ENVIRONMENTAL PARAMETERS RELATED TO GROWTH OF SUBMERSED

AQUATIC VEGETATION IN THE LOWER MOBILE DELTA, ALABAMA

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ENVIRONMENTAL PARAMETERS RELATED TO GROWTH OF SUBMERSED AQUATIC VEGETATION IN THE LOWER MOBILE DELTA, ALABAMA

Chad Haynes Newbolt

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ENVIRONMENTAL PARAMETERS RELATED TO GROWTH OF SUBMERSED

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VITA

Chad Haynes Newbolt, son of Jerry Newbolt and Charlene (England) Newbolt, was born August 21, 1979 in Natchez, Mississippi. He graduated from Hoover High School, Birmingham, Alabama, in 1997. He entered Auburn University in September of 1997 and received a Bachelor of Science in Wildlife Science in August of 2001. After working as a technician for Ducks Unlimited, Monroe, Louisiana, he entered Graduate School, Auburn University, in January 2003.

THESIS ABSTRACT

ENVIRONMENTAL PARAMETERS RELATED TO GROWTH OF SUBMERSED AQUATIC VEGETATION IN THE LOWER MOBILE DELTA, ALABAMA

Chad Haynes Newbolt

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Light availability and soils influence growth of submersed aquatic vegetation (SAV). My objectives in this study were to determine relationships between these environmental parameters and distribution and abundance of species of SAV in the lower Mobile River Delta, Alabama. I established sampling sites (n = 22) in Eurasian watermilfoil (*Myriophyllum spicatum*; n = 4), wild celery (*Vallisineria americana*; n = 5), Southern naid (*Najas guadalupensis*; n = 4), mixed species (n = 4; milfoil and native species were co-dominants), and sparsely vegetated areas (n = 5). I measured water depth, Secchi depth, surface temperature, velocity, salinity, turbidity, and total suspended solids (TSS)) twice monthly in June – August 2003 and in March – August 2004 at each site, and I estimated species composition and biomass of SAV at sites annually. I combined measurements of turbidity and TSS using principal component analysis and

used principal component (PC1) scores to estimate water clarity at sites. In April 2004, I placed experimental shade plots (1.8m^2) that produced three levels of shade (30%, 60%, and 90%) at mixed species sites to test relative effects of reduced light on biomass of milfoil and native SAV species. I also collected soil cores (5cm x 20cm) at sites in March 2004 and measured soil parameters (soil texture, total carbon (C), total nitrogen (N), extractable phosphorus (P), and pH).

PC1 scores of turbidity and TSS were lower at milfoil sites than at native SAV or sparsely vegetated sites on most sampling dates during the study period. PC1 scores also were greater during the early growing season (March-May) than during summer (June-August) in 2004. Total abundance of SAV was reduced by >69% in shade plots, but 30%, 60%, and 90% shade did not have different effects on growth of SAV species. Milfoil sites had greater amounts of C and N in soil cores than native SAV and sparsely vegetated sites. Milfoil sites also had greater amounts of clay and less P in soil cores (10-20 cm) than sparsely vegetated sites. My results identify differences between microhabitat conditions in milfoil, native SAV, and sparsely vegetated areas in the lower Mobile Delta, and these results provide evidence that milfoil and native SAV species may partition habitats in estuarine environments based on light availability and soil conditions.

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I. INTRODUCTION

Submersed aquatic vegetation (SAV) is an important component of estuarine ecosystems (Dennison and Orth 1993, Ailstock et al. 2000). SAV produces organic materials, removes nutrients, suspended sediments, and toxic materials from water, helps regulate flow, and provides habitat for many species of fish and wildlife (McRoy and Helfferich 1977, Stout 1979, Duffy and Baltz 1998, Knapton and Petrie 1999, Benedict and Hepp 2000, Wyda et al. 2002). The importance of SAV to ecological processes and their sensitivity to environmental conditions allow them to be used as indices of overall health in aquatic environments (Dennison and Orth 1993).

Estuaries worldwide have experienced declines in abundance of SAV (Litav and Agami 1976, Orth and Moore 1983, Cambridge and McComb 1984) and reduced abundance of SAV has raised concern for health of these environments. The tidal Potomac River and Chesapeake Bay, for example, have experienced dramatic losses of SAV due to declines in water quality (Carter and Rybicki 1990, Carter et al. 1994). Introductions of non-desirable exotic species of SAV, such as Eurasian watermilfoil (*Myriophyllum spicatum*) and hydrilla (*Hydrilla verticillata*), have led to declines in abundance of native species of SAV, and reduced abundance of native SAV has negatively affected populations of fish and wildlife (Bayley et al. 1978, Kemp et al. 1983, Zolcyznski and Eubanks 1990, Madsen et al. 1991, Ailstock et al. 2000, Hughes et al. 2002). A better understanding of how environmental conditions, such as water quality

and soils, influence abundance and distribution of species of SAV will allow for more effective restoration of native SAV communities and management of exotic SAV.

Factors Influencing Growth of SAV

SAV populations are spatially and temporally dynamic in terms of growth, distribution, and species composition (Carter et al. 1994). Growth and distribution of SAV is influenced by many factors, including water quality, growth substrate, weather, plant interactions, pathogens, and herbivory (Boeger 1992, Carter et al. 1994, Carr et al. 1997, Livingston et al. 1998). However, light availability has been identified as the most important factor limiting the growth and distribution of SAV (Goldsborough and Kemp 1988, Carter and Rybicki 1990, Dennison and Orth 1993, Carter et al. 1994). The amount of light that passes through the water column and epiphytic materials (i.e., percent light at leaf (PLL) determines the maximum depth at which SAV species can survive in non-tidal areas (Dennison and Orth 1993). In tidal areas, the maximum depth at which SAV species can survive also is a function of the mean low water level (Ailstock et al. 2000). SAV species have high minimum light requirements, ranging from 4 to 29% of incident light measures just below water surface (Dennison and Orth 1993). Minimum and optimal light requirements are consistent within species; however, they vary considerably across species (Dennison and Orth 1993). Wild celery (*Vallisneria americana*), for example, reaches maximum oxygen production under ambient conditions at a light measurement of 250 µE/ m^2/ s, whereas *Myriophyllum spicatum* does not reach maximum oxygen production until light levels reach 500 µE/ m^2/ s (Harley and Findlay 1994).

Light attenuation in the water column is influenced by incident irradiance and suspended solids (Carr et al. 1997). Although incident irradiance can influence light availability, suspended materials, such a phytoplankton and sediment, are the most important variables affecting light attenuation within the water column (Carter and Rybicki 1990). Phytoplankton and suspended sediments can be measured independently, or they can be estimated collectively using Secchi visibility, turbidity, and total suspended solids (Carter et al. 1994). Secchi visibility and turbidity provide an estimate of water clarity as a function of water color and suspended materials, whereas total suspended solids only estimate suspended materials. Habitat requirements of SAV in Chesapeake Bay for total suspended solids are <15 mg/L (Ailstock et al. 2000). Studies in the tidal Potomac River indicate that SAV growth is inhibited at Secchi depths < 0.65 m (Carter et al. 1994).

Light availability also is influenced by epiphytes on plant parts (Dennison and Orth 1993). Epiphytes on photosynthetically active plant parts reduce the ability of SAV to obtain light that passes through the water column (Ailstock et al. 2000). Studies in Chesapeake Bay indicate that epiphytic material contributes an additional 20 – 60 percent light attenuation in tidal fresh (< 0.5 ppt. (‰) and oligohaline (0.5 – 5 ‰) regions (Ailstock et al. 2000). Abundance of epiphytes is related to dissolved inorganic N and P concentrations; however, epiphyte biomass in tidal fresh and oligohaline regimes usually is limited by orthophosphate (Ailstock et al. 2000).

Salinity also influences growth and distribution of SAV (Haller and Barlowe 1974, Odum et al. 1984, Boeger 1992, Carr et al. 1997). Some SAV species have broad salinity tolerances; however, many species can survive only in specific salinity regimes

(Odum et al. 1984). Wigeongrass (*Ruppia maritima*), for example, can survive in polyhaline (18 – 30 ‰) and oligohaline regimes, whereas American pondweed (*Potamogeton nodosus*) is found only in tidal fresh environments (Odum et al. 1984). Diversity of SAV is greatest at salinities < 0.5 ‰ (Odum et al. 1984). Although most studies emphasize the importance of mean salinity, some studies indicate that growth of SAV also is limited by variations in salinity (Montague and Ley 1993). A study in Florida Bay, for example, indicated that SAV biomass decreased as the standard deviation of salinity measurements increased (Montague and Ley 1993).

Water velocity also influences growth of SAV (Madsen and Sondergaard 1983, Boeger 1992, Carr et al. 1997, Ailstock et al. 2000). Water flow decreases stagnant boundary layers on plant parts, which facilitates the exchange of gases and nutrients between plants and the surrounding environment (Madsen and Sondergaard 1983). Increased gas and nutrient exchange increases plant metabolic rates, which leads to increased plant production (Madsen and Sondergaard 1983, Boeger 1992). Flow also aids in the transportation of reproductive propagules (Boeger 1992). Some flow is beneficial to SAV; however, moderate to high water velocity can damage or dislodge plants (Boeger 1992). SAV tolerance of low and high water velocity varies by species (Boeger 1992). However, studies from Chesapeake Bay indicate that SAV survival is greatest in areas with current velocities between 1 and 50 cm/s (Ailstock et al. 2000).

Sediment texture, organic matter content, nutrient content, and pH influence the growth, distribution, and morphology of SAV (Barko and Smart 1983, 1986, Livingston et al. 1998, Ailstock et al. 2000). SAV responses to soil conditions are similar within species; however, plant responses to soils vary among species (Barko and Smart 1983).

Growth of most SAV species declines on inorganic sediments composed of >75% sand and with increasing sediment organic matter up to concentrations of 20% dry sediment mass (Barko and Smart 1986). Specific mechanisms of growth limitation on sand and organic sediment are not known; however, research suggests limitations are related to decreased nutrient availability or accumulation of toxins (Barko and Smart 1986). Nitrogen and P typically are the most important nutrients in aquatic soils since they usually are present in limited amounts (Boyd et al. 2002). Maximum nutrient availability in aquatic soils usually occurs at pH 7 (Boyd et al. 2002).

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II. RELATIONSHIPS BETWEEN LIGHT AVAILABILITY AND GROWTH OF EXOTIC AND NATIVE SPECIES OF SUBMERSED AQUATIC VEGETATION

INTRODUCTION

Submersed aquatic vegetation (SAV) is an important component of estuarine ecosystems (Dennison and Orth 1993, Ailstock et al. 2000). SAV produces organic materials, removes nutrients, suspended sediments, and toxic materials from water, helps regulate water flow, and provides habitat for many species of fish and wildlife (McRoy and Helfferich 1977, Stout 1979, Duffy and Baltz 1998, Knapton and Petrie 1999, Benedict and Hepp 2000, Wyda et al. 2002). Estuaries worldwide have experienced declines in SAV abundance (Litav and Agami 1976, Orth and Moore 1983, Cambridge and McComb 1984), which has raised concerns for the health of these systems. The tidal Potomac River and Chesapeake Bay, for example, have experienced dramatic losses of SAV communities due to declines in water quality (Carter and Rybicki 1990, Carter et al. 1994). Introductions of non-desirable exotic species of SAV, such as Eurasian watermilfoil (*Myriophyllum spicatum*, hereafter milfoil) and hydrilla (*Hydrilla verticillata*), also have contributed to reductions in abundance of native SAV (Bayley et al. 1978, Kemp et al. 1983, Zolcyznski and Eubanks 1990, Horton and Eichbaum 1991, Madsen et al. 1991, Ailstock et al. 2000, Hughes et al. 2002).

Light availability has been identified as the primary factor limiting growth of SAV (Dennison 1987, Carter and Rybicki 1990, Dennison and Orth 1993, Carr et al. 1997, Ailstock et al. 2000). The effects of eutrophication, such as increases in amounts of phytoplankton and epiphytes, often lead to reduced light availability and declines in abundance of SAV, and reduced amounts of dissolved nutrients and increases in available light can help restore submersed plant communities (Kemp et al. 1983, Carter and Rybicki 1985, 1986, Stevenson et al. 1993, Carter et al. 1994, Ailstock et al. 2000). Species of submersed plants often have different light requirements (Titus and Adams 1979, Madsen et al. 1991, Harley and Findlay 1994, Smart et al. 1994). Differences in light requirements have been reported for exotic canopy forming species, such as milfoil, and meadow forming native species, like American wild celery (*Vallisineria americana*), hereafter wild celery; Titus and Adams 1979, Madsen et al. 1991, Harley and Findlay 1994). Light-saturated net photosynthetic rates do not differ between wild celery and milfoil; however, milfoil requires significantly greater irradiances to reach maximum photosynthetic rates than does wild celery (Harley and Findlay 1994). Madsen et al. (1991) also reported higher light requirements for milfoil compared to native submersed plants, such as wild celery and large-leaved pondweed (*Potamogeton amplifolius*). Although milfoil has greater light requirements, it has been suggested that the surface canopy formed by the plant allows it to grow in more turbid environments (Smith and Barko 1990, Knapton and Petrie 1999).

Conservation and restoration of native SAV requires an understanding of factors that influence overall abundance of submersed plants and species-specific responses to these factors. Many studies have emphasized the importance of light availability on SAV

and have identified differences between light requirements of native and exotic species of SAV; however, relationships between light availability and abundance and distribution of species of SAV in natural environments remain unclear. In this study, we measured water quality variables during the growing season in milfoil and native SAV communities in the lower Mobile River Delta, Alabama, and examined the relationships between water clarity and abundance of native and exotic species of SAV. Next, we manipulated light levels using shade cloth and experimentally tested effects of reduced light on milfoil and native species of SAV.

STUDY SITE

The Mobile River System is the sixth largest river system in the United States, receiving flows from four states and having a watershed area of 111,369 km^2 (Lamb 1979; Fig 1). The confluence of the Tombigbee and Alabama Rivers in south Alabama marks the beginning of the Mobile River and Mobile River Delta (Fig. 1). The Mobile River Delta receives flows from several sources; however, about 95% of freshwater inflow comes from the Mobile River (Loyacano and Busch 1979). The Mobile River Delta is approximately 64 km long and 16 km wide and encompasses > 81,000 ha (Beshears 1979).

The lower Mobile Delta comprises approximately 25% (20,235 ha) of the total area of the Mobile River Delta and is generally described as the treeless area from Chuckfey Bay south to 4.0 km below US Highway 90 (Beshears 1979; Figs. 1 and 2). Large shallow bays with abundant submersed plant growth and areas of emergent marsh characterize the lower Delta (Beshears 1979). Average daily tidal range in the lower Mobile Delta is approximately 0.3 m.

Fifteen species of SAV are present in the lower Mobile River Delta, including the exotics hydrilla and milfoil (Zolczynski and Shearer 1997). Native species of SAV that are abundant in the Delta include wild celery, coontail (*Ceratophyllum demersum*), water stargrass (*Heteranthera dubia*), southern naiad (*Najas guadalupensis*), narrow-leaf pondweed (*Potamogeton pusillus*), and wigeongrass (*Ruppia maritima*; Zolczynski and Shearer 1997). Hydrilla was first identified in Mobile Delta in 1990 (Zolczynski and Shearer 1997). Milfoil was first observed in Mobile Delta in 1975 and has been associated with significant declines in native submersed plant abundance (Zolczynski and Eubanks 1990). In 1979, milfoil was the dominant submersed plant in the lower Mobile Delta and was estimated to cover at least 85% of shallow growing areas (Zolczynski and Eubanks 1990). Distribution and abundance of milfoil and native SAV vary annually in the Delta; however, submersed plant surveys in 1987 and 1994 identified milfoil as the dominant submersed plant (Zolczynski and Shearer 1997). Plant surveys conducted in 2002 indicate that milfoil remains an abundant submersed species in the lower Delta (Mapping of SAV in Mobile Bay and Delta 2004).

METHODS

Site selection

We intended to establish sampling sites early in the growing season in 2003; however, high water and turbidity during spring inhibited our ability to locate SAV communities until early summer. We established sampling sites (n = 22) in three bays (Big Bateau Bay, Chacaloochee Bay, and Justin's Bay) of the lower Mobile River Delta in June 2003 (Fig. 2). Sites were established in SAV communities visually identified as milfoil (n = 4), wild celery (n = 5), southern naiad (n = 4), and mixed species (milfoil

and native species were co-dominants; n = 4). Sampling sites (n = 5) also were established in sparsely vegetated areas.

Biomass and species composition of SAV

We estimated biomass and species composition of SAV at sampling sites in September 2003 and 2004. Subplots (0.25 m^2; n = 5) were placed at the center of each sampling site and 10 m from this point in each cardinal direction, and all above ground plant parts were collected by hand. Plant materials were placed in plastic bags, stored on ice, and transported to the laboratory at Auburn, Alabama where they were rinsed, sorted by species, and dried (60º C) to constant mass (0.1g).

Water parameters

We measured water depth, Secchi depth, surface temperature, velocity, turbidity, total suspended solids (TSS), and salinity at sampling sites every two weeks in June – August 2003 and in March - August 2004. Velocity (cm/s) was measured at a depth of 0.5 m (Speedtech® flowmeter). Water samples (500 ml) were collected 0.3 m below the surface, placed on ice, and transported to the laboratory at Auburn, Alabama to measure turbidity (NTU; Global Water® WQ770), TSS (mg/l; filtration method, ASTM 1999), and salinity (‰; hydrometer, 15.6º/15.6 ºC).

Experimental shade plots

In April 2004, we placed shade plots (3.3 m^2) at mixed species sites (n = 4) to test relative effects of reduced light on biomass of milfoil and native species of SAV. Shade plots were created using polyethylene shade cloth (Dewitt fabrics, Sikeston, MO) that produced three levels of shade (30%, 60%, and 90% of full sunlight exposure). Shade cloth was attached to floating PVC (4 cm diameter) frames with plastic tie straps. PVC

pipe (4 cm diameter, 3 m) was placed at each corner of the plots to restrict lateral movement but allow plots to rise and fall with fluctuating water levels. Amount of light transmitted through shade cloth was estimated with a LI-COR® photometer (model LI-189) and found to be similar to levels suggested by the manufacturer (Table 1). Plots were placed 20 m from the center of mixed species sites and at least 10 m from other shade plots. Two replicates of each shade level were placed at each site.

We estimated plant biomass and species composition of shade plots in September 2004 using subplots (0.25 m^2; $n = 1$) placed at the center of each plot. All above ground plant parts were collected by hand, placed in plastic bags, stored on ice, and transported to the laboratory at Auburn, Alabama. Plant samples were rinsed, sorted by species, and dried (60º C) to constant mass (0.1g).

Statistical analysis

Biomass of SAV

Each year we determined total plant dry mass and the dry mass of milfoil and native species of SAV at each sampling site. Native species of SAV included all species other than milfoil and hydrilla. Only trace (< 0.1g) amounts of hydrilla were found at sampling sites; therefore, we excluded hydrilla from the analysis. Paired t-tests were used to test for differences in dry mass of SAV between years.

Water parameters

TSS and turbidity provide measures of water clarity; therefore, we used principal component analysis (PROC PRINCOMP; SAS Institute 2003) of the correlation matrix of TSS and turbidity to produce a single variable representing water clarity. The first principal component (PC1) described a positive correlation between TSS and turbidity

and accounted for 95% of the total variance. We interpreted this correlation as variation in water clarity and used these PC1 scores as estimates of water clarity in subsequent statistical analyses. Repeated measures ANOVA (PROC MIXED; SAS Institute 2003) was used to test effects of sampling date, plant community, and their interactions on PC1 scores of turbidity and TSS for each year. Unstructured covariance structure was specified for the random variable (sampling sites) based on Akaike's Information Criterion (AIC; Littell et al. 1996). Interactions that were not significant were dropped from the final model. Differences between least squares means were determined using Tukey-Kramer tests.

We tested for year effects by restricting the analysis to data collected in June – August 2003 and 2004. We used repeated measures ANOVA (PROC MIXED; SAS Institute 2003) to test effects of year, sampling date, plant community, and their interactions on PC1 scores of turbidity and TSS. Autoregressive order 1 covariance structure was specified for the random variable based on Akaike's Information Criterion (AIC; Littell et al. 1996). Interactions that were not significant were dropped from the final model. Differences between least squares means were determined using Tukey-Kramer tests.

Experimental shade plots

Five shade plots were damaged during the study period and were eliminated. We restricted our analysis to five groups that had the full complement of shade plots (i.e., 30%, 60%, 90%, and control). The center of each mixed species site that had not been shaded was designated as the control (no shade, 0%). Three-way ANOVA (PROC GLM; SAS Institute 2003) was used to test effects of site, shade (0%, 30%, 60%, and 90%),

plant species (milfoil or native), and the interaction of shade and plant species on mean dry mass of plants. Differences between least squares means were determined using Tukey-Kramer tests. Tests were significantly different at $P \leq 0.05$.

RESULTS

Species composition and biomass of SAV

Milfoil was present in all plant communities in 2003 and 2004 (Table 2). We collected six native species of SAV, but southern naiad was the most widely distributed native species and was present in all plant communities in 2003 and 2004 (Table 2). Total dry mass of SAV was greater in 2004 than in 2003 (Mean diff. = 10.64 g / 0.25 m^2, SE = 3.71; $t_{21} = 2.87$, $P = 0.01$). Dry mass of milfoil was greater in 2004 than in 2003 (Mean diff. = 8.10 g / 0.25 m^2, SE = 2.71; $t_{21} = 2.99$, $P = 0.01$); however, dry mass of native species was similar between years (Mean diff. = 2.54 g / 0.25 m^2, SE = 3.08; $t_{21} = 0.82$, $P = 0.42$).

Water parameters

Water depth, Secchi depth, salinity, temperature, and velocity

Means and ranges of water parameters are presented to help characterize sampling sites in 2003 and 2004 (Tables 3 and 4). Sites were relatively shallow with very low flow and had low salinity (< 2 ‰). Yearly differences in these parameters are likely related to differences in the sampling periods (i.e., June - August 2003 vs. March - August 2004).

Turbidity and TSS

Lower PC1 scores corresponded to conditions of greater water clarity. In April 2004, for example, PC1 score of – 1.4 at milfoil sites corresponded to turbidity of 1.3 NTU and TSS of 2.4 mg/L, and PC1 score of 6.8 at sparsely vegetated sites in April 2004

corresponded to turbidity of 62.5 NTU and TSS of 77.8 mg/L (Fig. 3). PC1 scores varied with the interaction of sampling date and plant community in 2003 ($F_{16,17} = 6.77$, $P = 0.001$). Milfoil and mixed species consistently grew in areas with greatest water clarity in 2003 (Fig. 4). Water clarity at wild celery sites in 2003 was low in June and early July and increased during the later sampling dates (Fig. 4). Southern naiad and sparsely vegetated sites consistently had lower water clarity than milfoil sites in 2003 (Fig. 4).

Water clarity also varied with the interaction of sampling date and plant community in 2004 ($F_{44,17} = 6.01$, $P = 0.001$). Water clarity was low at milfoil sites during the first sampling date in March 2004; however, water clarity increased at milfoil sites during the remaining sampling dates (Fig. 3). Water clarity at wild celery, Southern naiad, mixed species, and sparsely vegetated sites generally was low during March and April and increased in May –August 2004 (Fig. 3). Milfoil and mixed species consistently grew in areas with greatest water clarity in 2004 (Fig. 3). We found no differences in water clarity between years (June – August; $F_{1,17} = 0.02$, $P = 0.9$).

Experimental shade plots

We collected seven species of SAV in experimental shade plots (Table 5). Total plant dry mass was greater in control plots than in shaded plots, but biomass did not differ among shaded treatments ($F_{3,28} = 7.76$, $P = 0.001$; Fig. 5). Abundance of milfoil and native species of SAV was similar within each level of shade ($F_{3,28} = 0.3$, $P = 0.83$; Fig. 6).

DISCUSSION

Similarity of water conditions during summer (June – August) 2003 and 2004 suggested that differences in early growing season (March – May) conditions may have been responsible for annual differences in plant biomass. Canopy forming species of SAV, such as milfoil, are especially vulnerable to high turbidity during the early growing season, and a short-term increase in turbidity during this period of time could have reduced growth of these species (Moore et al. 1997, Ailstock et al. 2000). Suspended sediment loads are influenced by multiple factors, such as local weather conditions and abundance of aquatic vegetation; however, discharges from dams can have a strong influence on water conditions in estuarine environments, including suspended sediments (Whitefield and Bruton 1989, Carter et al. 1994, Colonnello and Medina 1998, Day et al. 2000, Alber 2002). For example, low levels of freshwater discharges have been associated with increased water clarity in areas of the tidal Potomac River (Carter et al. 1994). To identify a potential turbidity event during the early growing season in 2003, we determined mean daily discharges by month during March – August 2003 and 2004 and 25-year mean daily discharges (1976 – 2001) using mean daily and mean monthly discharges from Claiborne Lock and Dam (USGS gauge # 02428400), Alabama River and Coffeeville Lock and Dam (USGS gauge # 02469761), Tombigbee River (USGS data obtained online at *waterdata.usgs.gov/al/nwis/rt*; Fig. 7). Both dams are located about 100 km upriver of the confluence at the Mobile River, and the Mobile River contributes approximately 95% of the freshwater inflow to the Delta (Loyacano and Busch 1979; Fig. 1). Mean daily discharges for each month from the two dams were

combined by month for each of the three time periods to provide an estimate of freshwater inflow to the Delta.

Combined mean daily discharges were higher during March – August 2003 than during the same months in 2004; however, annual differences in discharges were greater during March – May than during June – August (Fig. 7). Combined mean daily discharges were much greater (4,158 m^3) during May 2003 than during May 2004 (Fig. 7). High discharges from these dams during the early growing season could indicate that suspended sediment loads were higher and water clarity was lower in the Delta, which may have contributed to the low abundance of milfoil in 2003.

The higher and more variable PC1 scores during the early growing season (March – April 2004; Fig. 3) may have been related to differences in seasonal abundance of SAV. SAV reduces current velocity and wave action, which causes suspended sediments to be deposited and reduces the ability of wind to resuspend sediments in shallow areas (Fonesca and Cahalan 1992, Fonseca 1996). SAV is more abundant later in the growing season, and increased abundance of SAV during the summer may have led to less suspended sediments and lower PC1 scores. Differences between weather and tidal conditions during spring and summer also likely contributed to seasonal differences in PC1 scores. Wind and tidal range in the lower Delta generally are greater during spring than summer, which could have contributed to increased amounts of suspended sediments and higher PC1 scores during March - April.

It is likely that reduced current velocity and wave action at milfoil sites resulted in decreased amounts of suspended sediments and low PC1 scores (Fonseca 1996; Ailstock et al. 2000). However, our results suggest that factors other than growth of plants also

influenced PC1 scores. PC1 scores were lower in milfoil communities than wild celery communities at multiple sampling dates during 2003 (Fig. 4) despite similarities in overall abundance of SAV (Table 2). PC1 scores also were lower in milfoil communities than in communities dominated by native species of SAV and sparsely vegetated sites during early spring in 2004 when very little plant growth was present (Fig. 3). Overall abundance of SAV also was lower in 2003 than in 2004, but PC1 scores were similar during June – August 2003 and 2004.

Causal relationships between PC1 scores and growth of species of SAV are confounded by influences of submersed plants on the surrounding environment. Nonetheless, our results identify interesting relationships between water clarity and distribution and abundance of species of SAV. Milfoil was most abundant in areas with low PC1 scores, which suggests that milfoil may have been able to competitively exclude native SAV in areas with high water clarity. The ability of milfoil to displace native species of SAV appeared to be reduced in areas with higher PC1 scores; however, both milfoil and native species of SAV were least abundant at sites with the highest PC1 scores. These findings corroborate previous research suggesting that milfoil has high light requirements and meadow forming native species of SAV, such as wild celery, are able to grow in areas with lower levels of light (Madsen et al. 1991, Harley and Findlay 1994). Our results also support research indicating that light availability limits submersed plant growth in estuarine environments (Stevenson et al. 1993, Livingston et al. 1998, Ailstock et al. 2000).

It is possible that differences in water clarity played a role secondary to other factors, such as other water parameters or availability of plant propagules, in distribution

and abundance of SAV. However, our results did not suggest that water parameters, such as salinity and temperature, were different between plant communities, and previous research shows that growth of SAV is limited by factors other than propagule availability (Rybicki et al. 2001). Conclusions relating to light availability are limited to the influence of water clarity since we did not estimate other factors that attenuate available light, such as epiphytic loads (Ailstock et al. 2000).

Abundance and diversity of SAV species was lower in experimental shade plots than in full sun, demonstrating the importance of light availability to growth of SAV. These findings are consistent with previous research suggesting that diversity and biomass of SAV decrease as available light decreases (Spence 1976, Barko et al. 1982, Chambers and Kalff 1985, Dennison and Orth 1993, Carter and Rybicki 1990). Relatively small reductions in light availability had dramatic effects on abundance of SAV. A 30% reduction in ambient light resulted in a 69% reduction in SAV biomass (Fig. 5). Our analysis did not identify differences between the effects of 30%, 60%, and 90% shade on growth of SAV; however, small sample size and relatively small shade plots may have inhibited our ability to determine significant differences among these levels. Our data indicated that ≤ 30% reductions in available light have the greatest effects on SAV, and these results support other shading experiments indicating that ≤ 30% reductions in light reduce survival of many species of SAV (Congdon and McComb 1979, Goldsborough and Kemp 1988, Kimber et al. 1995). Our experiment also showed a tendency for a greater response of milfoil to the shade treatment than native SAV, but loss of plots and subsequent small sample size affected our ability to detect significant differences.

STUDY IMPLICATIONS

Numerous studies identify negative effects of anthropogenic inputs, such as nutrients and other pollutants, on health of rivers and estuarine environments; however, only recently have the impacts of river regulation received attention (Doering et al. 2002, Mattson 2002). Critical components of riverine ecosystems, such as natural streamflow variability and water quality, are altered in environments regulated by dams (Walker 1985, Resh et al. 1988, Power et al. 1995; Poff and Allan 1997, Day et al. 2000, Vorosmarty and Sahagian 2000, Alber 2002, Kimmerer 2002) and these alterations can negatively affect native biotic communities (Allen and Flecker 1993, Abramovitz and Peterson 1996, Poff et al. 1997, Collier et al. 2000). Changes in rivers associated with regulation of flows, such as altered sedimentation rates and water temperatures, contribute directly to losses in native communities (Cushman 1985, Greenberg et al. 1996, Stanford 1994); however, these changes may also contribute indirectly to losses by providing favorable conditions for exotic species (Ward and Stanford 1979, Walker 1985, Busch and Smith 1995, Moyle and Light 1996). For example, increased sediment loads and decreased number and magnitude of floods in the Rio Grande River below Elephant Butte Dam have allowed thickets of exotic tamarisk (*Tamari pentandra*) to replace much of the native cottonwood and willow communities (Howe and Knopf 1991; Collier et al. 2000).

The apparent ability of milfoil to displace native species of submersed plants in environments with high water clarity raises interesting questions concerning potential impacts of hydrologic alterations on growth of species of SAV in estuaries. It is possible that stabilization of natural variations of freshwater discharge in regulated environments

could result in alteration of suspended sediment loads, which in turn may lead to changes in light availability. Competitive advantages of high-light adapted exotic species of SAV, such as milfoil, may be increased if natural levels of light availability are increased as a whole or during critical periods, facilitating the spread of these species. Conversely, maintenance of natural stream flow variability may provide native species of SAV that are tolerant of lower levels of available light competitive advantages over some exotic submersed plants.

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Table 1. Mean (± SE) percent light (µmol) blocked by 30%, 60%, and 90% shade cloth.

	Percent light (µmol) blocked[b]		
Shade cloth[a]	*n*	$\bar{x}$	SE
30%	5	35.7	0.24
60%	5	70.9	0.37
90%	5	88.5	0.36

[a] Shade cloth manufactured by Dewitt fabrics (Sikeston, MO)
[b] Percent light estimated with LI-COR ® photometer (model LI-189)

Table 2. Mean dry mass (g) of species of submersed aquatic vegetation (SAV) collected in subplots (0.25 m^2) at sampling sites in SAV communities in the lower Mobile River Delta, Alabama, September 2003 and 2004.

			2003		2004	
Plant community[a]	*n*[b]	Species	$\overline{x}$	SE	$\overline{x}$	SE
Wild celery	5	*Vallisineria americana*	31.7	10.5	14.3	7.7
		Heteranthera dubia	1.8	1.8	11.0	10.9
		Ceratophyllum demersum	Tr[c]		0.2	0.2
		Myriophyllum spicatum	Tr		3.9	2.2
		Najas guadalupensis	Tr		4.2	2.6
		Potamogeton pusillus	Tr		Np[d]	
Southern naiad	4	*N. guadalupensis*	6.3	2.6	0.3	0.3
		P. pusillus	0.9	0.5	Np	
		V. americana	0.4	0.4	3.8	3.8
		M. spicatum	0.3	0.1	19.1	8.9
		Ruppia maritima	Tr		Tr	
Eurasian watermilfoil	4	*M. spicatum*	34.3	3.6	41.5	11.5
		N. guadalupensis	4.8	3.6	6.8	6.7
		C. demersum	1.3	1.2	7.2	2.2
		P. pusillus	Tr		Np	
Mixed species	4	*M. spicatum*	7.8	0.9	15.2	3.1
		N. guadalupensis	3.5	1.0	8.1	1.6
		V. americana	2.7	2.7	5.3	3.0
		C. demersum	1.8	1.7	15.6	9.0
		H. dubia	Tr		6.8	2.5
		Hydrilla verticillata	Tr		Tr	

Table 2. Continued

Plant community	*n*	Species	2003 $\bar{x}$	2003 SE	2004 $\bar{x}$	2004 SE
Sparsely vegetated	5	*N. guadalupensis*	1.0	0.3	Tr	
		C. demersum	Np		Tr	
		H. dubia	Np		6.0	6.0
		M. spicatum	Tr		5.2	3.4
		R. maritima	Tr		1.3	1.3
		V. americana	Np		Tr	

[a] Sampling sites placed into plant communities according to 2003 biomass. Mean dry mass of submersed plants in subplots was < 2g in sparsely vegetated communities. Species names indicate mean dry mass of plants was >2g and corresponding species comprised >75% of mean dry mass of plants in subplots. Exotic and native plants were present in subplots in mixed communities, but neither comprised > 75% of mean dry mass of plants.

[b] Sampling sites

[c] Trace amounts (dry mass < 0.1g)

[d] Not present

Table 3. Means (±SE) and ranges of water parameters measured at sampling sites in submersed plant communities during June – August 2003.

	Wild celery[a]				Southern naiad				Eurasian watermilfoil				Mixed species				Sparsely vegetated			
Parameters	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range
Salinity (‰)	30	0.8	0.1	(0-1.6)	20	0.7	0.1	(0-1.6)	24	0.6	0.1	(0-1.6)	24	0.6	0.1	(0-1.8)	26	0.5	0.1	(0-1.6)
Temperature (°C)	30	28.9	0.2	(28-32)	20	29.5	0.2	(28-31)	24	28.8	0.3	(26-31)	24	29.3	0.2	(28-31)	26	29.4	0.2	(28-32)
Velocity (cm/s)	30	0.9	0.2	(0-3)	20	0.8	0.2	(0-3)	24	0.0	0.0	(0)	24	0.7	0.2	(0-3)	26	0.7	0.2	(0-3)
Depth (m)	30	0.9	0.1	(0.3-1.3)	20	0.9	0.1	(0.7-1.5)	24	0.8	0.1	(0.6-1.1)	24	0.9	0.1	(0.5-1.7)	26	0.7	0.1	(0.3-1.2)
Secchi[b] (m)	24	0.5	0.1	(0.4-0.7)	20	0.5	0.1	(0.4-0.8)	7	0.8	0.1	(0.6-1.0)	20	0.7	0.1	(0.5-1.0)	22	0.5	0.1	(0.3-0.7)

[a] Sampling sites were placed into plant communities according to 2003 biomass. Mean total dry mass of submersed plants in subplots was < 2g in sparsely vegetated communities. Species names indicate total dry mass of plants was >2g and corresponding species comprised ≥75% of total dry mass of plants in subplots. Exotic and native plants were present in subplots in mixed communities, but neither comprises ≥ 75% of total dry mass of plants.

[b] Secchi depth was not estimitable at all sampling dates because of high water clarity or dense plant growth.

Table 4. Means (±SE) and ranges of water parameters measured at sampling sites in- submersed plant communities during March – August 2004.

	Wild celery[a]				Southern naiad				Eurasian watermilfoil				Mixed species				Sparsely vegetated			
Parameters	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range	*n*	$\bar{x}$	SE	Range
Salinity (‰)	60	1.4	0.1	(0.2-4.2)	48	1.5	0.1	(0.2-4.2)	48	1.1	0.1	(0.2-2.6)	48	1.4	0.1	(0.4-4.2)	60	1.5	0.1	(0.2-4.2)
Temperature (°C)	60	26.1	0.6	(15-33)	48	26.2	0.7	(16-33)	48	26.9	0.7	(16-33)	48	26.0	0.7	(16-33)	60	26.3	0.6	(16-33)
Velocity (cm/s)	60	1.0	0.1	(0-3)	48	0.4	0.1	(0-3)	48	0.4	0.1	(0-3)	48	0.3	0.1	(0-2)	60	0.6	0.1	(0-3)
Depth (m)	60	0.9	0.1	(0.3-1.3)	48	0.9	0.1	(0.6-1.3)	48	0.8	0.1	(0.4-1.0)	48	0.9	0.1	(0.5-1.3)	60	0.8	0.1	(0.4-1.2)
Secchi[b] (m)	54	0.6	0.1	(0.3-1.0)	38	0.6	0.1	(0.3-0.8)	4	0.6	0.1	(0.5-0.8)	28	0.6	0.1	(0.3-0.9)	54	0.5	0.1	(0.2-0.8)

[a] Sampling sites placed into plant communities according to 2003 biomass. Mean total dry mass of submersed plants in subplots was < 2g in sparsely vegetated communities. Species names indicate total dry mass of plants in subplots was >2g and corresponding species comprised ≥75% of total dry mass. Exotic and native plants were present in subplots in mixed communities, but neither comprises ≥ 75% of total dry mass.

[b] Secchi depth was not estimitable at all sampling dates because of high water clarity or dense plant growth.

Table 5. Mean (± SE) dry mass (g) of species of submersed aquatic vegetation (SAV) collected in subplots (0.25 m^2) in shade plots (3.3 m^2; n = 20) in the lower Mobile River Delta, Alabama, September 2004.

Percent shade	n[a]	Species	$\overline{x}$	SE
0	5	*Myriophyllum spicatum*	18.7	1.6
		Ceratophyllum demersum	16.9	10.1
		Najas guadalupensis	4.9	0.4
		Heteranthera dubia	2.7	1.3
		Vallisineria americana	0.4	0.2
		Hydrilla verticillata	Tr[b]	
30	5	*C. demersum*	8.6	5.5
		M. spicatum	4.2	2.7
		N. guadalupensis	0.2	0.2
		H. dubia	0.2	0.2
		V. americana	0.2	0.2
60	5	*C. demersum*	8.8	6.8
		M. spicatum	2.0	1.1
		H. dubia	1.7	1.0
		N. guadalupensis	1.4	1.0
		V. americana	Tr	
90	5	*H. dubia*	1.0	0.6
		N. guadalupensis	0.6	0.6
		M. spicatum	0.4	0.4
		C. demersum	0.2	0.2
		P. pusillus	Tr	

Table 5. Continued

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[a] Plots

[b] Trace amounts (dry mass < 0.1g)

Figure 1. Map of Mobile River Basin showing location of Mobile River Delta and lower Mobile River Delta, Alabama.

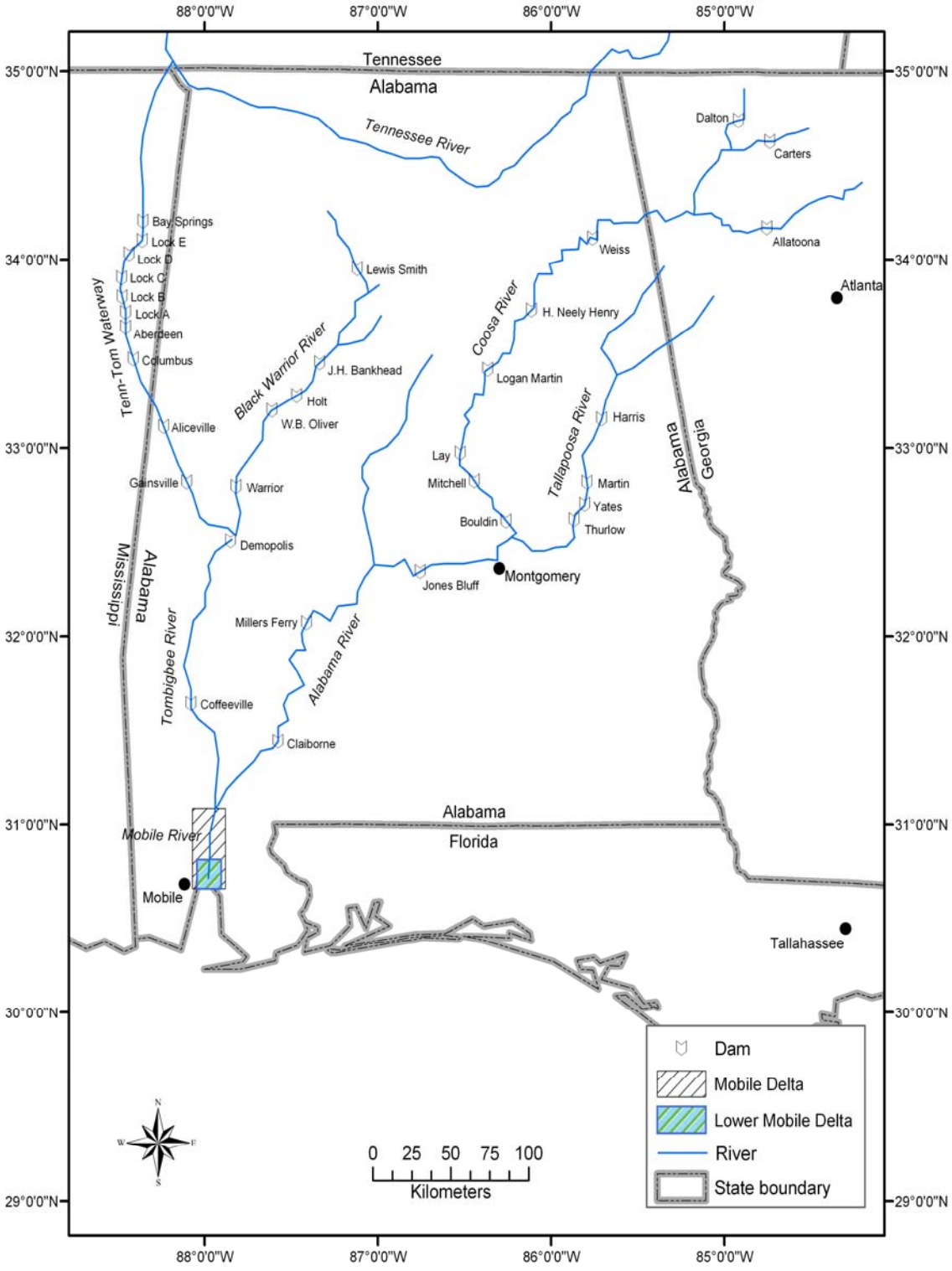

88°0'0"W
87°0'0"W
86°0'0"W
85°0'0"W
35°0'0"N
34°0'0"N
33°0'0"N
32°0'0"N
31°0'0"N
30°0'0"N
29°0'0"N
Tennessee
Alabama
Florida
Georgia
Tennessee River
Tenn-Tom Waterway
Black Warrior River
Coosa River
Tallapoosa River
Alabama River
Tombigbee River
Mississippi
Alabama
Mobile River
Bay Springs
Lock E
Lock D
Lock C
Lock B
Lock A
Aberdeen
Columbus
Aliceville
Gainsville
Lewis Smith
J.H. Bankhead
Holt
W.B. Oliver
Warrior
Demopolis
Millers Ferry
Coffeeville
Claiborne
Jones Bluff
Montgomery
Bouldin
Lay
Mitchell
Logan Martin
H. Neely Henry
Weiss
Harris
Martin
Yates
Thurlow
Dalton
Carters
Allatoona
Atlanta
Mobile
Tallahassee
0 25 50 75 100
Kilometers
Dam
Mobile Delta
Lower Mobile Delta
River
State boundary

Figure 2. Map of lower Mobile River Delta, Alabama showing locations of sampling sites.

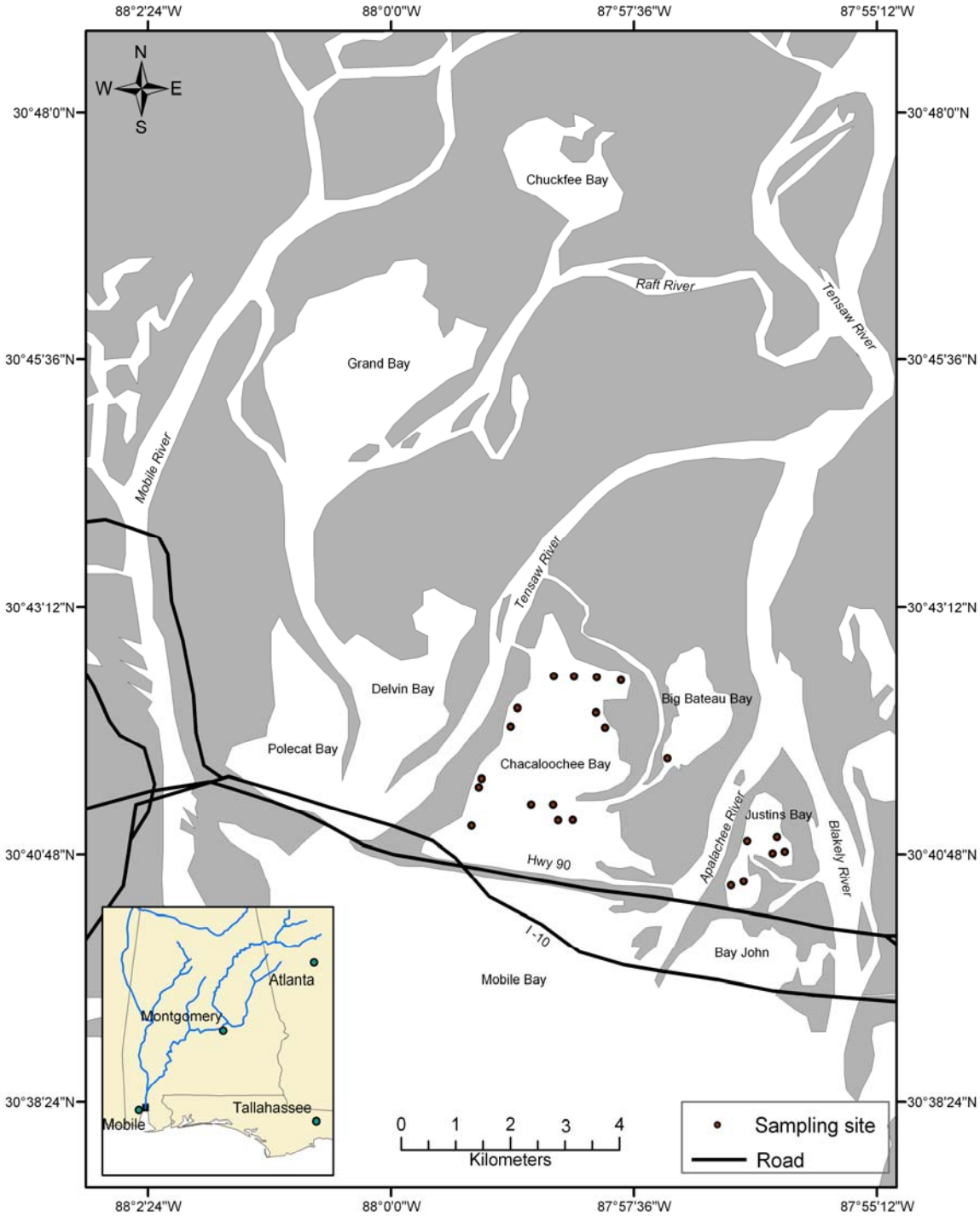

88°2'24"W
88°0'0"W
87°57'36"W
87°55'12"W
30°48'0"N
30°45'36"N
30°43'12"N
30°40'48"N
30°38'24"N
N
W
E
S
Chuckfee Bay
Raft River
Tensaw River
Grand Bay
Mobile River
Tensaw River
Delvin Bay
Big Bateau Bay
Polecat Bay
Chacaloochee Bay
Justins Bay
Apalachee River
Blakely River
Hwy 90
I-10
Bay John
Mobile Bay
Atlanta
Montgomery
Tallahassee
Mobile
0 1 2 3 4
Kilometers
Sampling site
Road

Figure 3. Least squares means (± SE) of principal component scores of turbidity (NTU) and total suspended solids (TSS)(mg/l) measured at sampling sites (n = 22) in submersed plant communities in the lower Mobile Delta, Alabama, March – August 2004. Lower PC1 values indicate greater water clarity.

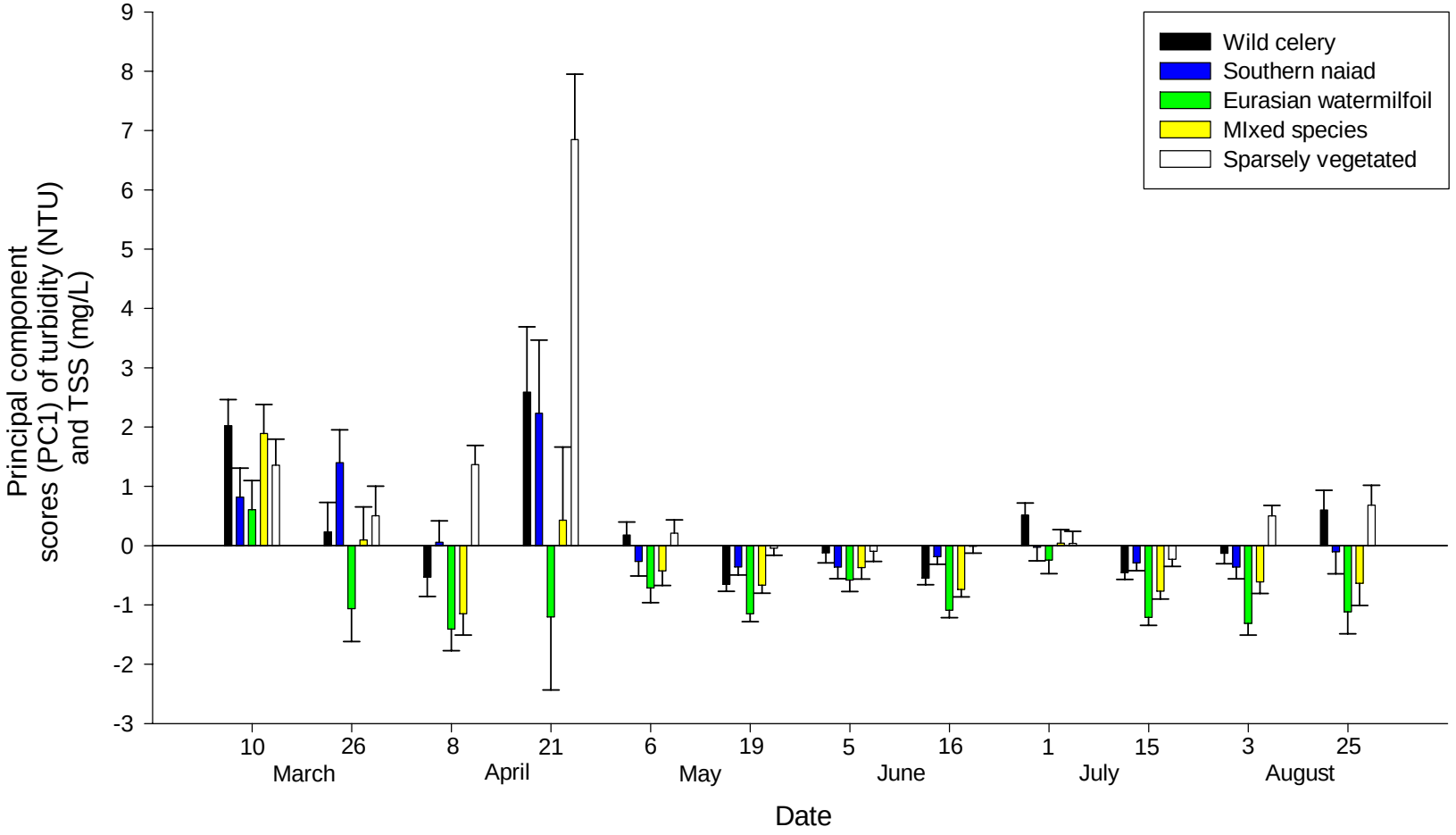

Principal component scores (PC1) of turbidity (NTU) and TSS (mg/L)
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
Wild celery
Southern naiad
Eurasian watermilfoil
MIxed species
Sparsely vegetated
10
26
8
21
6
19
5
16
1
15
3
25
March
April
May
June
July
August
Date

Figure 4. Least squares means (± SE) of principal component scores (PC1) of turbidity (NTU) and total suspended solids (TSS)(mg/L) measured at sampling sites (n = 22) in submersed plant communities in the lower Mobile Delta, Alabama, June – August 2003. Lower PC1 values indicate greater water clarity.

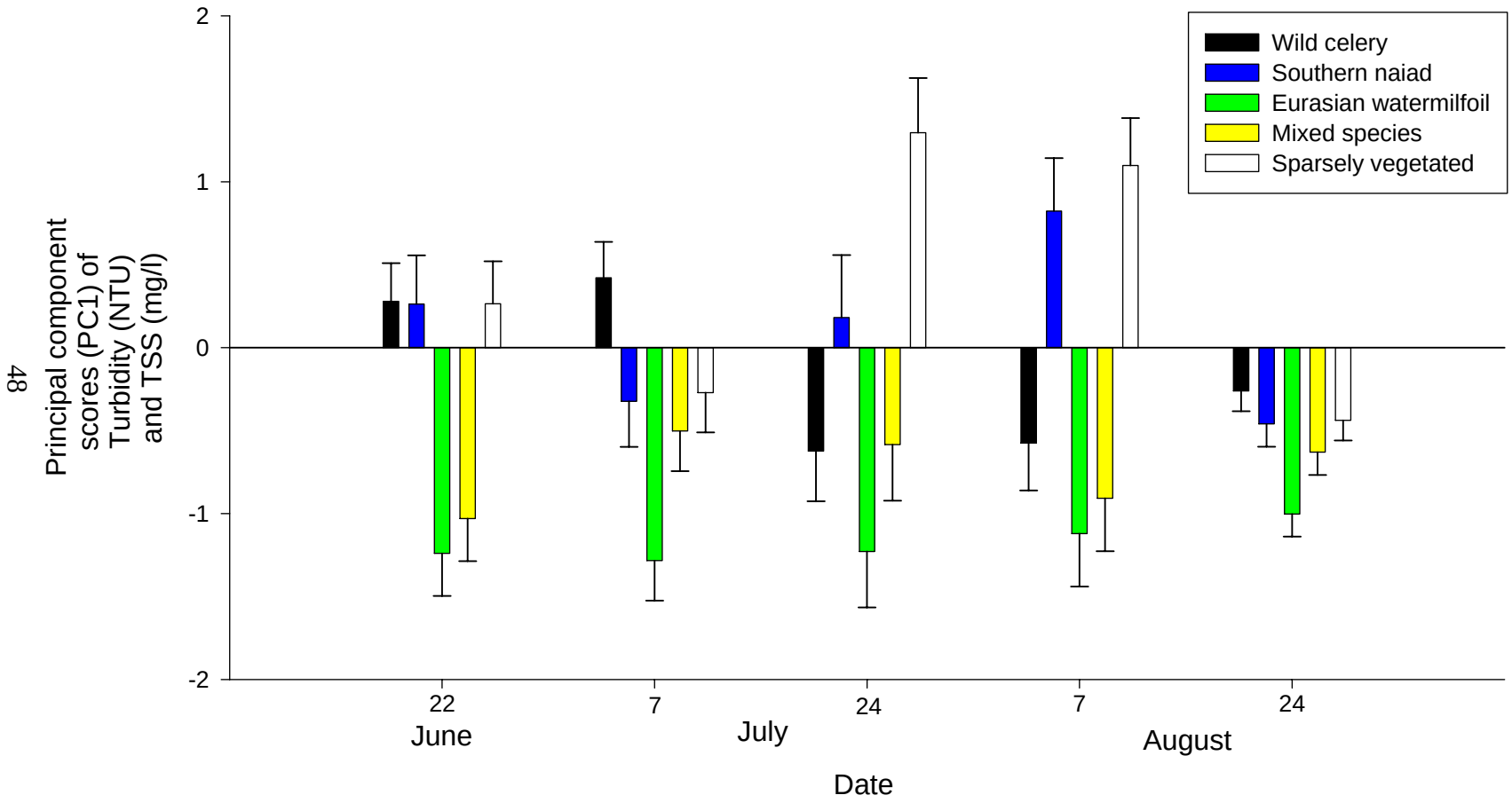

Wild celery
Southern naiad
Eurasian watermilfoil
Mixed species
Sparsely vegetated
Principal component scores (PC1) of Turbidity (NTU) and TSS (mg/l)
2
1
0
-1
-2
22
7
24
7
24
June
July
August
Date

Figure 5. Least squares means (± SE) of dry mass (g) of submersed aquatic vegetation (SAV) in full sun (control) and experimental shade plots in the lower Mobile River Delta, Alabama, September 2004. Means sharing same letter are not different ($P \leq 0.05$).

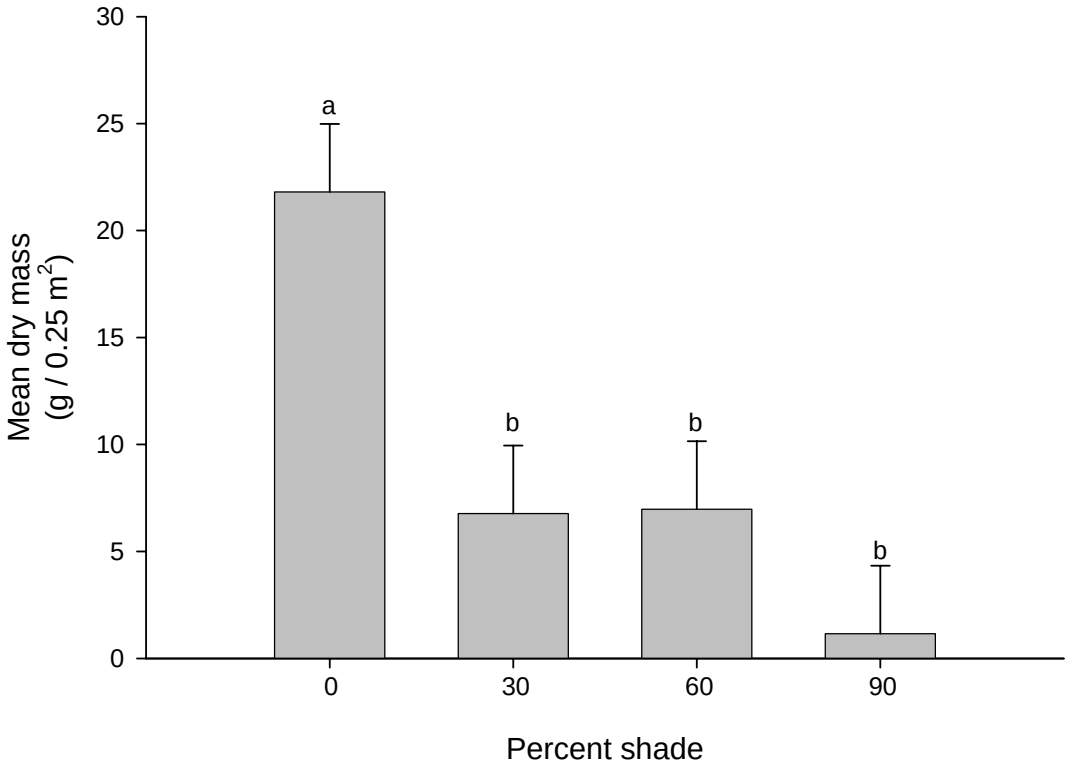

30
25
20
15
10
5
0
Mean dry mass
(g / 0.25 m2)
a
b
b
b
0
30
60
90
Percent shade

Figure 6. Least squares means (± SE) of dry mass (g) of Eurasian watermilfoil (*Myriophyllum spicatum*) and native species of submersed aquatic vegetation (SAV) in full sun (control) and experimental shade plots in the lower Mobile River Delta, Alabama, September 2004.

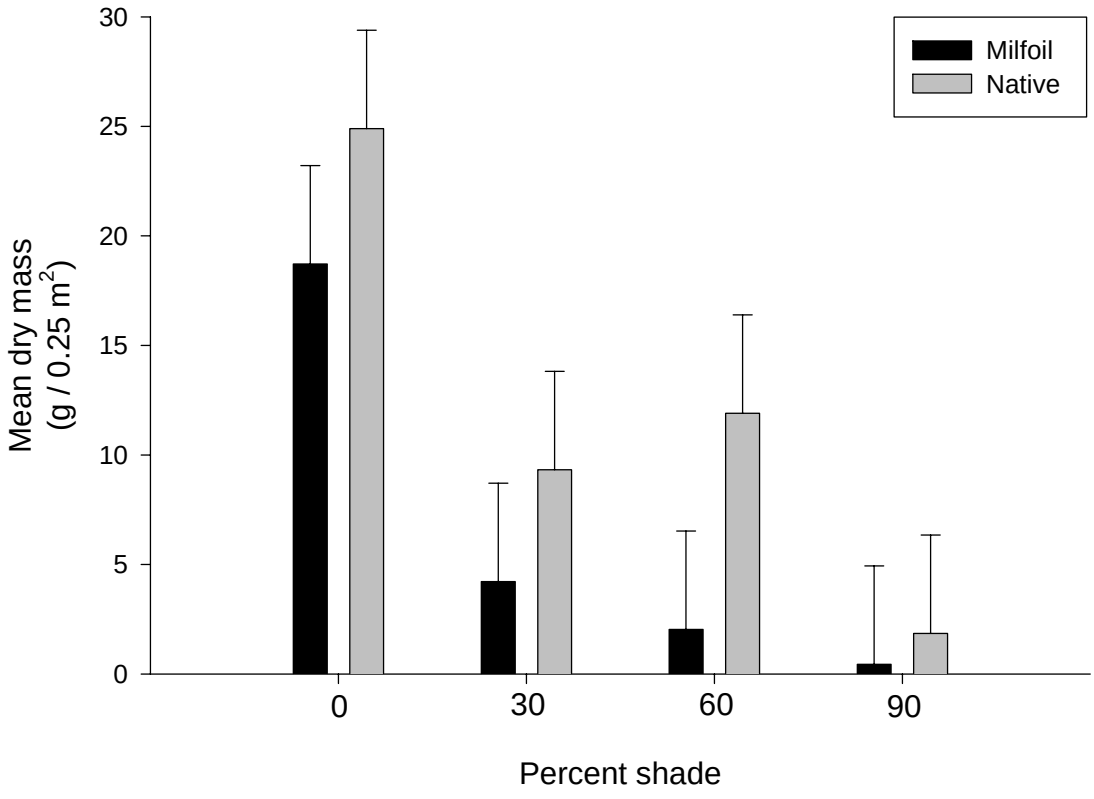
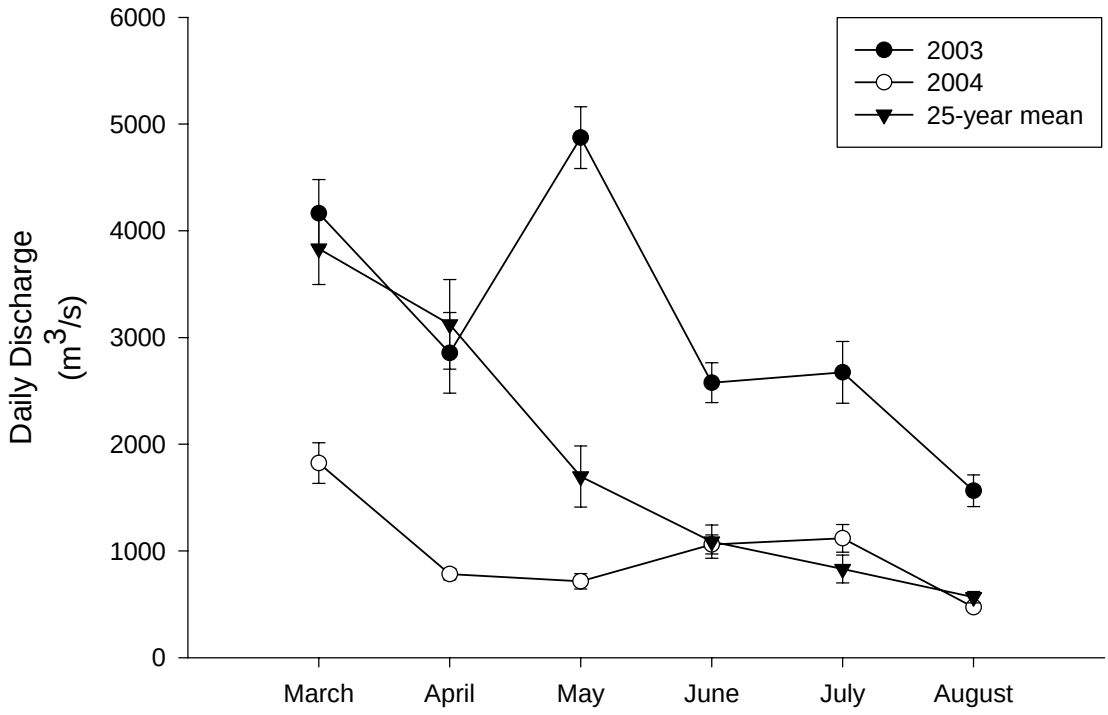

Milfoil
Native
Mean dry mass
(g / 0.25 m2)
30
25
20
15
10
5
0
0
30
60
90
Percent shade

Figure 7. Mean (± SE) combined daily discharges (m^3/s) by month from Claiborne Lock and Dam, Alabama River and Coffeeville Lock and Dam, Tombigbee River in 2003, 2004, and the 25-year average (1976-2001).


6000
5000
4000
3000
2000
1000
0
Daily Discharge
(m3/s)
2003
2004
25-year mean
March
April
May
June
July
August

III. CHARACTERISTICS OF SOILS ASSOCIATED WITH SUBMERSED AQUATIC VEGETATION (SAV) COMMUNITIES IN THE LOWER MOBILE RIVER DELTA, ALABAMA

INTRODUCTION

Eurasian watermilfoil (*Myriophyllum spicatum*) (hereafter milfoil) is an exotic species of submersed aquatic vegetation (SAV) that forms a dense canopy, grows rapidly, and has multiple mechanisms of propagation, enabling it to dominate native SAV communities (Couch and Nelson 1985, Nichols and Shaw 1986, Lillie 1990, Smith and Barko 1990, Madsen and Smith 1997). Establishment of milfoil often leads to declines in abundance and diversity of desirable native species of SAV, such as wild celery (*Vallisineria americana*), and reduced abundance of native SAV can negatively affect fish and wildlife (Aiken et al. 1979, Godfrey and Wooten 1981, Madsen et al. 1991, Duffy and Baltz 1998, Knapton and Petrie 1999, Getsinger et al. 2002). Milfoil also alters nutrient cycles (Seki et al. 1979; Getsinger et al. 2002, Madsen et al. 1991) and decreases water flow (Aiken et al. 1979), which can result in further habitat degradation.

Milfoil is a superior competitor to native SAV species under a wide range of environmental conditions; however, certain conditions may provide native plants advantages over milfoil (Titus and Adams 1979, Carpenter 1980, Madsen et al. 1991, Harley and Findlay 1994, Madsen and Smith 1997). Many native species of SAV, such

as wild celery and *Potamogeton* spp., for example, reach maximum photosynthetic rates at lower light levels than milfoil, which could give these plants competitive advantages in low light conditions (Madsen et al. 1991, Harley and Findlay 1994). Native species of SAV also are more tolerant of wave action than milfoil (Stewart et al. 1997; Ailstock et al. 2000). Consequently, spatial and temporal distribution of milfoil and native SAV species may vary according to environmental conditions (Titus and Adams 1979; Van et al. 1999)

In estuarine environments, water parameters, such as turbidity, salinity, and dissolved nutrients, frequently are the primary factors influencing growth of SAV (Carter and Rybicki 1990, Montague and Ley 1993, Carr et al. 1997). However, soil properties, such as texture and nutrient availability, also are important to SAV (Brunner and Batterson 1984, Barko and Smart 1986, McFarland and Barko 1987, Short 1987, Nichols 1994, Spencer 1990). Different responses of SAV species to soil conditions may influence their distribution and abundance (Barko and Smart 1980, 1983, 1986). Van et al. (1999), for example, demonstrated that the competitive abilities of wild celery and hydrilla (*Hydrilla verticillata*) were influenced by soil fertility. Wild celery was dominant on soils with low fertility, whereas hydrilla was dominant on soils with high fertility (Van et al. 1999).

In this study, we measured soil parameters at sparsely vegetated sites, and sites dominated by milfoil and native species of SAV in the lower Mobile Delta, Alabama. Our goal was to examine relationships between SAV abundance and various soil parameters. In particular, we predicted that milfoil would be more abundant than native species of SAV on sites with high fertility.

STUDY AREA AND METHODS

The study was conducted in the lower Mobile River Delta, Alabama (30˚ 41'N, 87˚ 58'W). The lower Mobile Delta comprises about 25% (20,235 ha) of the total area of the Mobile River Delta and is generally described as the treeless area from Chuckfey Bay south to 4.0 km below the causeway (Beshears 1979). Fifteen species of SAV are known to inhabit the lower Delta, including the exotics, Eurasian watermilfoil (*Myriophyllum spicatum*) and hydrilla (*Hydrilla verticillata*; Zolczynski and Shearer 1997). A detailed description of the study area is given in Chapter 2.

Site selection

In June 2003, sampling sites (n = 20) were established in three bays (Big Bateau, Chacaloochee Bay, and Justin's Bay) in the lower Mobile Delta. Sites were established in SAV communities visually identified as milfoil, native SAV, and sparsely vegetated.

Species composition and biomass of SAV

We used subplots (0.25 m^2; n = 5) to estimate plant biomass and species composition of SAV at sites in September 2003 and 2004. Subplots were placed at the center of each site and 10m from this point in each cardinal direction. All above ground plant parts were collected by hand, and plant materials were placed in plastic bags, stored on ice, and transported to the laboratory at Auburn, Alabama. Plant samples were rinsed, sorted by species, and dried (60º C) to constant mass (0.1g).

Soil sampling

We collected soil cores (n = 5) at sites in March 2004 using plastic tubes (5 x 20 cm). Soil cores were taken at the center of each site and 10m from this point in each cardinal direction. Each core was separated into three sections (0 – 5 cm, 5 – 10 cm, and

10 – 20 cm) and sections were placed in plastic bags, stored on ice, and transported to the laboratory at Auburn, Alabama.

Plant material was removed from 0 – 5 cm sections and all sections were dried (65º C) to constant mass (g). Dried cores were ground to pass a 2-mm stainless steel sieve, and a composite sample from each depth section at each site was used to determine substrate texture, pH, extractable phosphorus (mg/kg), total carbon (g/kg), and total nitrogen (g/kg). Texture was determined by the hydrometer method (Soil survey investigations staff 1991). Substrate pH was determined on 1:1 soil/water slurries with a pH meter and glass electrode. Extractable P was determined by extracting samples with a dilute double acid solution (Hue and Evans 1986) followed by inductively coupled argon plasma spectroscopy (SPECTRO CIROS, side on plasma, Germany). Total C and N were determined with a LECO CN-2000 analyzer (LECO Corp., St. Joseph, MI).

Statistical analysis

Each year we determined total dry mass and dry masses of milfoil and native species of SAV at each sampling site. Native species of SAV included all species except milfoil and hydrilla. Three-way ANOVA (PROC GLM; SAS Institute 2003) was used to test effects of site, plant community (milfoil, native SAV, or sparsely vegetated), core depth (0 – 5 cm, 5 – 10 cm, and 10 – 20 cm), and their interactions on soil parameters. Site was specified as a random variable, and plant community (site) was the error term used to test for plant community effects. Differences between least squares means were determined using Tukey-Kramer test. Tests were significantly different at $P \leq 0.05$.

RESULTS

Species composition and biomass of SAV

Seven species of SAV were encountered at sampling sites (Table 1). Milfoil was most abundant at milfoil sites, and wild celery and water stargrass (*Heteranthera dubia*) dominated native SAV sites (Table 1). Milfoil, wild celery, and Southern naiad (*Najas guadalupensis*) were most abundant at sparsely vegetated sites (Table 1). However, total dry mass of SAV at sparsely vegetated sites was much lower (>75%) than at either milfoil or native SAV sites (Table 1).

Texture

Percent sand varied from 72 ± 8.8 % at sparsely vegetated sites to 40 ± 8.8 % at milfoil sites, but differences among plant communities were not significant ($F_{2,17} = 3.37$, $P = 0.058$). Percent sand was greater at 0-5 cm than at 10-20 cm ($F_{2,34} = 4.87$, $P = 0.014$; Fig. 1 (A). Percent silt varied from 17 ± 5.4 % at sparsely vegetated sites to 33 ± 5.4 % at milfoil sites, but did not differ among plant communities ($F_{2,17} = 2.43$, $P = 0.118$) or core depths ($F_{2,34} = 0.57$, $P = 0.572$). Percent clay was greater at milfoil sites than sparsely vegetated sites ($F_{2,17} = 4.28$, $P = 0.031$; Fig. 2) and was greater at 10-20 cm than 0–5cm across all plant communities ($F_{2,34} = 9.18$, $P = 0.001$; Fig. 1 (B).

pH

pH was similar across plant communities ($F_{2,17} = 1.22$, $P = 0.319$) and core depths ($F_{2,34} = 0.37$, $P = 0.693$) and averaged 5.43 ± 0.09.

Carbon, nitrogen, and phosphorus

Total carbon ($F_{4,34} = 4.88$, $P = 0.003$) and total nitrogen ($F_{4,34} = 4.34$, $P = 0.006$) varied with the interaction of plant community and core depth. Total carbon and nitrogen

were higher at milfoil sites than at either native SAV or sparsely vegetated sites at depths of 0-5 cm and 5-10 cm, but not at 10-20 cm (Table 2, Fig. 3 (A,B). Total carbon and nitrogen did not differ ($P > 0.05$) between native SAV and sparsely vegetated sites at all core depths (Table 2, Fig. 3 (A,B). Extractable phosphorus also varied with the interaction of plant community and core depth ($F_{4,34}= 4.30$, $P = 0.006$). Phosphorus levels were greater at sparsely vegetated sites at 10 – 20 cm than milfoil sites at 10 – 20 cm and native SAV sites at 5 – 10 cm (Table 2, Fig. 3 (C).

DISCUSSION

Texture, pH, and carbon and nitrogen concentrations of soils were similar at sparsely vegetated and native SAV sites. Only phosphorus concentrations were different between these sites, and phosphorus was more abundant at sparsely vegetated sites than at native SAV sites. Similarities between soils at sparsely vegetated and native SAV sites and the abundance of phosphorus at sparsely vegetated sites suggest that these soil characteristics did not limit growth of native SAV at sparsely vegetated sites in the lower Mobile Delta. Soils also play a secondary role to other habitat conditions, such as light availability, in limiting growth of SAV in Chesapeake Bay (Dennison 1987, Stevenson et al. 1993, Ailstock et al. 2000).

After plant communities become established, soils in SAV communities are influenced by complex feedback mechanisms between growth of SAV and the surrounding environment (Almasi et al. 1987, Ailstock et al. 2000). Reduced current velocity and wave energy in SAV beds often result in high concentrations of fine particles, organic matter, and nitrogen (Scoffin 1970, Grady 1981, Wanless 1981,

Kenworthy et al. 1982, Fonseca and Cahalan 1992, Rybicki et al. 1997). The effects of SAV on the surrounding soil in turn influence growth of SAV (Ailstock et al. 2000).

Aquatic macrophytes influence soils differently (Moore et al. 1994, Wigand et al. 1997). Sediments colonized by wild celery, for example, retain more inorganic phosphorus than those occupied by milfoil and hydrilla (Wigand et al. 1997). SAV communities comprised of exotic canopy forming SAV species have lower current velocity and less wave action than those dominated by meadow-forming native species of SAV, which leads to high rates of sedimentation and an abundance of fine particles in exotic SAV communities (Ailstock et al. 2000). Soils with large amounts of clay have low porewater exchange with the water column, which can contribute to increased nitrogen concentrations (Kenworthy et al. 1982). In our study, higher sedimentation rates at milfoil sites possibly contributed to greater abundance of clay and higher levels of nitrogen at these sites than at sparsely vegetated sites. Milfoil also exhibits extensive leaf sloughing (Aiken et al. 1979), which, coupled with high rates of sedimentation, may have contributed to increased organic carbon and nitrogen concentrations at milfoil sites. Phosphorus concentrations were lower at both milfoil and native SAV sites than at sparsely vegetated sites, which may have been related to uptake of sediment phosphorus by SAV.

High levels of nitrogen, carbon, and clay in soils associated with milfoil raise questions concerning long-term impacts of milfoil infestations. Exotic canopy-forming SAV species often dominate nutrient-rich soils, and less productive soils often are occupied by native species of SAV (Hutchinson 1975; Van et al. 1999). The accumulation of nitrogen in soils associated with milfoil may provide exotic SAV species

further competitive advantages over native SAV species. SAV abundance is reported to decline as sediment organic content increases (Walker 1972, Wetzel 1979, Kight 1980, Barko and Smart 1983,1986), possibly due to nutrient limitations on soils with large amounts of fine particles (Barko and Smart 1986) or high concentrations of phytotoxic substances, such as sulfide, and soluble organic compounds (Barko and Smart 1983, Carlson et al. 1994). Barko and Smart (1986), for example, demonstrated that milfoil and hydrilla declined as sediment organic matter increased to 20% dry sediment mass. Concentrations of organic carbon in soils at milfoil sites in the lower Mobile Delta were within the known ranges for most SAV species (typically below 50g/kg) (Ward et al. 1984, Koch 1999, Ailstock et al. 2000); however, high rates of organic matter deposition and increased amounts of clay may contribute to declines in abundance of SAV. Milfoil often declines after dominating for a 5 – 10 year period, which may be partially related to the accumulation of organic matter in soils (Carpenter 1980, Smith and Barko 1990). Unfavorable soil conditions resulting from milfoil may also impede native SAV restoration, despite declines in milfoil abundance. Further, succession of aquatic plant communities from submersed to emergent is related to the accumulation of organic matter in soils (Wetzel 1979; Barko and Smart 1983), and milfoil may accelerate rates of succession in aquatic plant communities by increasing rates of organic matter deposition.

Soils can be an important contributing factor causing variation in abundance and distribution of SAV. Soil-plant relationships characterized in the lower Mobile Delta support results from other studies and suggest that milfoil is more abundant than native SAV in areas with high concentrations of carbon and nitrogen. Lower levels of phosphorus in soils in milfoil and native SAV communities than at sparsely vegetated

sites suggests that sediment phosphorus is important for growth of SAV. However, it is unlikely that sediment phosphorus limits growth of SAV since the plants can also utilize inorganic nutrients from the water (Denny 1972; Barko and Smart 1983). The abundance of carbon, nitrogen, and clay in soils associated with milfoil suggest that the plant may cause changes to aquatic soils that alter natural succession patterns in aquatic plant communities and potentially influence restoration of native SAV communities. Removal of exotic SAV species, like milfoil, may be important to reduce their impact on aquatic soils, thereby minimizing adverse ecologic impacts.

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Table 1. Dry mass ($\overline{x}$ ± SE) of submersed aquatic vegetation (SAV) collected in subplots (0.25 m^2) at sampling sites (*n* = 20) in SAV communities in the lower Mobile Delta, Alabama, September 2003 and 2004.

Plant Community[a]	n[b]	Species	Dry mass (g/ 0.25 m^2) $\overline{x}$	SE
Milfoil	7	*Myriophyllum spicatum*	27.8	5.6
		Najas guadalupensis	2.3	0.8
		Ceratophyllum demersum	2.2	1.3
		Vallisineria americana	0.8	0.8
		Potamogeton pusillus	0.1	0.1
		Heteranthera dubia	0.1	0.1
Native species	6	*Vallisineria americana*	21.4	8.8
		Heteranthera dubia	8.7	5.2
		Ceratophyllum demersum	4.1	4.0
		Myriophyllum spicatum	3.7	2.6
		Najas guadalupensis	1.4	0.7
		Hydrilla verticillata	Tr[c]	
		Potamogeton pusillus	Tr	
Sparsely vegetated	7	*Myriophyllum spicatum*	3.5	1.2
		Najas guadalupensis	1.6	0.8
		Vallisineria americana	1.1	1.1
		Ruppia maritima	0.5	0.5
		Potamogeton pusillus	0.1	0.1

Table 1. Continued

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[a] Sampling sites placed into plant communities according to mean dry mass of SAV collected in subplots September 2003 and 2004. Milfoil = mean dry mass of milfoil ≥60% of mean total dry mass, Native SAV = mean dry mass of native species of SAV ≥60% of mean total dry mass, and Sparsely vegetated = mean total dry mass of SAV < 15g.

[b] Sampling sites

[c] Trace amounts (< 0.1 g/ 0.25 m^2)

Table 2. Least squares means (± SE) of soil parameters measured at sampling sites in submersed aquatic vegetation (SAV) communities in the lower Mobile Delta, Alabama, March 2004.

		SAV Community		
Parameter	Core depth (cm)	Milfoil	Native SAV	Sparsely vegetated
Total carbon (g/ kg)	0 – 5	36.7 ± 2.2	16.9 ± 2.3	10.1 ± 2.2
	5 – 10	30.5 ± 2.2	17.4 ± 2.3	13.2 ± 2.2
	10 – 20	20.5 ± 2.2	16.3 ± 2.3	11.5 ± 2.2
Total nitrogen (g/ kg)	0 – 5	4.3 ± 0.3	1.9 ± 0.3	1.0 ± 0.3
	5 – 10	3.3 ± 0.3	1.7 ± 0.3	1.1 ± 0.3
	10 – 20	2.1 ± 0.3	1.4 ± 0.3	0.9 ± 0.3
Extractable phosphorus (mg/ kg)	0 – 5	12.4 ± 0.8	12.6 ± 0.9	12.3 ± 0.8
	5 – 10	11.9 ± 0.8	10.7 ± 0.9	13.1 ± 0.8
	10 – 20	9.2 ± 0.8	12.8 ± 0.9	15.1 ± 0.8

Figure 1. Mean (± SE) percents sand (A) and clay (B) in sections of soil cores collected in submersed aquatic vegetation (SAV) communities in lower Mobile Delta, Alabama, March 2004. Means sharing same letter are not different ($P \leq 0.05$).

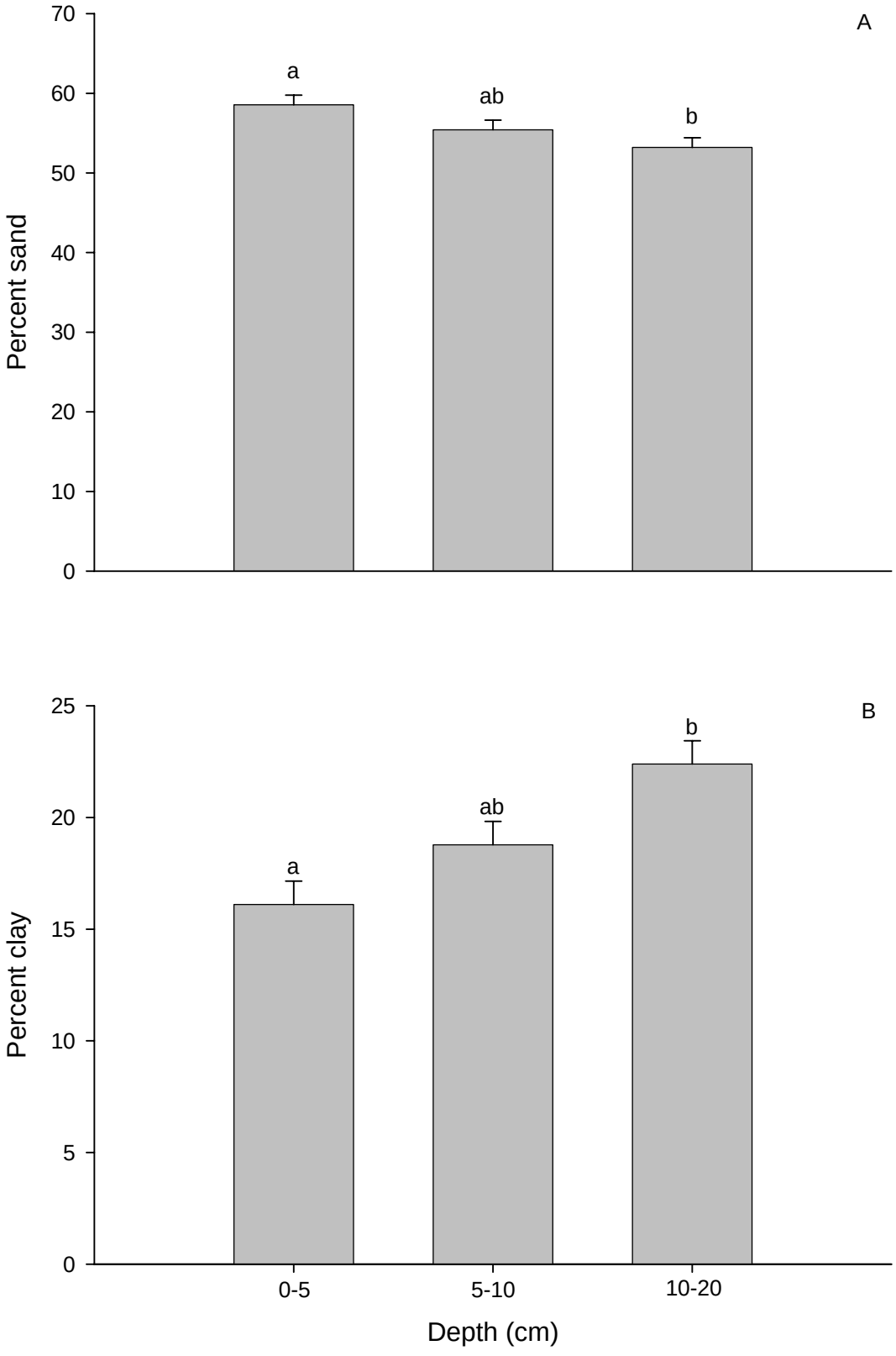

A
Percent sand
70
60
50
40
30
20
10
0
a
ab
b
B
Percent clay
25
20
15
10
5
0
a
ab
b
0-5
5-10
10-20
Depth (cm)

Figure 2. Mean (± SE) percent clay in soil cores collected in submersed aquatic vegetation (SAV) communities in lower Mobile Delta, Alabama, March 2004. Means sharing same letter are not different ($P \leq 0.05$).

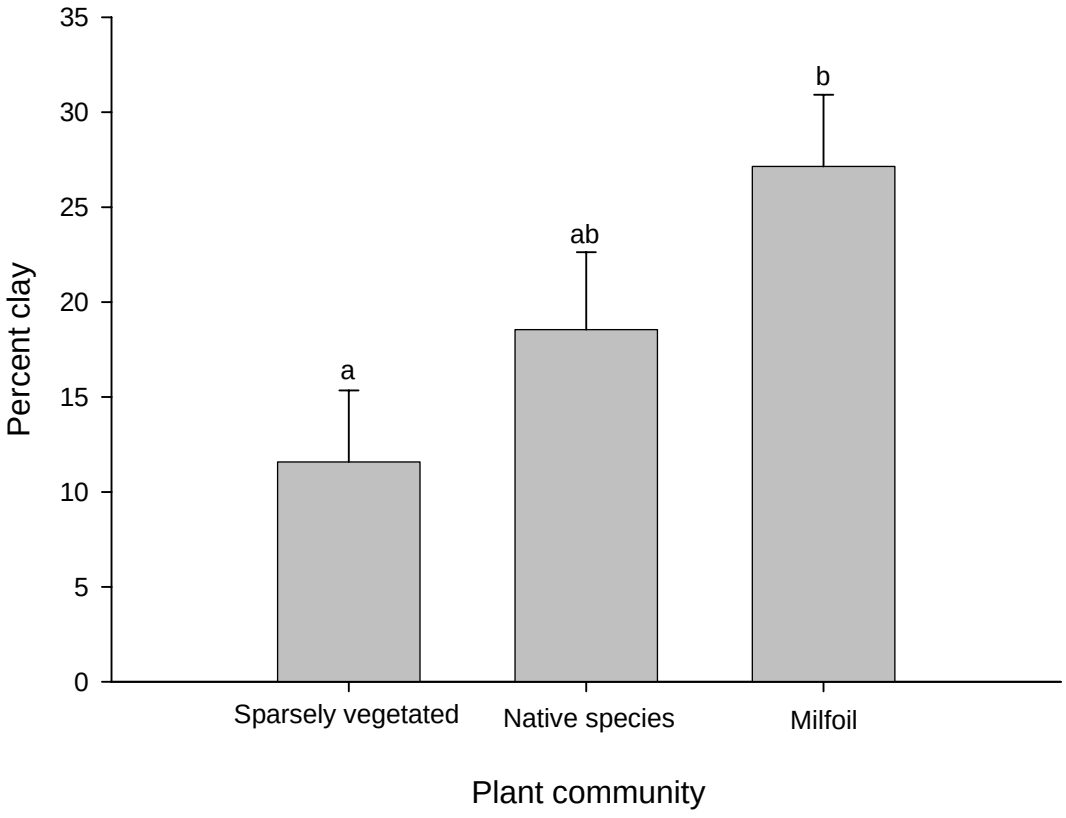
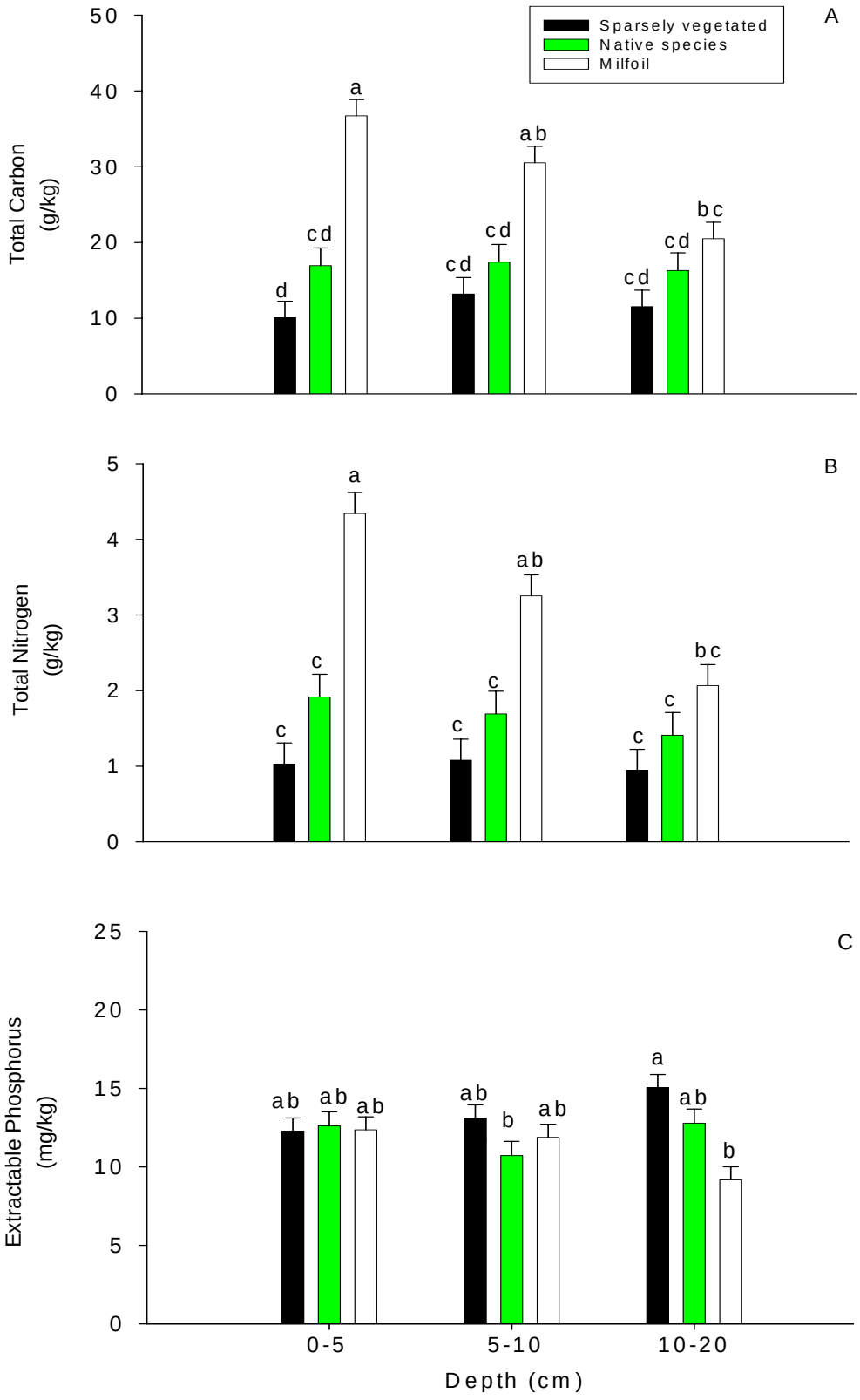

35
30
25
20
15
10
5
0
Percent clay
a
ab
b
Sparsely vegetated
Native species
Milfoil
Plant community

Figure 3. Mean (± SE) total carbon (A), total nitrogen (B), and extractable phosphorus (C) in sections of soil cores collected in submersed aquatic vegetation (SAV) communities in lower Mobile Delta, Alabama, March 2004. Means sharing same letter are not different ($P \leq 0.05$).


Sparsely vegetated
Native species
Milfoil
A
Total Carbon (g/kg)
50
40
30
20
10
0
d
cd
a
cd
cd
ab
cd
cd
bc
B
Total Nitrogen (g/kg)
5
4
3
2
1
0
c
c
a
c
c
ab
c
c
bc
C
Extractable Phosphorus (mg/kg)
25
20
15
10
5
0
ab
ab
ab
ab
b
ab
a
ab
b
0-5
5-10
10-20
Depth (cm)

APPENDIX A
PRODUCTION OF WINTER BUDS BY WILD CELERY IN COASTAL ALABAMA

INTRODUCTION

Vegetative reproduction is the primary method of propagation for most species of submersed aquatic vegetation (SAV)(Titus and Stephens 1983, Nichols and Shaw 1986, Smith and Barko 1990). Submersed plants use a variety of vegetative reproductive methods, including fragmentation, gemmipary, and stolon formation (Sculthorpe 1967, Aiken et al. 1979). Some SAV species also produce specialized vegetative structures, such as tubers and turions, when conditions are unsuitable for plant growth (Korschgen and Green 1988, Van Vierssen 1990). Turions are found both above and below ground and consist mostly of leaves, where as tubers are usually subterranean and consist primarily of stored carbohydrates (Sculthorpe 1967, Basiouny et al. 1978, Van Viersseen 1990). The formation of turions and tubers often is associated with decreased photoperiod and water temperature during late summer (Van et al. 1978, Steward 2000); however, other physiological stresses, such as nutrient deficiency, also are shown to increase turion production (Haller et al. 1976, Pieterse et al. 1984).

Wild celery (*Vallisineria americana*) is a submersed dioecious perennial plant that grows in rosettes of linear tape-shaped leaves (Lowden 1982, Korschgen and Green 1988). Wild celery primarily is found in eastern North America, but also occurs in select western states (Lowden 1982, Korschgen and Green 1988). Wild celery produces

subterranean turions (i.e. winter buds) that are an important source of food for many species of waterfowl, such as canvasback (*Aythya valisineria*; Korschgen and Green 1988). Wild celery has two growth forms, broad-leaved and narrow-leaved (Lowden 1982, Korschgen and Green 1988). The broad-leaved form has 10-25 mm wide leaves with 5-9 veins and conspicuously toothed margins, whereas the leaves on the narrow-leaved form are 10 mm wide with 3-5 veins and finely toothed margins (Lowden 1982, Korschgen and Green 1988). Broad-leaved plants are usually found inland in lakes and waterways where as narrow-leaved plants typically inhabit brackish coastal inlets and spring-fed waterways (Lowden 1982, Korschgen and Green 1988).

Wild celery ceases production of rosettes and produces winter buds during late summer in middle to northern lattitudes of its geographic range (Donnermeyer 1982, Titus and Stephens 1983, Rybicki and Carter 2002). Leaves break free after winter buds are formed and the plant remains dormant until water temperatures reach 10-14º C (Zamuda 1976, Titus and Adams 1979). Winter bud formation and dormancy play an essential role in survival where winter conditions inhibit photosynthetic production; however, the formation of over-wintering structures and dormancy may not be necessary for plants growing in areas where photosynthesis is possible year-round. Smart and Dorman (1993), for example, found that when grown under similar conditions, wild celery from Wisconsin produced winter buds and became dormant in the fall whereas plants from Texas never produced winter buds and remained viable throughout the study period.

In this study, we collected soil cores in stands of wild celery and estimated abundance of wild celery turions in the lower Mobile Delta, Alabama during winter 2003.

The primary goals of this study were to determine whether wild celery produced winter buds and evaluate the relative importance of the plant for waterfowl wintering in the Delta.

Study area

The Mobile River Delta begins at the confluence of the Tombigbee and Alabama Rivers in south Alabama and extends south about 64 km before opening into Mobile Bay (Beshears 1979). The delta is about 16 km wide and covers 81,000 ha (Beshears 1979). The lower Mobile Delta comprises about 25% (20,235 ha) of the total area of the Mobile River Delta and is generally described as the treeless area from Chuckfey Bay south to 4.0 km below the causeway (30˚ 41'N, 87˚ 58'W; Beshears 1979). Fifteen species of SAV are known to inhabit the lower Delta, including the exotics, Eurasian watermilfoil (*Myriophyllum spicatum*) and hydrilla (*Hydrilla verticillata*; Zolcyznski and Shearer 1997). In 2002, wild celery covered about 405 ha of the 1,902 ha of SAV in the lower Mobile Delta (Mapping of SAV in Mobile Bay and Delta 2004).

Temperatures in the Delta are characteristic of sub-tropical coastal environments found along the Gulf of Mexico (Table 1). Although temperatures in the region sometimes fall below 0º C, freezing conditions are few and of short duration.

METHODS

Winter buds

In September 2003, we established sampling sites in wild celery stands (n = 5) in the lower Mobile Delta. We collected soil cores (8 cm x 20 cm; n = 5) at each site monthly during November 2003 - January 2004. Soil cores were placed in plastic bags, iced, and transported to the laboratory at Auburn, Alabama for processing.

Any above ground plant material was removed from soil cores. Cores then were placed in a 4 mm sieve and rinsed to remove soil. Subterranean plant material retained in the sieve was visually examined for presence of winter buds, and below ground plant material was dried (60º C) to constant mass (g).

Statistical Analysis

We used repeated measures ANOVA (PROC MIXED; SAS Institute 2003) to test effects of site, collection date, and their interaction term on dry mass of subterranean plant material (Littell et al. 1996). This analysis allowed us to determine whether biomass of below ground plant material changed during the study period. Compound symmetric covariance structure was specified for the random variable (site) based on Akaike's Information Criterion (AIC; Littell et al. 1996). Differences between least squares means were determined using Tukey-Kramer tests.

RESULTS

Winter bud production

No wild celery winter buds were collected in soil cores during the study period. Dry mass of subterranean plant material also did not change during the study period (*collection date*; $F = 1.63$, $P = 0.21$) and averaged 0.58 ± 0.09 g/1005 cm^3

DISCUSSION

Absence of winter buds in cores and lack of change in dry mass of subterranean plant parts suggests that wild celery did not produce winter buds during the study period. Wild celery also had attached leaves throughout the study period, which indicates that plants remained photosynthetically active. Previous research indicates that wild celery from the Texas gulf coast also do not produce winter buds and remain viable during

winter (Smart and Dorman 1993). Smart and Dorman (1993) suggested ecotypic differentiation as a possible cause for latitudinal differences in winter growth strategy. It is possible that factors that initiate production of vegetative perennial organs and dormancy in wild celery, such as temperature and photoperiod, do not reach levels that support utilization of winter growth strategies in coastal Alabama (Aiken 1976; Weber and Noodén 1976; Van Vierssen 1990). However, recent unpublished data suggests that plants in the southeastern United States previously described as environmentally induced phenotypes of *V. americana* may actually be a distinct species (Haynes 1980; Mapping of SAV in Mobile Bay and Delta 2004). According to Mapping of SAV in Mobile Bay and Delta (2004), the upcoming Annotated Checklist of the Vascular Plants of Alabama will treat wild celery found in the Tennessee Valley in Northern Alabama as *V. americana*, while wild celery found in Southern Alabama will be identified as a new species, *V. neotropicalis*. However, this information is based on unpublished data and thus should be treated with caution until further verification.

MANAGEMENT IMPLICATIONS

Wild celery is an important source of food for many species waterfowl, such as canvasback and redhead (*Athya americana*), during migration and winter (Cottam 1939; Korschgen and Green 1988, Knapton and Petrie 1999). All parts of the plant are consumed; however, the carbohydrate rich winter buds are most important (Cottam 1939; Korschgen and Green 1988, Knapton and Petrie 1999). Although wild celery in southern climates likely provides some food for waterfowl during winter, the lack of winter bud production may decrease the relative importance of the plant as a source of food in these areas. In light of these findings, we suggest that individuals and organizations seeking to

provide carbohydrate-rich native foods for wintering waterfowl in southern habitats focus efforts on alternative plant species, such as delta duck potato (*Sagittaria platyphylla*).

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Table 1. Mean monthly and annual temperatures (ºC) at Mobile WSO Airport, Alabama (station # 015478) during 3/11/1900 – 3/31/2004 (Southeastern Regional Climate Center, *www.sercc.com*).

	Minimum Temp. (ºC) $\bar{x}$	Maximum Temp. (ºC) $\bar{x}$
Jan.	4.9	16.1
Feb.	6.5	18.0
Mar.	9.7	21.4
Apr.	13.7	25.4
May	18.0	29.3
Jun.	21.4	32.0
Jul.	22.7	32.8
Aug.	22.6	32.6
Sep.	20.3	30.4
Oct.	14.2	26.3
Nov.	9.0	21.1
Dec.	5.9	17.2
Annual	14.1	25.2