Biological Sciences

Spatial patterns of submerged macrophyte communities in select Florida spring-run streams: A review with new data

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Abstract Florida springs and the spring-run streams they create ("springs" for brevity) support extensive/dense communities of submerged aquatic vegetation (algae and macrophytes). Surveys of these communities in many springs using various methods have been conducted in the past, but no attempt has been made to conduct cross-system comparisons to elucidate spatial patterns in submerged aquatic vegetation among different springs. This study compared recent and prior submerged macrophyte community data from selected Florida springs and discussed spatial patterns observed. In particular, a distinct dichotomy was seen, with some spring macrophyte communities entirely dominated by *Sagittaria kurziana* and others by *Vallisneria americana*. In springs where both species occurred, *Sagittaria* was generally found to be the dominant plant in upstream reaches and *Vallisneria* was dominant or co-occurred with *Sagittaria* downstream. Comparison of data collected from prior field and mapping surveys of submerged vegetation conducted in these and other spring-run streams confirms these patterns. This dichotomy of "Sagittaria springs" versus "Vallisneria springs" prompts the question of what environmental drivers create these differences. A better understanding of this may help explain the shifts in vegetation that have been seen in spring-run streams over the past few decades.

Keywords Aquatic plant communities, Florida springs, spring ecology, stream ecology

Introduction

The springs of Florida and the streams they create (spring-run streams) have for centuries attracted the people who live in and visit the area. Ancient cultures, authors, artists, entrepreneurs, tourists, and scientists have all been drawn to Florida springs. The remarkable water clarity of these systems has been extolled by early explorers and visitors (Bartram 1791, Revels 2016) and has been scientifically investigated in both historic (LeConte 1861) and recent times (Duarte and Canfield 1990a, Szafraniec 2014). One of the first "modern" studies that defined the discipline of aquatic ecology was conducted in a Florida spring (Silver Springs; Odum 1957a); this and more recent studies (Duarte and Canfield 1990b) have shown that Florida springs are one of the most productive aquatic ecosystems on earth. More recently, a great deal of scientific and management attention has been

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devoted to Florida springs and spring-run streams due to documented declines in water quality (primarily significant increases in concentrations of nitrogen as nitrate), reductions in spring discharge, and changes in submerged aquatic vegetation communities including shifts from dominance by vascular macrophytes to a dominance of benthic filamentous algal mats or significant increases in epiphytic algal coverage (Florida Springs Task Force 2000, Scott et al. 2004, Munch et al. 2006).

While there has been a considerable body of research conducted on Florida springs, and the spring-run streams to which they give rise (hereafter, "springs" for brevity), there have been few cross-system comparisons of the hydrologic, chemical, and/or biological characteristics of springs, examining similarities and differences to elucidate patterns. In particular, the pioneering work of H.T. Odum in Florida springs "set the tone," in that he specifically remarked on the relatively constant physical (discharge) and chemical/water quality characteristics of springs (Odum 1957a, 1957b), leading to a perception that they are all similar and unvarying (Jacoby et al. 2008). Odum and his co-workers actually sampled a number of Florida springs under a grant from the Office of Naval Research (e.g., Odum 1957b), but much of those data are unpublished. The few cross-system studies among springs that have been published in fact indicate a diversity of aquatic ecosystems (Jacoby et al. 2008) with differences in water chemistry (Odum 1957b, Slack and Rosenau 1979, Woodruff 1993), algal and aquatic plant communities (Whitford 1956, Duarte and Canfield 1990b), and faunal communities (Walsh et al. 2009). A comprehensive literature review of the ecology of Florida springs has been conducted (Brown et al. 2008), but it was mainly focused on evaluating the impacts of nutrient enrichment on springs and not on a comparison among them, per se.

In this paper, data are presented from springs studies conducted by the St. Johns River Water Management District in Florida over the past decade and these are compared with existing published studies of springs to: 1) Examine spatial patterns in the submerged macrophyte (flowering, vascular plant) communities of Florida springs to evaluate similarities and differences; 2) Present results from a recent survey and annual monitoring of the submerged macrophyte communities of selected springs for the past decade to evaluate spatial patterns; 3) Review and compare these results with existing historical data from studies in springs to confirm spatial characteristics of springs macrophyte communities; 4) Identify physical/chemical characteristics that may be responsible for any botanical differences identified (or suggest avenues for further research).

Materials and Methods

The new work presented in this paper resulted from two projects conducted by the St. Johns River Water Management District (SJRWMD): (1) a synoptic biological survey of 14 spring-run streams in north and central Florida, and (2) annual surveys of submerged vegetation in springs within the St. Johns River basin.

Synoptic Biological Survey of 14 Springs. As part of a broader effort to understand and manage the springs of the St. Johns River basin, the SJRWMD contracted for a comprehensive biological survey in 14 spring-run stream ecosystems in north and central Florida (Table 1; hereafter the "synoptic study").

Table 1. Spring-run streams and site identifications in the SJRWMD Synoptic Study (2015). See Mattson et al. (2019) for site location coordinates.

Stream System	Upstream Transect	Downstream Transect	River Basin
Alexander Springs Creek	ALE1	ALE2	St. Johns
Volusia Blue Spring Run	VOL1	-	St. Johns
Gum Slough	GUM1	GUM2	S. Withlacoochee
Ichetucknee River	ICH1	ICH2	Santa Fe
Juniper Creek	JUN1	JUN2	St. Johns
Manatee Spring Run	MAN1	-	Suwannee
Rainbow River	RAI1	RAI2	S. Withlacoochee
Rock Springs Run	ROC1	ROC2	St. Johns
Silver River	SIL1	SIL2, SIL3	Ocklawaha
Silver Glen Spring Run	SLG1/SILG1	-	St. Johns
Wacissa River	WAC1	WAC2	Aucilla
Wakulla River	WAK1	WAK2	St. Marks
Weeki Wachee River	WEE1	WEE2	Southern Coastal
Wekiva River	WEK1	WEK2	St. Johns

In most systems, two transect locations were established; one near the headspring area and one downstream in the spring-run stream proper. Three transect locations were established on Silver River (one near the headspring complex and two downstream). These locations were selected to represent and capture the variability across different hydrogeomorphic patches or reaches, also called functional process zones, which control ecological structure within the spring-run stream ecosystem (Thorp et al. 2006). One transect location was established on systems with shorter spring runs (Manatee Spring, Volusia Blue Spring, and Silver Glen Spring) that did not feature multiple functional process zones. Two biological sampling efforts were conducted in the spring and fall of 2015.

Sampling at each transect involved systematic deployment of five replicate 1 m^2 quadrat locations across the stream channel perpendicular to the channel thalweg. Submerged macrophyte communities were sampled by estimating vegetation cover, by species, in the quadrats. Three replicate biomass samples of macrophytes (above-ground portion) were collected from within three of these quadrats using a modified Hess sampler, and returned to the laboratory on ice. In the laboratory, macrophytes were sorted by species, cleaned of algal epiphytes and epiphytic invertebrates, dried at 100 °C to constant weight, and dry weight measured. More detailed descriptions of sampling and analysis methods in this study were reported in AMEC (2016) and Mattson et al. (2019).

Because the data were collected non-randomly, conventional parametric and non-parametric statistics were considered inappropriate to use. Exploratory analyses were conducted by summarizing the data graphically (using a routine written in the R statistical package by M.Q. Guyette) and conducting multivariate analyses using the PRIMER™ software as described in Mattson et al. (2019).

Annual Surveys of Submerged Vegetation in St. Johns River Basin Springs. In 2009, SJRWMD staff began conducting annual surveys of submerged aquatic vegetation (SAV – algae and macrophytes) in five spring-run stream ecosystems in the St. Johns River basin (Table 2; hereafter the "annual surveys"). Silver River was added to this effort in 2012 and Blue Spring Run (Volusia County) was added in 2017. Transect locations were established systematically down the run of each stream, beginning at the headspring and finishing either at the confluence with another stream or at a downstream take-out location. Transects extended across the stream channel from bank-to-bank perpendicular to the thalweg.

At each transect, SAV cover was estimated using the Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974), a categorical scale which measures cover as: 1 – <5% cover, 2 – 5-25% cover, 3 – 25-50% cover, 4 – 50-75% cover, 5 – 75-100% cover. Cover was estimated in five (5) 0.25 m^2 quadrats deployed along the transect across the stream channel. Where the channel was <15 m in width, quadrats

Table 2. Spring-run streams sampled in the SJRWMD Annual Surveys (2009-2019). Contact the corresponding author for site location coordinates.

Stream System	Number of Transects	Sampling begun	County
Alexander Springs Creek	15	2009	Lake
Volusia Blue Spring Run	5	2017	Volusia
Juniper Creek	15	2009	Marion
Rock Springs Run	16	2009	Orange
Silver River	12	2012	Marion
Silver Glen Spring Run	10	2009	Marion/Lake
Wekiva River	25	2009	Orange/Seminole/Lake

were deployed systematically from bank-to-bank; where >15 m wide, quadrats were deployed randomly along the transect (using a random number table). Submerged macrophyte cover was estimated for each plant species. Cover data were graphically summarized, and raw data were transformed ($\log_{10}$ X+1), summarized by sampling site, and differences among springs were analyzed using one-way ANOVA and Tukey's Multiple Comparison Test. Graphical and statistical analyses were performed using Minitab™ version 18.

Results and Discussion

A total of 25 taxa of submerged plants have been historically reported from spring-run streams in Florida (Table 3). Two of these are genera of green algae (Chlorophyta) but are typically included as "macrophytes" due to their erect, branching habit (versus the filamentous, mat forming taxa of green algae). One genus is a bryophyte (*Fontinalis* spp.); the remainder are all flowering, vascular plants. Of these, nine taxa of submerged macrophytes were collected in the synoptic study and 14 taxa were observed over the 11 years of the annual surveys (2009-2019; Table 3). Some macrophytes, e.g., the grass *Zizania aquatica* and the floating-leaved *Nuphar advena* and *Hydrocotyle* spp. begin as submerged plants but eventually grow out of the water and become emergent plants; these were not included as "submerged macrophytes".

Total macrophyte cover ranged from 0 to 100% across all transects in the synoptic study. Volusia Blue Spring and Manatee Spring Runs did not support any macrophytes. Most frequently observed/collected taxa among the 12 springs supporting macrophytes (in both spring and fall 2015) were *Vallisneria americana*, *Sagittaria kurziana*, and the exotic *Hydrilla verticillata* (Mattson et al. 2019). These will be referred to by genus. Mean total dry weight biomass (all macrophyte species combined) ranged from 0 to 1,267 g/m^2 (the latter at SIL1, the upstream Silver River transect in fall 2015). Duarte and Canfield (1990b) sampled submerged macrophytes across 31 different Florida springs and observed a range from 0 to 1,562 g/m^2 mean dry weight (the high value in Wacissa River). They reported their data as wet weight; these were converted to dry weight by multiplying their values by a conversion factor of 0.061 (obtained from Odum 1957a). They did not report standing crop by individual SAV species or taxa.

In the synoptic study, a pronounced dichotomy was found in the occurrence and abundance of *Sagittaria* versus *Vallisneria* among the springs which supported one or both. In some springs, *Sagittaria* was the dominant plant, by both cover

Table 3. List of submerged macrophytes recorded from Florida spring-run streams. 1-collected in SJRWMD synoptic study; 2-observed in SJRWMD annual surveys. **- may have been identified as *Rorippa* spp. in historic surveys.

Chlorophyta	Najadaceae
Chara spp. [1,2]	*Najas guadalupensis* [1, 2]
Nitella spp. [2]	
	Nymphaceae
Bryophyta	*Cabomba* spp.
Fontinalis spp. [2]	
	Onagraceae
Angiospermophyta	*Ludwigia repens*
Alismataceae	
Sagittaria kurziana [1, 2]	Potamogetonaceae
Sagittaria subulata/graminea [2]	*Potamogeton diversifolius*
	Potamogeton illinoensis [1]
Ceratophyllaceae	*Potamogeton pectinatus* (*Stuckenia pectinata*) [1, 2]
Ceratophyllum demersum [1, 2]	*Potamogeton pusillus*
Cruciferae	Ruppiaceae
Nasturtium spp.**	*Ruppia maritima* [2]
Halagoraceae	Scrophulariacea
Myriophyllum heterophyllum	*Bacopa caroliniana*
Myriophyllum spicatum	*Gratiola virginica* [2]
Myriophyllum sp. [2]	*Micranthemum* sp.
Hydrocharitaceae	Zannichelliaceae
Egeria densa	*Zannichellia palustris* [2]
Hydrilla verticillata [1, 2]	
Vallisneria americana [1, 2]	
Lentibulariaceae	
Utricularia sp.	

(Figure 1) and dry weight standing crop (Figure 2), while in others, *Vallisneria* was dominant (Figures 1 and 2). In two springs (the Ichetucknee and Wakulla Rivers), *Sagittaria* was more dominant at the upstream transect and *Vallisneria* at the downstream (Figures 1 and 2). In two springs (Rainbow and Silver Rivers), *Sagittaria* was dominant upstream and *Vallisneria* co-occurred with *Sagittaria* at the downstream transect (Figures 1 and 2). These spatial patterns were seen in both spring and fall 2015 for both cover and dry weight. Cluster analysis of these data using the PRIMER software (Figures 3 and 4) showed two significant groupings of streams (both spring and fall 2015); those on the mainstem of the St. Johns River (SJR streams), and those not connected to the St. Johns (O for "Other" streams). ANOSIM analysis revealed the differences to be significant in both the spring and the fall (Cover - Spring: Global test R=0.418, sig.=0.002; Fall: Global test R=0.346, sig.=0.003; Dry Weight – Spring: Global test R=0.375, sig.=0.005; Fall: Global test R=0.310, sig.=0.006). In all analyses, SIMPER analysis revealed the main factor

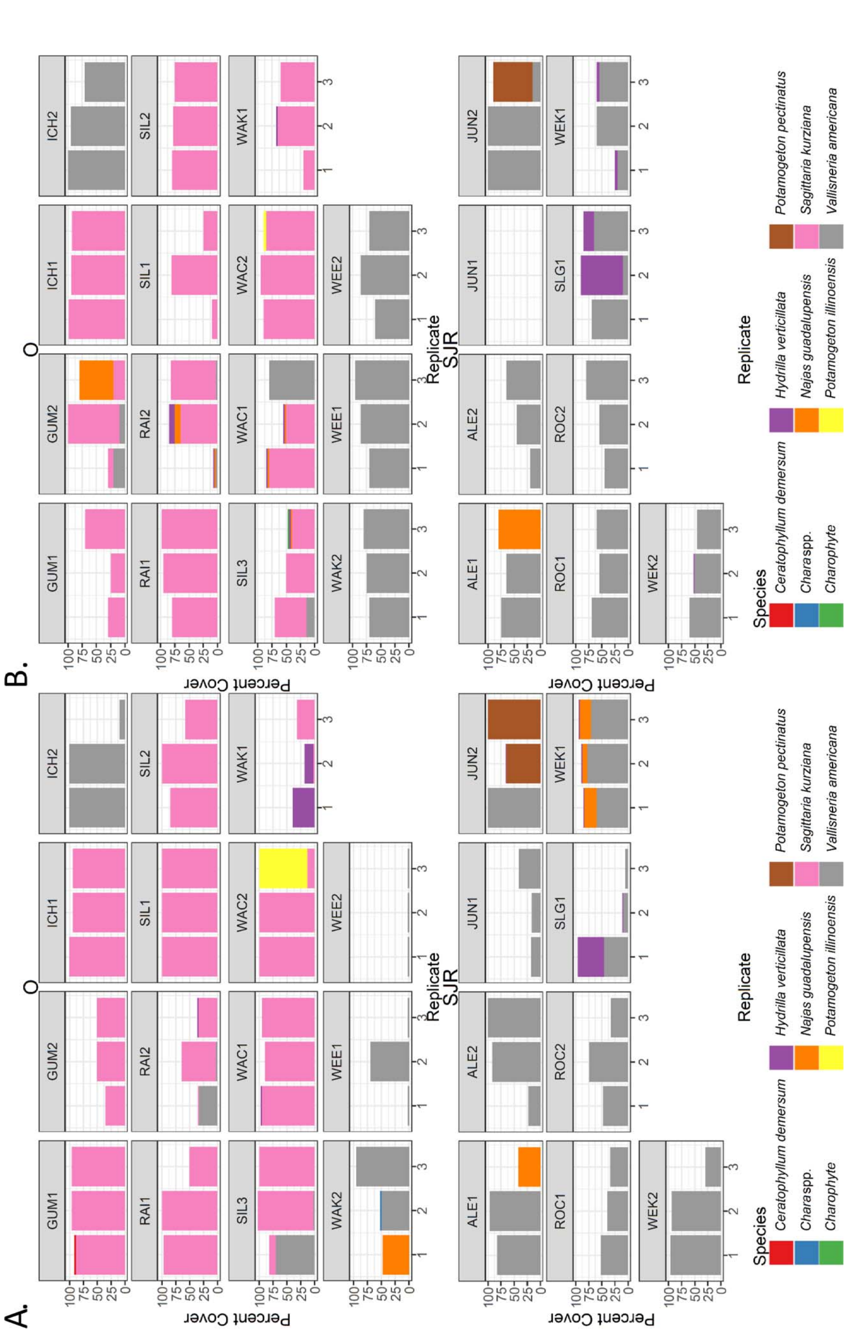


Figure 1. Percent cover of submerged macrophytes from 12 springs surveyed in the SJRWMD synoptic study in (A) spring and (B) fall 2015. Note that individual replicate samples are shown (X-axis) to enable assessment of variation. SJR – St. Johns River springs; O – Other springs (not on the St. Johns River). Station names in Table 1.

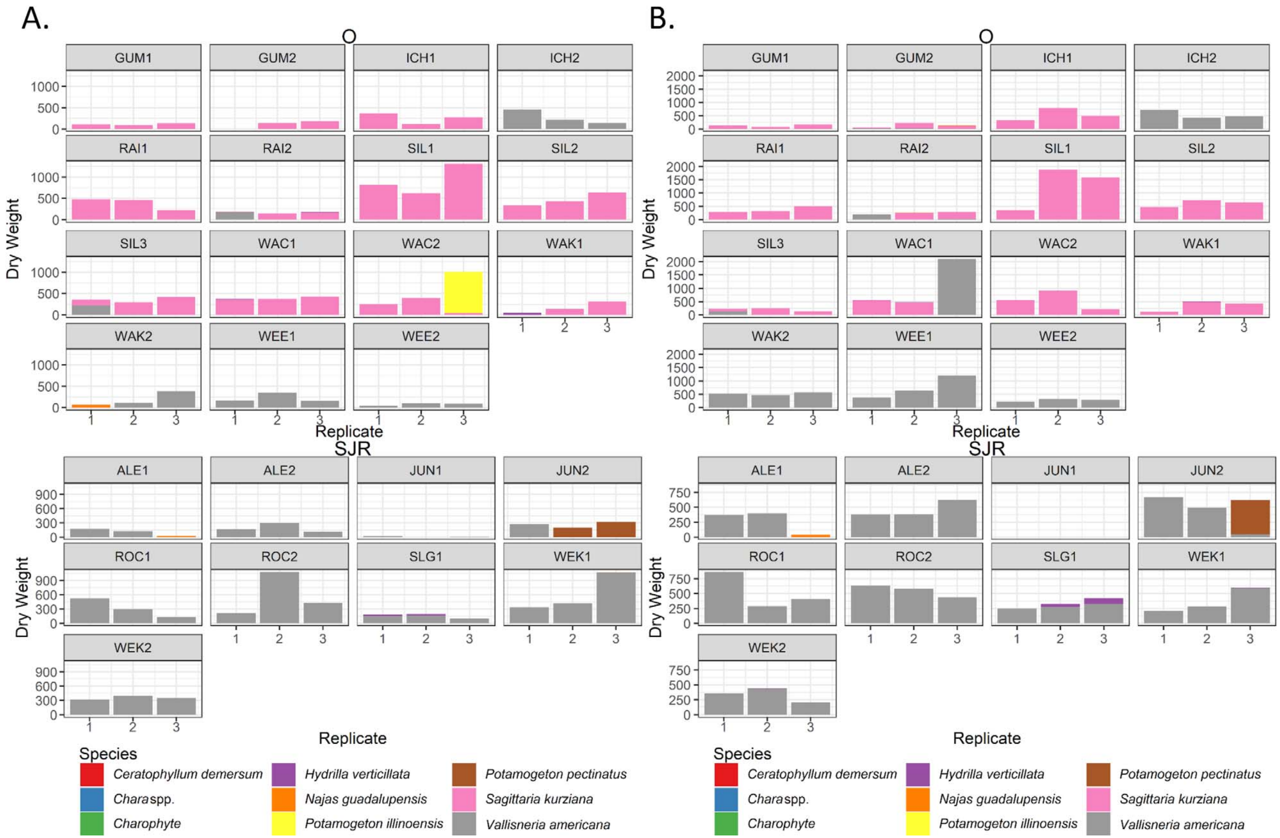


Figure 2. Dry weight (g/m^2) of submerged macrophytes from 12 springs surveyed in the SJRWMD synoptic study in (A) spring and (B) fall 2015. Note that individual replicate samples are shown (X-axis) to enable assessment of variation. SJR – St. Johns River springs; O – Other springs (not on the St. Johns River). Station names in Table 1.

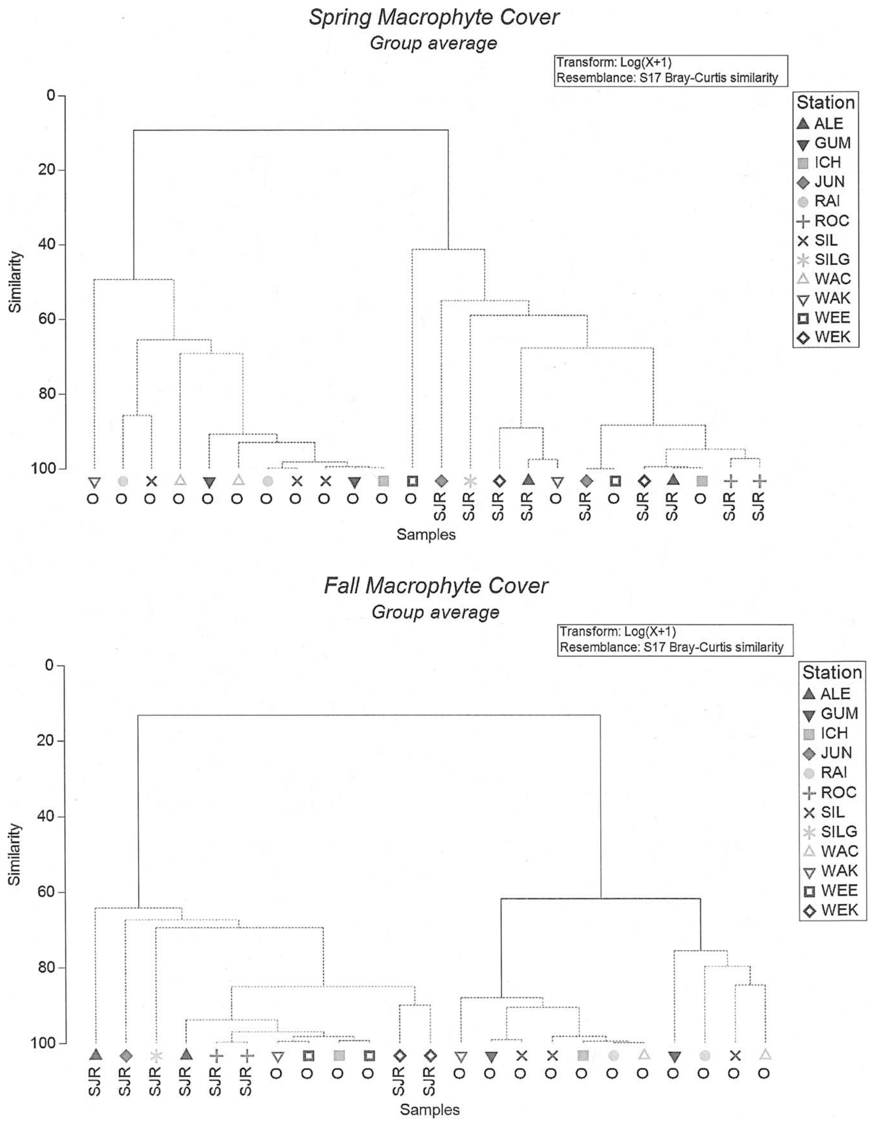


Figure 3. Cluster analysis diagrams of cover data spring and fall 2015. Clusters connected with a solid line are significantly different. SJR – St. Johns River springs; O – Other springs (not on the St. Johns River). Station names in Table 1.

driving the differences among springs was the abundance/dominance of *Vallisneria* or *Sagittaria*.

To support and assess the findings from the 2015 synoptic study, data on coverage of *Vallisneria* and *Sagittaria* from the SJRWMD annual surveys were summarized for selected sites from the 2015 annual surveys on Alexander Springs

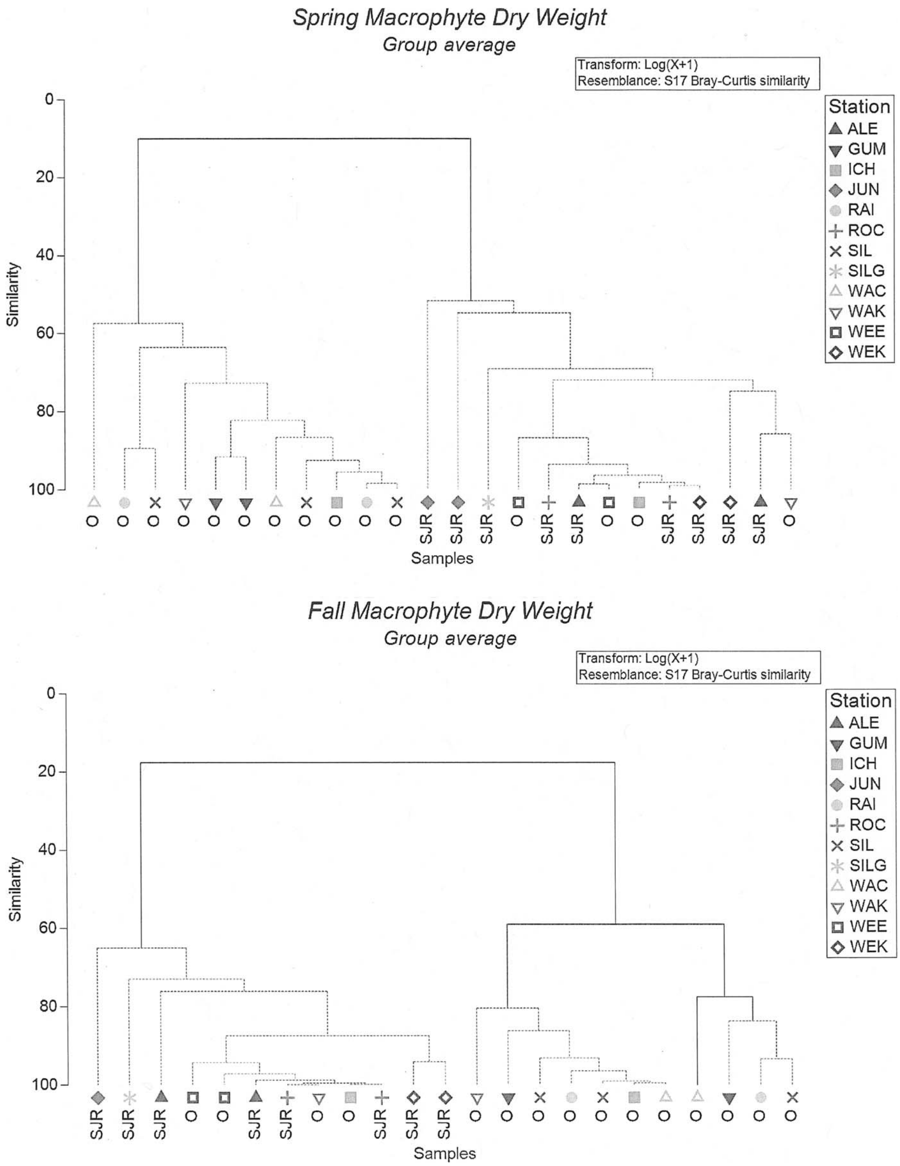
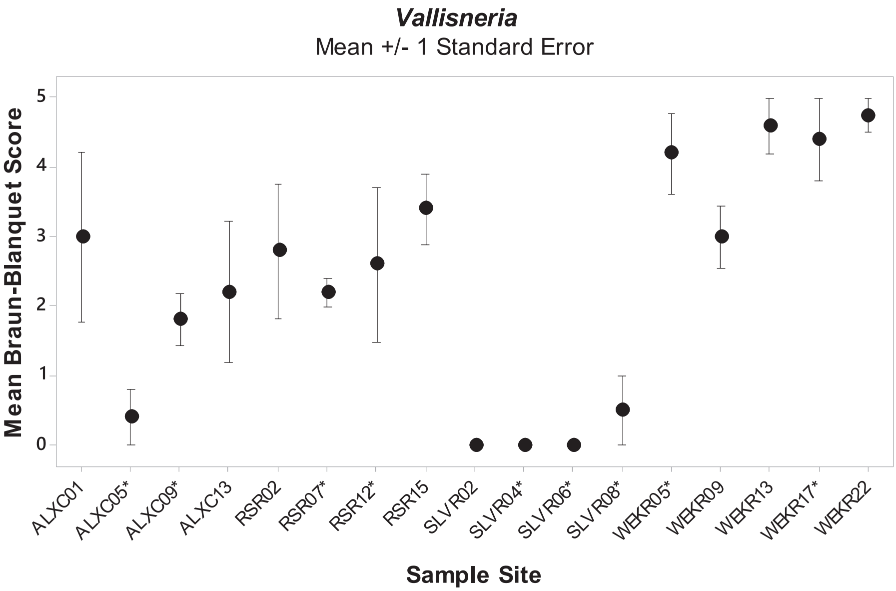


Figure 4. Cluster analysis diagrams of dry weight spring and fall 2015. Clusters connected with a solid line are significantly different. SJR – St. Johns River springs; O – Other springs (not on the St. Johns River). Station names in Table 1.

Creek (ALXC), Rock Springs Run (RSR), Silver River (SLVR), and Wekiva River (WEKR). The selected sites covered wide stretches of these springs (and encompassed the locations of the synoptic study transects), from the headspring to downstream locations near the terminus of the stream (RSR, SLVR, and WEKR)



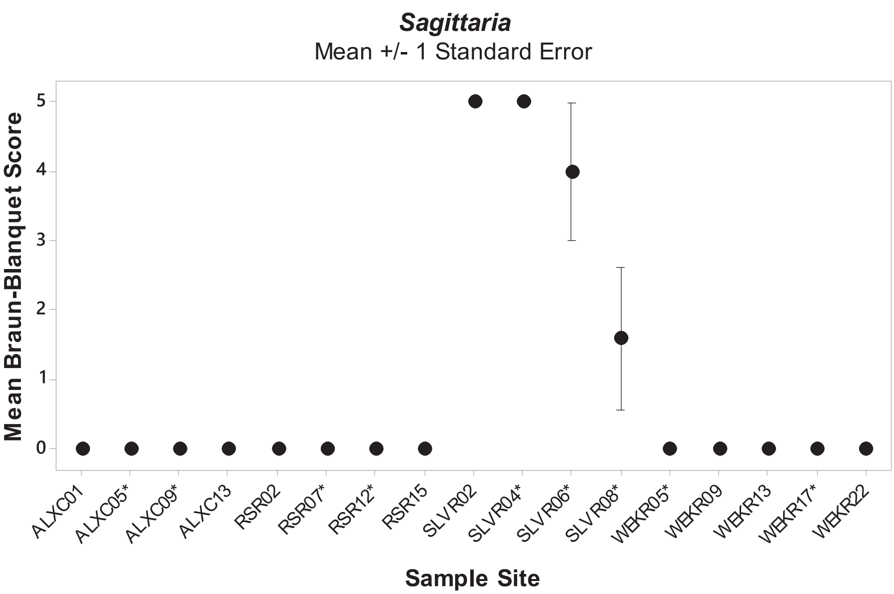


Figure 5. Mean cover (as Braun-Blanquet Score) of *Vallisneria* and *Sagittaria* at multiple sites (upstream-lower numbers to downstream-higher numbers) on Alexander Springs Creek (ALXC), Rock Springs Run (RSR), Silver River (SLVR) and Wekiva River (WEKR) from the 2015 SJRWMD annual surveys. N=5 at each sample site. * - indicates approximate location of 2015 synoptic study transects.

or the take-out point (ALXC). *Vallisneria* dominated coverage throughout ALXC, RSR, and WEKR (Figure 5). *Sagittaria* was dominant at all SLVR transects but declined in cover downstream and *Vallisneria* was present at the downstream locations (Figure 5). These results support those of the synoptic study. *Vallisneria* cover was significantly higher at ALXC, RSR, and WEKR ($F=30.01$; $P<0.001$; all sites combined on each stream), while *Sagittaria* cover was significantly higher on SLVR ($F=77.45$; $P<0.001$; all sites combined on each stream). Although not shown, *Vallisneria* dominated macrophyte cover in 2015 at all transects on Silver Glen Run; *Vallisneria* was generally dominant or co-dominant (with *Najas guadalupensis* or *Potamogeton pectinatus*) at many of the transects on Juniper Creek. *Sagittaria* was not observed in either Silver Glen or Juniper. These findings corroborate those of the synoptic study.

As a final "verification" of the occurrence of a spatial pattern within springs, data were reviewed from SAV mapping studies conducted on Alexander Springs Creek, Juniper Creek, Rock Springs Run, Silver Glen Run and Wekiva River in 2008 (Dial, Cordy and Associates 2008), Ichetucknee River in 2003 (PBS&J and UF 2003), and Rainbow River in 2005 (PBS&J and Woithe 2007). *Vallisneria* dominated the overall acreage of submerged macrophytes throughout the lengths of Alexander, Rock, Silver Glen and Wekiva, including the locations of the 2015 synoptic study transects (Dial, Cordy and Associates 2008). It was co-dominant with other taxa in Juniper. In the Ichetucknee River, *Sagittaria* dominated the acreage in the reach around ICH1 in the synoptic study (and generally throughout the mapped reach of the Ichetucknee), and *Vallisneria* co-dominated the acreage with *Sagittaria* in the reach around ICH2 (PBS&J and UF 2003). In the Rainbow River, *Sagittaria* dominated the overall acreage river-wide, and the river reach with RAI1, while *Vallisneria* co-occurred with *Sagittaria* in the reach with RAI2 and exhibited higher overall cover in the lower half of the river for the period 1996-2005 (PBS&J and Woithe 2007). These mapping studies support the findings of the synoptic survey, suggesting a long-term pattern of submerged macrophyte occurrence and stability regarding the distribution of *Vallisneria* and *Sagittaria* in Florida springs.

Other studies of submerged macrophytes in springs further support the occurrence of these spatial patterns (Table 4). Jackson Blue Spring (Jackson County), the Homosassa and Chassahowitzka Rivers support or supported only or predominantly *Vallisneria* (Frazer et al. 2006, Wetland Solutions, Inc. 2010), as does the Crystal River (Hauxwell et al. 2007). A 2014 survey of 20 transects down the length of the Silver River (Cohen et al. 2017) found *Sagittaria* to be the dominant plant, occurring in 80.2% of their sample quadrats, while *Vallisneria* occurred in 17.4% of their samples, indicating the dominance of *Sagittaria* in this stream. A 2003 survey of 31 transects in the Ichetucknee River (PBS&J and UF 2003) found *Sagittaria* occurring at 54% of the sample quadrats they surveyed (mainly at upstream transects; Table 4) and *Vallisneria* at 10% (mainly downstream transects; Table 4). Historically, Manatee Spring Run supported primarily beds of *Sagittaria* (PBS&J and UF 2003, R.A. Mattson, pers. observation). Frazer et al. (2006) showed that occurrence of *Sagittaria* was greater at upstream and that of *Vallisneria* at downstream locations on the Weeki

Table 4. Occurrence of *Vallisneria* and *Sagittaria* by locations from multiple spring-run stream studies. Note sampling locations in the different studies are not similar, except Station 1 is always at/near headspring; shaded square indicates the downstream-most station.

Vallisneria americana

Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Alexander[1]	X		X		X		X	X	X	X	X	X	X	X	X								
Chassahowitzka[2]	X	X	X	X	X	X	X	X															
Homosassa[2]			X	X	X	X	X	X	X	X													
Ichetucknee[3]																X		X			X	X	X
Juniper[1]	X	X	X	X		X	X		X		X				X								
Rainbow[5]	X	X	X	X	X	X	X	X	X	X													
Rock Springs[1]		X	X		X	X	X					X	X	X	X	X							
Silver[1,4]	X	X	X		X	X	X	X	X	X	X	X	X	X		X	X	X		X			
Silver Glen[1]	X	X		X	X	X	X	X	X	X													
Weeki Wachee[2]							X	X	X	X													
Wekiva[1]					X	X	X		X	X	X	X	X	X	X		X	X	X	X		X	

Sagittaria kurziana

Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Alexander[1]																							
Chassahowitzka[2]	X	X	X	X	X																		
Homosassa[2]																							
Ichetucknee[3]	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X
Juniper[1]																							
Rainbow[5]	X	X	X	X	X	X	X	X	X	X													
Rock Springs[1]																							
Silver[1,4]	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			
Silver Glen[1]																							
Weeki Wachee[2]	X	X	X	X																			
Wekiva[1]																							

1-SJRWMD annual surveys (2009-2019); 2-Frazer et al. 2006 (1998-2005); 3-PBS&J and UF 2003 (2003); 4-Cohen et al. 2017 (2014); 5-PBS&J and Woithe 2007 (1996-2005).

Wachee River (Table 4). Recent restoration efforts by the Southwest Florida Water Management District (SWFWMD) planted *Vallisneria* in upstream reaches on the Weeki Wachee River (Chris Anastasiou, SWFWMD, personal communication April 2018). This plant was the dominant macrophyte collected in the synoptic study on that river, although the upstream transect location was not in any of the planted areas. *Sagittaria* appears to have historically been more abundant in the upper reaches of Weeki Wachee but has declined over the past decade (S. Notestein, SWFWMD, personal communication April 2018). *Sagittaria* occurred in the Chassahowitzka River (Frazer et al. 2006); but in terms of frequency of occurrence it was a minor component of the SAV community and was found only in upstream reaches (Table 4). *Vallisneria* occurred throughout the Silver and Rainbow Rivers (Table 4), but overall it was more abundant downstream (Figure 5) and *Sagittaria* is the dominant submerged macrophyte in these rivers (this study and Cohen et al. 2017, PBS&J and Woithe 2007)

No other study to date has called attention to these spatial patterns within and among springs. *Sagittaria* or *Vallisneria* are often described as being the dominant submerged macrophyte in a particular spring and its run (Clewell 1991), but the spatial patterns in the distribution of these two plants within and among springs has not been specifically identified. Some spring-run streams are or were dominated by *Sagittaria* (Silver River, Rainbow River, Ichetucknee River, Manatee Spring Run), while others are or were dominated by *Vallisneria* (Alexander Springs Creek, Chassahowitzka River, Homosassa River, Rock Springs Run, Wekiva River). In streams where the two co-occur, the tendency is for *Sagittaria* to be more prevalent/dominant upstream and *Vallisneria* more prevalent/dominant downstream (i.e., Ichetucknee, Wakulla, Silver, and Rainbow rivers).

What factors may be responsible for these patterns? Analysis of water quality data collected concurrent with the biological data in the synoptic survey indicated that the SJR springs generally had higher conductivity (Mattson et al. 2019), and it is known that many springs of the St. Johns River have a higher dissolved solids content due to the presence of an underlying layer of relict seawater beneath the river corridor (Slack and Rosenau 1979, Woodruff 1993). This could be one reason for the plant community differences, although the chemistry of some SJR springs (e.g., Rock Springs, Wekiwa Springs) is similar to O springs, such as Weeki Wachee, Rainbow, and Silver. The Homosassa and Chassahowitzka Rivers and their springs are also characterized by higher dissolved solids concentrations (Frazer et al. 2006, Woodruff 1993), and they are dominated by *Vallisneria* as well. The salinity tolerance of *Vallisneria* has been well-studied (Bortone et al. 1998), and this species is frequently found in upper-estuarine and tidal reaches of Florida rivers. However, the salinity tolerance of *Sagittaria* does not appear to be as well studied.

Light regime is a major factor influencing the occurrence and abundance of submerged macrophytes in streams (Hynes 1970), including Florida springs (Odum 1957a, Duarte and Canfield 1990b, Szafraniec 2014). Where both *Vallisneria* and *Sagittaria* occur in the same stream, the lower reaches, where *Vallisneria* is more abundant, may experience periods of reduced water clarity (higher color and turbidity) due to surface water influence, either via watershed runoff and/or backwater "intrusion" from a downstream river (e.g., the lower Silver River is influenced by the adjacent Ocklawaha River). *Sagittaria* appears to have more narrow light requirements than *Vallisneria* (Szafraniec 2014), suggesting it cannot tolerate the periods of reduced light occasionally present in downstream reaches of springs. Szafraniec (2014) evaluated the effects of the various components influencing the submerged light regime and found that the dissolved organic carbon that contributes to water color intercepts light primarily in the blue portion of the spectrum. This may have implications for occurrence of *Sagittaria*, as it has a particular minimum light requirement in the blue portion of the light spectrum for growth and production (Szafraniec 2014). Streams where *Vallisneria* is predominant throughout, even if fed largely by lower-conductivity springs, may occasionally experience periods of high color during higher flows (upper Wekiva River, Rock Springs Run). This may explain the lack of *Sagittaria* in these streams.

Sediment type/composition is known to be an important determinant of the occurrence of submerged macrophytes in streams (Butcher 1933, Hynes 1970), but there appears to be very little research done on the interaction of sediments and macrophytes in Florida springs. Cohen et al. (2017) conducted correlative analyses on bottom sediment properties and submerged macrophyte cover from 20 stations sampled down the length of the Silver River and found that sediment characteristics explained a relatively low amount of the variation in macrophyte cover (~18%). Macrophyte cover was negatively correlated with % clay content of sediment; this could relate to a plethora of physical-chemical conditions including sediment redox, porewater chemistry, nutrient availability, and toxin accumulation. Sediment conditions downstream of “the lagoon” in the upper Wekiva River appear to have been altered substantially (higher % silt and sediment organic content), possibly due to hydrilla control activities (Wetland Solutions, Inc. 2008). The occurrence and abundance of macrophytes in this reach of the Wekiva River appears to be more ephemeral (SJRWMD unpublished data from the annual surveys), which could be due to these sediment properties.

Current is a known factor influencing occurrence and abundance of submerged macrophytes in streams (Butcher 1933, Hynes 1970). Vegetative studies in the Chassahowitzka, Homosassa and Crystal Rivers showed that submerged macrophyte occurrence and distribution was influenced by current (Hoyer et al. 2004). Szafraniec (2014) found that current may be a factor influencing occurrence and abundance of *Sagittaria* versus *Vallisneria* in the Rainbow and Weeki Wachee Rivers. However, a recent study using data from multiple springs studies (Reaver et al. 2019) found no relationship between current velocity and macrophyte abundance. This is a subject that may benefit from additional investigations.

Historic increases in concentrations of nitrate in many springs initially led to the belief that these elevated nitrogen levels were contributing to the observed changes in the submerged vegetation communities (declines in macrophytes and increases in filamentous algal mats; Stevenson et al. 2007). Evidence specifically linking these two is inconclusive (Brown et al. 2008, Heffernan et al. 2010) and recent work has failed to identify specific linkages (Cohen et al. 2017). Elevated nitrate may also act to inhibit macrophyte growth due to various physiological effects (Osborne et al. 2017a), but subsequent work growing *Vallisneria* and *Sagittaria* in mesocosms under various nitrate concentrations failed to detect an effect (Osborne et al. 2017b), but nonetheless there exists evidence that nitrate “toxicity” on macrophyte growth could be a factor (Osborne et al. 2017a). Evidence also exists that elevated nitrate concentrations do result in higher algal growth rates and/or abundance (Cowell and Dawes 2004, Stevenson et al. 2007, Osborne et al. 2017b), which could affect macrophyte abundance.

Studies using both mesocosm and field experiments would be valuable to better elucidate the environmental forcing functions influencing the distribution of *Vallisneria* and *Sagittaria* among and within springs. This knowledge may be helpful in explaining the vegetation changes that have been observed to occur in springs (shifts from macrophyte-dominated to filamentous algae-dominated) and help guide restoration efforts. In addition, implementation of long-term monitoring of spring SAV communities is needed to provide additional data for better spring management.

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