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Effects of Storm-induced Salinity Changes on Submersed Aquatic Vegetation in Kings Bay, Florida

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ABSTRACT: Hurricanes and other major storms cause acute changes in salinity within Florida's streams and rivers. Wind-driven tidal surges that increase salinities may have long-lasting effects on submersed aquatic vegetation (SAV) and the associated fauna. We investigated potential effects of salinity pulses on SAV in Kings Bay, Florida, by subjecting the three most common macrophytes, *Vallisneria americana*, *Myriophyllum spicatum*, and *Hydrilla verticillata*, to simulated salinity pulses. In Kings Bay, we documented changes in salinity during three storms in September 2004 and measured biomass and percent cover before and after these storms. During experiments, macrophytes were exposed to salinities of 5‰, 15‰, or 25‰ for 1, 2, or 7 d, with a 28-d recovery period in freshwater. Relative to controls, plants subjected to salinities of 5‰ exhibited few significant decreases in growth and no increase in mortality. All three species exhibited decreased growth in salinities of 15‰ or 25‰. *H. verticillata* exhibited 100% mortality at 15‰ and 25‰, irrespective of the duration of exposure. *M. spicatum* and *V. americana* exhibited increased mortality after 7-d exposures to 15‰ or any exposure to 25‰. Maximum daily salinities in Kings Bay approached or exceeded 15‰ after each of the three storms, with pulses generally lasting less than 2 d. Total aboveground biomass and percent cover of vascular plants were reduced following the storms. *M. spicatum* exhibited an 83% decrease in aboveground biomass and an 80% decrease in percent cover. *H. verticillata* exhibited a 47% and 15% decline in biomass and percent cover, respectively. *V. americana* exhibited an 18% increase in aboveground biomass and a 37% increase in percent cover, which suggests greater tolerance of salinity pulses and release from competition with the invasive *H. verticillata* and *M. spicatum*. Our results indicate that rapid, storm-induced pulses of high salinity can have important consequences for submersed aquatic vegetation, restoration efforts, and management of invasive species.

Introduction

Biotic and abiotic factors and their interactions through ecological processes determine the structure and function of biological communities. In estuaries and other coastal aquatic ecosystems, the forces shaping submersed aquatic plant assemblages are important because these assemblages play critical roles in supporting healthy ecosystems and human activities (Williams and Heck 2001).

Restoration of disturbed vegetated habitats and management of invasive plants represent two critical issues at the interface of abiotic and biotic influences on submersed aquatic vegetation (SAV). Changes in water quality and physical disturbance have reduced the extent of SAV worldwide (Bayley et al. 1978; Duarte 1995; Short and Wyllie–Echeverria 1996; Valiela et al. 1997). Managers are undertaking numerous efforts to restore these vegetated habitats. In addition to removing native vegetation, disturbances often provide a foothold for exotic and nuisance species. Invasive species can gain or lose a foothold following changes in temperature, salinity, water clarity, selective herbivory, or other environmental factors (Van et al. 1978, 1998, 1999; Titus and Adams 1979; Barko et al. 1991). Once established, invasive aquatic plants (including both angiosperms and algae) outcompete native species by exhibiting allelopathy, faster growth, aggressive reproduction, or other superior characteristics (Haller and Sutton 1975; Titus and Adams 1979; Elakovich 1989; Gopal and Goel 1993; Doyle et al. 2003).

The situation in Kings Bay, a tidally influenced, spring-fed system along Florida's Gulf coast, highlights the issues noted above, and it provides a model system for investigations of processes that affect the structure of submersed plant communities. SAV in Kings Bay was once dominated by wild celery, *Vallisneria americana*, according to anecdotal accounts from local residents and long-time recreational users of the bay (see Hauxwell et al. 2004a). Recent investigations indicate that nuisance algae and nonnative, invasive vascular plants have, for the most part, replaced this native species (Notestein et al. 2005). *Myriophyllum spicatum* (Eurasian water milfoil) and *Hydrilla verticillata* are now more prominent than *V. americana*. Both of these invasive plants were introduced into the Kings Bay-Crystal

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River system within the past several decades (Blackburn and Weldon 1967; Haller 1978; Langeland 1990). Ongoing research has assessed the feasibility of restoring *V. americana* to its earlier dominance, but *M. spicatum* and *H. verticillata* still occupy much of the system (Mataraza et al. 1999; Hoyer et al. 2001; Hauxwell et al. 2004a,b; Notestein et al. 2005).

Several factors probably contributed to the initial displacement of *V. americana* in Kings Bay. Decreased water clarity and light availability, grazing by herbivores, and competitive exclusion by nonnative macrophytes and macroalgae probably all played important roles (Haller and Sutton 1975; Bowes et al. 1977; Barko et al. 1991; Blanch et al. 1998; Hauxwell et al. 2004a). Acute and chronic changes in salinity may exacerbate or ameliorate changes in the bay's vegetation (Mataraza et al. 1999; Frazer et al. 2001b).

Salinities do affect SAV in Kings Bay, Crystal River, and other adjacent spring-fed river systems. The abundances of many plants decline in areas where salinities reach or exceed 3‰ (Hoyer et al. 2004). Although salinities near the mouth of Kings Bay may typically stay below 3‰, salinities can rise to 5‰ and 15‰ during droughts and storms (Yobbi and Knochenmus 1989; Frazer et al. 2001b).

Investigators have observed correlations between widespread declines in plant and algal biomass in Kings Bay and major storm events (Terrell and Canfield 1996; Mataraza et al. 1999). Mataraza et al. (1999) also noted differences in the recovery of different submersed aquatic plants. The presence of tidal surges suggested that salinity caused these effects, but field measurements of salinity were not available, which means that the conclusions remain speculative.

Studies characterizing the salinity tolerances of *M. spicatum*, *H. verticillata*, and *V. americana* lend support to the hypothesis that salinity changes may affect their abundances and distributions (Haller et al. 1974; Twilley and Barko 1990; Kraemer et al. 1999; Doering et al. 1999, 2001). *M. spicatum* and *V. americana* are generally considered salt-tolerant, freshwater species, whereas *H. verticillata* does not tolerate higher salinities as well. Differences in salinity tolerance among these three species probably plays an important role in determining the patterns in their biomass and distribution within Kings Bay and other tidally influenced systems where they co-occur. Salinity may be a primary factor mediating their relative competitive success.

Salinity tolerances in macrophytes have been derived primarily from studies carried out under static conditions, which may not reflect responses to rapid changes like those driven by normal tidal cycles during droughts or acute storms. Doering et al. (2001) conducted an experiment in which *V. americana* plants were gradually exposed to a salinity of 18‰ for varying times and then returned to a base salinity of 3‰ for a 30-d recovery period. Shoot numbers and blade densities decreased relative to control plants only after exposures of 20 d or longer. Similar data are not available for *M. spicatum* or *H. verticillata*.

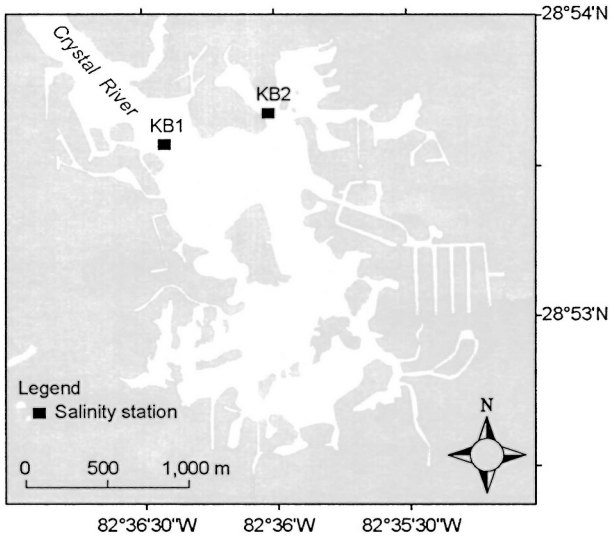

Fig. 1. Map of Kings Bay-Crystal River with solid squares depicting locations of continuous salinity recorders.

This study addresses the effects of rapid salinity change on *V. americana*, *H. verticillata*, and *M. spicatum*. It incorporates multiple, experimental treatments with field surveys before and after major storms to achieve a better understanding of how salinity drives patterns in biomass and distribution of these species in Kings Bay. Such an improved understanding can guide future research, revegetation efforts, and management of aquatic invasive plants.

Study Location

The Kings Bay and Crystal River system is located in Citrus County approximately 97 km north of Tampa, Florida (Fig. 1). Kings Bay, which covers approximately 1.91 km^2, serves as the origin of freshwater flow for Crystal River (Hoyer et al. 2001). At least 30 known springs and sinks combine to form the fourth largest spring discharge in the state and contribute up to 99% of the freshwater entering the bay (Rosenau et al. 1977; Hammet et al. 1996). Variations in discharge result from variations in local rainfall, groundwater levels, and tidal cycles (Mann and Cherry 1969). The average total spring discharge about 4.8 km downstream of Kings Bay was greater than 27 $m^3 s^{-1}$ between 1965 and 1977, but the average discharge at the mouth of Kings Bay dropped to less than 14 $m^3 s^{-1}$ during 2000, which

was during a drought (Yobbi and Knochenmus 1989; Frazer et al. 2001b).

Tides influence all of Crystal River and Kings Bay, and the downstream flow of freshwater commonly reverses during high tides not only in the river but also in the man-made canals and ditches along the shoreline (Mann and Cherry 1969; Yobbi and Knochenmus 1989; Hammet et al. 1996; Frazer et al. 2001b). Yobbi and Knochenmus (1989) reported diurnal tidal ranges of about 0.8 m at the mouth of Crystal River and fluctuations of 0.5 to 0.6 m approximately 4.8 km below Kings Bay. Hammet et al. (1996) found that water levels in Kings Bay changed less than 1.2 m between low and high tides. During Hurricane Donna in September 1964, Mann and Cherry (1969) observed a maximum water level that was 1.5 m above mean sea level, suggesting that storm winds may drive large amounts of high salinity water up the river and into Kings Bay.

Salinities in Kings Bay respond to the balance between freshwater flow and the influence of tides or storms. From March 1984 to March 1986, Yobbi and Knochenmus (1989) reported salinities less than 3‰ at the head of Crystal River just below Kings Bay. These investigators suggested that reduced freshwater discharge in Kings Bay would allow an increase in saltwater intrusion and higher salinities in the upper river and Kings Bay. Measurements over the last 10 yr indicate that salinity in Kings Bay can exceed 5‰ during normal tidal oscillations, perhaps because of decreased spring discharges (Frazer et al. 2001b; Hoyer et al. 2001). Between July 2000 and June 2001, a period of drought in north-central Florida, bottom salinities at the mouth of Kings Bay reached or exceeded 3‰ more than 10% of the time and 5‰ more than 2% of the time (Frazer et al. 2001b). These data demonstrate that relatively high salinity water can enter Kings Bay under normal tidal regimes during drought conditions. In addition to salinity changes driven by normal tidal exchange, episodic storms can significantly alter salinity conditions. Frazer et al. (2001b) reported bottom salinities in excess of 15‰ at the mouth of Kings Bay coincident with the passage of Tropical Storm Gordon in 2000.

Methods

Experimental Salinity Pulses

Experiments simulating pulsed salinity events took place during September 2004 in outdoor, 900-l, concrete tanks (2.5 m long × 1.5 m wide × 1.5 m deep) located in Gainesville, Florida. Synthetic sea salt (Instant Ocean, Aquarium Systems, Inc., 8141 Tyler Boulevard, Mentor, Ohio, 44060) was added to groundwater supplied from an on-site well (salinity < 1‰) to create four salinity treatments (<1‰ or control, 5‰, 15‰, and 25‰). In all tanks treated with salt, submersible water pumps mixed the water and maintained a homogeneous salinity environment. Salinity was monitored daily, and when needed, the salinity was adjusted with Instant Ocean or well water. Translucent shade cloth covering each tank reduced ambient light to a level similar to that in Kings Bay. Temperature (°C), dissolved oxygen (mg l^{-1}) and pH were monitored daily with a handheld YSI model 650 Multiparameter Display System equipped with appropriate sensors (YSI Incorporated, 1700/1725 Brannum Lane, Yellow Springs, Ohio, 45387).

Whole *V. americana* plants, apical fragments of *M. spicatum*, and females of the dioecious biotype of *H. verticillata* were collected from Kings Bay, during August 2004 (prior to the major storms). For *Hydrilla* and *Myriophyllum*, 4-cm apical sections were cut from each fragment, blotted dry, weighed, and then planted with at least 2 nodes below the sediment and approximately 3 cm of the stem and associated leaf material exposed. For *Vallisneria*, the blades of each plant were trimmed to 3 cm, roots were clipped to 2 cm, and any rhizomes were removed at the crown. The remaining blades were counted, and each shoot was blotted dry, weighed, and planted. All specimens were planted in 1-quart, plastic nursery pots lined with fabric to prevent leakage of 900 g of sand fertilized with 0.1% (0.9 g) Osmocote (Scotts Consumer Service, 14111 Scottslawn Road, Marysville, Ohio, 43041) through predrilled drainage holes. Specimens were acclimated for 28 d in tanks filled with groundwater (salinity < 1‰).

Six plants of each species were haphazardly placed in the treatment tanks so that they were separated from each other and the sides of the tanks by approximately 0.5 m to minimize interactions between plants and edge effects. This design allowed 2 plants from each of 2 tanks to be subjected to each of 4 salinities for 1, 2, and 7 d (i.e., n = 4 for each combination of salinity and duration of exposure).

Following exposure, plants from treatment tanks were placed into four designated recovery tanks, i.e., pre-conditioned tanks containing groundwater from an on-site well (salinity < 1‰). Plants from each treatment were placed into at least two recovery tanks to avoid pseudoreplication. Plants remained in recovery for 28 d following simulated salinity pulses.

At the conclusion of the experiment, plants were removed from their respective pots and rinsed. The number of blades and clones for *Vallisneria*, the number of branches and turions for *Hydrilla*, and the number of branches for *Myriophyllum* were

counted. The length of longest blade or stem was recorded for all plants. After processing, plants were split into belowground and aboveground portions, and each set of material was dried at 60°C for 48 h prior to being weighed to the nearest gram to yield aboveground and belowground biomasses.

Statistical analyses examined changes in parameters that characterize growth. Calculations involved subtracting initial values from final values and dividing by the sum of the durations of the appropriate treatment and recovery periods. Daily rates standardize measures across unequal treatment periods, an approach that assumes plants of all initial sizes exhibited linear responses over the finite study period. Gains in stem or blade length in cm d^{-1}, gains in aboveground and belowground biomass in g dry weight (dw) d^{-1}, changes in number of blades and clones d^{-1} for *Vallisneria*, changes in number of branches d^{-1} for *Hydrilla* and *Myriophyllum*, and changes in number of turions d^{-1} for *Hydrilla* were treated as separate dependent variables in 2 × 2 factorial analyses of variance (ANOVA), with salinity and duration of exposure as fixed effects (PROC GLM; SAS Institute, Inc. 2002). Student–Newman–Kuels multiple comparison tests identified significantly different means following significant ANOVA (Zar 1974). Significance levels were set at $p < 0.05$ unless otherwise indicated.

Field Sampling

Water quality parameters were recorded at the mouth of Kings Bay (Station KB1; approximate position 28°53.62′N, 82°36.36′W; Fig. 1) from August 12, 2004 through December 31, 2004 with a YSI model 6600 Multiparameter Water Quality Monitor designed for long-term, in situ monitoring and profiling (YSI Incorporated, 1700/1725 Brannum Lane, Yellow Springs, Ohio, 45387). Sensors measured salinity ± 0.1‰, temperature ± 0.15°C, and depth ± 0.018 m. Following calibration in the laboratory, the instrument package was secured to the post of a channel marker, with the sensors located 0.5 m off the bottom. Data were recorded at 30-min intervals, and average hourly values were used in analyses.

Although sampling at Station KB1 was most likely to capture pulses of high salinity water entering Kings Bay via Crystal River because the sensor was near the bottom and the middle of the channel, an additional instrument (same model and sensor specifications) was deployed within the bay in Cedar Cove (approximate position 28°53.73′N, 82°35.97′W; Fig. 1). This second instrument was deployed to further characterize the duration of high salinity events that can result from storm surges associated with tropical storms in late summer and early fall.

SAV was sampled in February, May, July, and October of 2004 and 2005 at 71 stations previously established by Frazer and Hale (2001). At each of the 71 sampling stations in each sampling period, divers estimated the percent cover of all SAV within 3 replicate 0.25-m^2 quadrats that were positioned haphazardly within 10 m of the anchor, which was located at the coordinates of the station (Frazer and Hale 2001; Notestein et al. 2005). Separate estimates were made for total SAV (the combination of all angiosperms and macroalgae), filamentous algae (a composite group dominated by *Lyngbya* sp.), and individual taxa, i.e., *Ceratophyllum demersum*, *Chara* sp., *H. verticillata*, *M. spicatum*, *Najas guadalupensis*, *Potamogeton pectinatus*, *Potamogeton pusillus*, *Ruppia maritima*, and *V. americana*. We restrict subsequent discussion to the dominant angiosperms as they were the focus of the experimental work described above. Following in situ estimates of cover, the aboveground biomass within each of the quadrats was removed, placed into uniquely labeled plastic bags, and transported to the University of Florida for subsequent processing. In the laboratory, samples were rinsed with fresh water, sorted by taxon, and dried at 65°C to a constant dry weight as measured to the nearest 0.001 g.

Analyses of pre-hurricane and post-hurricane SAV biomass and cover in Kings Bay were carried out using standard ANOVA procedures and Tukey–Kramer (HSD) tests as pairwise follow-up tests (SAS Institute, Inc. 2002). Before analyses, biomass data were $\log_{10}$ transformed and percent cover data were arcsine transformed to improve normality and homoscedasticity. Significance levels were set at $p < 0.05$.

Results

Experimental Salinity Pulses

Midday incident light levels at the surface of the tanks ranged between 1,750 and 2,000 μE m^{-2} s^{-1}. Shade cloth placed over each tank reduced these levels by approximately 70% (525 to 600 μE m^{-2} s^{-1} at midday), which simulated in situ light levels near the bottom in Kings Bay. Mean midday water temperatures in the tanks varied between 21°C and 26°C throughout the experiment. These values were similar to temperatures recorded in Kings Bay during the study period. Salinity values in control and recovery tanks were always < 0.2‰. Salinities in 5‰ and 15‰ treatment tanks were always within 1‰ of the prescribed level, and salinities in the 25‰ treatment tanks were always within 2‰ of the prescribed level. Mean midday dissolved oxygen concentrations and pH values ranged between 7.5–10.0 mg l^{-1} and 7.5–8.5, respectively; these values are typical of Kings Bay.

TABLE 1. Results of two-factor ANOVAs used to test for effects of salinity and duration of exposure on gains in number of blades (clones included), blade length, number of clones, aboveground biomass, and belowground biomass for *Vallisneria americana*. An asterisk (*) indicates statistical significance at $p < 0.05$. dw = dry weight.

Gain factor	df	MS	F	p
Number of blades d^{-1}				
Salinity	3	2.925	31.00	< 0.001*
Duration	2	0.006	0.06	0.942
Salinity × Duration	6	0.057	0.60	0.725
Error	36	0.094		
Blade length cm d^{-1}				
Salinity	3	1.325	66.29	< 0.001*
Duration	2	0.052	2.59	0.089
Salinity × Duration	6	0.078	3.89	0.004*
Error	36	0.020		
Number of clones d^{-1}				
Salinity	3	0.072	27.09	< 0.001*
Duration	2	1.0 E^{-5}	0.01	0.995
Salinity × Duration	6	9.0 E^{-4}	0.34	0.912
Error	36	0.003		
Aboveground biomass g dw d^{-1}				
Salinity	3	7.2 E^{-4}	36.67	< 0.001*
Duration	2	1.9 E^{-5}	0.96	0.393
Salinity × Duration	6	1.2 E^{-5}	0.60	0.728
Error	36	2.0 E^{-5}		
Belowground biomass g dw d^{-1}				
Salinity	3	2.6 E^{-4}	46.87	< 0.001*
Duration	2	1.0 E^{-7}	0.02	0.983
Salinity × Duration	6	6.1 E^{-6}	1.10	0.379
Error	36	5.6 E^{-6}		

Measures of *V. americana* growth were all significantly affected by increased salinity (Table 1). Regardless of the duration of exposure, gains in number of blades, number of clones, aboveground biomass, and belowground biomass all decreased significantly when salinities were raised to 15‰ (Table 2). Multiple comparisons among the 12 means comprising the interaction of duration and exposure showed that gains in blade length decreased as plants were exposed to higher salinities over longer periods, with unequivocal decreases found only for the 7-d 15‰ treatment and all 25‰ treatments (Fig. 2 and Table 2).

All measures of *H. verticillata* growth were significantly affected by salinity regardless of the duration of exposure (Table 3). Gains in number of branches were significantly higher in the control tanks than in 5‰, and plants subjected to 15‰ and 25‰ did not add branches (Table 4). Gains in stem length, aboveground biomass, and belowground biomass were significantly lower when salinities were raised to 15‰ and 25‰. Gain in number of turions was affected by increased salinity, but multiple comparisons indicated an overlap among the means (Tables 3 and 4). Similar to other measures, gains in number of turions decreased with increased salinity and fell to zero in salinities of 15‰ and 25‰ (Table 4).

TABLE 2. Means (± SD) for gains in number of blades (all clones included), blade length, number of clones, aboveground biomass, and belowground biomass for *Vallisneria americana*. Means followed by different letters are statistically different at $p < 0.05$ according to Student–Newman–Kuels follow-up tests. dw = dry weight.

Gain	Control	5‰	15‰	25‰
Number of blades d^{-1}	1.088 a (0.500)	0.737 a (0.239)	0.218 b (0.184)	0.000 b
Blade length cm d^{-1}				
1 day	0.596 b (0.139)	0.897 a (0.214)	0.325 c (0.126)	0.000 d
2 days	0.480 b,c (0.091)	0.622 b (0.152)	0.356 c (0.238)	0.000 d
7 days	0.721 a,b (0.182)	0.652 b (0.192)	0.023 d (0.034)	0.000 d
Number of clones d^{-1}	0.169 a (0.075)	0.114 a (± 0.052)	0.029 b (0.031)	0.000 b
Aboveground biomass g dw d^{-1}	0.0168 a (0.0071)	0.0117 a (± 0.0042)	0.0029 b (0.0024)	0.0000 b
Belowground biomass g dw d^{-1}	0.0093 a (0.0034)	0.0077 a (0.0030)	0.0010 b (0.0009)	0.0000 b

Growth of *M. spicatum* was significantly affected by increased salinity (Table 5). Regardless of the

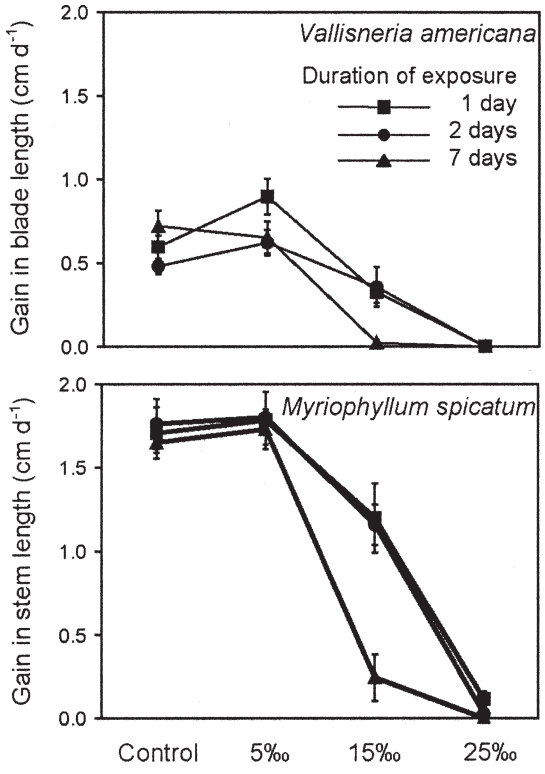

Fig. 2. Mean (± SE) gains in blade length (cm d^{-1}) for *Vallisneria americana* subjected to different salinities for different durations. Mean (± SE) gains in stem length (cm d^{-1}) for *Myriophyllum spicatum* subjected to different salinities for different durations.

TABLE 3. Results of two-factor ANOVAs used to test for effects of salinity and duration of exposure on gains in number of branches, stem length, number of turions, aboveground biomass, and belowground biomass for *Hydrilla verticillata*. An asterisk (*) indicates statistical significance at $p < 0.05$. dw = dry weight.

Gain factor	df	MS	F	p
Number of branches d^{-1}				
Salinity	3	11.023	84.43	< 0.001*
Duration	2	0.010	0.07	0.929
Salinity × Duration	6	0.209	1.60	0.175
Error	36	0.131		
Stem length cm d^{-1}				
Salinity	3	7.105	54.55	< 0.001*
Duration	2	0.216	1.66	0.205
Salinity × Duration	6	0.090	0.69	0.658
Error	36	0.130		
Number of turions d^{-1}				
Salinity	3	3.0 E^{-3}	9.66	< 0.001*
Duration	2	3.9 E^{-4}	1.26	0.295
Salinity × Duration	6	2.8 E^{-4}	0.93	0.488
Error	36	3.1 E^{-4}		
Aboveground biomass g dw d^{-1}				
Salinity	3	2.8 E^{-3}	60.34	< 0.001*
Duration	2	9.5 E^{-5}	2.05	0.144
Salinity × Duration	6	7.6 E^{-5}	1.64	0.164
Error	36	4.6 E^{-5}		
Belowground biomass g dw d^{-1}				
Salinity	3	2.6 E^{-4}	29.30	< 0.001*
Duration	2	2.4 E^{-5}	2.69	0.081
Salinity × Duration	6	1.1 E^{-5}	1.22	0.319
Error	36	8.8 E^{-6}		

duration of exposure, gains in number of branches decreased significantly when salinity was raised to 15‰ or 25‰ (Table 6). Gains in aboveground biomass and belowground biomass also decreased significantly at salinities of 15‰ and 25‰ regardless of the duration of exposure. Gains in stem length varied among combinations of salinity and duration of exposure (Tables 5 and 6). Less growth was recorded for all treatments of 15‰ and 25‰, with the 7-d, 15‰ treatment being statistically similar to all 25‰ treatments (Fig. 2 and Table 6).

Mortality was observed after some treatments and a 28-d recovery period (Table 7). All three species survived exposures to control and 5‰ treatments for 1, 2, and 7 d. *H. verticillata* did not survive exposure to 15‰. *V. americana* and *M. spicatum* did not exhibit mortality after 1-d and 2-d exposures to 15‰. At least half of the *M. spicatum* plants survived a 7-d exposure to 15‰ and a 1-d exposure to 25‰.

TABLE 4. Means (± SD) for gains in number of branches, stem length, turions, aboveground biomass, and belowground biomass for *Hydrilla verticillata*. Means followed by different letters are statistically different at $p < 0.05$ according to Student–Newman–Kuels follow-up tests. dw = dry weight.

Gain	Control	5‰	15‰	25‰
Number of branches d^{-1}	1.340 b (0.625)	1.888 a (0.391)	0.000 c	0.000 c
Stem length cm d^{-1}	1.456 a (0.689)	1.181 a (0.201)	0.000 b	0.000 b
Number turions d^{-1}	0.033 a (0.028)	0.016 a, b (0.021)	0.000 b	0.000 b
Aboveground biomass g dw d^{-1}	0.0220 a (0.0102)	0.0298 a (0.0103)	0.0000 b	0.0000 b
Belowground biomass g dw d^{-1}	0.0085 a (0.0047)	0.0074 a (0.0041)	0.0000 b	0.0000 b

TABLE 5. Results of two-factor ANOVAs used to test for effects of salinity and duration of exposure on gains in number of branches, stem length, aboveground biomass, and belowground biomass for *Myriophyllum spicatum*. An asterisk (*) indicates statistical significance at $p < 0.05$. dw = dry weight.

Gain Factor	df	MS	F	p
Number of branches d^{-1}				
Salinity	3	0.906	46.18	< 0.001*
Duration	2	0.017	0.89	0.420
Salinity × Duration	6	0.022	1.13	0.366
Error	36	0.020		
Stem length cm d^{-1}				
Salinity	3	7.924	139.77	< 0.001*
Duration	2	0.441	7.78	0.002*
Salinity × Duration	6	0.252	4.45	0.002*
Error	36	0.057		
Aboveground biomass g dw d^{-1}				
Salinity	3	4.4 E^{-3}	54.10	< 0.001*
Duration	2	1.3 E^{-4}	1.55	0.226
Salinity × Duration	6	1.1 E^{-4}	1.36	0.257
Error	36	8.2 E^{-5}		
Belowground biomass g dw d^{-1}				
Salinity	3	4.3 E^{-4}	25.99	< 0.001*
Duration	2	4.7 E^{-5}	2.82	0.073
Salinity × Duration	6	2.3 E^{-5}	1.40	0.240
Error	36	1.7 E^{-5}		

TABLE 6. Means (± SD) for gains in number of branches, stem length, aboveground biomass, and belowground biomass for *Myriophyllum spicatum*. Means followed by different letters are statistically different at $p < 0.05$ according to Student–Newman–Kuels follow-up tests. dw = dry weight.

Gain	Control	5‰	15‰	25‰
Number of branches d^{-1}	0.554 a (0.183)	0.575 a (0.180)	0.169 b (0.111)	0.029 b (0.032)
Stem length cm d^{-1}				
1 day	1.706 a (0.306)	1.782 a (0.341)	1.198 b (0.415)	0.114 c (0.092)
2 days	1.762 a (0.301)	1.800 a (0.100)	1.159 b (0.240)	0.027 c (0.053)
7 days	1.651 a (0.126)	1.729 a (0.183)	0.244 c (0.282)	0.000 c
Aboveground biomass g dw d^{-1}	0.0373 a (0.0141)	0.0341 a (0.0120)	0.0052 b (0.0030)	0.0004 b (0.0005)
Belowground biomass g dw d^{-1}	0.0124 a (0.0061)	0.0102 a (0.0059)	0.0019 b (0.0019)	0.0003 b (0.0007)

TABLE 7. Percent mortality of *Vallisneria americana*, *Hydrilla verticillata*, and *Myriophyllum spicatum* after different exposures to different salinities and a 28-d recovery period.

	Vallisneria			*Hydrilla*			*Myriophyllum*		
Salinity	1 day	2 days	7 days	1 day	2 days	7 days	1 day	2 days	7 days
Control	0	0	0	0	0	0	0	0	0
5‰	0	0	0	0	0	0	0	0	0
15‰	0	0	75	100	100	100	0	0	50
25‰	100	100	100	100	100	100	25	75	100

Hurricane Effects on Kings Bay

In September 2004, an interval which captured three hurricanes, depths at the mouth of Kings Bay (Station KB1) ranged from 0.70 to 3.02 m with a mean value of 2.02 m (all depth measurements were corrected to account for the position of the sensor off the bottom). Bottom temperatures during the same time period ranged from 23.7°C to 29.4°C with a mean value of 25.8°C; values were typical of the area at the mouth of Kings Bay in fall without the influence of a storm (Frazer et al. 2001a).

The passage of Hurricanes Ivan, Frances, and Jeanne, altered salinities in Kings Bay. Near the bottom at the mouth of the bay (Station KB1), salinities increased markedly reaching maxima of 14‰, 14‰, and 19‰, respectively (Fig. 3). In each case, the initial pulse of high salinity water persisted for approximately 24 h, and was followed by a series of smaller amplitude pulses (maximum salinities of 4–10‰) that lasted less than 12 h and tracked the tidal cycle. Continuous records of bottom salinity in Cedar Cove (Station KB2) showed a similar influx of high salinity water coincident with each storm event and a more gradual return to pre-storm conditions, generally within 2.5 d. This pattern is indicative of mixing and dilution due to the large volume of freshwater entering Kings Bay from the spring system.

Hurricanes altered the biomass and percent cover of some SAV in Kings Bay in an unusual manner (Fig. 4). The post-hurricane declines in biomass and percent cover of *M. spicatum* and *H. verticillata* were not repeated between more typical summer and fall sampling periods in 2005.

In July 2004, before the hurricanes, the mean aboveground biomass of all vascular plants and macroalgae was estimated to be 226.5 g dw m^{-2}. The mean percent cover derived from samples collected at 71 stations was 70.4%. Filamentous algae, primarily *Lyngbya* sp., dominated the bay in terms of biomass (180.5 g dw m^{-2}) and cover (38.3%; mean cover per station). The dominant macrophytes were *M. spicatum* (aboveground biomass of 18.6 g dw m^{-2} and mean cover of 18.8% per station), *H. verticillata* (aboveground biomass of 9.5 g dw m^{-2} and mean cover of 8.0% per station), and *V. americana* (aboveground biomass of 4.7 g dw m^{-2} and mean cover of 5.4% per station). In combination, these three species accounted for ca. 84% of the vascular plant biomass.

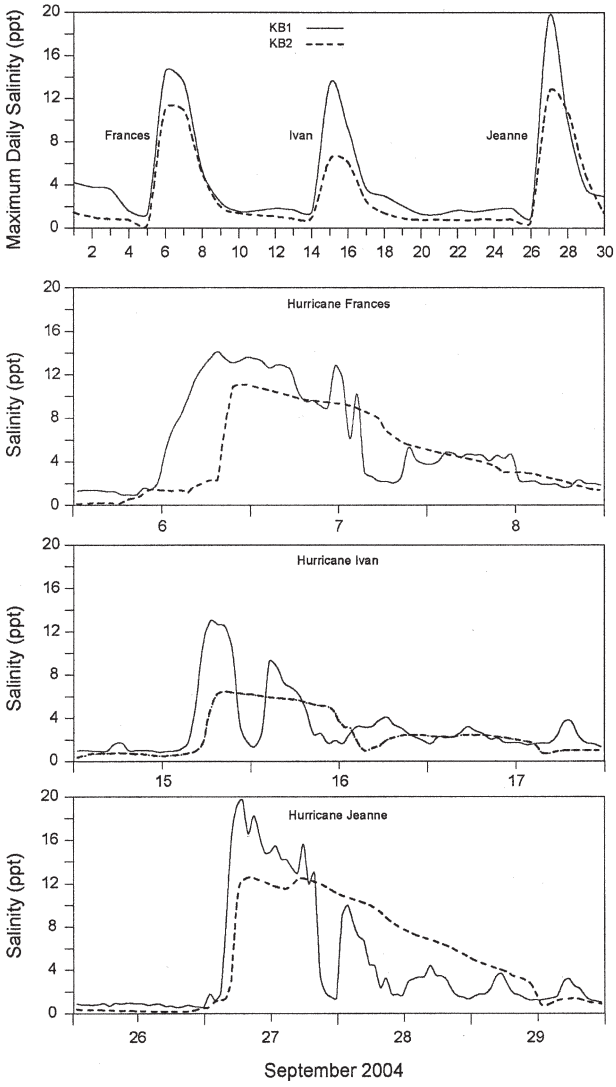

Fig. 3. Salinities recorded in Kings Bay in association with Hurricanes Frances, Ivan, and Jean. Solid lines are for station KB1 (mouth of the bay) and dashed lines are for station KB2 (interior of the bay).

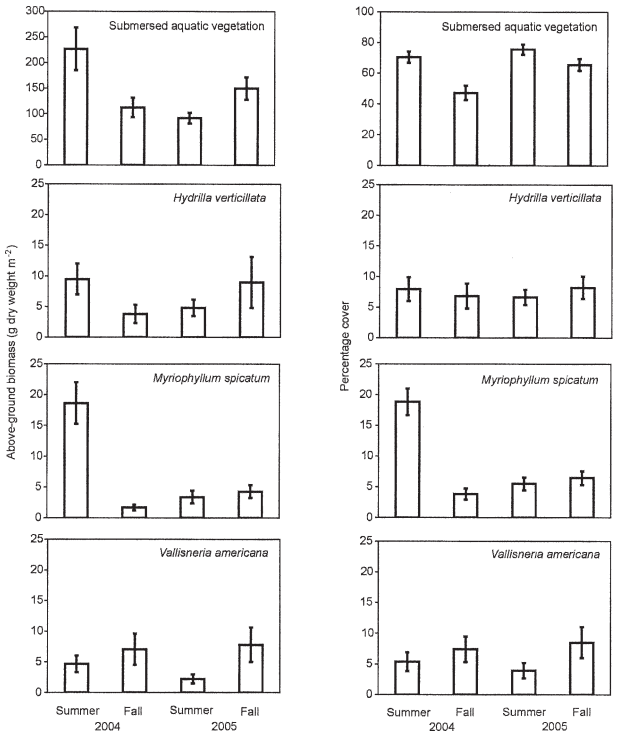

Fig. 4. Mean aboveground biomass and percent coverage (± SE) for total submersed aquatic vegetation (SAV), *Hydrilla*, *Myriophyllum*, and *Vallisneria* in Kings Bay during summer 2004 (pre-hurricanes) and fall 2004 (post-hurricanes). Data for summer and fall 2005 (a time interval in which no storms affected Kings Bay) are provided for comparison. Biomass values for total SAV, *Hydrilla*, *Myriophyllum*, and *Vallisneria* are given in panels a–d, respectively.

In October 2004, following the passage of Hurricanes Frances, Ivan, and Jeanne, mean aboveground biomass of all SAV in Kings Bay was estimated to be 112.3 g dw m^{-2}, a significant 51% reduction from the pre-storm sampling period (ANOVA, df = 3, MS = 51.4, $p < 0.0001$; Tukey–Kramer HSD follow-up pairwise test, $p < 0.05$). Macroalgal and vascular plant biomass were reduced by 48% and 60%, respectively. The mean percent cover derived from samples collected at 71 stations was 47.2%, i.e., a significant, 33% reduction from the pre-storm estimate (ANOVA, df = 3, MS = 25631.7, $p < 0.0001$; Tukey–Kramer HSD follow-up pairwise test, $p < 0.05$). With regard to vascular plants, *M. spicatum* was particularly affected; it exhibited a statistically significant 83% decrease in aboveground biomass (ANOVA, df = 3, MS = 81.6, $p < 0.0001$; Tukey–Kramer HSD follow-up pairwise test, $p < 0.05$). The aboveground biomass of *H. verticillata* also declined significantly after the storms, but only by 47% (ANOVA, df = 3, MS = 6.8, $p < 0.0117$; Tukey–Kramer HSD follow-up pairwise test, $p < 0.05$). *V. americana* exhibited an 18% increase in aboveground biomass, although changes in biomass for this species were not statistically significant (ANOVA, df = 3, MS = 5.1, $p > 0.3481$). Mean cover estimates for *M. spicatum* declined by 79.8% between the pre-hurricane and post-hurricane sampling periods (ANOVA, df = 3, MS = 28526.3, $p < 0.0001$; Tukey–Kramer HSD follow-up pairwise test, $p < 0.05$). Although cover estimates for *H. verticillata* decreased by 15.0% during the same interval, this change was not statistically significant (ANOVA, df = 3, MS = 258.9, $p < 0.3580$). Consistent with the observed increase in biomass, mean cover estimates for *V. americana* increased by 37.0%. Although a significant effect on *V. americana* cover was evident in the general test, the pairwise follow-up was not significant (ANOVA, df = 3, MS = 671.6, $p < 0.0511$; Tukey–Kramer HSD follow-up pairwise test, $p > 0.05$).

Discussion

Salinity represents a primary determinant of long-term patterns in the abundance and distribution of plants in spring-fed rivers along Florida's Gulf coast (Hoyer et al. 2004). In the Crystal River system, Haller et al. (1974) observed that both *H. verticillata* and *M. spicatum* were present at the head of the river in Kings Bay, but *H. verticillata* disappeared in the lower river and *M. spicatum* became dominant. Based on laboratory work to estimate salinity tolerances, they postulated that differences in this trait could explain the distribution of these two plants. Other observations support these results. In the Potomac River estuary, *H. verticillata* does not exist at salinities greater than 2‰ (Rybicki et al. 1985). Although Haller et al. (1974) observed suppressed growth of *V. americana* in salinities as low as 6.66‰ and mortality in 13.32‰, their study was carried out over 4 wk under static conditions. Their findings probably do not reflect the ability of this species to tolerate storm-induced tidal surges and other short-term variations in salinity. As noted by Twilley and Barko (1990, p. 319), ''fluctuations in salinity may be as important a factor as mean concentrations in determining the distribution of these eurysaline macrophytes in estuarine waters.''

There is indirect evidence that short-term changes in salinity can alter the distribution of plants in the Crystal River system. Terrell and Canfield (1996) analyzed presence-absence data for SAV in Kings Bay collected between 1979 and 1994, and they attributed precipitous declines in *Hydrilla* and filamentous algae during March and April 1993 to a catastrophic storm, the ''Storm of the Century.'' *V. americana* and *M. spicatum* were not immediately affected by this storm. Although field data were not available, the extensive flooding

caused by tidal surges driven by the storm suggested that increased salinity contributed to the observed changes. In a subsequent study, Mataraza et al. (1999) suggested that declines in SAV in Kings Bay following three separate storms, i.e., Hurricane Elena in September 1985, the ''Storm of the Century'' in March 1993, and Tropical Storm Josephine in October 1996, were due to increased salinity as a consequence of tidal surges, but they also lacked salinity data to substantiate their claim.

Short-term changes in SAV may have long-term effects on vegetation patterns. Mataraza et al. (1999) suggested that high salinities associated with catastrophic storms might eliminate dominant macrophytes, allow other species to proliferate, and maintain plant diversity in Kings Bay, i.e., act as intermediate forms of disturbance (Connell 1978; Sousa 1979). These investigators observed that some common macrophytes and algae in Kings Bay responded differently to storms. *M. spicatum* recovered more quickly than did *H. verticillata* after Hurricane Elena, and *V. americana* appeared to be largely unaffected by acute disturbance.

Our study combines controlled experiments and field data to elucidate responses of SAV to pulsed salinity events. The study also generates insights into the intermediate disturbance hypothesis and competition between introduced and native species because it provides data for two invasive and one native species.

Experiments showed that short-term (1–7 d) exposures to salinities of 15‰ or 25‰ significantly affected growth and survival of *V. americana*, *H. verticillata*, and *M. spicatum*. Measures of growth for all three species decreased significantly, except for elongation of blades in *V. americana* following 1-d or 2-d exposures to 15‰ and addition of turions by *H. verticillata* in all treatments. These exceptions may be related to a lack of statistical power in the follow-up tests rather than a lack of response to higher salinities because ANOVAs indicated a significant effect overall and growth decreased following exposure to 15‰ and 25‰. *H. verticillata* was particularly sensitive to higher salinities because all plants died following even 1-d exposures to 15‰. Although all *V. americana* and *M. spicatum* plants survived 1-d and 2-d exposures to 15‰, 25% to 100% of these plants died following exposures of 7 d to 15‰ or 1, 2, or 7 d to 25‰. Other studies also point to similar variation in salinity tolerance among these species. Twilley and Barko (1990) found that growth of *V. americana* was unaffected by salinities up to 12‰, and Doering et al. (1999) reported growth in salinities up to 15‰. In a subsequent study, Doering et al. (2001) found that mortality of *V. americana* occurred at salinities of 18‰, but duration of exposure was important. Field observations suggest that *M. spicatum* can withstand salinities up to 15‰ (Twilley and Barko 1990), but Haller et al. (1974) noted that plants stopped growing when exposed to 13.32‰ and died when exposed to 16.65‰ for 4 wk. *H. verticillata* plants did not grow in 6.66‰ and died when exposed to 10‰ (Haller et al. 1974). These findings clearly indicate that rapid, storm-induced changes in salinity have the potential to markedly influence the growth and survival of these three macrophytes, which, in combination with filamentous macroalgae, comprise the bulk of the SAV in Kings Bay (Notestein et al. 2005).

Field data showed that hurricanes raised salinities at the mouth of Kings Bay to near or above 15‰ for three 1-d periods during October 2004. Such events may occur on a regular basis. In September 2000, Tropical Storm Gordon passed west of Crystal River, and bottom salinities in excess of 15‰ were recorded at the mouth of Kings Bay (Frazer et al. 2001b). The shallow sill near the mouth of the bay acts as a natural barrier that serves to temporarily entrain high-density salt water forced into the bay during storms (Frazer et al. 2001b). Salinities near the bottom in the bay's interior remain elevated for more than 2 d following each storm, albeit decreasing from the maximum measured at the mouth of Kings Bay due to dilution from the continuous discharge of groundwater out of the numerous springs in the system.

Our experiments predicted the observed declines in the biomass and coverage of *H. verticillata* and *M. spicatum* in Kings Bay following three hurricanes in 2004. Our results are consistent with findings reported by Mataraza et al. (1999). Our experiments did not predict that *M. spicatum* biomass and percent cover would decrease more than biomass and percent cover of *H. verticillata*. Experiments indicated that *H. verticillata* was more sensitive to salinity pulses and *M. spicatum* should survive 1–2 d exposures to salinities of 15‰. *M. spicatum* exhibited marked decreases in growth when exposed to salinities of 15‰ or higher. The mean aboveground biomass added by *M. spicatum* exposed to salinities of 15‰ was approximately an order of magnitude less than that for plants exposed to lower salinities. Haller et al. (1974) observed that *M. spicatum* subjected to salinities of approximately 13‰ for 4 wk did not grow, and McGahee and Davis (1971) reported a reduced capacity for photosynthesis at 16‰. In combination, these findings suggest that salinities of 15‰ or higher cause considerable stress in *M. spicatum*. Multiple exposures to high salinities caused by a series of hurricanes and a compounding of stress may explain the precipitous decline in biomass and coverage of this macrophyte in Kings Bay during 2004. We are not aware of studies investigating the effects of multiple high-salinity

pulses on *M. spicatum* or other aquatic plants. Such studies may clarify the influence of salinity on the abundance and distribution of SAV in estuaries.

In our experiments, *V. americana* added fewer blades, exhibited shorter blade lengths, had fewer clones, and less aboveground and belowground biomass after short-term exposure to salinities of 15‰ or higher, but plants died only after exposures to 15‰ for 7 d or exposures to 25‰. Overall these results lead to a prediction that this species would be stressed, but able to tolerate rapid, short-lived (< 2 d) pulses of high salinity water, such as those resulting from the storm events in 2004. *V. americana* survived the storm-induced salinity pulses in 2004, and its biomass and percent cover increased during pre-hurricane and post-hurricane samplings. Mataraza et al. (1999) also observed no significant effects on the frequency of occurrence of *V. americana* in Kings Bay following three separate storms, and Doering et al. (2001) observed that *V. americana* acclimated to 18‰ persisted for more than 11 d without significant affects on growth when plants were returned to more typical salinities. *V. americana* appears to survive or adapt to higher salinities fairly readily, which may provide a competitive advantage over *H. verticillata* and *M. spicatum.*

Although our study does not directly address competition between the *H. verticillata*, *M. spicatum*, and *V. americana*, other studies indicate that *V. americana* may compete with the invasive *H. verticillata* and *M. spicatum*. In low salinity conditions, *H. verticillata* can form dense canopies that inhibit growth of other submersed macrophytes including *V. americana* (Van et al. 1999; see also Rybicki and Carter 2002), and *M. spicatum* has been shown to exclude *V. americana* in Kings Bay and elsewhere (Lind and Cottam 1969; McFarland and Rogers 1998; Hauxwell et al. 2004a). In combination with the results of our experiments and field sampling, these results suggest that pulses of higher salinity may act as intermediate disturbances that allow *V. americana* to outcompete invasive species, and they suggest that slightly higher salinity may support efforts to revegetate Kings Bay with *V. americana* (cf. Mataraza et al. 1999).

The results of our study provide insights into how acute salinity pulses due to major storm events can drive patterns in biomass and distribution of key species, influence interactions among invasive and native species, and affect restoration. These insights point to the value of competition experiments with salinity as a mediating factor when managing aquatic invasive plants or designing revegetation efforts.

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