FINAL REPORT

Otter Point Creek Submerged Aquatic Vegetation Grid Study
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INTRODUCTION

Submersed aquatic vegetation is an important component of aquatic ecosystems because it has the capacity to provide habitat for fish and wildlife, buffer shores from erosion and enhance water quality. Realizing its effects on ecosystems, researchers and managers in the Chesapeake Bay watershed focus considerable attention on restoring and managing submersed aquatic macrophytes throughout the Bay. To this end, several research and monitoring projects have been initiated in 2002 at the Chesapeake Bay National Estuarine Research Reserve sites in Maryland (CBNERR-MD). In its fourth year at Otter Point Creek, one of the three CBNERR-MD sites, the time is appropriate to analyze the collected data, evaluate whether sample design is adequate, and synthesize the data into reports that can be published in peer-reviewed journals. The goal of the project was therefore to establish a productive collaboration between CBNERR/MD and UMCES to specifically:

1. Conduct regular meetings and coordinate activities among staff to evaluate data availability and needs, and discuss approaches to analyzing the data;
2. Compile existing data so that it can be used in statistical analyses;
3. Perform statistical analyses and share techniques and approaches;
4. Submit reports and prepare a manuscript for publication.

Grid Study: A sampling grid was created in summer 2002 at Otter Point Creek to monitor the submersed aquatic vegetation community at the site. Initially 64 sampling stations, the study was expanded in 2004 to include 106 sampling stations sampled 4 times during the growing season (May, June, August and October). The goals of this ongoing monitoring effort are to 1) establish sites suitable for long-term monitoring and change detection, and 2) track the distribution, diversity and density of SAV throughout the marsh in a spatially explicit way.

Water quality monitoring: Coinciding with the vegetation monitoring study, a tidal water quality monitoring program was initiated in 2002. The goals of this program are to 1) establish long-term monitoring sites capable of detecting changes in water quality over time, and 2) quantify the spatial and temporal variability of water quality throughout the marsh. Six sites were established and are monitored twice monthly during the SAV growing season (April to October). Top and bottom measurements are made for salinity, conductivity, temperature and dissolved oxygen. Discrete water samples are also taken at the same time and analyzed for total suspended solids/total volatile solids, chlorophyll a, dissolved inorganic phosphorus, dissolved inorganic nitrogen, total nitrogen and total phosphorus. pH and light attenuation are also recorded.

Float Study: An experiment was conducted in June 2002 to identify 1) which species are most suited for restoration based on survival, growth and vegetative expansion, and 2) the optimal planting depth for each species. Nine floats, containing five different species of SAV (*Vallisneria americana*, *Heteranthera dubia*, *Potamogeton perfoliatus*, *Potamogeton nodosus*, and *Elodea canadensis*) were suspended at three separate depths at OPC. Single shoots of each species were transplanted and left in the floating trays for

approximately 2 months before they were harvested. Fifteen plants of each species from each of three depths were harvested at the end of the study and length, and number of shoots and biomass measured.

RESULTS

Task 1 – Meetings: Project personnel (Katia Engelhardt, Bob Hilderbrand, Julie Bortz) met regularly at least once per quarter. Data needs were discussed as were potential papers emerging from data analyses. We believe that these regular meetings strengthened a productive relationship between CBNERR-MD and the University of Maryland Center for Environmental Science that we hope will continue in the future.

Task 2 – Sample collection and data compilation: Samples (vegetation and water) were collected in summer 2005, sent out for analysis, and compiled either at the Appalachian Laboratory or at CBNERR-MD. Through these efforts, we gained an appreciation for the richness of the data that are collected at Otter Point Creek on a regular basis. The spatial and temporal extent of the vegetation and water quality sampling, and possibilities for integrating the two datasets are unique. We therefore hope that these monitoring efforts continue with the same rigor in future years.

Task 3 – Statistical analyses: Data from the float study was analyzed in depth. We found that not one of the five species planted in floats at different depths was a superior species. Rather, survival, growth, and vegetative expansion differed across species, suggesting that a mix of species may be the best approach to ensuring restoration success of submersed aquatic macrophyte beds.

The grid study data was analyzed using geostatistical procedures. This resulted in maps of spatial patterns of vegetation (Figures 1, 2, and 3). Relative density of vegetation, measured with rake grabs, increased from 2002 to 2004 but declined in 2005. To identify 1) what effects this invasion of vegetation might have on water quality, and 2) how water quality may have affected vegetation density across years and seasons, we examined water quality parameters at 5 water quality monitoring stations at 6 spatial scales for the four sampled seasons in 2004 and 2005 (Figure 4). We found that greater vegetation density decreases the concentration of nutrients and particulates but that this effect is strongly linked to the season and the spatial scale of inference (Table 1). Nitrogen concentrations (nitrate, nitrite, ammonium, and total nitrogen) were only associated with vegetation in the spring and early summer when growth rate of vegetation is the highest. Total suspended and volatile solids, and total phosphorus, on the other hand, were associated with vegetation in the summer months. Chlorophyll a was positively associated with vegetation in spring and negatively in the fall. Scale of inference was especially important in early summer, where larger spatial scales generally increased explanatory power. The same trends are generally true for the variability of water quality parameters in a given season (Table 2).

SAS code for the statistical analyses of the float and the grid study can be found in Appendix A.

Task 4 – Submit reports and write manuscript: We submitted a manuscript summarizing the results of the float study to Estuaries in November 2005. The manuscript is included in this report as Appendix B. We are still waiting to hear back from the journal.

The October 2005 water quality data has not been received yet, which constrained some of the data analysis efforts of the grid study, and, thus, the preparation of a manuscript. Two manuscripts may result from further data analysis, but these efforts are beyond the current scope of work.

RECOMMENDATIONS

Restoration: Results of the float study suggest that not one species is the best for SAV restoration planting at OPC. Rather a mix of species that increase the chances of survival, grow fast and expand vegetatively should be considered. We recommend a mix of *V. americana*, *Heteranthera dubia*, and *Potamogeton perfoliatus*. While *P. nodosus* did well in the experiment, we recommend against the species because it is currently not found in Chesapeake Bay and the wave and tidal energy at OPC be too high for the long-term survival of the species. We recommend further experimentation with these and other species.

Vegetation sampling grid: The current extent and resolution of the grid is adequate for examining the spatial distribution of vegetation at Otter point Creek. Hence, the sample design does not need to be altered. However, we do recommend the use of echosounder technology to add greater rigor to the measurement of vegetation density. The data shows the initial invasion of *Hydrilla verticillata* and its subsequent decline in 2005, which is a pattern similar to the one observed in the Potomac River. We recommend continuing the sampling each year and during the four seasons (spring, early summer, summer, and fall) for the next 3 years to monitor the long-term vegetation dynamics of the system.

Water quality monitoring: The water quality monitoring stations are important in assessing the health of Otter Point Creek and in monitoring a potential switch of the system from a turbid algal dominated state to a clear macrophyte dominated state. The current locations of the stations are adequate with the only weakness being that all but one station are located close to shore. Managers at OPC may want to consider adding 2 more stations and to consult Figure 4 on the most appropriate placement of these stations. Because early summer is the period during the growing season when vegetation and water quality are most strongly associated, we recommend weekly sampling between mid-June and mid-July to further elucidate relationships during this critical period.

Table 1. The association of mean vegetation density around 5 water quality stations at 6 spatial scales ("buffer" measured as diameter (m) of a circle surrounding each station; see Figure 4) and the average of water quality data. Correlation coefficients are reported when significant (o = (P<0.1), * = (P<0.05), ** = (P<0.01), ***=(P<0.001). "–" represents negative and "+" positive associations. October water quality data for 2005 is missing and statistics are not presented.

	buffer	PO4	NO2	NO3	NH4	TSS	TVS	TP	TN	chl-a
Spring	25	-	+	0.67**, -	-	-	-	+	0.57*, -	0.87***, +
	50	-	+	0.68**, -	-	-	-	+	0.57*, -	0.87***, +
	75	-	+	0.69**, -	-	-	-	+	0.57*, -	0.88***, +
	100	-	+	0.69**, -	-	-	-	+	0.56*, -	0.89***, +
	150	-	+	0.70**, -	-	-	-	+	0.54*, -	0.91***, +
	200	-	+	0.68**, -	-	-	-	+	0.51*, -	0.91***, +
Early Summer	25	-	0.57*, -	0.39^{o}, -	0.46*, -	0.48*, -	0.48*, -	0.49*, -	0.80**, -	-
	50	-	0.59**, -	-	0.41*, -	0.43*, -	0.45*, -	0.48*, -	0.54*, -	-
	75	-	0.62**, -	-	0.49*, -	0.53*, -	0.56*, -	0.58*, -	0.49*, -	-
	100	-	0.63**, -	-	0.57*, -	0.63**, -	0.68**, -	0.66**, -	0.43*, -	-
	150	-	0.60**, -	-	0.65**, -	0.73**, -	0.80***, -	0.74**, -	0.35^{o}, -	-
	200	-	0.57*, -	-	0.69**, -	0.78***, -	0.84***, -	0.76**, -	0.31^{o}, -	-
Summer	25	-	+	+	-	0.46**, -	-	0.24^{o}, -	-	-
	50	-	+	+	-	0.47**, -	-	0.27*, -	-	-
	75	-	+	+	-	0.49**, -	-	0.31*, -	-	-
	100	-	+	+	-	0.51**, -	0.21^{o}, -	0.35*, -	-	-
	150	-	+	+	-	0.53**, -	0.26*, -	0.41**, -	+	0.21^{o}, -
	200	-	+	0.20^{o}, +	-	0.54***, -	0.31*, -	0.46**, -	+	0.20^{o}, -
Fall	25									0.71**, -
	50									0.72**, -
	75									0.75**, -
	100									0.75**, -
	150									0.76***, -
	200									0.76***, -

Table 2. The association of mean vegetation density around 5 water quality stations at 6 spatial scales ("buffer" measured as diameter (m) of a circle surrounding each station; see Figure 4) and the standard deviation of water quality data. Correlation coefficients are reported when significant (o = (P<0.1), * = (P<0.05), ** = (P<0.01), ***=(P<0.001). "–" represents negative and "+" positive associations. October water quality data for 2005 is missing and statistics are not presented.

	buffer	PO4	NO2	NO3	NH4	TSS	TVS	TP	TN	chl-a
Spring	25	-	+	0.67**, -	-	-	-	+	0.57*, -	0.87***, +
	50	-	+	0.68**, -	-	-	-	+	0.57*, -	0.87***, +
	75	-	+	0.69**, -	-	-	-	+	0.57*, -	0.88***, +
	100	-	+	0.69**, -	-	-	-	+	0.56*, -	0.89***, +
	150	-	+	0.70**, -	-	-	-	+	0.54*, -	0.91***, +
	200	-	+	0.68**, -	-	-	-	+	0.51*, -	0.91***, +
Early Summer	25	-	0.57*, -	0.39^{o}, -	0.46*, -	0.48*, -	0.48*, -	0.49*, -	0.80**, -	-
	50	-	0.59**, -	-	0.41*, -	0.43*, -	0.45*, -	0.48*, -	0.54*, -	-
	75	-	0.62**, -	-	0.49*, -	0.53*, -	0.56*, -	0.58*, -	0.49*, -	-
	100	-	0.63**, -	-	0.57*, -	0.63**, -	0.68**, -	0.66**, -	0.43*, -	-
	150	-	0.60**, -	-	0.65**, -	0.73**, -	0.80***, -	0.74**, -	0.35^{o}, -	-
	200	-	0.57*, -	-	0.69**, -	0.78***, -	0.84***, -	0.76**, -	0.31^{o}, -	-
Summer	25	-	+	+	-	0.46**, -	-	0.24^{o}, -	-	-
	50	-	+	+	-	0.47**, -	-	0.27*, -	-	-
	75	-	+	+	-	0.49**, -	-	0.31*, -	-	-
	100	-	+	+	-	0.51**, -	0.21^{o}, -	0.35*, -	-	-
	150	-	+	+	-	0.53**, -	0.26*, -	0.41**, -	+	0.21^{o}, -
	200	-	+	0.20^{o}, +	-	0.54***, -	0.31*, -	0.46**, -	+	0.20^{o}, -
Fall	25									0.71**, -
	50									0.72**, -
	75									0.75**, -
	100									0.75**, -
	150									0.76***, -
	200									0.76***, -

Figure 1. Kriged maps of relative vegetation density (percent) measured in August from 2002 to 2005.

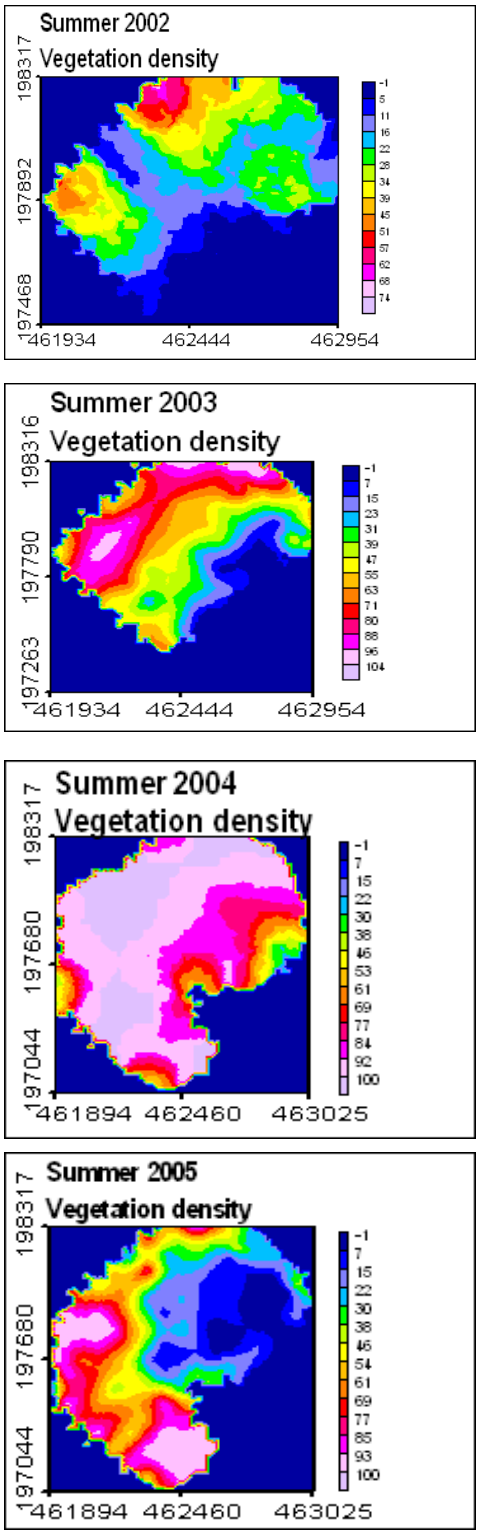


Figure 2. Kriged maps of relative vegetation density (percent) measured in four seasons in 2004. x and y axes are UTM coordinates.

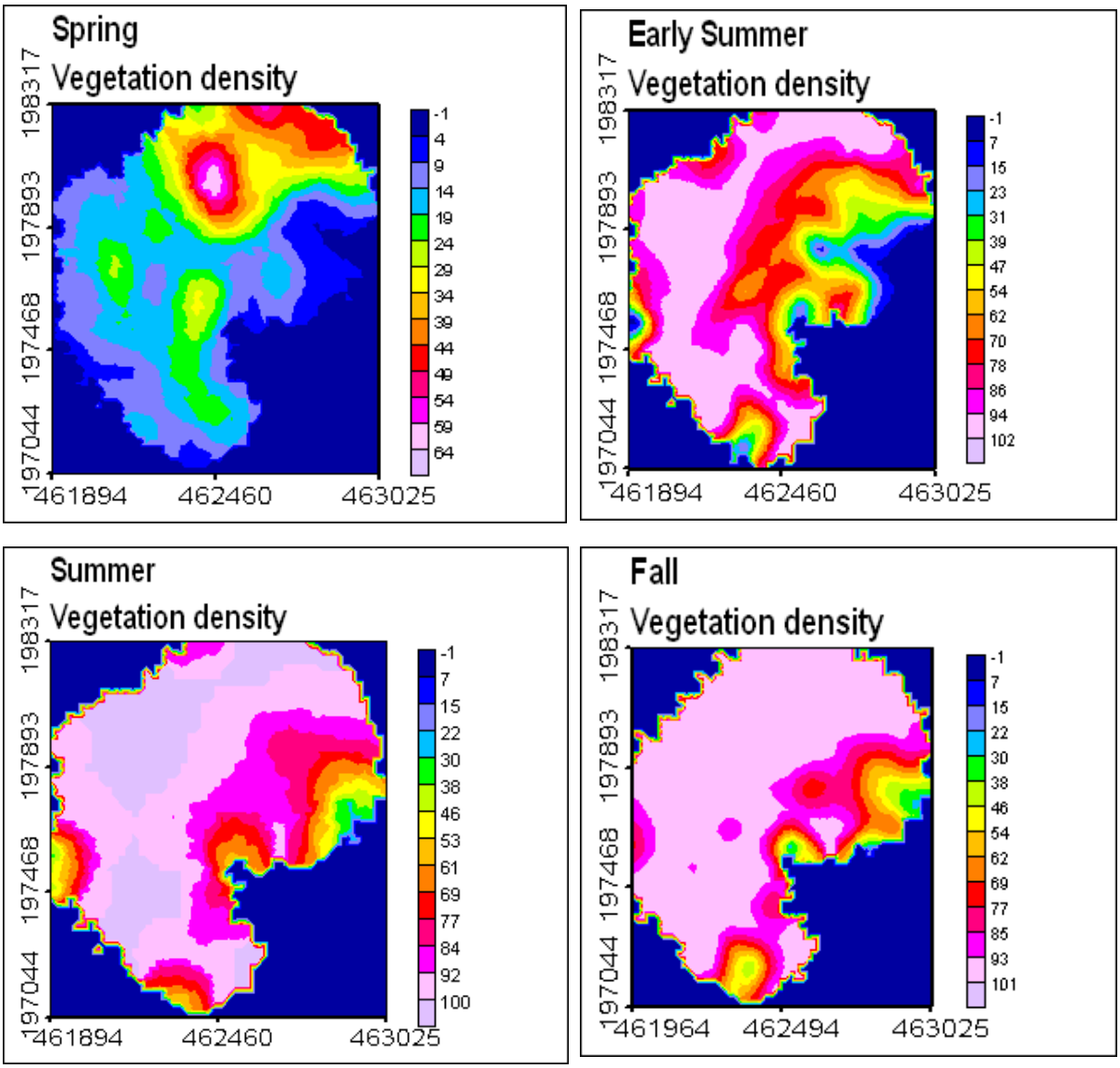


Figure 3. Kriged maps of relative vegetation density (percent) measured in four seasons in 2005. x and y axes are UTM coordinates.

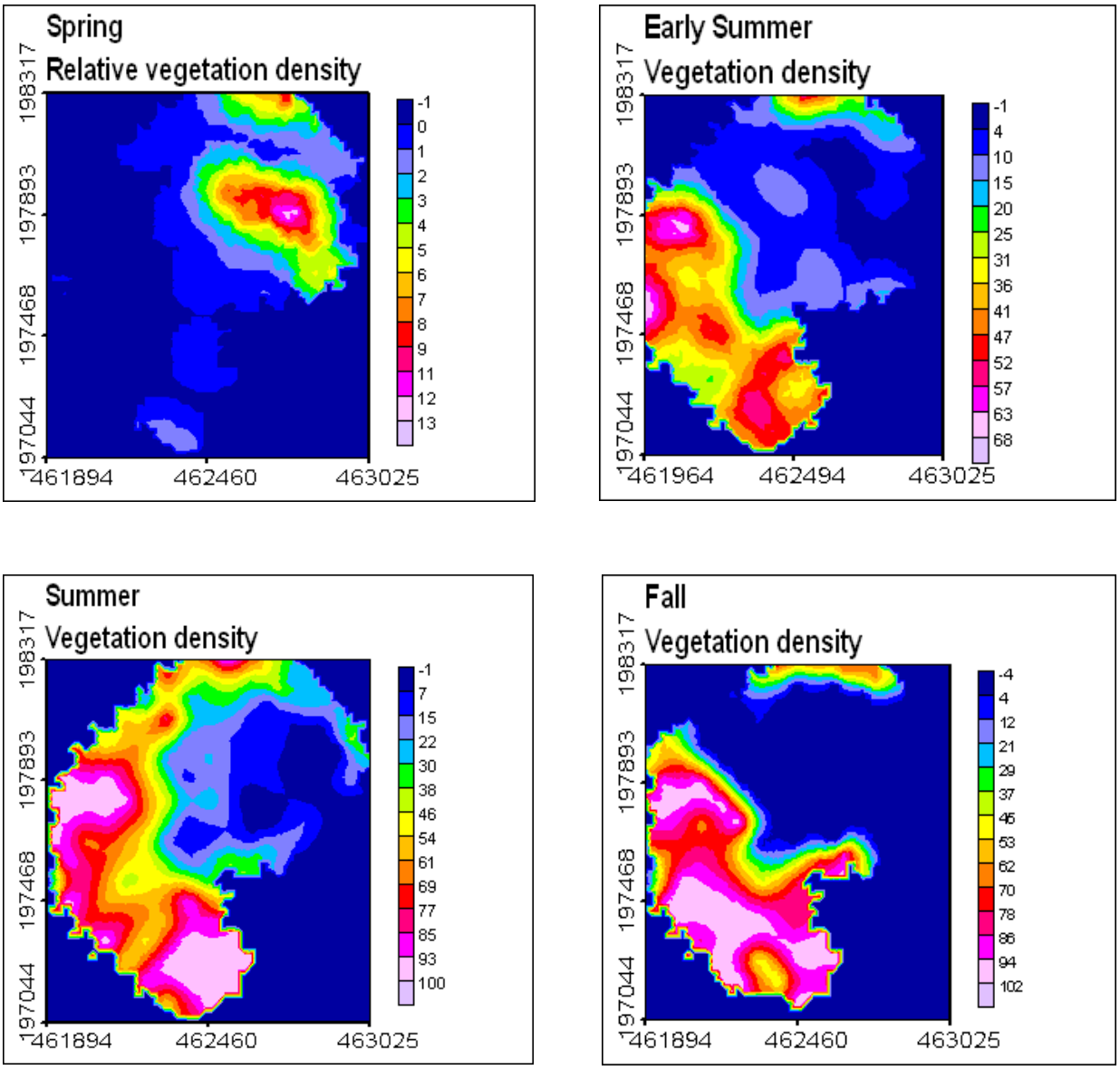
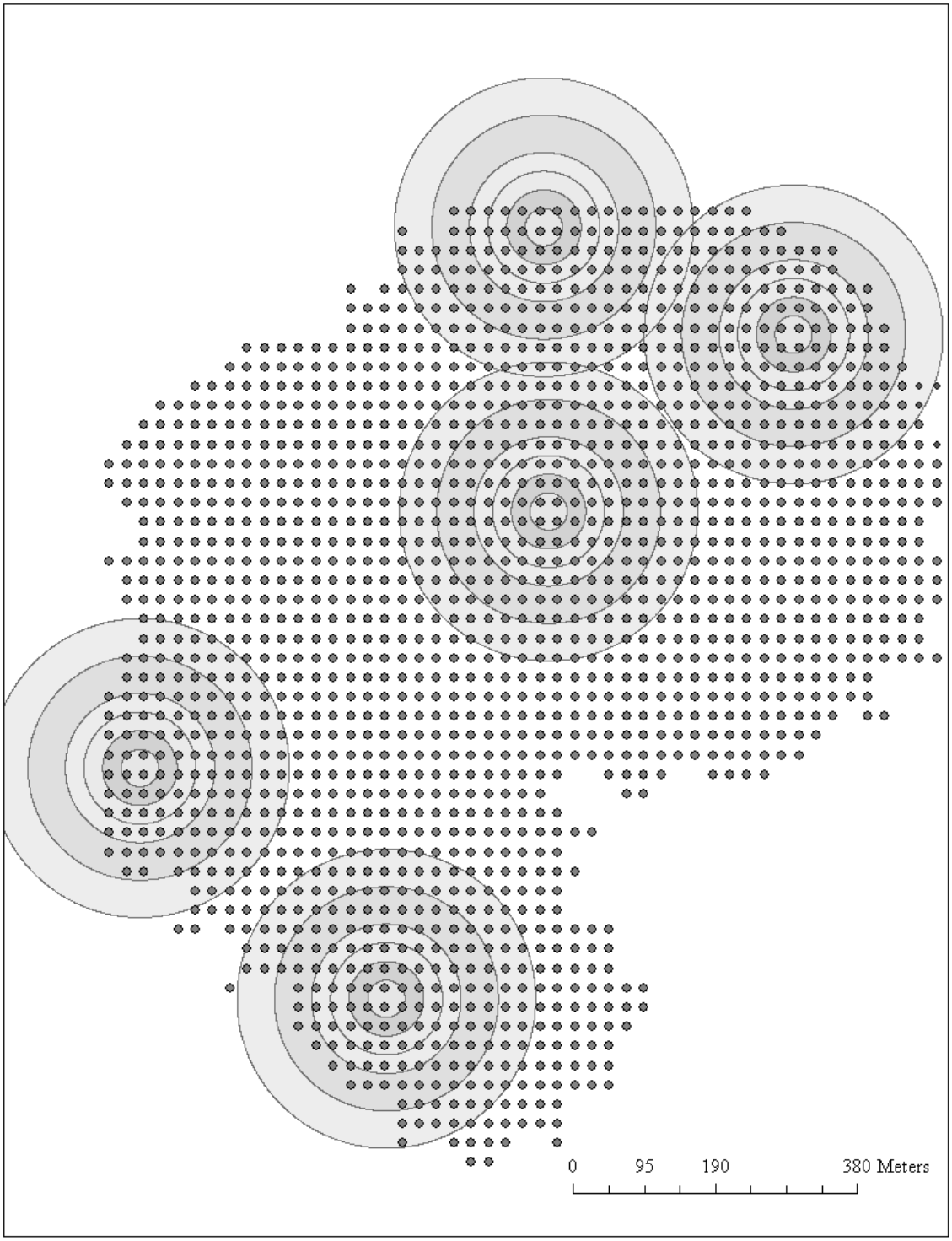


Figure 4. Location of the water quality stations and their buffers of different diameters. Grey dots represent the locations of 2500 points that predict vegetation density throughout the marsh through kriging. The buffers allow to test whether vegetation density and water quality are related at different spatial scales.



Appendix A. SAS code for statistical tests for the analysis of the float study.

```
data b;
set sasuser.float;
if drywt = 0 then delete;

relupwt = ((abovewt-avgdrywt)/avgdrywt);
rellength = ((len-avglen)/avglen);

title1 'total weight analysis';
proc mixed;
class float depth species;
model drywt = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;


title1 'above ground biomass analysis';
proc mixed;
class float depth species;
model abovewt = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;


title1 'below ground biomass analysis';
proc mixed;
class float depth species;
model belowwt = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;


title1 'relative above ground biomass analysis';
proc mixed;
class float depth species;
model relupwt = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;


title1 'length analysis';
proc mixed;
class float depth species;
model len = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;


title1 'shoots analysis';
proc mixed;
```

```
class float depth species;
model shoots = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;



title1 'relative length analysis';
proc mixed;
class float depth species;
model rellength = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;

****traits analysis
proc corr spearman;
var rellength shoots relupwt;
run;

****root to shoot analysis
data b;
set sasuser.float;
if drywt = 0 then delete;

rtsratio = (belowwt/abovewt);

title1 'root to shoot ratio analysis';
proc mixed;
class float depth species;
model rtsratio = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;



****survival analysis
data b;
set sasuser.floatsurv;
if drywt = 0 then delete;

title1 'survival analysis';
proc mixed;
class float depth species;
model survival = depth species depth*species;
random float(depth);
lsmeans species depth species*depth / pdiff adjust = tukey;
run;
```

Appendix B. SAS code for statistical tests for the analysis of the grid study.

Analysis of mean in vegetation in relation to mean water quality

```
data nuta; set sasuser.vegnutavg;
proc sort;
by buffer month;

proc glm data = nuta;
model po4 no23 no2 no3 nh4 tss tvs tp tn chl_a = mean;
by buffer month;
run;
```

Analysis of mean in vegetation in relation to variability in water quality

```
data nuta; set sasuser.vegnutavg;
proc sort;
by buffer month;

proc glm data = nuta;
model stdpo4 stdno23 stdno2 stdno3 stdnh4 stdtss stdtvs stdtp stdtn
stdchl_a = mean;
by buffer month;
run;
```

Appendix C. Manuscript of the float study that was submitted to Estuaries in November 2005.

SHORT-TERM EXPOSURE TO A TURBID ENVIRONMENT: RESPONSE OF SPECIES AND IMPLICATIONS FOR RESTORATION

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ABSTRACT: Submersed aquatic macrophyte populations have been declining in estuarine and coastal systems throughout the world. Their decline has been attributed to higher inputs of nutrients and sediments to aquatic systems that increase turbidity and lower the amount of light available at leaf surfaces of submersed plants. Our goal was to explore the ability of aquatic macrophyte species to survive short-term (6 weeks) exposure to a turbid environment in a replicated field experiment. We planted five freshwater species in floats at three water depths (0.3, 0.5, 0.7m below the water surface) in a turbid estuary of Chesapeake Bay to test a) how survival, biomass accumulation and vegetative expansion are affected by species identity and b) whether depth of planting influences performance of species. Survival of *Vallisneria americana* and *Heteranthera dubia* was highest across all water depths. *Potamogeton nodosus* and *H. dubia* accumulated the most aboveground biomass whereas *V. americana* accumulated the highest root biomass. *Potamogeton perfoliatus* showed the greatest potential to expand vegetatively. Water depth had no effect on survival and growth, but negatively affected vegetative expansion in *P. perfoliatus* and induced *H. dubia* to develop longer shoots at greater depths. Not one species stood out as the best species to tolerate short-term exposure to a high turbidity environment. Our results draw attention to the importance of species identity in understanding the short-term response of submersed aquatic macrophyte beds to low light environments. They also suggest that restoration of a mix of species, including species that transplant well, grow fast, expand rapidly, and are morphologically plastic, are crucial considerations for enhancing restoration success and effectively restoring the health of freshwater estuarine habitats.

Introduction

Recent analyses (Ricciardi and Rasmussen 1999) and syntheses (Sala et al. 2000) project that global freshwater diversity will decrease at much faster rates than terrestrial systems. These unprecedented declines are attributed in large part to land-use change and concomitant increases in nutrients, sediments, and contaminants to aquatic systems (Kemp et al. 1983, Sala et al. 2000, Sand-Jensen et al. 2000). Submersed aquatic macrophytes are particularly sensitive to changes in nutrient and sediment loading, and population declines have been documented in North America (Stevenson and Confer 1978; Kemp et al. 1983; Orth and Moore 1983, 1984; Brush and Hilgartner 2000), Europe (Giesen et al. 1990; Sand-Jensen et al. 2000), and Australia (Cambridge and McComb 1984). However, not all species respond the same to environmental stress such that some species have become rare or extinct while others have invaded or increased in abundance (Sand-Jensen et al. 2000). Because submersed aquatic macrophyte beds provide many important ecosystem services, such as buffering shorelines, enhancing nutrient retention, and providing food and shelter to commercially important organisms (Carpenter and Lodge 1986; Wigand et al. 1997), their preservation and restoration has become a major management priority for freshwater, estuarine and coastal systems throughout the world (Batiuk et al. 1992; Yap 2000; Cho and Poirrier 2005). Understanding how different species respond to changes in environmental conditions will be important to develop effective conservation and restoration strategies and management priorities.

In estuarine environments, submersed aquatic macrophytes are predominantly, but not exclusively (Koch 2001), limited by light attenuation (Kd) through the water column (Batiuk et al. 1992; Dennison et al. 1993; Stevenson et al. 1993), which influences the depth distribution for submersed macrophytes (Meyers et al. 1943; Chambers and Kalff 1985). Species differ in

their minimum light requirements and maximum depth tolerances depending on their morphological and physiological adaptations to low light conditions and how well they can acclimate to changing light levels by changing their morphology or photosynthetic efficiency (Barko et al. 1982; Barko and Filbin 1983). For example, canopy-forming species, such as *Potamogeton perfoliatus* and *Stuckenia pectinata*, may better survive in turbid water than low-growing, meadow-forming species, such as *Vallisneria americana*, owing to a canopy-former's greater capacity to access light higher up in the water column (Titus and Adams 1979; Goldsborough and Kemp 1988; Sand-Jensen et al. 2000; Lougheed et al. 2001; Kemp et al. 2004). Relationships between habitat and the morphology of species are either identified with controlled experiments on single species (Dennison and Alberte 1982, 1986; Goldsborough and Kemp 1988; French and Moore 2003) or are based on observational data that correlate a variety of different species and their morphologies with the habitats in which they are abundant (Sand-Jensen et al. 2000; Lougheed et al. 2001). Survival and growth of species of different morphologies and growing within the same environment are generally not compared. However, such a study would identify communities and species that can withstand chronic or short-term changes in environmental conditions and would therefore highlight those ecosystems that are more resistant and resilient to short-term disturbances or long-term environmental change.

We conducted a replicated field experiment in 2002 that explored the ability of native submersed aquatic macrophytes to survive for a short period of time (6 weeks) in a highly turbid environment at Otter Point Creek, a freshwater tidal marsh in Chesapeake Bay. In addition to identifying differences among species, our study was motivated by the observation that most restoration efforts in freshwater portions of Chesapeake Bay focus on a single species, *Vallisneria americana*. The success of these restoration efforts has been mixed, leading us to

question whether the restoration of a diverse freshwater community may enhance restoration success in turbid environments. We monitored the survival, growth and vegetative expansion of five submersed aquatic macrophytes native to the Chesapeake Bay watershed growing at three water depths. We tested the hypothesis that species differ in their short-term tolerance to a turbid environment measured as survival, growth and expansion of individuals growing at different water depths. If differences existed, we tested the hypothesis that morphology was related to a species' tolerance to turbid conditions, where canopy-forming species perform better than meadow-forming species.

Materials and Methods

STUDY LOCATION

The study was conducted in the Maryland portion of Chesapeake Bay (39°27' N, 76°16' W) at Otter Point Creek (OPC), a tidal freshwater marsh managed by the National Estuarine Research Reserve (NERR) System. OPC supports 106ha of tidal freshwater wetlands. Maximum depth at the site is 1.5m and water depth fluctuates by 30cm during a tidal cycle. Median Secchi depth at the study location was 0.51m. Total suspended solids and chlorophyll *a* content of the water column increased from 14.4 to 20.5mg/L and from 9.88 to 26.95µg/mL, respectively, during the study period. Dissolved inorganic nitrogen and dissolved inorganic phosphorus remained relatively constant at 0.8mg/L and 0.06mg/L, respectively (NERR, *unpublished data*). Percent Light at Leaf (Batiuk et al. 2000; Kemp et al. 2004) was calculated using these parameters to evaluate light limitation at the three depths and at different times of the experiment (Fig. 1). The submersed aquatic plant community at OPC in summer 2002 listed from most abundant to least abundant was *Myriophyllum spicatum*, *Hydrilla verticillata*, *Ceratophyllum demersum*, *Elodea canadensis*, *Heteranthera dubia*, and *Potamogeton pusillus*.

H. verticillata was sampled at OPC for the first time in 2001 and started to spread rapidly in 2002.

EXPERIMENTAL DESIGN

A replicated field experiment was conducted to explore the ability of 5 species to survive, produce biomass and vegetatively expand at three water depths (0.3m, 0.5m, 0.7m). The five species (*Potamogeton nodosus*, *P. perfoliatus*, *Vallisneria americana*, *Heteranthera dubia*, and *Elodea canadensis*) were suspended by floats deployed at the three depths. A sixth species, *Najas guadalupensis*, did not transplant well into the experimental units and was therefore not used in the actual experiment. The species differ in their growth form, where *P. nodosus* produces a canopy of floating leaves at the water surface with some sparse submersed leaves; *P. perfoliatus*, *H. dubia*, and *E. canadensis* produce biomass throughout the water column but can form a canopy at the water surface through dense branching of upper stems; and *V. americana* is a rosette-forming species that forms "meadows" of varying heights.

Bare-root shoots of *Vallisneria americana* were harvested from outdoor grow-out tanks because shoot cuttings do not produce roots. The other four species were harvested as 8-12" unrooted cuttings from outdoor grow-out tanks. Grow–out tanks are used at OPC and elsewhere in the Chesapeake Bay region to mass propagate species for transplantation and environmental education purposes. All individuals were kept cool until they were transplanted into 10cm x 10cm x 10cm plastic planting pots within 24h after harvesting. Each planting pot was filled with topsoil and capped with sand. Individual shoots from the 5 species were transplanted into 81 planting pots per species and housed in nine 30cm x 50cm plastic planting trays (9 pots per tray; Fig. 2). One tray of each species was randomly placed into each of nine

floats (120cm x 180cm; Fig. 2). A tray containing pots without plants was also included in each float to fill out the space and to test for colonization from outside the experimental units. Once plants were transplanted into planting pots, put in trays and placed in the floats, the floats were left to rest on the marsh bottom at approximately 0.30m depth and allowed to acclimate and root prior to being deployed as floats one week later. All plants were alive at the time of float deployment. After deployment at OPC, three floats suspended the experimental units at 30cm below the water surface, three floats at 50cm and three floats at 70cm (Fig. 2). Water depth remained constant during the tidal cycle. Floats and their respective depth treatment were randomly placed within a grid consisting of three rows of three floats each. Floats were deployed July 31, 2002 and retrieved 6 weeks later on September 17, 2002.

Survival, vegetative expansion, and biomass production was measured at the end of the experiment. Length of above-ground tissues was measured to determine whether shoots were able to grow tall enough to gain access to the water surface. Survival was measured by counting the number of pots supporting above-ground macrophyte biomass. Vegetative expansion was measured by counting the number of shoots per pot for all pots that supported one or more shoots. Five pots from each species x depth treatment combination were then randomly selected for harvesting. If a selected pot did not contain above-ground tissue because the plant had died, another pot was randomly selected until n = 5 or until no more pots were available for harvesting. Harvested biomass was rinsed and separated into above and below ground plant biomass. The biomass was dried at 60^{o}C for 72 hours and then weighed to obtain a dry weight.

To effectively determine biomass accumulation over the course of the experiment, we initially collected more individuals than we intended to plant and measured length and wet and dry biomass on 15 randomly selected individuals per species. Total biomass accumulation, B_{tot},

per tray was calculated as $B_{tot} = B_e - B_i$, where B_i = average initial biomass and B_e = average ending biomass per experimental unit (tray containing pots). To account for inherent differences in the size of individuals per species, we calculated relative biomass accumulation as $B_{rel} = B_{tot} / B_i$. Relative changes in maximum shoot length, L_{rel}, was calculated the same way as B_{rel} but substituting length for biomass.

STATISTICAL ANALYSIS

Within the experimental design, individual plants were subsamples rather than replicates, so we used a mixed model analysis of variance (ANOVA) where trays (replicates) of each species were nested within each depth. We tested for among-group differences in species, depths, and their interaction. Our response variables were number of planted individuals that survived to the end of the experiment, total and relative biomass accumulation, total and relative above- and below-ground biomass accumulation, maximum length of shoots, and number of planted individuals that expanded vegetatively. All analyses were considered statistically significant at $P<0.05$.

Results

All species experienced some mortality; however, *H. dubia* suffered the least loss, followed by *V. americana*, *P. nodosus*, *P. perfoliatus*, and *E. canadensis* (ANOVA; $F_{4,24}=6.74$, $P<0.001$; Fig. 3a). In contrast, depth did not significantly affect survival of individuals (ANOVA; $F_{2,6}=2.74$, $P=0.14$) even though survival across all species tended to decrease with depth (Fig. 3a).

Heteranthera dubia and *V. americana* consistently produced higher total biomass (above- and belowground) than the other species (Fig. 3b). However, the biomass allocation was

markedly different among the species. Experimental units planted with *H. dubia* supported the greatest total above-ground biomass over all other species followed by *V. americana*. *P. perfoliatus*, *P. nodosus*, and *E. canadensis* (ANOVA; $F=55.0$; $P<0.001$). When comparing relative above ground biomass, *H dubia* and *P. nodosus* produced the greatest amounts followed by the remaining species (ANOVA; $F=32.3$; $P<0.001$; Fig 1c). In contrast, *V. americana* produced the greatest below-ground biomass followed by *H. dubia* and then the remaining three species (ANOVA; $F=89.8$; $P<0.001$; Fig 1d). Similar to survival results, water depth did not influence biomass accumulation or allocation. We could not compare relative below ground biomass because all species except for *V. americana* were planted as rootless cuttings (i.e., $B_i = 0$).

All pots were planted with only one shoot; thus, a count of shoots greater than one within each pot indicates that an individual is vegetatively expanding by producing more ramets. *E. canadensis* was excluded from statistical analyses on vegetative expansion because it did not produce additional shoots. Vegetative expansion was clearly influenced by species (ANOVA; $F_{3,153}=9.73$, $P<0.001$). *P. perfoliatus* expanded the most, followed by *P. nodosus*. Vegetative expansion did not differ between *H. dubia* and *V. americana* and was the lowest among the four species (Fig. 3f). An interaction between species and water depth was also observed (ANOVA; $F_{6,153}=2.51$, $P=0.02$), which was influenced by lower shoot production of *P. perfoliatus* at greater water depths.

A relative change in maximum shoot length shows whether a species' morphology is plastic enough to respond to an environmental gradient, in our case water depth. Species differed in shoot elongation (ANOVA; $F_{4,194}=282.07$, $P<0.001$), where *H. dubia* shoots increased significantly in length over the course of the study period compared to the other species (Fig. 3e).

In contrast, shoot length of the other four species decreased in length, especially for *P. perfoliatus* (Fig. 3e). Water depth also had an impact on shoot elongation (ANOVA; $F_{2,6}$=28.78, P<0.001), where average shoot length increased with water depth for *H. dubia*, but did not change for the other species (Fig. 3e). This resulted in a significant species by depth interaction (ANOVA; $F_{8,194}$=20.69, P<0.001; Fig. 3e).

Discussion

Species are adapted to a range of environmental conditions and should therefore differ in how they respond to environmental gradients. Indeed, our study shows that five submersed aquatic macrophyte species differed in their short-term response to a turbid estuarine environment. However, contrary to expectations, the identity of species had a greater effect on survival and biomass accumulation than did water depth.

SPECIES IDENTITY

Our study specifically focuses on the short-term effects of a light-limited (Fig. 1) but nutrient-rich estuarine environment on the survival, growth, and vegetative expansion of establishing individuals. Short-term increases in turbidity occur frequently and are common after storms, especially during spring high flow events and fall hurricanes, when increased sediment loads are carried to estuaries or are resuspended. If species respond differently to such conditions, then richness and abundance of submersed aquatic macrophyte beds may be driven by these short-term changes in light attenuation (Dennison and Alberte 1885; Zimmerman et al. 1995; Moore et al. 1996, 1997; Moore and Wetzel 2000; Cabello-Pasini 2002). Survival of *Heteranthera dubia* and *Vallisneria americana* were the highest of the five species that we compared, suggesting that submersed aquatic macrophyte beds supporting these two species may

be more resistant to short-term decreases in light attenuation. Our experiment is admittedly limited in describing long-term population dynamics which are described elsewhere (Sand-Jensen et al. 2000) and suggest that fast growing canopy-forming species may be favored in turbid environments. However, we found no evidence to suggest that morphology was related to a species' tolerance to turbid conditions. The meadow-forming species, *V. americana*, performed just as well and sometimes better than some of the canopy-forming species. Likewise, Johnson and Ostrofsky (2004) showed that deep sites were dominated by *V. americana* and shallow sites by *H. dubia*, which is opposite from what one might expect from a meadow-forming and a canopy-forming species. Sand-Jensen et al. (2000) developed a morphological index (e.g., floating leaves, plant height) to correlate morphology with changes in species abundance patterns in eutrophic lakes. They found that morphological indices were not adequate in explaining systematic alterations of species abundances towards a taller growth form in turbid eutrophic conditions. Thus, morphology appears to be a poor indicator of a species' tolerance to turbid conditions or deeper water.

Restoration efforts in freshwater portions of Chesapeake Bay focus predominantly on planting *Vallisneria americana*. This is an excellent species for submersed aquatic macrophyte bed restoration, not only because it is easily propagated and of high wildlife value, but also because it can acclimate to lower light conditions (French and Moore 2003). *V. americana* had one of the highest survival rates in our experiment (Fig. 3a). It also produced the highest root biomass and root/shoot ratio, which allows the species greater access to sediment nutrients and to anchor the substrate and decrease resuspension of sediments. Our results, however, may have been in part confounded by *V. americana* having been planted with an intact root system rather

than as cuttings. Nevertheless, *V. americana* is known for producing a large root system (Wigand et al. 1997) and is clearly a good candidate species for freshwater habitat restoration.

Even though *V. americana* performed well, other species performed as well, if not better. *Heteranthera dubia* survival was the highest of all species and, with *P. nodosus*, accumulated the highest relative above-ground biomass. In contrast, *P. perfoliatus* survival and biomass accumulation was low; however, the species produced more new stems over the study period than any of the other species, especially at the shallow water depth. Vegetative expansion ensures that restoration efforts create healthy beds that expand and colonize new areas over time. Thus, low survival was compensated for by greater shoot production in *P. perfoliatus*. This phenomenon has been observed in other studies as well (Neundorfer and Kemp 1993; Sturgis and Murray 1997), where transplanted shoots frequently died, but were replaced by numerous new ramets. *Elodea canadensis* was clearly a poorly performing species on all accounts; this result was unexpected considering that the environmental conditions at OPC clearly favor *Hydrilla verticillata*, a close relative.

Our results suggest that single-species restoration may not be the best strategy for enhancing restoration success. For example, focusing on the restoration of *V. americana* at Otter Point Creek would enhance survival and provide structure to the sediments; however, it would not develop as much above ground structure or expand as quickly as some of the other species. In contrast, restoration of *H. dubia* would enhance survival and provide above-ground structure but would not expand as quickly as *P. perfoliatus* or bind the sediments as well as *V. americana*. Planting a mix of species may increase the chances of a successful restoration by introducing species with different responses to environmental conditions that can change through time. This tactic increases the response diversity of the system (Elmqvist et al. 2003) and helps to increase

the overall system resilience to maintain integrity in the face of a changing environment. The results also suggest that preliminary trials are important to exclude those species from the potential species pool, in our case *E. canadensis*, that would not be favored by the environmental conditions at the restoration site, or that do not transplant well, in our case *Najas guadalupensis*.

PHENOTYPIC PLASTICITY

Freshwater macrophyte species have the capacity to change their morphology to respond to environmental variability ("phenotypic plasticity"; Idestam-Alquist and Kautsky 1995; Barrat-Segretain 2001; Pilon and Santamaria 2002; Cronin and Lodge 2003; Dorken and Barrett 2004). For example, in field manipulation experiments (Cronin and Lodge 2003), internode length of shoots of *Potamogeton amplifolius* was longer under shaded conditions. The species allocated relatively more resources to shoots than roots when light was limiting as witnessed by 40% lower root/shoot ratios under low light conditions compared to a high light environment (Cronin and Lodge 2003). Similarly, a laboratory experiment (Pilon and Santamaria 2002) observed that *Stuckenia pectinata* grew longer stems when the species was grown under low light conditions. French and Moore (2003) showed that *V. americana* increased leaf length and width under low light conditions, and Goldsborough and Kemp (1988) observed similar changes in *P. perfoliatus*. The height of the water column above the experimental planting units may also affect elongation of shoots irrespective of light attenuation (Kemp et al. 2004). In our study, maximum length of shoots increased substantially with increasing depth, but only in one species, *Heteranthera dubia* (Fig. 3e). Since biomass allocation to shoots and roots did not perceptibly change with depth, we can conclude that *H. dubia* is the species with the greatest capacity to respond to changes in light and/or water depth by growing stems and leaves higher in

the water column where light intensity is greater. Indeed, shoot length was positively related to above ground biomass accumulation ($r=0.65$; $P<0.0001$), suggesting that a longer stem may allow greater photosynthate production and hence higher biomass accumulation.

WATER DEPTH

Contrary to expectations, we did not observe an effect of water depth or an interaction between depth and species identity on survival or biomass accumulation. Our findings contrast with an observational study conducted by Van den Berg et al. (2003) who documented that species cover and occurrence decreased with depth for some species, whereas other species showed an optimum response to water depth. We did observe, however, that vegetative expansion was affected by species identity and depth, and an interaction between species identity and depth, that was driven by *P. perfoliatus*, a species known for its tolerance of turbid conditions (Goldsborough and Kemp 1988; Lehmann et al. 1997). An overall lack of a survival and growth response to the depth gradient may have three alternative explanations: (1) Only *H. dubia* and *P. nodosus* accumulated aboveground biomass over the study period. The other species either maintained or lost biomass (Fig. 3c). Similarly, only *H. dubia* increased in length while shoot length of the other species decreased (Fig. 3e). Water clarity values (see Study Location description) and light level at the leaf surface (Fig. 1) were generally below restoration criteria for submersed aquatic macrophytes (Batiuk et al. 1992), especially for the deepest treatment at 0.7m. Thus, three of the five species may have been stressed by the low light environment even at the shallow water depth and may not have been able to respond to increasing water levels. However, plants had an advantage of initial height from having been transplanted. Survival was higher than 50% for all species at all water depths, casting doubt on

the general validity of this explanation. Alternatively, (2) species tolerances to turbid conditions and low irradiance may not have encompassed the entire depth gradient, i.e., the water depth gradient may have been too narrow to induce a detectable species response. None of the species could have theoretically survived at a depth beyond their physiological limit; this depth was clearly not reached in our experiment. Nevertheless, the deepest water depth treatment at 0.7m below the water surface provided only a marginal light environment during the entire study period (Fig. 1). Thus, the survival, growth, and vegetative response we observed even in the deep treatment attests to the wide tolerance levels of the five species. Finally, (3) the study may not have been long enough (6 weeks) for some of the species to show a significant response to the depth gradient. The three alternative explanations are all plausible; however, we can confidently conclude that for the range of conditions at Otter Point Creek and during plant establishment, water depth did not influence survival and growth of plants as much as species identity.

MANAGEMENT IMPLICATIONS

Freshwater habitats support a diverse group of submersed aquatic macrophytes, but restoration projects in the freshwater portions of Chesapeake Bay generally focus on restoring single species that can be relatively easily propagated. Single species restoration may be the economically and logistically most feasible strategy. However, no single species is superior under all conditions. Since water quality, climate, and turbidity may change from year to year, long-term restoration costs may actually be lower for multiple species restorations because of their increased likelihood to deal with changing environments. This may increase the resistance and resilience of SAV communities to environmental stress and may speed establishment and recovery. Thus restoration strategies in freshwater portions of estuaries may need to combine

assessment of habitat suitability with identification of species combinations that are resistant to the common environmental perturbation of the area. Such a restoration strategy will enhance restoration success of submersed aquatic macrophyte beds, increase the long-term sustainability of submersed macrophyte beds and enhance the health of estuaries worldwide.

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Legend

Fig. 1. Percent Light at Leaf (Batiuk et al. 2000) at the three experimental water depth at the beginning (August 7, 2002), middle (August 28, 2002) and end (September 5, 2002) of the experiment.

Fig. 2. Experimental set-up of the field floats. Floats were suspended at three water depths (0.3m, 0.5m, 0.7m). Each float received 6 trays, one per species and one unplanted. Each tray contained 9 planted pots. Placement of floats and trays were random.

Fig. 3. The influence of species identity (*Elodea canadensis*, *Heteranthera dubia*, *Potamogeton nodosus*, *P. perfoliatus*, *Vallisneria americana*) and water depth on % survival (A), total biomass accumulation (B), relative accumulation of aboveground biomass (C), below-ground biomass accumulation (D), maximum length of stem (E), and number of ramets (F).

Figure 1

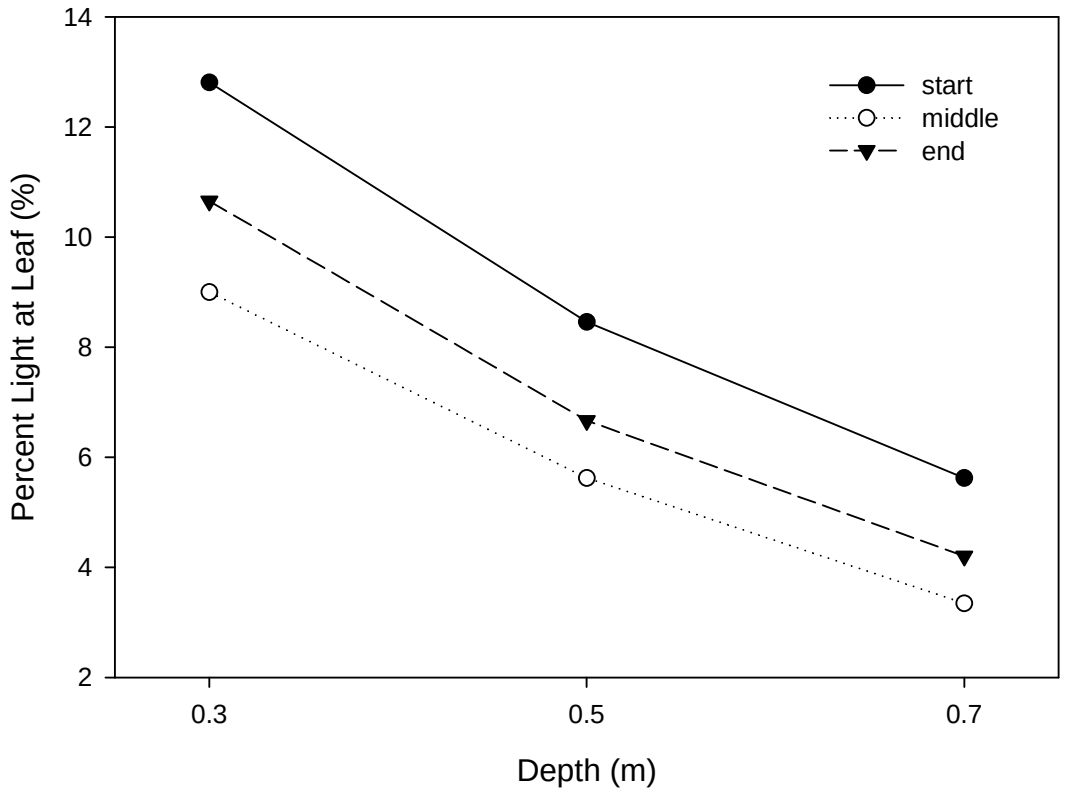

14
12
10
8
6
4
2
Percent Light at Leaf (%)
0.3
0.5
0.7
Depth (m)
start
middle
end

Figure 2.

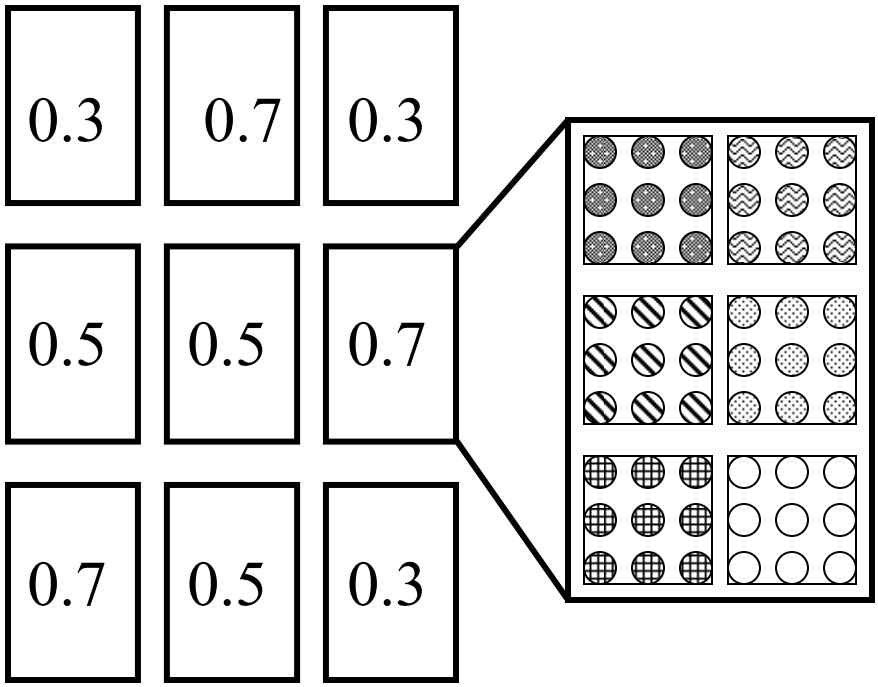
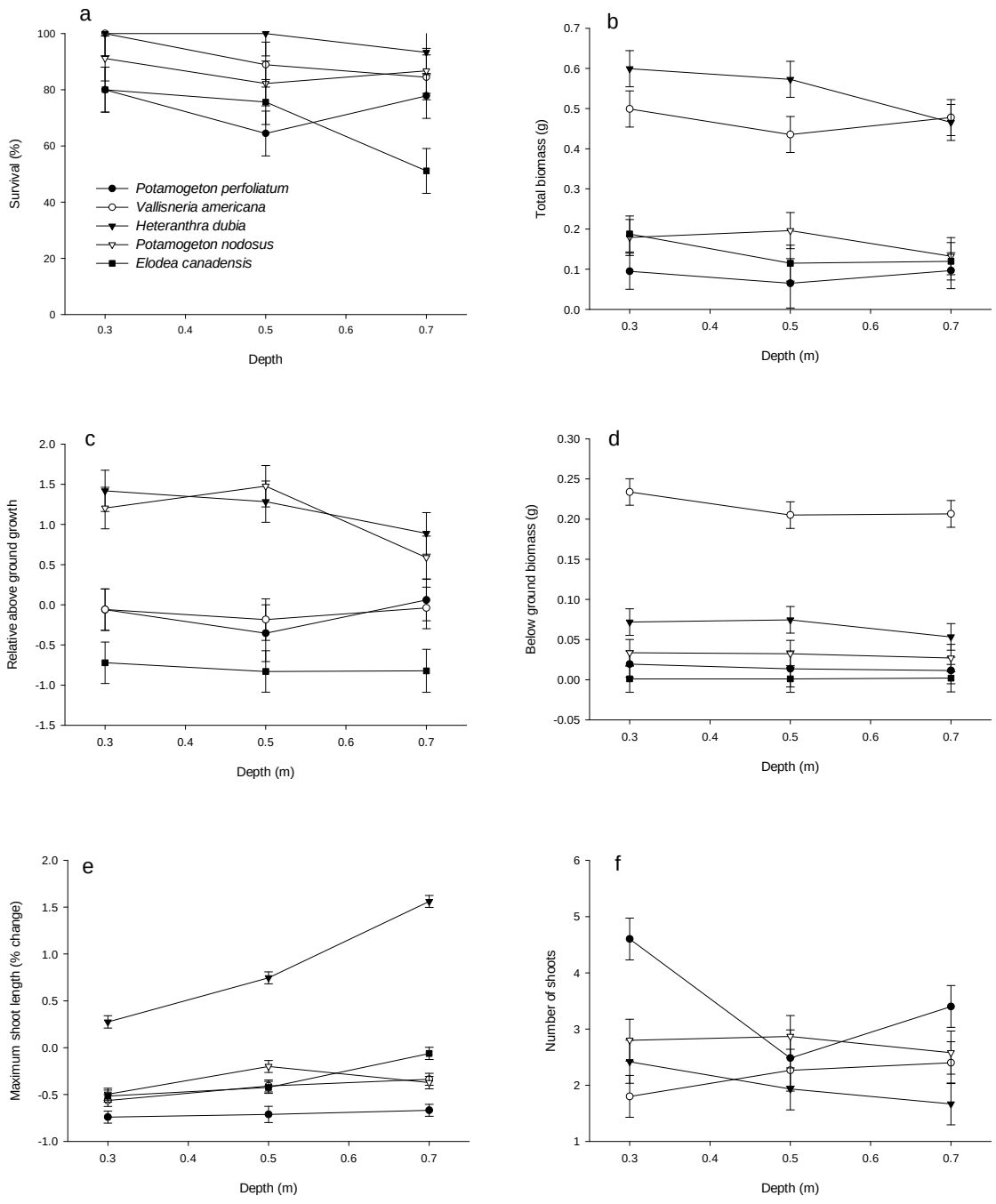


Figure 3.


a
Survival (%)
Depth
Potamogeton perfoliatum
Vallisneria americana
Heteranthra dubia
Potamogeton nodosus
Elodea canadensis
b
Total biomass (g)
Depth (m)
c
Relative above ground growth
Depth (m)
d
Below ground biomass (g)
Depth (m)
e
Maximum shoot length (% change)
Depth (m)
f
Number of shoots
Depth (m)