

2016

## Effects of sediment and salinity on the growth and competitive abilities of three submersed macrophytes

Erin C. Shields  
*Virginia Institute of Marine Science*

Ken Moore

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Aquaculture and Fisheries Commons](#)

---

### Recommended Citation

Shields, Erin C. and Moore, Ken, "Effects of sediment and salinity on the growth and competitive abilities of three submersed macrophytes" (2016). *VIMS Articles*. 798.  
<https://scholarworks.wm.edu/vimsarticles/798>

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact [scholarworks@wm.edu](mailto:scholarworks@wm.edu).

1

2

3

4 Effects of sediment and salinity on the growth and competitive abilities of three  
5 submersed macrophytes

6

7

8

9

Erin C. Shields<sup>1\*</sup> and Kenneth A. Moore<sup>1</sup>

10

11

12

13

14 <sup>1</sup>Virginia Institute of Marine Science, School of Marine Science, College of William and  
15 Mary, 1375 Greate Road, Gloucester Point, Virginia 23062-1346, USA

16

[eshields@vims.edu](mailto:eshields@vims.edu); [moore@vims.edu](mailto:moore@vims.edu)

17

18

19

20

\*Corresponding author: [eshields@vims.edu](mailto:eshields@vims.edu), ph: 804-684-7702

21

**22 Abstract**

23           Submersed macrophytes are generally found in multispecies beds, with the  
24 dominance of individual species varying in both space and time. In estuarine  
25 environments, these plants can grow across a range of environmental conditions which  
26 may alter species interactions. Three species common to the Chesapeake Bay region,  
27 *Vallisneria americana* (wild celery), *Heteranthera dubia* (water stargrass), and *Stuckenia*  
28 *pectinata* (sago pondweed), were planted in a microcosm designed to test their growth  
29 and interactions (relative yielding) under a range of conditions of salinity (0, 5, or 10),  
30 sediment type (mud or sand), and species combinations. *H. dubia* was most sensitive to  
31 elevated salinity, while sediment type impacted only *V. americana*, performing better in  
32 mud compared with sand. *V. americana* and *H. dubia* were strong competitors,  
33 overyielding in many treatments when grown in mixture, while *S. pectinata* never  
34 overyielded and frequently underyielded. Interspecific competition was only strong  
35 between *H. dubia* and *S. pectinata* under 0 salinity, regardless of sediment type. *V.*  
36 *americana* on the other hand, showed strong interspecific competition with *S. pectinata*  
37 across multiple salinity and sediment types, indicating that this species is able to compete  
38 well across a wider range of environmental conditions. Our results suggest that *H. dubia*  
39 and *V. americana* are strong candidates for multi-species restoration, as positive  
40 interactions were observed when grown together. This measure of complementarity  
41 provides evidence for increased mixed bed plant performance under environmental  
42 conditions that would typically be more stressful to each growing alone.

43 Key words: submersed aquatic vegetation; complementarity; competition; restoration;  
44 Chesapeake Bay

45

## 46 **1. Introduction**

47 Submersed aquatic vegetation (SAV) growing in low-salinity and freshwater  
48 systems are typically not found in monotypic communities, but in multispecies beds, with  
49 the dominance of individual species varying in both space and time (Moore et al., 2000;  
50 Chambers et al., 2008; Orth et al., 2009; Arthaud et al., 2013). This suggests that there is  
51 a range of suitable environmental conditions among the diversity of species in these beds.  
52 This may allow for greater natural survival or restoration under a wider range of  
53 environmental conditions when compared to monotypic communities.

54 Changing environmental conditions may alter the competitive advantage of one  
55 species over another, because each species may have different requirements for their  
56 growth or tolerate a different range of conditions. Within an estuarine system such as the  
57 Chesapeake Bay, parameters related to light, temperature, nutrients, salinity, and  
58 sediment may all play roles in the SAV community dynamics (Kemp et al., 2004).  
59 Historically, light availability has been a primary focus when studying SAV habitat  
60 requirements (Carter and Rybicki, 1990; Korschgen et al., 1997; Moore et al., 1997;  
61 Moore and Wetzel, 2000). Salinity and sediment requirements have not received as  
62 much attention, but are likely to be very important in estuarine environments due to their  
63 variability in both space and time and their differing effects on individual SAV species.

64 SAV communities in the Chesapeake Bay are typically distributed by salinity,  
65 with *Zostera marina* and *Ruppia maritima* occurring in meso and polyhaline regions, and  
66 a variety of freshwater mixed species occurring in oligohaline and tidal fresh regions.  
67 Within the oligohaline and tidal fresh regions, over 15 species of SAV have been  
68 identified (Moore et al., 2000). Many of these species have been shown to have differing

69 salinity tolerances (Teeter, 1965; Haller et al., 1974; Kantrud, 1990; Twilley and Barko,  
70 1990; French and Moore, 2003; Bergstrom et al., 2006; Frazer et al., 2006) as well as a  
71 range of suitable sediment conditions for their growth (Barko and Smart, 1983; Hoover,  
72 1984; Barko and Smart, 1986; Chambers and Prepas, 1990; Batiuk et al., 2000; Jarvis and  
73 Moore, 2008).

74         It is not well understood how different local sediment composition and salinity  
75 levels might affect SAV bed growth or how these conditions might affect SAV  
76 restoration success when species are planted both singly and in competition with other  
77 species. Typically, restoration of SAV has been conducted using a single species  
78 approach, while the potential positive interactions of planting multiple species together  
79 has generally been overlooked (Halpern et al., 2007). Previous work has determined that  
80 there is considerable potential for SAV restoration in the major Chesapeake Bay  
81 tributaries including the James River using both whole plants and seeds (Moore and  
82 Jarvis, 2007; Moore et al., 2010). It is still poorly known if mixed plantings would be  
83 more successful by providing a broader range of bed tolerance when subject to varying  
84 environmental conditions. It has been reported that in many regions experiencing re-  
85 growth of SAV that *Vallisneria americana* can be found growing in combination with  
86 other SAV, including *Hydrilla verticillata*, *Myriophyllum spicatum*, *Heteranthera dubia*,  
87 and *Ceratophyllum demersum* (Moore et al., 2000; Rybicki and Landwehr, 2007). This  
88 suggests that mixed plantings may improve restoration success through complementarity  
89 among species in resource utilization.

90         Plants exhibit positive complementarity when their combined performance is  
91 greater than what would be expected from them individually (Loreau et al., 2001). This

92 is due to resource partitioning and facilitative interactions, and has been observed in SAV  
93 communities (Salo et al., 2009; Gustafsson and Boström, 2011; Hao et al., 2013). On the  
94 other hand, multi-species assemblages may not increase overall productivity, bed  
95 resilience or restoration success due to interspecific competition, which has been shown  
96 to be strong in both temperate and tropical SAV communities (Titus and Stephens, 1983;  
97 Moen and Cohen, 1989; Van et al., 1999; Spencer and Ksander, 2000; Barrat-Segretain  
98 and Elger, 2004).

99         Here we present results from a microcosm that was designed to test the growth  
100 and competitive abilities of low-salinity and freshwater SAV under varying conditions of  
101 salinity and sediment type. We address the following research questions: a) What effect  
102 will different salinity and sediment types have on plants growing separately in  
103 monoculture? b) How will the different treatments alter species interactions when plants  
104 are grown in combination? Our goals were to examine the degrees of competition and  
105 complementarity among three different species exposed to variable environmental  
106 conditions, and to improve the site selection criteria and success of restoration efforts of  
107 freshwater and low-salinity tolerant SAV.

## 108 **2. Methods**

109         An outdoor microcosm was used for the experiment which was conducted in the  
110 summer and located at the Virginia Institute of Marine Science, Gloucester Point,  
111 Virginia (37°14.8'N, 76°30.3'W). 20-liter white translucent containers with a height of  
112 37 cm and diameter of 30 cm were used for each individual experimental unit, and all the  
113 containers were housed in a shallow nursery tank approximately 8.5 m x 3 x 0.5 m filled  
114 with freshwater to allow for consistent temperatures among the experimental units. Three

115 main treatments were established. Sediment type consisted of two levels (mud and sand),  
116 salinity consisted of three levels (0, 5, 10) and species combinations included all  
117 combinations of three species (three monocultures, three bicultures, one triculture) for a  
118 total of 42 treatments. Each treatment was replicated three times for a total of 126  
119 experimental units. *Heteranthera dubia* (water stargrass) and *Vallisneria americana* (wild  
120 celery) plants were taken from adjacent outdoor nursery tanks grown from local  
121 Chesapeake Bay stock, and *Stuckenia pectinata* (sago pondweed) was harvested from two  
122 outdoor ponds located on the Chesapeake Bay at the University of Maryland Center for  
123 Environmental Science Horn Point Laboratory, Cambridge, Maryland (38°35.5'N,  
124 76°08.8'W). These were brought back to Virginia and planted in an outdoor SAV  
125 restoration nursery pond next to other ponds containing the other species. Prior to the  
126 start of the experiment, oligohaline estuarine sediment was collected from the  
127 Chickahominy River, Virginia. Sediments were obtained from two sites where SAV  
128 occur, with target organic content of > 8 % for the muddy site (37°17.5'N, 76°51.8'W)  
129 and < 2 % for the sandy site (37°15.5'N, 76°52.4'W). At the time of collection, percent  
130 organic content was determined through loss on ignition (Erftemeijer and Koch, 2001).  
131  $\text{NH}_4^+$  concentrations were determined using a Lachat auto analyzer (Liao, 2001, revised  
132 2002) and  $\text{PO}_4^{3-}$  concentrations were determined spectrophotometrically at 880nm  
133 (VIMS, 1991).

134 Sediment was homogenized, and each container was filled approximately 10 cm  
135 deep with sediment, and then filled with filtered freshwater. Plants were sorted within  
136 species to a similar length (*V. americana* 16.8 cm  $\pm$  1.2; *H. dubia* 17.6 cm  $\pm$  1.4; *S.*  
137 *pectinata* 44.3 cm  $\pm$  2.2). A subset of 30 plants from each species was sampled for dry

138 weight measurements of above and belowground biomass (*V. americana* 0.068 gDW; *H.*  
139 *dubia* 0.042 gDW; *S. pectinata* 0.074 gDW per plant). A total of 12 plants were planted  
140 in each container in a replacement series design. With this design, the total number of  
141 plants in each container was kept constant, but the number of plants per species was  
142 altered according to their species combination treatment. For example, in biculture, six  
143 plants of each species were used, and in triculture four plants of each species were used.  
144 This planting density was chosen based on a literature review of densities of natural plant  
145 populations of these species (Moen and Cohen, 1989; Van et al., 1999; Jarvis and Moore,  
146 2008).

147       After planting, each container was placed in the tank in a randomized design. The  
148 tank was filled with freshwater, and a drain pipe ensured the water level in the tank never  
149 rose above the rim of the containers. This served as a water bath to help keep temperature  
150 constant in the containers. The containers were allowed to sit for two days to allow  
151 sediment settlement, and then individual air bubblers and aquarium foam/floss, carbon,  
152 and zeolite filters were connected to each container. These filters were routinely rinsed  
153 and were replaced halfway through the experiment. Clear plexiglass sheets were placed  
154 over each container to minimize evaporation and to protect the containers from rain. A  
155 neutral density (50% light reduction) shade cloth was placed over the top of the tank to  
156 minimize algal growth and to better mimic natural field light availability.

157       The experiment started on 17-June and ran for 11 weeks. Plants were kept in  
158 freshwater until 10-July, when salinity treatments began, in order to allow the plants to  
159 recover from any transplant stress. Salinity was elevated in increments over the course of  
160 the next 19 days using Forty Fathoms© Crystal Sea® salt. This was done to parallel rates



161 of salinity change which have been observed under natural field conditions in the region  
162 (Shields et al., 2012). The 5 salinity treatments were increased by 1 and the 10 salinity  
163 treatments were increased by 2 every 3-4 days during the 19 days until the final  
164 concentrations were reached. Salinity was monitored every 3-4 days during this period  
165 using a handheld YSI 6000 (Yellow Springs Instrument, Inc.). Additionally, temperature,  
166 dissolved oxygen, and pH were also monitored biweekly throughout the experiment.

167 At the end of the experiment prior to harvesting, sediment was sampled for  
168 percent organic content and  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$ . All plant material was harvested and  
169 brought to the lab for measurements of maximum shoot length, shoot density, and above  
170 and belowground biomass. Biomass was determined by drying the plants at  $60^\circ\text{C}$  until a  
171 constant weight was obtained.

## 172 *2.1. Data Analyses*

173 Relative growth rate (RGR) was determined based on natural logarithm  
174 transformed dry weights of total biomass (above and below ground). Initial dry weights  
175 were subtracted from final dry weights and divided by the length in days of the  
176 experiment ( $\text{gdw gdw}^{-1} \text{ day}^{-1}$ ). Multivariate analyses of variance (MANOVA) were run  
177 for all species separately in monoculture for RGR, density, and length, with salinity and  
178 sediment as fixed factors. Where appropriate, univariate ANOVAs were then used to  
179 analyze treatment effects on individual response variables. Tukey's HSD tests were run  
180 when significant differences were found. Before testing, residual plots and QQ plots  
181 were observed to ensure normality and homoscedasticity.

182 Relative yield (RY) and relative yield totals (RYT) were calculated for RGR  
183 based on Hooper (1998) and Engelhardt and Ritchie (2002) in order to analyze the degree

184 of competition and complementarity among species in the different treatments. To  
185 calculate an individual RY, the mean RGR of a species in monoculture was calculated  
186 individually for all treatments, and this number was used as the expected mean. Next, the  
187 RGR of that species in mixture was calculated by accounting for differences in initial  
188 planting densities; i.e. biomass in biculture was multiplied by 2, and by 3 in triculture.  
189 This number was then divided by the expected mean of the species in monoculture to  
190 calculate the RY. Interspecific competition was strong when one species significantly  
191 overyielded while another underyielded in mixture. Relative yield totals (RYT) were used  
192 to define species complementarity, and were calculated by averaging the RYs of all the  
193 species in each treatment. When  $RYT > 1$ , species were considered complementary as  
194 long as each had an individual  $RY > 1$ . One-sided 95% confidence intervals were  
195 performed for all RYs and RYTs to test if the value was significantly different from 1.  
196 All data analyses were performed in RStudio (R Core Team, 2012).

### 197 **3. Results**

#### 198 *3.1. Environmental Conditions*

199 Temperature, pH and dissolved oxygen remained consistent throughout the experiment  
200 with no differences among treatments or planting combinations observed. Mean  
201 temperature during the dates measured ranged from 26.3 °C to 28.6 °C, mean pH ranged  
202 from 8.40 to 8.75, and mean dissolved oxygen ranged from 7.37 mg l<sup>-1</sup> to 8.46 mg l<sup>-1</sup>.  
203 Mean salinity concentrations in the containers prior to their increase were constant for all  
204 three salinity treatments at 0.23. After the increases were performed, the target  
205 concentrations were met, with mean salinity values always within 0.5 of targets. The  
206 mud treatments had higher mean organic content, higher NH<sub>4</sub><sup>+</sup> concentrations, and lower

207  $\text{PO}_4^{3-}$  concentrations compared with the sand treatments, both at the beginning and at the  
208 end of the experiment (Table 1).

### 209 3.2. Individual species response in monocultures

210 Salinity had significant effects on the performance of *H. dubia*, but not sediment  
211 (Fig. 1, Table 2). Salinity impacted both RGR and density, with 0 and 5 treatments  
212 greater than 10 for both parameters. Length showed no significant response. *S. pectinata*  
213 was not significantly impacted by sediment or salinity (Fig. 1, Table 2). For *V.*  
214 *americana*, sediment showed significant effects (Table 2), with plants growing taller in  
215 mud compared with sand, while RGR and density were unaffected (Fig. 1).

### 216 3.3. Relative Yield

217 *V. americana* and *H. dubia* were the most competitive species, significantly  
218 overyielding in 6 and 7, respectively, of the possible 18 treatments, and never  
219 underyielding (Fig. 2). *S. pectinata* was a weak competitor, never overyielding and  
220 significantly underyielding in 8 of the treatments (Fig. 2).

221 Interspecific competition was strong in five of the treatments (Fig. 2). With *H.*  
222 *dubia*, significant overyielding paired with significant *S. pectinata* underyielding only  
223 occurred in 0 salinity treatments, regardless of sediment type. On the other hand,  
224 significant *V. americana* overyielding paired with significant *S. pectinata* underyielding  
225 occurred across a variety of salinity and sediment types (Fig. 2). Complementarity  
226 occurred in both the *V. americana/H. dubia* biculture and triculture grown in sand in 10  
227 salinity. Here,  $\text{RYT} > 1$ , and the individual RYs for *V. americana* and *H. dubia* were  $> 1$   
228 in both the biculture and triculture. *S. pectinata* remained unchanged in the triculture  
229 with a  $\text{RY} = 1$ .

230 Salinity appeared to play a different role in the competitive ability of *H. dubia*  
231 compared with *V. americana*. *H. dubia* significantly overyielded in mixture primarily in 0  
232 salinity treatments. On the other hand, the majority of cases in which *V. americana*  
233 significantly overyielded were in the 10 salinity treatments (Fig. 2).

#### 234 **4. Discussion**

235 The three species studied here demonstrated the wide range of tolerances and  
236 competitive abilities which have been found among low-salinity SAV. All survived and  
237 grew throughout the summer-long experiment. When each was grown in monoculture,  
238 without competition from the other species, there were no interactions observed in the  
239 species growth responses to the levels of salinity and sediment tested here. This suggests  
240 that the factors of sediment type and salinity may be affecting the plants through different  
241 ways. For example, sediment type may be influencing the rates of nutrient uptake (Barko  
242 et al., 1991), while salinity levels may be influencing plant respiration or photosynthesis  
243 (French and Moore, 2003).

244 Both *S. pectinata* and *H. dubia* performed equally as well in muddy and sandy  
245 sediment types, and *V. americana* and *S. pectinata* grew well across a range of salinities.  
246 However, *H. dubia* growth was reduced in the 10 salinity treatment compared to lower  
247 salinity levels, and *V. americana* growth was reduced in the sand treatment in comparison  
248 to its growth in mud. Morphologically, each species responded differently to these  
249 stressful conditions. *H. dubia*'s low overall growth rate under high salinity was driven by  
250 a decrease in clonal reproduction, with shoot lengths remaining unchanged among  
251 treatments. On the other hand, *V. americana*'s reduced overall growth in sand was driven  
252 by a decline in shoot elongation, while clonal reproduction did not change across

253 sediment type. These changes in growth morphology may have important implications  
254 for their competitive abilities or responses to other environmental stressors, such as  
255 reduced light availability where an elongated shoot length could be important, or physical  
256 disruption where rapid clonal spread may be necessary.

257         While single species responses to environmental conditions are important,  
258 evidence exists for both competition and environmental conditions as drivers for species  
259 interactions and distributions in aquatic macrophyte communities (Anderson and Kalff,  
260 1986; Chambers and Prepas, 1990; McCreary, 1991; Gopal and Goel, 1993). Our study  
261 showed examples of both, with interspecific competition being the driving force in some  
262 cases, and salinity stress in others. Both *V. americana* and *H. dubia* were stronger  
263 competitors than *S. pectinata*, though the degree of competition varied with  
264 environmental condition. *V. americana* was able to outcompete *S. pectinata* across all  
265 sediment and salinity treatments, while *H. dubia* typically only outcompeted in 0 salinity.  
266 *S. pectinata* proved to be the least competitive species, as it significantly underyielded in  
267 mixtures in many of the multi-species treatments, and never overyielded. Engelhardt and  
268 Ritchie (2002) found opposite results in their experiment, where *S. pectinata* was the  
269 dominant species, overyielding in all mixed plantings. Their experiment differed from  
270 ours in that they did not include *V. americana* or *H. dubia*, which appear to be much  
271 stronger competitors than the other species they used (*Potamogeton nodosus*,  
272 *Potamogeton crispus*, *Zannichellia palustris*). This illustrates the broad range of  
273 competitive abilities that may exist among low-salinity SAV communities.

274         Competitive abilities of plants have been shown to vary along environmental  
275 gradients, but how the intensity of competition changes with increasing abiotic stress has

276 proven inconsistent (Gaudet and Keddy, 1995; Greiner La Peyre et al., 2001; Hooper and  
277 Dukes, 2004; Elmendorf and Moore, 2007). For *H. dubia*, our results provide evidence  
278 that interspecific competition is stronger when abiotic stress is less. This species was  
279 typically a strong competitor at 0 salinity, which was the least stressful for this species.  
280 As salinity increased, the degree of competition decreased, as the stress of salinity  
281 became the driving factor affecting its performance. *V. americana* on the other hand, was  
282 able to outcompete *S. pectinata* under a variety of sediment and salinity conditions,  
283 indicating that it is able to outcompete weaker competitors under a wider range of  
284 conditions than *H. dubia*.

285       When grown separately in monoculture, *H. dubia* did not perform well in the 10  
286 salinity treatment, and *V. americana* did not perform well in the sand treatment, however  
287 when grown together both in biculture and in triculture, these species exhibited positive  
288 interactions. They performed relatively better in mixture than they did by themselves,  
289 allowing them to perform well in what would otherwise be stressful conditions. This  
290 suggests that these two species are complementary in their resource use and under  
291 stressful abiotic conditions this allows them to individually access resources, such as light  
292 or nutrients, which would be more limiting to each when growing monotypically  
293 (Hooper, 1998; Spehn et al., 2000). Morphologically, each species responded differently  
294 to these stressful conditions when grown in monoculture, as *H. dubia* decreased clonal  
295 reproduction while *V. americana* decreased shoot elongation. When grown in mixture in  
296 sand and 10 salinity, *H. dubia*'s low shoot density and *V. americana*'s stunted shoot  
297 height may have worked in complementary ways, allowing maximum resource

298 allocation, though the exact mechanism behind this is beyond the scope of this  
299 experiment.

300         This work was done in an experimental setting in relatively small containers  
301 rather than a field setting, in order to control and be able to more precisely manipulate the  
302 different treatment combinations and to more accurately measure the species interactions.  
303 In these types of confined spaces, interspecific competition may be stronger and positive  
304 plant interactions weaker than what would be observed in a natural field setting.  
305 Previous studies have indeed demonstrated the importance of spatial scale in aquatic  
306 plant communities, with competition dominating at smaller “patch” scales, and positive  
307 facilitative interactions dominating at “bed” scales (van de Koppel et al., 2006; Hengst et  
308 al., 2010). The fact that positive plant interactions were measured between *H. dubia* and  
309 *V. americana* even in a microcosm setting, provides evidence for these interactions  
310 perhaps becoming even stronger at the larger bed scale in a natural field setting, and  
311 provides a framework for future larger scale studies.

312         Results from this study can be used to improve restoration techniques for these  
313 species and other similar low-salinity SAV in estuarine environments. Here we show that  
314 species typically found growing together in multispecies beds respond differently to  
315 changing environmental conditions, so using generalized SAV habitat requirements for  
316 restoration targets may have limited success in diverse communities. Individual salinity  
317 tolerances should especially be considered, and in estuarine areas where higher salinities  
318 (5-10) can be expected occasionally, of the species studied here, *V. americana* should be  
319 considered as a primary restoration species. All three species tolerated a broad range of  
320 sediment conditions, so organic content, for example, may not be as limiting a factor for

321 restoration targets as previously indicated. For example, previous SAV habitat  
322 requirement studies (Batiuk et al., 2000; Koch, 2001; Kemp et al., 2004) suggested that  
323 sediments for freshwater SAV restoration in the Chesapeake Bay should consist of less  
324 than 5% organic matter. While high organic sediments may be deleterious for seagrasses  
325 growing under high salinity conditions due to potentially high sediment sulfide  
326 concentrations (Borum et al., 2005), this would not be expected to be as great an issue  
327 under oligohaline or freshwater conditions. Therefore the sediment habitat requirements  
328 for freshwater SAV restoration in some areas may need to be re-evaluated.

329         Typically, restoration of SAV has been conducted using a single-species  
330 approach. This study provides strong support for using *H. dubia* and *V. americana*  
331 together in co-plantings when habitat conditions may occur in the ranges of those studied  
332 here. When planted together, both species either performed equally as well, or better,  
333 than they did when grown by themselves, especially when stressed. This capacity for  
334 complementarity is important as restoration efforts are costly, and improvements to the  
335 resiliency of restored beds are critical for success, especially in physically variable  
336 estuarine habitats.

### 337 **Acknowledgments**

338 Funding for this project was provided by the U.S. Army Engineer Research and  
339 Development Center (ERDC) in Vicksburg, MS. We also thank Jessie Jarvis, Brittany  
340 Haywood, Steve Snyder, Voight Hogge, Betty Neikirk, Willy Reay, Jim Goins, Dave  
341 Parrish, Annie Markwith, Elizabeth Francis, Amber Knowles, and Jeremiah Walawender  
342 for help with microcosm construction, field collection, experimental sampling and



343 processing. This is contribution No. XXXX from the Virginia Institute of Marine  
344 Science, School of Marine Science, College of William and Mary.

345 **References**

346 Anderson, M.R., Kalff, J., 1986. Regulation of submerged aquatic plant distribution in a  
347 uniform area of a weedbed. *J. Ecol.* 74, 953-961.

348 Arthaud, F., Vallod, D., Robin, J., Wezel, A., Bornette, G., 2013. Short-term succession  
349 of aquatic plant species richness along ecosystem productivity and dispersal  
350 gradients in shallow lakes. *J. Veg. Sci.* 24(1), 148-156.

351 Barko, J.W., Smart, R.M., 1983. Effects of organic matter additions to sediment on the  
352 growth of aquatic plants. *J. Ecol.* 71, 161-175.

353 Barko, J.W., Smart, R.M., 1986. Sediment-related mechanisms of growth limitation in  
354 submersed macrophytes. *Ecology* 67(5), 1328-1340.

355 Barko, J.W., Gunnison, D., Carpenter, S.R., 1991. Sediment interactions with submersed  
356 macrophyte growth and community dynamics. *Aquat. Bot.* 41, 41-65.

357 Barrat-Segretain, M.H., Elger, A., 2004. Experiments on growth interactions  
358 between two invasive macrophyte species. *J. Veg. Sci.* 15, 109-114.

359 Batiuk, R.A., Bergstrom, P., Kemp, M., Koch, E., Murray, L., Stevenson, J.C.,  
360 Bartleson, R., Carter, V., Rybicki, N.B., Landwehr, J.M., Gallegos, C., Karrh,  
361 L., Naylor, M., Wilcox, D., Moore, K.A., Ailstock, S., Teichberg, M., 2000.  
362 Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-  
363 Based Requirements and Restoration Targets: A Second Technical Synthesis.  
364 Environmental Protection Agency, Annapolis, Maryland.

- 365 Bergstrom, P.W., Murphy, R.F., Naylor, M.D., Davis, R.C., Reel, J.T., 2006. Underwater  
366 Grasses in Chesapeake Bay and Mid-Atlantic Coastal Waters. Guide to  
367 Identifying Submerged Aquatic Vegetation. Maryland Sea Grant College. College  
368 Park, MD. 76pp.
- 369 Borum, J., Pedersen, O., Greve, T.M., Frankovich, T.A., Zieman, J.C., Fourqurean, J.W.,  
370 Madden, C.J., 2005. The potential role of plant oxygen and sulphide dynamics in  
371 die-off events of the tropical seagrass, *Thalassia testudinum*. J. Ecol. 93(1), 148-  
372 158.
- 373 Carter, V., Rybicki, N.B., 1990. Light attenuation and submersed macrophyte distribution  
374 in the tidal Potomac river and estuary. Estuaries 13(4), 441-452.
- 375 Chambers, P.A., Prepas, E.E., 1990. Competition and coexistence in submerged aquatic  
376 plant communities: the effects of species interactions versus abiotic factors.  
377 Freshwater Biol. 23, 541-550.
- 378 Chambers, P.A., Lacoul, P., Murphy, K.J., Thomaz, S.M., 2008. Global diversity of  
379 aquatic macrophytes in freshwater. Hydrobiologia 595, 9-26.
- 380 Elmendorf, S.C., Moore, K.A., 2007. Plant competition varies with community  
381 composition in an edaphically complex landscape. Ecology 88, 2640-2650.
- 382 Engelhardt, K.A.M., Ritchie, M.E., 2002. The effect of aquatic plant species richness  
383 on wetland ecosystem processes. Ecology 83(10), 2911-2924.
- 384 Erfemeijer, P.L.A., Koch, E.W., 2001. Sediment geology methods for seagrass habitat,  
385 in: Short, F.T., Coles, R.G., Global Seagrass Research Methods. Elsevier Science  
386 B.V., Amsterdam, pp. 345-367.

- 387 Frazer, T.K., Notestein, S.K., Jacoby, C.A., Littles, C.J., Keller, S.R., Swett, R.A., 2006.  
388 Effects of storm-induced salinity changes on submersed aquatic vegetation in  
389 Kings Bay, Florida. *Estuar. Coast.* 29(6A), 943-953.
- 390 French, G.T., Moore, K.A., 2003. Interactive effects of light and salinity stress on the  
391 growth, reproduction, and photosynthetic capabilities of *Vallisneria americana*  
392 (wild celery). *Estuaries* 26(5), 1255-1268.
- 393 Gaudet, C.L., Keddy, P.A., 1995. Competitive performance and species distribution in  
394 shoreline plant communities: a comparative approach. *Ecology* 76(1), 280-291.
- 395 Gopal, B., Goel, U., 1993. Competition and allelopathy in aquatic plant communities.  
396 *Bot. Rev.* 59, 155-210.
- 397 Greiner La Peyre, M.K., Grace, J.B., Hahn, E., Mendelssohn, I.A., 2001. The importance  
398 of competition in regulating plant species abundance along a salinity gradient.  
399 *Ecology* 82(1), 62-69.
- 400 Gustafsson, C., Boström, C., 2011. Biodiversity influences ecosystem functioning in  
401 aquatic angiosperm communities. *Oikos* 120: 1037-1046.
- 402 Haller, W.T., Sutton, D.L., Barlowe, W.C., 1974. Effects of salinity on growth of several  
403 aquatic macrophytes. *Ecology* 55, 891-894.
- 404 Halpern, B.S., Siliman, B.R., Olden, J.D., Bruno, J.P., Bertness, M.D. 2007.  
405 Incorporating positive interactions in aquatic restoration and conservation. *Front.*  
406 *Ecol. Environ.* 5, 153-160.
- 407 Hao, B., Wu, H., Shi, Q., Liu, G., Xing, W., 2013. Facilitation and competition among  
408 foundation species of submerged macrophytes threatened by severe  
409 eutrophication and implications for restoration. *Ecol. Eng.* 60: 76-80.

- 410 Hengst, A., Melton, J., Murray, L. 2010. Estuarine restoration of submersed aquatic  
411 vegetation: the nursery bed effect. *Restor. Ecol.* 18, 605-614.
- 412 Hooper, D. U., 1998. The role of complementarity and competition in ecosystem  
413 responses to variation in plant diversity. *Ecology* 79, 704–719.
- 414 Hooper, D.U., Dukes, S.J., 2004. Overyielding among plant functional groups in a long-  
415 term experiment. *Ecol. Lett.* 7, 95-105.
- 416 Hoover, D.T., 1984. Reproductive ecology of two submersed macrophytes in varying pH  
417 regimes. M.A. thesis, State University of New York, Binghamton. 87pp.
- 418 Jarvis, J.C., Moore, K.A., 2008. Influence of environmental factors on *Vallisneria*  
419 *americana* seed germination. *Aquat. Bot.* 88, 283-294.
- 420 Kantrud, H.A., 1990. Sago Pondweed (*Potamogeton pectinatus* L): A literature review.  
421 Fish and Wildlife Service Resource Publication 176, Washington, DC.
- 422 Kemp, W.M., Batiuk, R., Bartleson, R., Bergstrom, P., Carter, V., Gallegos, C.L.,  
423 Hunley, W., Karrh, L., Koch, E.W., Landwehr, J.M., Moore, K.A., Murray, L.,  
424 Naylor, M., Rybicki, N.B., Stevenson, J.C., Wilcox, D.J., 2004. Habitat  
425 requirements for submerged aquatic vegetation in Chesapeake Bay: Water  
426 quality, light regime, and physical-chemical factors. *Estuaries* 27(3), 363-377.
- 427 Koch, E.W., 2001. Beyond light: Physical, geological, and geochemical parameters as  
428 possible submersed aquatic vegetation habitat requirements. *Estuaries* 24(1),  
429 1-17.
- 430 Korschgen, C.E., Green, W.L., Kenow, K.P., 1997. Effects of irradiance on growth and  
431 winter bud production by *Vallisneria americana* and consequences to its  
432 abundance and distribution. *Aquat. Bot.* 58, 1-9.

- 433 Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity  
434 experiments. *Nature* 412, 72-76.
- 435 Liao, N., 2001. Revised 2002. Determination of ammonia in brackish or seawater by flow  
436 injection analysis. QuikChem Method 31-107-06-1-B. Lachat Instruments,  
437 Milwaukee, WI, USA.
- 438 McCreary, N.J., 1991. Competition as a mechanism of submersed macrophyte  
439 community structure. *Aquat. Bot.* 41, 177-193.
- 440 Moen, R.A., Cohen, Y., 1989. Growth and competition between *Potamogeton*  
441 *pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems.  
442 *Aquat. Bot.* 33, 257-270.
- 443 Moore, K.A., Wetzel, R.L., Orth, R.J., 1997. Seasonal pulses of turbidity and their  
444 relations to eelgrass (*Zostera marina* L.) survival in an estuary. *J. Exp. Mar. Biol.*  
445 *Ecol.* 215, 115-134.
- 446 Moore, K.A., Wetzel, R.L., 2000. Seasonal variations in eelgrass (*Zostera marina* L.)  
447 responses to nutrient and reduced light availability in experimental ecosystems.  
448 *J. Exp. Mar. Biol. Ecol.* 244, 1-28.
- 449 Moore, K.A., Wilcox, D.J., Orth, R.J., 2000. Analysis of the abundance of submersed  
450 aquatic vegetation communities in the Chesapeake Bay. *Estuaries* 23(1), 115-127.
- 451 Moore, K.A., Jarvis, J.C., 2007. Techniques for the Use of Seeds in the Propagation and  
452 Restoration of *Vallisneria americana* Michaux (wild celery) in the Chesapeake  
453 Bay. COE Technical Report Series. ERDC/TN SAV-07-2.

- 454 Moore, K.A., Shields, E.C., Jarvis, J.C., 2010. The role of habitat and herbivory on the  
455 restoration of tidal freshwater submerged aquatic vegetation populations. *Restor.*  
456 *Ecol.* 18(4), 596-604.
- 457 Orth, R.J., Wilcox, D.J., Whiting, J.R., Nagey, L.S., Owens, A.L., Kenne, A.K., 2009.  
458 2008 distribution of submerged aquatic vegetation in Chesapeake Bay and coastal  
459 bays. Virginia Institute of Marine Science Special Scientific Report #149,  
460 Gloucester Point, VA.
- 461 R Core Team (2012). R: A language and environment for statistical computing. R  
462 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0,  
463 URL <http://www.R-project.org/>.
- 464 Rybicki, N.B, Landwehr, J.M., 2007. Long-term changes in abundance and diversity  
465 of macrophyte and waterfowl populations in an estuary with exotic macrophytes  
466 and improving water quality. *Limnol. Oceanogr.* 52(3), 1195-1207.
- 467 Salo, T., Gustafsson, C., Boström, C., 2009. Effects of plant diversity on primary  
468 production and species interactions in brackish water angiosperm communities.  
469 *Mar. Ecol. Prog. Ser.* 396, 261-272.
- 470 Shields, E.C., Moore, K.A., Parrish D.B., 2012. Influences of salinity and light  
471 availability on abundance and distribution of tidal freshwater and oligohaline  
472 submerged aquatic vegetation. *Estuar. Coast.* 35, 515-526.
- 473 Spehn, E.M., Joshi, J., Schmidt, B., Diemer, M, Korner, C., 2000. Above-ground  
474 resource use increases with plant species richness in experimental grassland  
475 ecosystems. *Funct. Ecol.* 14, 326-337.
- 476 Spencer, D.F., Ksander, G.G., 2000. Interactions between American Pondweed and

- 477 monoecious *H. verticillata* grown in mixtures. *J. Aquat. Plant. Manage.* 38, 5-13.
- 478 Teeter, J.W., 1965. Effects of sodium chloride on the Sago Pondweed. *J. Wildlife.*  
479 *Manage.* 29(4), 838-845.
- 480 Titus, J.E., Stephens, M.D., 1983. Neighbor influences and seasonal growth patterns  
481 for *Vallisneria americana* in a mesotrophic lake. *Oecologia* 56, 23-29.
- 482 Twilley, R.R., Barko, J.W., 1990. The growth of submersed macrophytes under  
483 experimental salinity and light conditions. *Estuaries* 13(3), 311-321.
- 484 van de Koppel, J., Altieri, A.H., Siliman, B.R., Bruno, J.F., Bertness, M.D. 2006. Scale-  
485 dependent interactions and community structure on cobble beaches. *Ecol. Lett.* 9,  
486 45-50.
- 487 Van, T.K., Wheeler, G.S., Center, T.D., 1999. Competition between *Hydrilla verticillata*  
488 and *Vallisneria americana* as influenced by soil fertility. *Aquat. Bot.* 62, 225-233.
- 489 Virginia Institute of Marine Science. Nutrient Analysis Laboratory Procedure Manual.  
490 Orthophosphate procedure, Revision No. 3, 1991.
- 491

492 Table 1

493 Mean  $\pm$  SE for sediment nutrients and organic content for the mud and sand treatments.

494 Initial values were taken in the field at the time of sediment collection, and final values

495 were taken at the time of harvest at the end of the experiment.

496

	Mud	Sand
<b>Initial</b>		
NH <sub>4</sub> <sup>+</sup> ( $\mu$ M)	178.2 $\pm$ 18.3	20.5 $\pm$ 6.2
PO <sub>4</sub> <sup>3-</sup> ( $\mu$ M)	0.17 $\pm$ 0.0	0.45 $\pm$ 0.2
Organic (%)	9.8 $\pm$ 0.2	0.52 $\pm$ 0.1
<b>Final</b>		
NH <sub>4</sub> <sup>+</sup> ( $\mu$ M)	74.6 $\pm$ 12.6	24.0 $\pm$ 2.6
PO <sub>4</sub> <sup>3-</sup> ( $\mu$ M)	0.46 $\pm$ 0.0	1.1 $\pm$ 0.3
Organic (%)	9.2 $\pm$ 0.4	1.0 $\pm$ 0.8



497 Table 2  
 498 MANOVA results for all response variables (RGR, density, and length) for three species  
 499 under different sediment and salinity conditions. Significant results are highlighted in  
 500 bold.

	df	Wilks	F	p value
<b><i>H. dubia</i></b>				
Sediment	1	0.77	0.91	0.47
Salinity	2	0.17	4.25	<b>&lt; 0.01</b>
Sediment x Salinity	2	0.52	1.15	0.37
<b><i>S. pectinata</i></b>				
Sediment	1	0.85	0.57	0.65
Salinity	2	0.38	2.08	0.10
Sediment x Salinity	2	0.53	1.25	0.32
<b><i>V. americana</i></b>				
Sediment	1	0.34	6.57	<b>&lt; 0.01</b>
Salinity	2	0.40	1.92	0.13
Sediment x Salinity	2	0.35	2.29	0.08

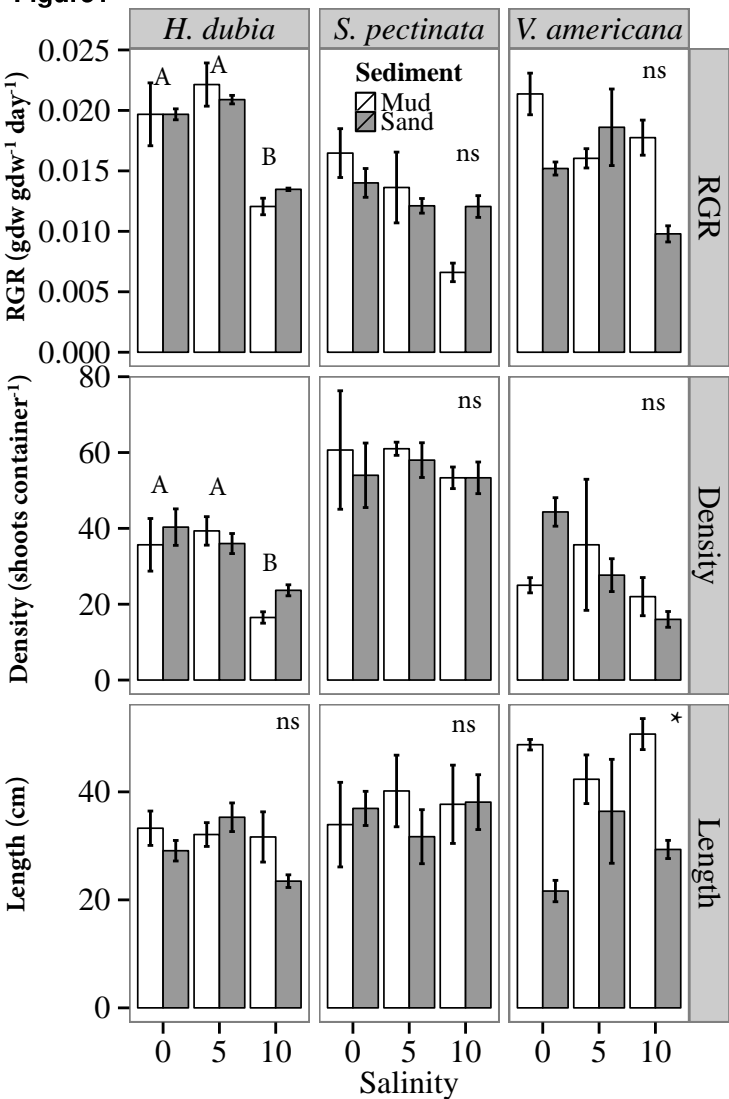
501

502 **Fig. 1.** Relative growth rate (RGR), density, and length of all species in monoculture  
503 (*Heteranthera dubia* left; *Stuckenia pectinata* middle; *Vallisneria americana* right) across  
504 all salinity and sediment treatments. Values are mean  $\pm$  1 SE, n = 3. Different letters  
505 indicate significant differences among salinity treatments, and the star indicates that the  
506 results were significantly different between sediment types. NS = not significant.

507

508 **Fig. 2.** Relative yield calculated based on relative growth rate for each species in all  
509 salinity (x-axis) and sediment (left and right panel) treatments. Species combination  
510 treatments are in order from top to bottom: *H. dubia*/*S. pectinata* biculture; *H. dubia*/*V.*  
511 *americana* biculture; *S. pectinata*/*V. americana* biculture; all species in triculture. White  
512 is *H. dubia*, black is *S. pectinata*, gray is *V. americana*. Values are mean  $\pm$  1 SE, n = 3.  
513 A line is drawn across a relative yield of 1 which represents a species performing equally  
514 well in mixture compared with monoculture. Stars indicate significant overyielding or  
515 underyielding with a 95% confidence interval.

516

**Figure 1**

**Figure2**

