+06	2.22E+06	6.37E+06
J4	6.26E+05	2.76E+06	1.33E+06	3.59E+06	J4	1.01E+07	8.08E+06	2.87E+06	6.81E+06
J9	4.57E+05	2.44E+06	7.54E+05	4.00E+06	J9	4.59E+06	3.77E+06	1.42E+06	4.94E+06
P1	3.75E+05	6.70E+05	4.23E+05	3.16E+06	P1	2.22E+06	2.34E+06	1.76E+06	7.90E+06
P6					P6	5.08E+06		2.22E+06	9.57E+06
P8		3.02E+05	4.01E+05	2.55E+06	P8	2.98E+06	3.13E+06	1.94E+06	7.51E+06
P2	1.22E+06	5.81E+05	4.87E+05	4.10E+06	P2				
P4	1.34E+06		6.19E+05	3.88E+06	P4	3.55E+06	2.32E+06	2.16E+06	7.12E+06
P9	5.91E+05	3.81E+05	5.42E+05	4.51E+06	P9	3.33E+06	2.47E+06	1.03E+06	9.59E+06
PC1	4.93E+05	8.82E+05	1.61E+06	4.03E+06	PC1	2.00E+06	2.86E+06	1.99E+06	6.00E+06
PC2	7.90E+05	1.11E+06	1.33E+06	4.41E+06	PC2	3.41E+06	2.46E+06	1.88E+06	7.06E+06
PC3	5.40E+05	1.35E+06	9.65E+05		PC3				

Appendix II - Frequency distribution of bacterial biomass measurements within each vegetation zone at time zero and time 24 hours for the July 24 bioassay. Biomass measurements from individual sippers were combined.

TSI=0		SSI=0		Jt=0		Pt=0		PCt=0	
Bin	μ ³	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL
0	0	0	0.00	0	0.00	0	0.00	0	0.00
0.02	32	0.2667	2.76	35	0.407	25.67	138	0.4876	26.83
0.04	23	0.1917	3.96	21	0.2442	30.81	56	0.1979	21.77
0.06	13	0.1083	3.36	9	0.1047	19.81	24	0.0848	14.00
0.08	14	0.1167	4.82	10	0.1163	29.34	24	0.0848	18.66
0.1	8	0.0667	3.45	4	0.0465	14.67	8	0.0283	7.78
0.12	4	0.0333	2.07	1	0.0116	4.40	8	0.0283	9.33
0.14	6	0.05	3.62	0	0.00	0.00	7	0.0247	9.52
0.16	4	0.0333	2.76	1	0.0116	5.87	6	0.0212	9.33
0.18	6	0.05	4.65	1	0.0116	6.60	0	0.00	0.00
0.2	0	0.00	0.00	1	0.0116	7.34	1	0.0035	1.94
0.22	3	0.025	2.84	0	0.00	0.00	0	0.00	0.00
0.24	2	0.0167	2.07	0	0.00	0.00	0	0.00	0.00
0.26	0	0.00	0.00	0	0.00	0.00	1	0.0035	2.72
0.28	1	0.0083	1.21	0	0.00	0.00	0	0.00	0.00
0.3	0	0.00	0.00	0	0.00	0.00	1	0.0035	3.11
0.32	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
0.34	0	0.00	0.00	0	0.00	0.00	2	0.0071	7.00
0.36	1	0.0083	1.55	0	0.00	0.00	0	0.00	0.00
0.38	1	0.0083	1.64	0	0.00	0.00	0	0.00	0.00
0.4	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
0.42	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
0.44	1	0.0083	1.90	0	0.00	0.00	0	0.00	0.00
0.46	0	0.00	0.00	0	0.00	0.00	1	0.0035	4.47

Appendix II - Continued

TS t=0		SS t=0		J t=0		P t=0		PC t=0	
Bin	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
0.48	0	0.00	0	0.00	1	0.0035	0	0.00	0
0.5	0	0.00	0	0.00	0	0.00	1	0.0066	0
0.52	0	0.00	0	0.00	0	0.00	1	0.0066	0
0.54	0	0.00	0	0.00	1	0.0035	0	0.00	0
0.56	0	0.00	0	0.00	0	0.00	0	0.00	0
0.58	0	0.00	0	0.00	0	0.00	0	0.00	0
0.6	0	0.00	0	0.00	0	0.00	0	0.00	0
0.62	0	0.00	0	0.00	0	0.00	0	0.00	0
0.64	1	0.0083	0	0.00	0	0.00	0	0.00	0
0.66	0	0.00	1	0.0116	0	0.00	0	0.00	0
0.68	0	0.00	0	0.00	0	0.00	0	0.00	0
0.7	0	0.00	0	0.00	0	0.00	0	0.00	0
0.72	0	0.00	0	0.00	0	0.00	0	0.00	0
0.74	0	0.00	1	0.0116	0	0.00	0	0.00	0
0.76	0	0.00	0	0.00	1	0.0035	0	0.00	0
0.78	0	0.00	0	0.00	0	0.00	0	0.00	1
0.8	0	0.00	0	0.00	0	0.00	0	0.00	0
0.82	0	0.00	0	0.00	0	0.00	0	0.00	0
0.84	0	0.00	0	0.00	0	0.00	0	0.00	0
0.86	0	0.00	0	0.00	0	0.00	0	0.00	0
0.88	0	0.00	0	0.00	0	0.00	0	0.00	0
0.9	0	0.00	0	0.00	0	0.00	0	0.00	0
0.92	0	0.00	0	0.00	0	0.00	0	0.00	0
0.94	0	0.00	0	0.00	0	0.00	0	0.00	0

Appendix II - Continued

Bin	TS t=0		SS t=0		J t=0		P t=0		PC t=0	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
0.96	0	0	0.00	1	0.0116	36.21	0	0	0.00	0
0.98	0	0	0.00	0	0	0.00	1	0.0036	9.52	0
1	0	0	0.00	0	0	0.00	0	0	0.00	0
1.02	0	0	0.00	0	0	0.00	1	0.0036	9.91	0
1.04	0	0	0.00	0	0	0.00	0	0	0.00	0
1.06	0	0	0.00	0	0	0.00	0	0	0.00	0
1.08	0	0	0.00	0	0	0.00	0	0	0.00	0
1.1	0	0	0.00	0	0	0.00	0	0	0.00	0
1.12	0	0	0.00	0	0	0.00	0	0	0.00	0
1.14	0	0	0.00	0	0	0.00	0	0	0.00	0
1.16	0	0	0.00	0	0	0.00	0	0	0.00	0
1.18	0	0	0.00	0	0	0.00	1	0.0036	11.66	0
1.2	0	0	0.00	0	0	0.00	1	0.0036	185.06	151
Totals	120	1	45.396	86	1	232.53	283	1	185.06	151

Appendix II - Continued

Bin		TS t=24		SS t=24		J t=24		P t=24		PC t=24	
μ^2	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
0	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
0.02	12	0.0719	39	0.1242	18	0.0933	33	0.1875	36	0.1158	8.28
0.04	14	0.0838	35	0.1115	24	0.1244	25	0.142	48	0.1543	22.07
0.06	5	0.0299	16	0.051	20	0.1036	25	0.142	35	0.1125	24.14
0.08	8	0.0479	12	0.0382	24	0.1244	12	0.0682	46	0.1479	42.31
0.1	14	0.0838	15	0.0478	24	0.1244	18	0.1023	37	0.119	42.54
0.12	12	0.0719	11	0.035	15	0.0777	11	0.0625	23	0.074	31.73
0.14	9	0.0539	16	0.051	15	0.0777	7	0.0398	19	0.0611	30.58
0.16	3	0.018	10	0.0318	9	0.0466	6	0.0341	12	0.0386	24.83
0.18	7	0.0419	20	0.0637	10	0.0518	8	0.0455	9	0.0289	20.69
0.2	4	0.024	10	0.0318	4	0.0207	5	0.0284	3	0.0096	7.59
0.22	7	0.0419	12	0.0382	3	0.0155	2	0.0114	4	0.0129	11.04
0.24	4	0.024	5	0.0159	6	0.0311	2	0.0114	2	0.0064	5.98
0.26	4	0.024	10	0.0318	4	0.0207	0	0.0114	4	0.0096	10.35
0.28	7	0.0419	10	0.0318	2	0.0104	0	0.0227	3	0.0064	7.36
0.3	1	0.006	8	0.0255	0	0	1	0.0057	2	0.0032	3.91
0.32	1	0.006	4	0.0127	0	0.0052	1	0.0057	6	0.0193	24.83
0.34	3	0.018	4	0.0127	1	0.0052	5	0.0284	1	0.0032	4.37
0.36	2	0.012	8	0.0255	3	0.0155	1	0.0057	0	0	0.00
0.38	6	0.0359	2	0.0064	3	0.0155	0	0	0	0.0032	4.83
0.4	3	0.018	1	0.0032	0	0	0	0.0057	1	0.0032	0.00
0.42	0	0	1	0.0159	0	0	1	0.0057	0	0	0.00
0.44	4	0.024	5	0.0159	0	0.0052	0	0	0	0	0.00
			4	0.0127	1	0.0052	0	0	0	0	0.00
			12.65		6.71		7.24				

Appendix II - Continued

Appendix II - Continued														
Bin	TS t=24			SS t=24			J t=24			P t=24			PC t=24	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	
0.46	0	0	0.00	1	0.0032	1.75	2	0.0104	15.14	1	0.0057	3.82	0	0.00
0.48	3	0.018	10.35	1	0.0032	1.83	1	0.0052	7.90	1	0.0057	3.99	1	0.0032
0.5	1	0.006	3.59	4	0.0127	7.62	0	0	0.00	0	0	0.00	1	0.0032
0.52	1	0.006	3.74	1	0.0032	1.98	0	0	0.00	0	0	0.00	1	0.0032
0.54	2	0.012	7.76	4	0.0127	8.23	1	0.0052	8.88	0	0.0057	4.65	0	0.00
0.56	3	0.018	12.07	3	0.0096	6.40	1	0.0052	9.21	1	0.0057	4.82	0	0.00
0.58	1	0.006	4.17	0	0	0.00	0	0	0.00	1	0.0057	4.98	1	0.0032
0.6	2	0.012	8.62	4	0.0127	9.15	2	0.0104	19.74	1	0.0057	5.15	1	0.0032
0.62	0	0	0.00	1	0.0032	2.36	0	0	0.00	0	0	0.00	0	0.00
0.64	1	0.006	4.60	0	0	0.00	0	0	0.00	0	0	0.00	0	0.00
0.66	0	0	0.00	0	0	0.00	0	0	0.00	1	0.0057	5.65	0	0.00
0.68	0	0	0.00	3	0.0096	7.77	0	0	0.00	1	0.0057	5.81	1	0.0032
0.7	2	0.012	10.06	1	0.0032	2.67	0	0	0.00	0	0	0.00	0	0.00
0.72	2	0.012	10.35	3	0.0096	8.23	1	0.0052	11.85	0	0	0.00	0	0.00
0.74	2	0.012	10.64	3	0.0096	8.46	0	0	0.00	0	0	0.00	0	0.00
0.76	0	0	0.00	1	0.0032	2.90	0	0	0.00	0	0	0.00	1	0.0032
0.78	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00	0	0.00
0.8	1	0.006	5.75	1	0.0032	3.05	0	0	0.00	0	0	0.00	0	0.00
0.82	1	0.006	5.89	1	0.0032	3.12	0	0	0.00	0	0	0.00	0	0.00
0.84	0	0	0.00	0	0	0.00	0	0	0.00	1	0.0057	7.14	0	0.00
0.86	1	0.006	6.18	0	0	0.00	0	0	0.00	0	0	0.00	0	0.00
0.88	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00	0	0.00
0.9	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00	0	0.00
0.92	0	0	0.00	2	0.0064	7.01	0	0	0.00	0	0	0.00	0	0.00

Appendix II - Continued

Bin	TS t=24		SS t=24		J t=24		P t=24		PC t=24	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
0.94	0	0	0.00	1	0.0032	3.58	0	0	0.00	0
0.96	1	0.006	6.90	0	0	0.00	0	0	0.00	0
0.98	0	0	0.00	1	0.0032	3.73	0	0	0.00	0
1	0	0	0.00	0	0	0.00	0	0	0.00	0
1.02	1	0.006	7.33	0	0	0.00	0	0	0.00	0
1.04	0	0	0.00	0	0	0.00	0	0	0.00	0
1.06	3	0.018	22.85	1	0.0032	4.04	1	0.0052	17.44	0
1.08	0	0	0.00	0	0	0.00	0	0	0.00	0
1.1	0	0	0.00	1	0.0032	4.19	0	0	0.00	0
1.12	0	0	0.00	2	0.0064	8.54	0	0	0.00	0
1.14	0	0	0.00	0	0	0.00	0	0	0.00	0
1.16	0	0	0.00	0	0	0.00	0	0	0.00	0
1.18	1	0.006	8.48	3	0.0096	13.49	0	0	0.00	0
1.2	1	0.006	8.62	0	0	0.00	0	0	0.00	0
1.22	1	0.006	8.77	0	0	0.00	0	0	0.00	0
1.24	0	0	0.00	0	0	0.00	0	0	0.00	0
1.26	0	0	0.00	0	0	0.00	0	0	0.00	0
1.28	0	0	0.00	0	0	0.00	0	0	0.00	0
1.3	0	0	0.00	0	0	0.00	0	0	0.00	0
1.32	1	0.006	9.49	1	0.0032	5.03	0	0	0.00	0
1.34	0	0	0.00	0	0	0.00	0	0	0.00	0
1.36	0	0	0.00	0	0	0.00	0	0	0.00	0
1.38	0	0	0.00	1	0.0032	5.26	0	0	0.00	0
1.4	0	0	0.00	0	0	0.00	0	0	0.00	0

Appendix II - Continued

Bin	TS t=24		SS t=24		J t=24		P t=24		PC t=24	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
1.42	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.44	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.46	0	0	0.00	1	0.0032	5.56	0	0.00	0	0.00
1.48	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.5	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.52	0	0	0.00	1	0.0032	5.79	0	0.00	0	0.00
1.54	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.56	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.58	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.6	0	0	0.00	1	0.0032	6.10	0	0.00	0	0.00
1.62	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.64	0	0	0.00	1	0.0032	6.25	0	0.00	0	0.00
1.66	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.68	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.7	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.72	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.74	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.76	0	0	0.00	1	0.0032	6.78	0	0.00	0	0.00
1.78	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.8	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.82	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.84	1	0.006	13.22	0	0.00	0	0.00	0	0.00	0
1.86	0	0	0.00	0	0.00	0	0.00	0	0.00	0
1.88	0	0	0.00	0	0.00	0	0.00	0	0.00	0

Appendix II - Continued

Bin		TS t=24		SS t=24		J t=24		P t=24		PC t=24	
μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
1.9	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
1.92	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
1.94	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
1.96	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
1.98	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2	0	0.00	1	0.0032	0	0.00	0	0.00	0	0.00	0
2.02	0	0.00	1	0.0032	0	0.00	0	0.00	0	0.00	0
2.04	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.06	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.08	0	0.00	1	0.0032	0	0.00	0	0.00	0	0.00	0
2.1	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.12	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.14	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.16	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.18	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.2	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.22	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.24	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.26	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.28	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.3	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.32	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.34	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
2.36	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0

Appendix II - Continued

Bln		TS t=24		SS t=24		J t=24		P t=24		PC t=24	
μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	
2.38	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.4	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.42	0	0.00	1	0.0032	0	0.00	0	0.00	0	0.00	
2.44	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.46	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.48	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.5	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.52	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.54	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.56	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.58	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.6	0	0.00	1	0.0032	0	0.00	0	0.00	0	0.00	
2.62	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.64	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.66	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.68	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.7	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.72	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.74	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.76	1	0.006	0	0.00	0	0.00	0	0.00	0	0.00	
2.78	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.8	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	
2.82	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	

Appendix II - Continued

Bln	TS t=24		SS t=24		J t=24		P t=24		PC t=24	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
2.84	0	0	0.00	0	0	0	0	0	0.00	0
2.86	0	0	0.00	0	0	0	0	0	0.00	0
2.88	0	0	0.00	0	0	0	0	0	0.00	0
2.9	0	0	0.00	0	0	0	0	0	0.00	0
2.92	0	0	0.00	0	0	0	0	0	0.00	0
2.94	0	0	0.00	0	0	0	0	0	0.00	0
2.96	1	0.006	21.27	0	0	0	0	0	0.00	0
2.98	0	0	0.00	0	0	0	0	0	0.00	0
3	0	0	0.00	0	0	0	0	0	0.00	0
3.02	0	0	0.00	0	0	0	0	0	0.00	0
3.04	0	0	0.00	0	0	0	0	0	0.00	0
3.06	0	0	0.00	0	0	0	0	0	0.00	0
3.08	0	0	0.00	0	0	0	0	0	0.00	0
3.1	0	0	0.00	0	0	0	0	0	0.00	0
3.12	0	0	0.00	0	0	0	0	0	0.00	0
3.14	0	0	0.00	0	0	0	0	0	0.00	0
3.16	0	0	0.00	0	0	0	0	0	0.00	0
3.18	0	0	0.00	0	0	0	0	0	0.00	0
3.2	0	0	0.00	0	0	0	0	0	0.00	0
3.22	0	0	0.00	0	0	0	0	0	0.00	0
3.24	1	0.006	23.28	0	0	0	0	0	0.00	0
3.26	0	0	0.00	0	0	0	0	0	0.00	0

Appendix II - Continued

Bin	TS t=24		SS t=24		J t=24		P t=24		PC t=24	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
3.28	0	0	0.00	0	0	0	0	0	0	0.00
3.3	0	0	0.00	0	0	0	0	0	0	0.00
3.32	0	0	0.00	0	0	0	0	0	0	0.00
3.34	0	0	0.00	0	0	0	0	0	0	0.00
3.36	0	0	0.00	0	0	0	0	0	0	0.00
3.38	1	0.006	24.29	0	0	0.00	0	0	0	0.00
3.4	0	0	0.00	0	0	0.00	0	0	0	0.00
3.42	0	0	0.00	0	0	0.00	0	0	0	0.00
3.44	0	0	0.00	0	0	0.00	0	0	0	0.00
3.46	0	0	0.00	0	0	0.00	0	0	0	0.00
3.48	0	0	0.00	0	0	0.00	0	0	0	0.00
3.5	0	0	0.00	0	0	0.00	0	0	0	0.00
3.52	0	0	0.00	0	0	0.00	0	0	0	0.00
3.54	0	0	0.00	0	0	0.00	0	0	0	0.00
3.56	0	0	0.00	0	0	0.00	0	0	0	0.00
3.58	0	0	0.00	0	0	0.00	0	0	0	0.00
3.6	0	0	0.00	0	0	0.00	0	0	0	0.00
3.62	0	0	0.00	0	0	0.00	0	0	0	0.00
3.64	0	0	0.00	0	0	0.00	0	0	0	0.00
3.66	0	0	0.00	0	0	0.00	0	0	0	0.00
3.68	0	0	0.00	0	0	0.00	0	0	0	0.00
3.7	0	0	0.00	0	0	0.00	0	0	0	0.00
3.72	0	0	0.00	0	0	0.00	0	0	0	0.00
3.74	0	0	0.00	0	0	0.00	0	0	0	0.00

Appendix II - Continued

Bln	TS t=24		SS t=24		J t=24		P t=24		PC t=24	
	μ^3	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.	ngC/mL	freq.
3.76	0	0	0.00	0	0	0	0	0	0	0
3.78	0	0	0.00	0	0	0	0	0	0	0
3.8	0	0	0.00	0	0	0	0	0	0	0
3.82	0	0	0.00	0	0	0	0	0	0	0
3.84	0	0	0.00	0	0	0	0	0	0	0
3.86	0	0	0.00	0	0	0	0	0	0	0
3.88	0	0	0.00	0	0	0	0	0	0	0
3.9	0	0	0.00	0	0	0	0	0	0	0
3.92	0	0	0.00	0	0	0	0	0	0	0
3.94	0	0	0.00	0	0	0	0	0	0	0
3.96	0	0	0.00	0	0	0	0	0	0	0
3.98	0	0	0.00	0	0	0	0	0	0	0
4	0	0	0.00	0	0	0	0	0	0	0
4.02	0	0	0.00	0	0	0	0	0	0	0
4.04	0	0	0.00	0	0	0	0	0	0	0
4.06	0	0	0.00	1	0.0032	0	0	0	0	0
Totals	167	1	432.45	314	1	373.06	194	1.0052	440.6	176

Appendix III a - Carbon dioxide evolved in sealed vials over 24 hours for individual sippers within each vegetation zone for each sampling date. Control values represent samples acidified prior to incubation. Live values represent samples acidified after incubation.

mg C/L	6/7/95		7/8/95		7/24/95	
	Abiotic	Total	Abiotic	Total	Abiotic	Total
TS1			26.42	44.44		
TS2		28.82	25.62	36.03	28.02	44.44
TS3		27.22	28.82	20.02	22.02	34.43
SS1		43.24	73.26	37.63	44.04	47.24
SS2			46.44		43.64	59.25
SS3			49.64	34.43	51.64	52.84
J1		19.22	28.02	26.42	16.01	53.64
J2		22.82	42.44	28.02	32.03	38.43
J3		27.22	12.41		17.21	30.43
P1		32.03			13.21	18.02
P2		28.82	40.03	42.44		
P3		22.82	14.01	27.22	22.02	25.22
PC1		24.42	21.62	16.41	1.6	14.41
PC2		24.42	18.82	43.64	15.21	26.42
PC3		19.22	23.62			

Appendix III b - Carbon dioxide evolved in sealed vials over 24 hours for individual sippers within experimentally flooded plots. Control values represent samples acidified prior to incubation. Live values represent samples acidified after incubation.

mg C/L

7/25/95

Abiotic Total

J1	-34	15.21
J6	-16.8	26.02
J8	14.01	
J2	5.61	11.21
J4	-20	26.42
J9	12.01	21.62
P1	4	13.61
P6	11.21	7.21
P8	-21.6	8.01
P2		
P4	11.21	4.8
P9	-14	28.02
PC1	2	26.82
PC2	-8.81	46.04
PC3		

Appendix IV a - Dissolved Organic Carbon values for individual sippers within each vegetation zone for each sampling date and subsampling time.

	Initial mg/L	t=0 mg/L	t=6 mg/L	t=12 mg/L	t=24 mg/L		Initial mg/L	t=0 mg/L	t=6 mg/L	t=12 mg/L	t=24 mg/L
8/6/1995						10/17/1995					
TS1	31.74					TS1	10.88				
TS2	28.89					TS2	18.28				
TS3	28.13					TS3					
SS1	35.48					SS1	25.14				
SS2	27.58					SS2	30.39				
SS3	38.13					SS3	25.8				
J1	19.2					J1	36.74				
J2	40.15					J2	18.32				
J3	27.56					J3	19.8				
P1	78.76					P1	9.02				
P2	49.84					P2	39.63				
P3	33.49					P3	31.61				
PC1						PC1					
PC2						PC2					
PC3						PC3					
2/4/1995						3/5/1995**					
TS1	30.46					TS1	204.44				
TS2						TS2					
TS3	30.95					TS3	40.1				
SS1	23.85					SS1	16.27				
SS2	30.69					SS2	41.38				
SS3	22.44					SS3	14.83				
J1	29.95					J1	20.42				
J2						J2	286.43				
J3	28.1					J3					
P1	78.29					P1	85.95				
P2	40					P2	27.77				
P3	48.15					P3	26.61				
PC1	14.49					PC1	24.11				
PC2	11.58					PC2	388.71				
PC3						PC3	7.04				

Appendix IV a - Continued

	Initial mg/L	t=0 mg/L	t=6 mg/L	t=12 mg/L	t=24 mg/L		Initial mg/L	t=0 mg/L	t=6 mg/L	t=12 mg/L	t=24 mg/L
						7/24/95					
7/8/95						TS1	17.92				
TS1	10.92	10.7	15.51	16.47	7.01	TS2	12.49	9.96	8.09	8.35	8.27
TS2	8.95	14.04	14.35	16.11	5.79	TS3	10.16	7.43	1.06	0.82	6.24
TS3	7.65	3.43	8.53	10.42	4.13	SS1	28.23	18.11	15.76	16.81	17.07
SS1	31.05	26.54	21.6	18.37	19.14	SS2	47.59	13.07	13.33	15.13	16.82
SS2	25.49	25.59		15.61	13.98	SS3	38.75		19.55	18.09	16.33
SS3	31.99	27.03	24.15	16.67	15.42	J1	29.95	15.75	11.99	13.23	12.21
J1	21.88	8.94	9.38	10.96	11.06	J2	49.66	22.36	24.01	19.13	17.41
J2	37.96	16.28	13.29	14.68	15.84	J3	26.2	1.43	12	9.78	7.76
J3	22.88	10.54	9.7	9.56	9.73	P1	27.83	10.28	7.07	11.73	15.64
P1						P2					
P2	39	18.37		29.71	1.3	P3	48.9	13.68	15.97	20.25	21.36
P3	42.55	18.74	20.45	28.15	31.48	PC1	7.1	2.05	3.66	0.03	6.21
PC1	3.04	6.01	11.46	11.78	4.01	PC2	0.63	5.53	2.62	4.19	4.8
PC2				10.64	6.43	PC3	1.14	1.77	0.15	3.46	5.93
PC3	4.64	2.67	11.51	2.96	4.64	PC4	3.25	3.81		3.7	5.37

Appendix IV b - Dissolved Organic Carbon values for individual sippers within experimentally flooded plots for each sampling date and subsampling time.

	Initial mg/L	t=0 mg/L	t=6 mg/L	t=12 mg/L	t=24 mg/L		Initial mg/L	t=0 mg/L	t=6 mg/L	t=12 mg/L	t=24 mg/L
5/24/95						7/25/95					
J1	22.61	13.57	10.05	19.66	14.13	J1	20.28	13.85	14.94	15.36	13.39
J6	20.07	57.7	8.52	16	8.55	J6	27.28	10.13	13.48	13.95	13.66
J8	22.61	24.33	13.77	16.86	10.2	J8	22.81	20.83	20.87	18.52	14.69
J2						J2	16.01	9.04	8.35		9.48
J4	18.56	27.82	13.72	5.14	9.54	J4	15.84	9.84	8.01	10.82	10.78
J9	17.76	11.05	11.99	14.27	9.45	J9	13.86	8.09	8.62	8.56	9.18
P1	26.7	22.31	23.33	50.48	24.14	P1	21.21	11.16	13.22	12.31	13.04
P6	26.54	28.9	13.59	21.38	16.68	P6	21.38	14.35	12.97	10.94	12.2
P8	25.25	11.08	22.14	12.89	17.88	P8	16.9	12.53	10.77	10.38	11.84
P2	42.16	13.95	26.8	23.92	18.77	P2					
P4	17.23	8.01	20.85	40.14	11.55	P4	1.39	7.5	9.34	9.34	1.08
P9	24.2	11.24	22.81	28.82	11.21	P9	5.73	5.64	8.31	7.27	6.04
PC1	2.32	3.24	4.64	8.5	8.98	PC1	7.1	2.05	3.66	0.03	6.21
PC2	1.17	0.37	2.07	1.4	7.39	PC2	0.63	5.53	2.62	4.19	4.8
PC3	2.68	4.02	2.87	7.58	4.33	PC3	1.14	1.77	0.15	3.46	5.93
						PC4	3.25	3.81		3.7	5.37

2495		
TS1	3.04	6.53
TS2		
TS3	4.83	10.53
SS1	35.9	46.71
SS2	12.72	49.53
SS3	4.91	23.9
J1	11.47	2.44
J2		0.62
J3	2.26	0.9
P1	48.31	0.8
P2	7.8	0.35
P3	7.49	0.9
PC1		
PC2		
PC3		

3/26/95			
TS1			
TS2			
TS3	19.77	27.46	25
SS1	25.91		34
SS2			35
SS3	8.28	2.33	34
J1	3.56		21
J2	6.24		30
J3	3.41		21
P1	71.7		21
P2	2.93		16
P3	6.55		22
PC1		1.12	31
PC2			31
PC3			

Appendix Va - Continued

	NH ₄ μM	PO ₄ μM	H ₂ S μM	salinity ‰	pH	PEP mV	NH ₄ μM	PO ₄ μM	H ₂ S μM	salinity ‰	pH	PEP mV
4/21/85							5/24/95					
TS1	22.92	13.06	17.82				TS1		48.7			
TS2							TS2	23.08	21.75			
TS3	23.07	48.09					TS3		37.42			
SS1	78.31	28.33	0.29				SS1	98.04	19.24			
SS2	93.73	12.91					SS2	35.2	0.01			
SS3	38.97	12.21	-0.06				SS3	144	3.89			
J1	18.2	0.78	0.21				J1	6.23	-0.12			
J2	14.42	4.07	1.33				J2	16.46	1.43			
J3	16.94	1.3	0.004				J3	5.75	-0.07			
P1	62.41	1.82	-0.12				P1		-3.01			
P2	8.6	1.47	0.1				P2	6.7	-0.12			
P3	15.68	1.3	-0.1				P3	30.15	-0.12			
PC1	0.57	0.6	-0.18				PC1	10.63	-0.13			
PC2	0.56	0.78	-0.2				PC2	11.11	-0.17			
PC3	0.26	0.78	-0.2				PC3		-0.17			

6/7/85							6/21/95					
TS1							TS1	40.7	185.5	27		
TS2	21.74	21.38	66.38	30			TS2	47.45	8.2	118.2	29	
TS3	11.77	14.51	6.15	30			TS3	14.03	14.47	77.82	32	
SS1							SS1	90.3	25.74	2.55	37	
SS2	4.36	1.09	-2.13	36			SS2	-1.77				
SS3			6.81				SS3	62.76	2.715	-9.23	37	
J1	1.79	0.66	-0.56	22			J1	3.82	1.06	1.18	24	
J2	13.43	0.77	-1.65	23			J2	9.79	3.35	2.61	25.5	
J3	3.81	0.89	-0.79	23			J3	4.01	1.06	2.57	26	
P1	2.7	0.35	-2.16	20			P1	33.19	1.79	0.3	25	
P2	19.48	0.58	-2	21			P2	5.94	0.82	-0.23	25	
P3	7.23	0.14	-2.16	19			P3	15.47	0.87	0.09	24	
PC1	6.78	0.88	-2.18	32			PC1	6.32	1.02	-0.52	33	
PC2	5.57	0.96	-2.18	32			PC2	4.78	1.06	-0.55	32.5	
PC3	7.23	0.88	-2.18	32			PC3	5.07	2.04	-0.55	32	

Appendix V b - Chemical and physical values for individual sippers within experimentally flooded plots for each sampling date.

	NH ₄ μM	PO ₄ μM	H ₂ S μM		NH ₄ μM	PO μM	H ₂ S μM
5/24/95				7/25/95			
J1	3.08		0.1	J1	9.9	0.4	-0.01
J6				J6	42.74	5.6	10.13
J8	3.86		-0.15	J8	24.63	0.7	3.73
J2				J2	13.09	0.3	1.81
J4			-0.18	J4	29.96	0.6	-0.17
J9	4.49		-0.1	J9	7.95	0.5	0.39
P1	7.54		5.22	P1	8.83	0.4	0.06
P6	14.73			P6	20.73	3	12.97
P8	35.52		25.75	P8	9.01	0.7	22.1
P2	2.92		-0.07	P2			
P4			-0.12	P4	15.22	2	5.17
P9	10.63			P9	12.38	0.5	13.8
PC1	10.63		-0.15	PC1	12.74	0.9	-0.22
PC2	11.11		-0.17	PC2	25.16	0.9	-0.31
PC3			-0.17	PC3			

Appendix VI - Water depth measured at the base of each slipper over partial daily tidal cycles.

cm	7:10	8:10	9:10	10:10	11:10	12:10	13:10	14:10	15:10	16:10	17:10	18:10	19:10
6/14/95													
TS1	2.5	3	27	49	54	35.5	14.5	2	1	0	0	0	0
TS2	0.5	4.5	31.5	50.8	56	42	16	0.2	0.5	0.2	0	0	0
TS3	0	0.8	28	50	58	37	18.5	0	0	0	0	0	0
SS1	0	0.5	1	22	28.8	3.3	1	0.8	0.8	0.5	0.2	0	0
SS2	0	0.8	1.2	22	28.5	4	1	1	1	0.5	0.5	0.5	0.5
SS3	0.2	0.5	2.2	22.5	29	4	0.5	0.5	0.5	0	0	0	0
J1	3.5	3.8	3.5	3.5	8.8	3.8	3.5	3.5	3.5	3	3	3.2	3.2
J2	2	1.8	1.5	1.5	6.8	2	2.3	2.3	1	2	1.5	2	2
J3	3	2.6	2	2.8	6	2	2	2	2	1.8	2.3	1.5	1.8
P1	0	0.5	0.5	0.7	0.7	1	0.5	0	0	0	0	0	0
P2	0	1	0.8	1	1	1	1.1	0.5	1	0.5	0.2	0.2	0.5
P3	0	0	0	0	0	0	0	0	0	0	0	0	0
6/15/95													
TS1	0	0	0	12.3	32	33	26	1.5	1.5	2	2	2	2
TS2	0	0	0	16	34	38.5	17.5	0.5	0	0	0	0	0
TS3	0	0	0	14.8	34	35	17	0	0	0	0	0	0
SS1	1	1	1	1	7	7.5	1	1	0.3	0	0	0	0
SS2	0.8	0.8	0.8	0.8	7.5	7.5	1	1	1	0.5	0.3	0	0
SS3	0	0	0	0	7.7	8.2	0.5	0.5	0	0	0	0	0
J1	3.3	3.5	3.5	3.5	3.5	3.5	3	3.5	3	2	3	3	3
J2	1.7	2.3	2.3	2	1.8	1	1	1.5	1	1.5	1.3	1.3	1.3
J3	2	2.5	2	2	2	2	1.8	2	1.8	1.5	1	1.3	1
P1	0	0	0.5	0.5	0.5	0.3	0.3	0.3	0	0	0	0	0
P2	1	1	1	1	1	1	0.7	0.7	0.7	0.7	0.5	0.5	0.3
P3	0	0	0	0	0.3	0.3	0.3	0.2	0	0	0	0	0

Appendix VI - Continued

	7:00	7:30	8:00	8:30	9:00	9:30	10:00	10:30	11:00		20:00	20:30	21:00	21:30
7/26/95														
TS1			6.4	11.7	13.1	8.2	0.4	0.2	0.2		18	24.6	32	33
TS2			13.8	19.5	21	15.8	0.2	0	0		25.2	32.5	37.6	40.8
TS3			6.1	11.9	13.4	7.8	0	0	0		18.3	24.7	30.5	33.2
SS1			0	0	0	0	0	0	0		0	0	7	4.5
SS2			0	0	0	0	0	0	0		0	0	6	8.3
SS3			0	0	0	0	0	0	0		0.3	0.3	0.3	0.2
J1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5		0	0	0	0
J2	0	0	0	0	0	0	0	0	0		0	0	0	0
J3.	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7		0	0	0	0
P1			0	0	0	0	0	0	0		0	0	0	0
P2			0	0	0	0	0	0	0		0	0	0	0
P3			0	0	0	0	0	0	0		0	0	0	0

[illegible]

Appendix VII a - Apparent bacterial growth rate constants calculated from bacterial abundances for individual sippers within each vegetation zone for each sampling date.

	μ 3/5/95	3/26/95	4/21/95	6/7/95	7/8/95	7/24/95
TS1	0.1137		0.0886		0.0533	
TS2			0.113	0.0969	0.0466	-0.0117
TS3	0.1294	0.1159	0.132	0.0961	0.1149	0.0551
SS1	0.0996	0.1558	0.0916	0.102	0.0514	-0.0387
SS2		0.1373	0.1123		0.1329	-0.0414
SS3	0.1101	0.1212	0.1633		0.1221	-0.0363
J1	0.1213	0.1031	0.0723	0.0906	0.129	-0.0124
J2	0.1046		0.12	0.0921	0.1587	0.0242
J3		0.0423	0.0882	0.0844	0.1384	0.0074
P1	0.1054	0.0316	0.1109	0.1097		-0.0533
P2	0.0701	0.0965	0.0922	0.0897	0.1069	
P3	0.0868	0.0902	0.0951	0.0965	0.1319	0.0184
PC1	0.0804	0.1075	0.1018	0.1012	0.0964	0.0428
PC2	0.0989	0.1216	0.1133	0.1017	0.0654	0.0576
PC3		0.0858	0.1039	0.084	0.1043	