J. Aquat. Plant Manage. 58: 135–145

Patterns in submerged aquatic vegetation in the lower St. Johns River, Florida, from 2001 to 2019

NISSE GOLDBERG* AND TIFFANY TRENT

ABSTRACT

To understand resiliency of submerged aquatic vegetation (SAV) communities with distance from the river mouth, SAV monitoring data, consisting of nine taxa, were analyzed in the lower St. Johns River, Florida, from 2001 to 2019. Patterns were evaluated with changes in salinity, turbidity, and weather events (e.g., hurricanes). Beginning just north of the Ortega River (30.2884°N, 81.7060°W) to the inlet of the Ocklawaha River (29.4858°N, 81.6751°W), SAV bed width perpendicular from shore, taxon richness, canopy length, and water depth were recorded from 124 transects stratified by 10 river kilometer sections (RKMs) of 15-km lengths between RKM 48 to 179 from the river mouth. Mean annual salinity and turbidity values per RKM were compared with SAV parameters. SAV bed extent and taxon richness were smallest in sections farther upriver (RKM 144 to 159) and highest in RKM 64 to 79. Salinity and turbidity had significantly higher values in sections closest to the river mouth (RKM 48 to 79). Southern naiad [*Najas guadalupensis* (Spreng.) Magnus] and wild celery (*Vallisneria americana* Michx.) were the most abundant and ubiquitous in all river sections, irrespective of environmental conditions. Canopy length and growing depth per taxon were variable among river sections and years, indicating differing tolerances to turbidity, salinity, and physical disturbance from extreme storm events. The number of sites present per taxon declined in the later years, which supports global trends that reduced water quality and habitat availability, and changes in salinity and flow regimes may exacerbate SAV recovery following repeated disturbance events.

Key words: *Hydrilla*, *Najas*, *Ruppia*, SAV, *Vallisneria*, *Zannichellia*.

INTRODUCTION

Submerged aquatic vegetation (SAV) are angiosperms that grow underwater in estuarine and fresh waters. SAV can form beds that provide habitat for invertebrates, fishes, and other animals and contribute to estuarine food chains (Orth et al. 2010). In addition to carbon and nutrient cycling, SAV beds provide other important ecological services that include sediment retention and attenuation of wave energy from wind, currents, and passing vessels (Poirrier et al. 2017).

In riverine to estuarine habitats, changes in SAV abundance and species diversity have been associated with droughts and episodic storm events that expose taxa to pulses of increased and fluctuating salinity concentrations, changes in light availability, and the increased likelihood of displacement by currents and turbulence or burial by sediment deposition (Orth et al. 2010). Species tolerant to variability in salinity levels, such as southern naiad [*Najas guadalupensis* (Spreng.) Magnus] and wild celery (*Vallisneria americana* Michx.) may survive brief exposures to salinities of 10 to 18 ppt; however, reduced growth or mortality is likely (Morris and Dobberfuhl 2012). For other species, high salinity values may be deleterious. The freshwater species coontail (*Ceratophyllum demersum* L.) can tolerate gradual increases in salinity levels (i.e., 2 ppt; Izzati 2016). In the Upper Escambia Bay, Florida, drought conditions in 2000 increased salinity to $>$ 10 practical salinity units (PSU), which is comparable to ppt, resulting in extensive areal loss of wild celery (Lores and Sprecht 2001). Pulses of high salinity from hurricane-induced surges were correlated with declines in the freshwater species hydrilla [*Hydrilla verticillata* (L.f.) Royle] and wild celery in Kings Bay, Florida (Frazer et al. 2006, Poirrier et al. 2010). Morris and Dobberfuhl (2012) and Boustany et al. (2010) reported that wild celery can recover from salinity stress with new growth from below-ground reserves.

In addition to salinity concentrations, light availability can also limit SAV vegetative growth and growing depths. Longer blades (hereafter referred to as canopy length) of wild celery, irrespective of depth, are indicative of reduced exposure to salinity and low turbidity (Twilley and Barko 1990, Blanch et al. 1998, Boustany et al. 2010). In rivers that have high tannins from colored dissolved material, reduced light attenuation through the water column contributes to SAV species growing in shallower depths as has been recorded in the lower St. Johns River (LSJR), Florida (Dobberfuhl 2007, Sagan 2007). In addition to tolerance to salinity variability, wild celery can persist in light levels as low as 1% of surface light in depths of 1.4 to 1.7 m (Carter and Rybicki 1985) and 20 nephelometric turbidity units (NTU; Kreiling et al. 2007). Light attenuation can be further reduced by plankton blooms, resulting in reduced growth as has been recorded for coontail (Poirrier et al. 2017). Surface mat-forming SAV taxa coontail, hydrilla, and southern naiad (Poirrier et al. 2010) can outcompete subsurface species, such as wild celery, for light (Blanch et al. 1998).

---

*First author: Professor, Department of Biology and Marine Science, Jacksonville University, Jacksonville, FL 32211. Second author: Environmental Scientist, St. Johns River Water Management District, P.O. Box 1429, Palatka, FL32178-1429. Corresponding author's E-mail: ngoldbe@ju.edu. Received for publication January 7, 2020 and in revised form March 20, 2020.

Following disturbances from storm events and high and variable salinity pulses, SAV recovery depends on germination from seed bank populations, vegetative growth from starch reserves stored below ground in roots and stolons, or recolonization from propagules dispersed from other source populations (Blanch et al. 1998, Morris and Dobberfuhl 2012). Although untested, species that depend on seed germination to maintain populations (e.g., horned pondweed [*Zannichellia palustris* L.] and southern naiad) are likely to be more vulnerable to recovery than those that recruit via vegetative and clonal growth (e.g., wild celery). For example, the persistence of the annual horned pondweed depends on successful germination from shallow ($<$ 2 cm substratum depth) seed banks and calm waters to prevent dislodgment of the shallow roots (Spencer and Ksander 2002). By comparison, 93% of wild celery relied on vegetative growth (93% of shoot production) from below-ground reserves (Hauxwell et al. 2004).

The objective of this study was to describe changes in the distribution and composition of SAV assemblages along sections of the LSJR from 2001 to 2019 and to compare these findings with available water quality data. The LSJR varies in salinity with increasing distance from the river terminal in the Atlantic Ocean. The oligohaline to mesohaline region spans the region from the river mouth to approximately 68 km, freshwater lacustrine from 69 to 126 km, and freshwater riverine farther upstream (Sagan 2007). SAV bed extent, a measure of bed width perpendicular from shore, and taxon richness were compared among river sections between 48 to 175 km from the river mouth and years. Bed width was used as an indicator of SAV bed coverage (Morris and Dobberfuhl 2012). In addition, plant parameters of growing depth and canopy length among the nine taxa were predicted to differ as a function of tolerance to environmental conditions with increasing distance from the river mouth. Merino et al. (2009) had observed that salinity and depth were the strongest predictors of SAV communities from samples in the Gulf of Mexico in 2001 and 2002. Similar to the findings in Chesapeake Bay, SAV assemblages were expected to increase in low-salinity regions, fluctuate in mid-salinity regions, and decline in high-salinity regions (Orth et al. 2010).

In addition to changes in salinity with distance from the river mouth, we compared patterns in SAV distribution and abundance with turbidity (a proxy for light availability) per river kilometer section. Poor water clarity from eutrophic conditions and suspended sediments have contributed to global SAV declines (Dennison et al. 1993, Cho and May 2008). In the tannin-rich waters of the LSJR, low-light conditions are further impacted by persistent phytoplankton blooms from excessive nutrients and suspended sediments following storm events (Gallegos 2005, SRR 2019). Temporal and spatial patterns of wild celery have been described in the LSJR (Morris and Dobberfuhl 2012, Goldberg et al. 2018), but no comparable diversity study has been published that covers the spatial extent of the LSJR for the period studied in this paper.

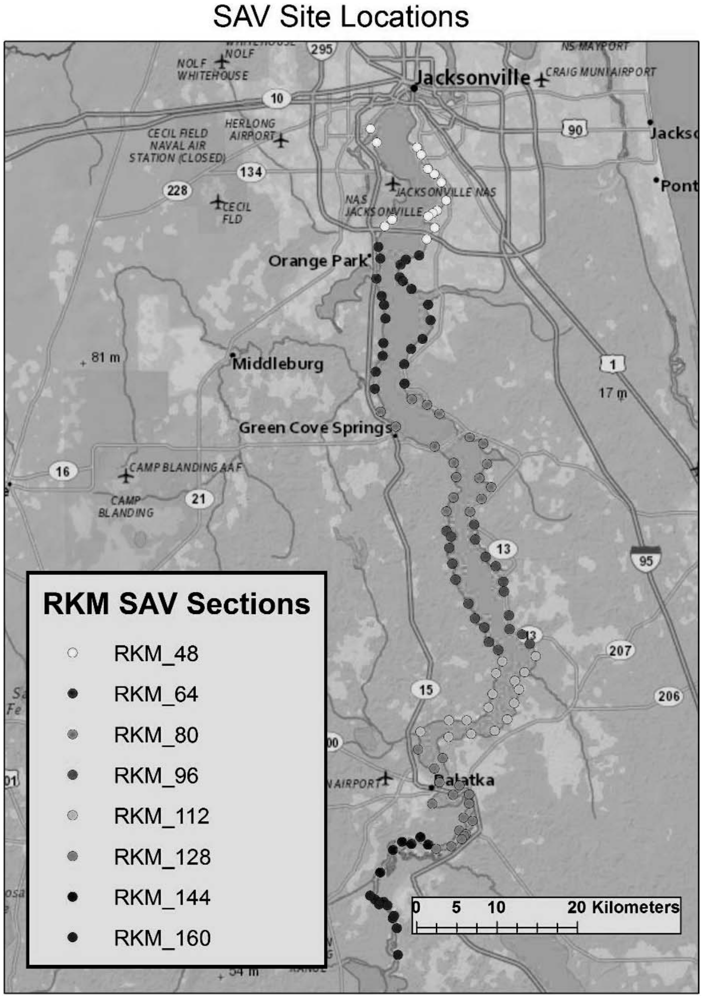

Figure 1. Map of sampling sites in the lower St. Johns River, Florida, indicating river kilometer (RKM) sections with distance from the river mouth (RKM 48 to 63, 64 to 79, 80 to 95, 96 to 111, 112 to 127, 128, 144 to 159, and 160 to 175).

MATERIALS AND METHODS

Site description

The extent of the study area in the LSJR, Florida, encompassed the river section of 48 km (30.2883°N, 81.7060°W; just north of the Ortega River) to 175 km (29.4858°N, 81.6751°W; inlet of the Ocklawaha River) from the river mouth (Figure 1). The littoral margins are wide with gradual slopes, and currents are slower in the stretch from 48 to 111 km than 112 to 176 km from the river mouth (Sagan 2001, 2007). Substratum is sandy throughout the study area with humic clay and silt in 70 to 176 km from the river mouth (unpubl. data). River depths can reach 4 m (Sagan 2001). SAV species common in the LSJR include wild celery, southern naiad, coontail, Charophytes, hydrilla, *Micranthemum* sp., widgeon grass (*Ruppia maritima* L.), awlleaf arrowhead (*Sagittaria subulata* (L.) Buchenau), and horned pondweed. Populations of small pondweed (*Potamogeton pusillus* L.), sago pondweed [*Stuckenia pectinata (L.) Börner*], Illinois pondweed (*Potamogeton illinoensis* Morong), and *Elodea*

Table 1. River sections sampled for submerged aquatic vegetation in the lower St. Johns River, Florida, during the study period from 2001 to 2019 (excluding 2012 to 2014), including number of sites per river kilometer section (RKM) and Water Body Identification (WBID) station(s) sampled for salinity and turbidity.

River section (RKM)	Distance from the river mouth (km)	2001 to 2007 (no. of sites)	2008 to 2019 (no. of sites)	Water Body Identification station (WBID no.)
RKM 48	48 to 63	14	17	2213E
RKM 64	64 to 79	14	17	2213G
RKM 80	80 to 95	7	18	2213H/I
RKM 96	96 to 111	10	20	2213J/K
RKM 112	112 to 127	6	14	2213L
RKM 128	128 to 143	4	6	2213M
RKM 144	144 to 159	6	10	2213N
RKM 160	160 to 175	6	10	2213N

sp. are variable and relatively uncommon (Sagan 2007) and therefore not included in the study.

Sampling

SAV data were collected by the St. Johns River Water Management District (SJRWMD) at permanent sites from 2001 to 2019, excluding the years 2012 to 2014 when monitoring efforts were paused (Table 1). SAV surveys were conducted during summer months (June to September), with most sites sampled in June and July. A transect tape was placed from the water's edge at each site and extended perpendicular to the shoreline to an approximate depth of 1.3 m. Along the transect, SAV taxa were inspected visually from the water surface at approximate intervals of 0.1 m. If water clarity or color prevented surveyors from recognizing SAV taxa, a small sample would be uprooted for identification. In addition to documenting the presence of SAV taxa along the transect line, canopy length (cm) and growing depth (m, hereafter referred to as depth present) per taxon were measured at 10 equidistant intervals and then the mean per transect was calculated and used for analyses.

Salinity (ppt) and turbidity (NTU) measurements were compiled from Water Body Identification Number (WBID) stations 2213E to 2213N (Table 1), using the STORage and RETrieval database managed by the Florida Department of Environmental Protection (FDOT 2019). The annual means of weekly measurements were compared among the years 2001 to 2017, excluding 2012 to 2014. Data were unavailable for 2018 and 2019.

Analyses

Permanent site locations within the LSJR were stratified in eight river kilometer sections (RKM) for analyses: RKM 48 to 63, 64 to 79, 80 to 95, 96 to 111, 112 to 127, 128 to 143, 144 to 159, and 160 to 175 (hereafter each RKM section is indicated by the first kilometer; Table 1). To test for differences among RKM sections during the study period, mean SAV bed extent, proportion of sites, and taxon richness, depth present, and canopy length per site were compared among RKM sections ($n = 8$ river sections) and years ($n = 16$ years). Proportion of sites per taxon was calculated based on the total number of sites sampled per year (Table 1). Salinity and turbidity estimates were also compared among WBID stations per RKM and years 2001 to 2017 (Table 1). Because SAV, salinity, and turbidity data did not meet the assumptions of normality even after transforming the data, the nonparametric Kruskal-Wallis test was used to test separately for differences among years and sections. If significant differences ($P < 0.05$) were present, Dunn's pairwise comparisons were conducted and illustrated with figures.

RESULTS AND DISCUSSION

Patterns in salinity and turbidity

Salinity differed significantly among RKM sections ($P < 0.001$) and among years ($P < 0.001$). The river section closest to the river mouth (RKM 48) had significantly greater salinity values than in upstream sections (RKM 80 section to RKM 144 and 160, $P < 0.001$; Figure 2A). Mean salinity estimates from all WBID stations in the study area were > 1.5 ppt in 2002, 2006, 2007, 2011, and 2017 (Figure 2B).

In the LSJR, turbidity differed among RKM sections ($P < 0.001$) and years ($P < 0.040$). Persistent plankton blooms (SRR 2019) and suspended sediments were evident in river sections closest to the river mouth where turbidity values > 6.5 NTU were recorded (2213E, G, and H/I; $P < 0.001$; Figure 2A) and in 6 of the 14 years measured in this study (Figure 2B). In addition, the years 2004, 2005, and 2011 were also characterized by > 7.0 NTU (Figure 2B).

Spatial patterns in SAV distribution

SAV bed extent and taxon richness varied with distance from the river mouth. SAV bed extent from shore differed significantly among river sections and not among years ($P < 0.001$; $P = 0.069$, respectively; Figure 3). The narrowest sections were measured in RKM 128 to 160 (12.1 ± 1.2 m) where the river was narrow (Figure 1) and widest in the RKM 64 section (89.9 ± 7.1 m; Dunn pairwise test, $P < 0.040$; Figure 3). Similarly, total number of taxa differed among river sections ($P < 0.001$) but not among years ($P = 0.073$; Figure 4). Taxon richness in the middle sections RKM 64 and 96 was significantly greater than in sections closest and farthest from the river mouth (RKM 48, 128, 144, and 160; Dunn pairwise test, $P < 0.050$, Figure 4). The proportion of sites per SAV taxon was significantly different among river sections for six taxa except for awlleaf arrowhead, coontail, and *Micrantheum* sp. ($P < 0.05$; Figure 5). Wild celery, southern naiad, and horned pondweed were the most common species, present in all river sections and years (Figures 5 and 6), and only *Micrantheum* sp. was not recorded in the later years. The persistence of SAV populations suggests a resiliency among the nine SAV taxa to disturbance and eutrophic conditions.

The high-salinity region closest to the river mouth (RKM 48 to 80) was associated with decreased water clarity and fewer SAV records, a pattern similar to SAV distributions in

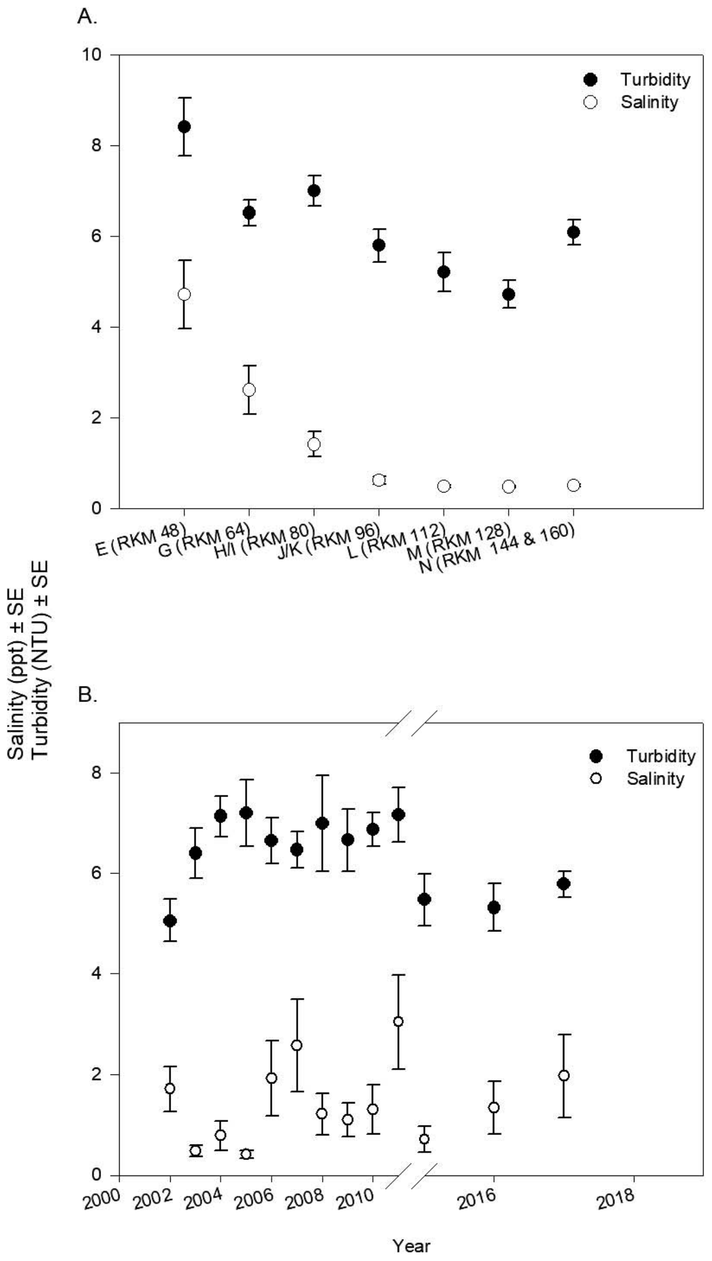

Figure 2. Mean turbidity (NTU) and salinity (ppt) ± SE per (A) Water Body Identification Number (WBID) 2213 E–N stations during the study period 2001 to 2019, excluding 2012 to 2014 and (B) year ($n = 9$ stations) in the lower St. Johns River, Florida. River kilometer section (RKM) in parentheses.

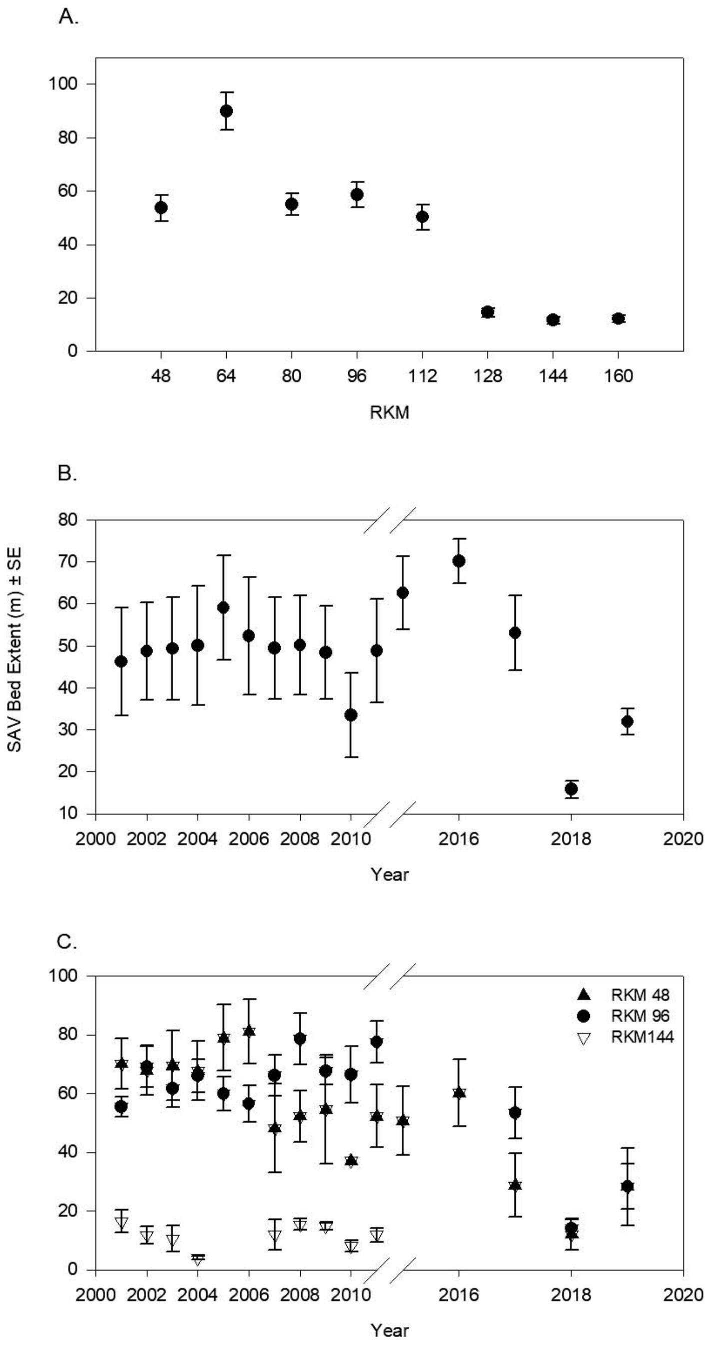

Figure 3. Mean submerged aquatic vegetation bed extent (m) ± SE with (A) river kilometer section (RKM), (B) year, and (C) RKM and year in the lower St. Johns River, Florida, during the study period 2001 to 2019, excluding 2012 to 2014.

Chesapeake Bay (Figures 2 and 4; Orth et al. 2010). Hardened shorelines (e.g., rip rap and sea walls) were first noted in 2015 (unpubl. data). In 2007, 2011, and 2017, maximum salinity values were > 15.0 ppt and turbidity values were > 10 NTU, which may have contributed to fewer species present (Figure 4C). In this region, SAV assemblages were represented by wild celery, southern naiad, widgeon grass, horned pondweed, and *Micrantheum* sp. (Figure 5). These species are tolerant to variability in salinity exposure and turbidity. Southern naiad populations persisted in greater salinity (> 3.5 ppt) in the LSJR and Gulf of Mexico estuaries (> 5 ppt; Merino et al. 2009) than reported in Jean Lafitte National Historical Park and Preserve, Louisiana (Poirrier et al. 2010), and had longer canopy lengths than wild celery (21.02 ± 4.50 cm, 10.29 ± 2.07 cm, respectively). For freshwater SAV taxa, Poirrier et al. (2017) recorded horned pondweed in lower salinities (3.2 to 5.4 ppt) in Chesapeake Bay than observed in this study. As expected, the halophyte widgeon grass was recorded in a greater number of sites in RKM 48 and 64 than farther

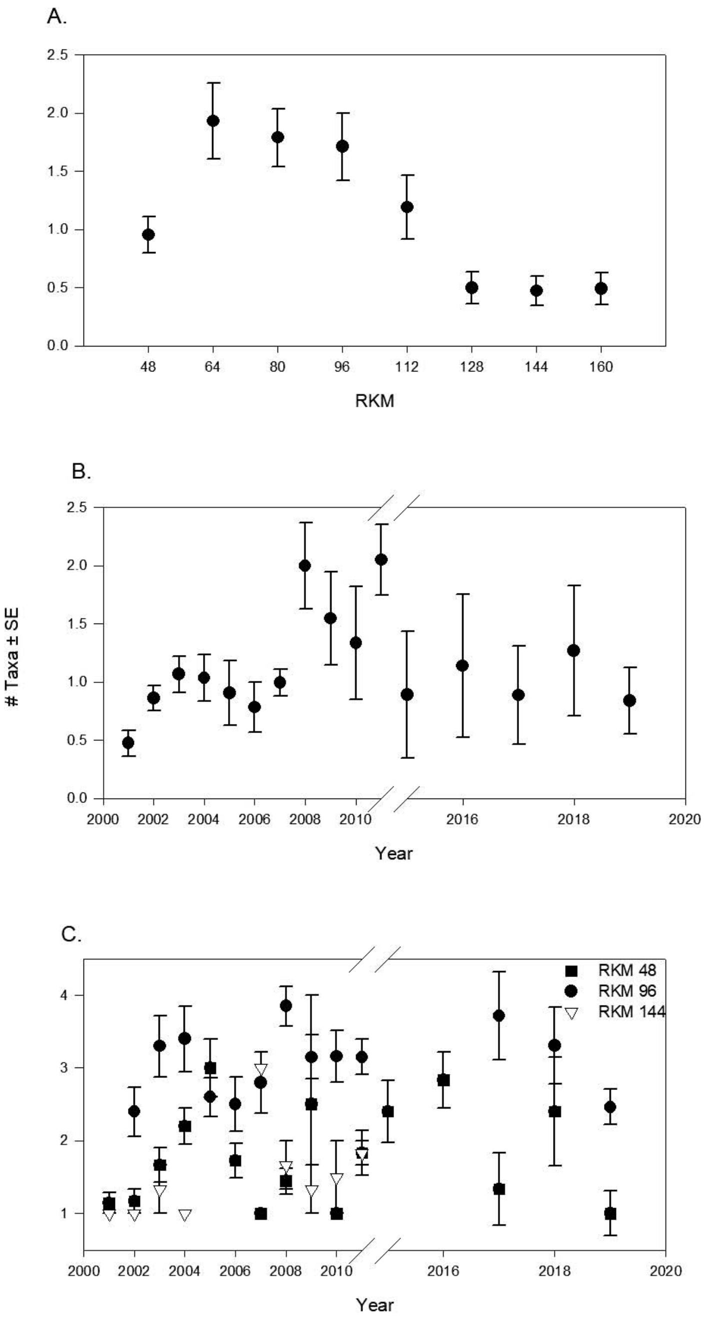

Figure 4. Mean submerged aquatic taxon richness ± SE with (A) river kilometer section (RKM), (B) year, and (C) RKM and year in the lower St. Johns River, Florida, during the study period 2001 to 2019, excluding 2012 to 2014.

upriver in RKM 112, 128, 144, and 160 ($P < 0.001$, Dunn pairwise test, $P < 0.005$; Figure 5C). Although described as tolerant to low salinity (≤ 5 ppt; Merino et al. 2009, Izzati 2016, Hillman et al. 2019) and calm conditions (Koch 2001, Poirrier et al. 2010, 2017), coontail was recorded in RKM 48 and 64 and growing in shallower depths where exposure to storm wave energy is more likely (Figure 5C and Table 2). Similarly, hydrilla was recorded in < 3% of the sites in RKM 48, 64, and 80 and may persist from underground reserves and propagules.

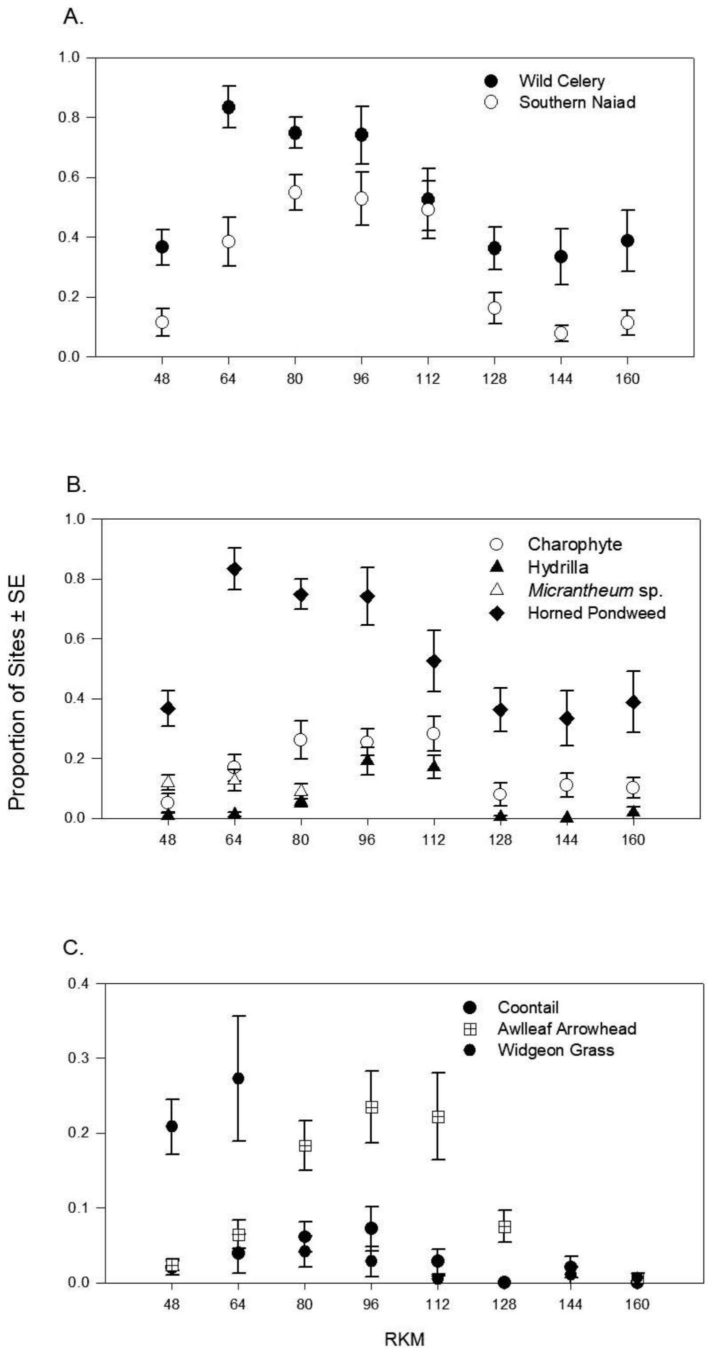

Figure 5. Submerged aquatic taxon mean proportion of sites ± SE per river kilometer section (RKM) in the lower St. Johns River, Florida ($n = 16$ years), during the study period 2001 to 2019, excluding 2012 to 2014.

The greatest taxon richness was observed in the mid-salinity regions of the LSJR, with environmental conditions more favorable for SAV communities (Figure 4), a pattern also observed by Hillmann et al. (2019) in the Gulf of New Mexico estuaries. Salinity and turbidity values were lower than in sections closer to the river mouth (Figure 2), and the littoral shelves are relatively wide with beds extending farther from shore (Figures 1 and 3) where water exchange would be greater (Sagan 2001, Kreiling et al. 2007, Cho and May 2008).

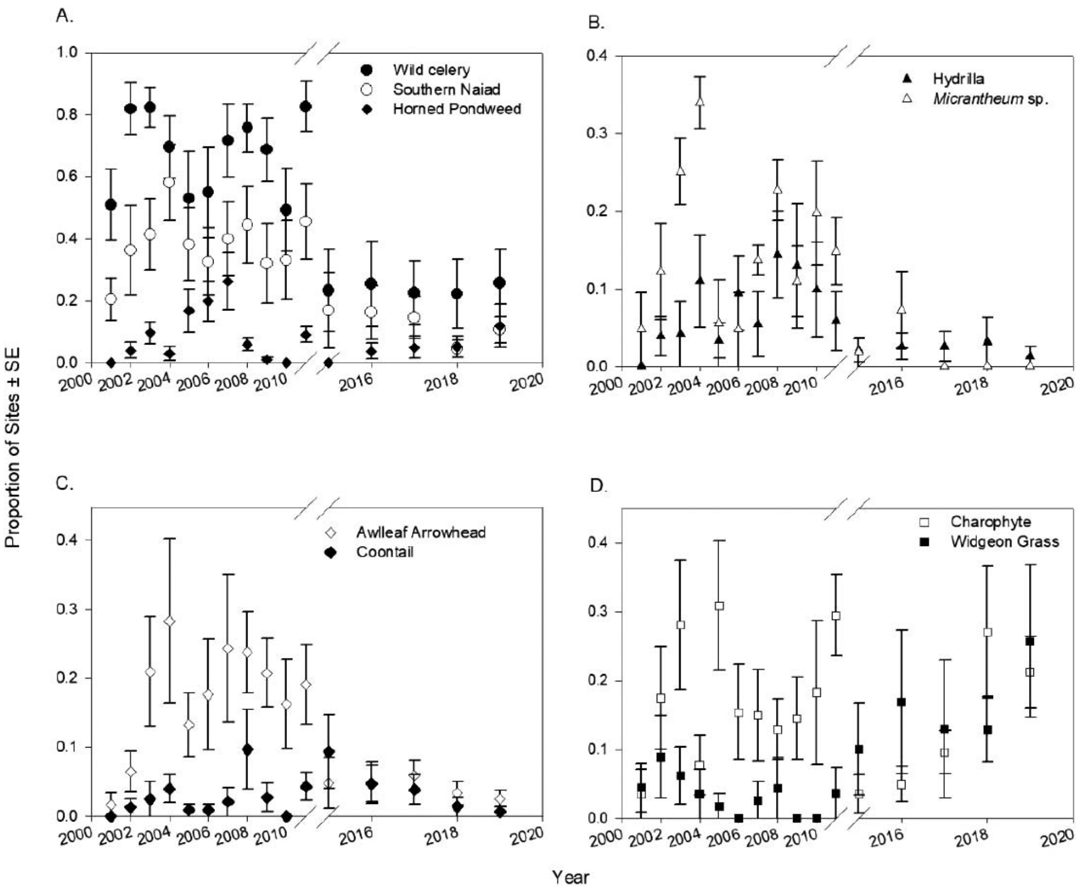

Figure 6. Submerged aquatic taxon mean proportion of sites ± SE per year, during the study period 2001 to 2019, excluding 2012 to 2014 ($n = 8$ river sections).

Gurbisz et al. (2016) reported a positive "bed effect" or feedback loop across SAV beds wherein water quality parameters (e.g., suspended sediments and chlorophyll *a*) decreased with increases in SAV biomass. Goldberg et al. (2018) speculated that the wider beds dominated by wild celery along the western sides of the LSJR may be a function of wind fetch enabling nutrient exchange.

Five taxa were common in the more taxon-rich middle sections of RKM 80 to 112. In particular, meadow-forming southern naiad and wild celery were more abundant (252 records) than the remaining seven species (185 records). Wild celery occurred in significantly greater proportions of sites than in the RKM 48, and 138 to 160 sections ($P < 0.001$; Dunn pairwise test, $P < 0.030$, Figure 5A). Similarly, the proportion of sites with hydrilla ($P < 0.001$; Dunn pairwise test, $P < 0.040$) and Charophytes ($P < 0.001$; Dunn pairwise test, $P < 0.050$) were significantly greater than in RKM 48 and farther upstream river sections (Figure 5B). The proportion of sites was significantly greater in RKM 64 to 96 than upriver RKM 128 to 160 sections for wild celery ($P < 0.001$; Dunn pairwise test, $P < 0.050$; Figure 5A) and horned pondweed ($P = 0.034$; Dunn pairwise test, $P < 0.050$; Figure 5B). Although horned pondweed is more tolerant to current flow (< 50 cm s^{-1}) than wild celery (< 7 cm s^{-1}; Koch 2001), the wider SAV beds in the midregion of the LSJR may help to dampen current flow in shallower waters and enable persistence of wild celery, Charophytes, hydrilla, and coontail (Kreiling et al. 2007, Patrick et al. 2018; Figure 5).

TABLE 2. MEAN TAXON DEPTH (M) AND CANOPY LENGTH (CM) PER RIVER KILOMETER SECTION (RKM) IN THE LOWER ST. JOHNS RIVER, FLORIDA, DURING THE STUDY PERIOD FROM 2001 TO 2019 (EXCLUDING 2012 TO 2014; $N = 8$ SECTIONS; RKM 48 TO 160).

Taxon	Depth (m per RKM) mean ± SE (range)	Canopy length (cm per RKM) mean ± SE (range)
Wild celery	0.59 ± 0.03 (0.47 to 0.69)	23.70 ± 3.90 (10.29 to 40.80)
Southern naiad	0.50 ± 0.04 (0.30 to 0.65)	12.31 ± 1.63 (7.22 to 21.02)
Charophytes	0.50 ± 0.02 (0.43 to 0.56)	10.05 ± 0.53 (8.58 to 11.78)
Hydrilla	0.49 ± 0.04 (0.37 to 0.65)	19.57 ± 4.28 (1.00 to 31.83)
Horned pondweed	0.51 ± 0.02 (0.43 to 0.60)	3.89 ± 0.53 (2.31 to 7.26)
Widgeon grass	0.51 ± 0.03 (0.43 to 0.56)	6.05 ± 1.27 (3.25 to 10.23)
Awlleaf arrowhead	0.36 ± 0.05 (0.23 to 0.63)	5.27 ± 0.21 (4.48 to 6.13)
Micranthemum sp.	0.26 ± 0.09 (0.04 to 0.44)	13.30 ± 2.63 (6.00 to 18.21)
Coontail	0.47 ± 0.06 (0.31 to 0.73)	27.46 ± 5.50 (16.00 to 50.00)

Compared to increases in abundances in low-salinity regions in Chesapeake Bay (Orth et al. 2010), SAV beds in RKM 128 to 160 had reduced taxon richness (Figure 4A), despite relatively low and stable salinity values (Figure 2). The combination of faster currents and narrower margins may have contributed to reduced available habitat (Figures 1 and 3A; Sagan 2001, 2007). In addition, SAV taxa growing

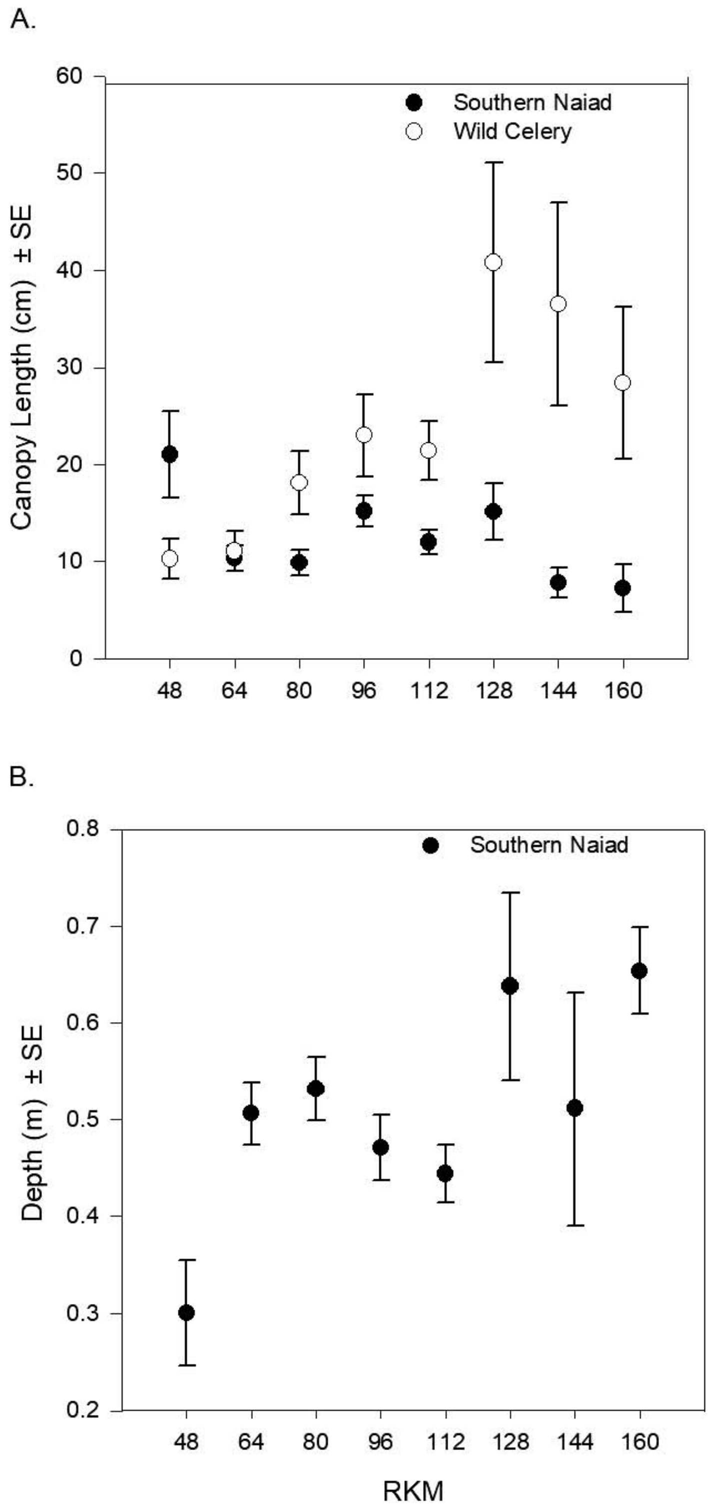

Figure 7. (A) Mean canopy length (cm) ± SE for southern naiad and wild celery and (B) mean depth present (m) ± SE for southern naiad per river kilometer section (RKM) in the lower St. Johns River, Florida, during the study period 2001 to 2019, excluding 2012 to 2014.

beneath the water surface may be light-limited due to persistent phytoplankton blooms from 1997 to 2016 (SRR 2019). Poirrier et al. (2017) reported that coontail abundances were negatively impacted by phytoplankton blooms. Yet Merino et al. (2009) recorded coontail growing in Gulf of Mexico estuaries with turbidity reaching 65.6 NTU. In this river section, wild celery and coontail grew in shallower waters ($<$ 28 cm depth) and may be more competitively dominant for space and light than species with shorter canopy lengths such as horned pondweed, Charophytes, and southern naiad (Figure 7 and Table 2). Despite being tolerant to low salinities, hydrilla was present in fewer records than in RKM 96 and 112, indicating that other factors (e.g., turbidity) were negatively impacting abundances (Figure 5C). Merino et al. (2009) reported that hydrilla was present in turbidity as high as 4.0 NTU, which is lower than mean values recorded in RKM 144 and 160 (Figure 2).

Temporal patterns in SAV distribution

SAV bed extent and number of SAV taxa declined in coverage in the later years in the LSJR (Figures 3 and 4). In 2015 to 2018, nine tropical storms or hurricanes swept through the region. Exposure to eutrophic conditions characterized by persistent phytoplankton blooms and recurring extreme storm events with associated stressors of scour and reduced water clarity likely contributed to observed reductions in SAV distribution and abundance. For example, epiphytes and phytoplankton blooms were recorded in 2004, 2006, 2008, and 2011 (unpubl. data). In comparing annual differences within RKM 48, 96, and 144, bed extent in RKM 48 and RKM 96 was significantly narrower in 2018 and 2019 relative to the earlier years (Dunn pairwise test, $P < 0.040$; Figure 4C).

Although common in the LSJR, significantly fewer records of wild celery, southern naiad, and horned pondweed were noted in the later years between RKM 48 to 160 ($P < 0.038$; Dunn pairwise test, $P < 0.050$; Figure 6). *Micrantheum* sp. was not present in 2017 to 2019 (Figure 6). Repeated disturbance from storm energy in the later years may have contributed to the absence of *Micrantheum* sp. and reduced populations of horned pondweed, which is described as less tolerant to wave energy than wild celery (Joanen and Glasgow 1965, Koch 2001).

With the hurricanes in 2018 and 2019, physical disturbance that uprooted SAV biomass rather than increased salinity (Figure 2B) may have contributed to the reduced canopy lengths of Charophytes, wild celery, and hydrilla (Figure 8). Shorter canopy lengths can be indicative of repeated exposures to pulses of $\geq$ 15 ppt salinity (Frazer et al. 2006) from storm-induced surge. Increased records of widgeon grass in 2019 (Figure 6) may be a function of recruitment from exposed seed banks following scour of sediment layers, in addition to growing in a broad range of depths (10 to 120 cm) and turbidity levels (as high as 280 NTU; Cho et al. 2009, Merino et al. 2009).

Taxon level patterns in growing depth and canopy length

Wild celery and southern naiad were the most common taxa with 682 and 394 records, respectively (Figures 5A and

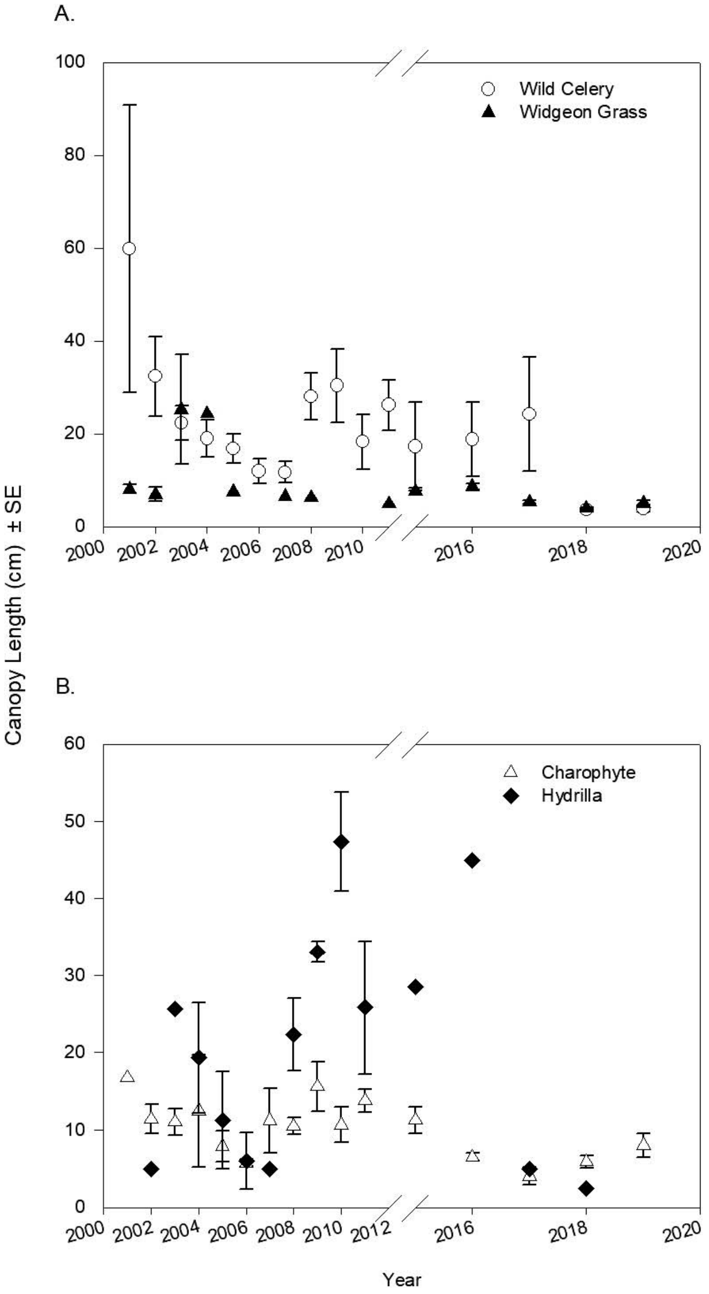

Figure 8. Mean canopy length (cm) ± SE per year for (A) wild celery and widgeon grass and (B) charophyte and hydrilla in the lower St. Johns River, Florida, during the study period 2001 to 2019, excluding 2012 to 2014 ($n = 8$ river sections).

Table 3. Mean taxon depth (m) and canopy length (cm) per year from 2001 to 2019, excluding 2012 to 2014, in the lower St. Johns River, Florida.

Taxon	Depth (m per year) mean ± SE (range)	Canopy length (cm per year) mean ± SE (range)
Wild celery	0.57 ± 0.03 (0.44 to 0.72)	21.50 ± 4.67 (3.60 to 59.80)
Southern naiad	0.51 ± 0.03 (0.39 to 0.73)	11.05 ± 1.54 (3.00 to 16.00)
Charophytes	0.51 ± 0.04 (0.29 to 0.73)	10.18 ± 1.28 (4.00 to 16.75)
Hydrilla	0.46 ± 0.03 (0.31 to 0.73)	20.12 ± 3.89 (2.50 to 47.37)
Horned pondweed	0.53 ± 0.04 (0.30 to 0.72)	4.06 ± 0.47 (1.50 to 07.92)
Widgeon grass	0.48 ± 0.03 (0.26 to 0.70)	9.23 ± 1.95 (3.90 to 25.20)
Awlleaf arrowhead	0.32 ± 0.04 (0.26 to 0.74)	5.32 ± 0.26 (4.25 to 6.75)
Micranthemum sp.	0.39 ± 0.03 (0.44 to 0.7)	16.10 ± 2.86 (7.33 to 42.00)
Coontail	0.43± 0.04 (0.14 to 0.68)	21.58 ± 4.13 (0.06 to 49.00)

6A). Similar to the findings of Cho et al. (2010) and Hillmann et al. (2019), the two species were commonly found growing together in the lower Pascagoula River and Pearl River, Mississippi, and coastal Louisiana. Canopy lengths of wild celery and southern naiad ($P = 0.005$) were significantly different among river sections ($P = 0.007$), with opposite patterns in canopy lengths with distance from the river mouth (Figure 7A), indicating different physiological responses with salinity and turbidity. Canopy lengths of southern naiad were shorter in RKM 144 and 160 (Figure 7). Among years, canopy length of wild celery was significantly different ($P = 0.025$) with a range of 3.60 ± 0.35 cm to 59.90 ± 30.90 cm (Figure 8A). By comparison, canopy length for southern naiad was not significantly different among years ($P = 0.088$; Table 3). Depth present of wild celery was not significantly different among river sections ($P = 0.074$; Table 2) or among years ($P = 0.080$; Table 3), indicating that variability was greatest among sites. By comparison, depths present for southern naiad were significantly different ($P = 0.001$) with greater depths farther from the river mouth (Figure 7) and among years ($P = 0.015$; Figure 9A). In the Gulf of Mexico estuaries, Merino et al. (2009) reported greater mean depths for wild celery (0.67 m) than for southern naiad (0.47 m). The significant differences in growing depths between the Gulf of Mexico and LSJR sites underscore that populations are likely responding to local conditions.

Charophytes were present in every river section throughout the study period and represented the third most common taxa with 181 records and greater numbers recorded in RKM 80 to 112 (Figure 5A). Canopy length ($P = 0.011$) and depth present ($P = 0.020$) were significantly different among years (Figures 8B and 9B), which may be a function of reduced light availability. Frankovich et al. (2011) estimated 5% of surface light for maintenance of *Chara* communities. Among river sections, depth present and canopy length were not significantly different ($P > 0.720$ Table 2) due to site-specific variability.

Hydrilla was the fifth most common taxon present with 77 records and was present in every river section except RKM 144 and not present in 2001 (Figures 5B and 6B). Merino et al. (2009) reported hydrilla in salinities as high as 20.7 ppt, indicating a broader tolerance to salinity. However, Patrick et al. (2018) reported that hydrilla is a predictor of freshwater salinities. Canopy length varied significantly among years ($P = 0.046$), with a range of 2.50 cm to 47.37 ± 6.45 cm (Figure 8B). Longer canopy lengths may be indicative of reduced light availability with depth, as suggested by Hillmann et al. (2019). However, depth present and canopy length were not significantly different among river sections ($P > 0.490$; Table 2), and depth present was not significantly different among years ($P = 0.616$; Table 3). Merino et al. (2009) recorded hydrilla in greater mean depth of 0.85 m in the Gulf of Mexico than mean depths reaching 0.65 m recorded in this study. Hydrilla is described as an early successional species following disturbances, enabling

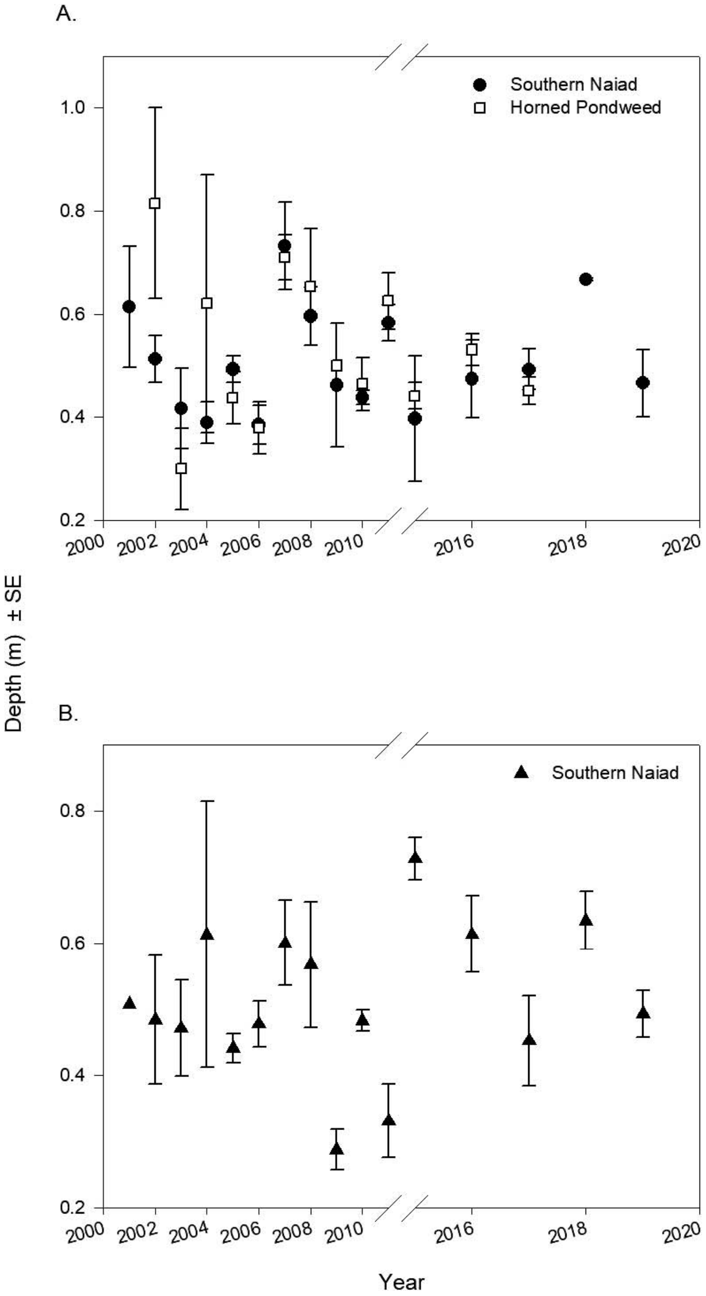

Figure 9. Mean depth present (m) ± SE per year for (A) southern naiad and horned pondweed, (B) Charophyte in the lower St. Johns River, Florida, during the study period 2001 to 2019, excluding 2012 to 2014 ($n = 8$ river sections).

species like coontail and southern naiad to establish in Chesapeake Bay (Patrick et al. 2018).

The opportunistic horned pondweed was present in all river sections with proportion of sites differing among river sections and was not recorded in 2001, 2010, and 2015 (Figures 5B and 6A). Similar to the findings of Cho et al. (2010), horned pondweed grew together with southern naiad and wild celery in the Pascagoula River, Mississippi. Of the species studied, horned pondweed was the sixth most common species with 75 records. Depth present differed significantly among years ($P = 0.031$; Figure 9A). Depth present in 2003 (0.30 ± 0.08 m) was shallower than in 2007, 2008, and 2016 (0.63 to 0.71 m, $P < 0.05$). Depth present and canopy length were not significantly different among river sections ($P > 0.148$), and canopy length did not differ among years ($P = 0.098$; Tables 2 and 3). Patrick et al. (2018) suggested that the persistence of horned pondweed may be a function of dispersal from source populations and tolerance to eutrophic conditions and a wide range in salinity concentrations.

As expected, widgeon grass was abundant in river sections closest to the river mouth (Figure 5C) with 44 records, where turbidity and salinity values were the greatest (Figure 2). Merino et al. (2009) reported widgeon grass present in turbidity values as high as 380 NTU, indicating a broad tolerance to low-light conditions. Similar to the findings of Cho et al. (2010), widgeon grass was associated with wild celery and was tolerant to a range of salinities. The halophyte was not recorded in RKM 128 and in the years 2006, 2009, and 2010 (Figures 5C and 5D). Canopy length was variable throughout the study period ($P = 0.050$). Depth present was not significantly different among RKM 48 to 96 ($P = 0.120$) or among years ($P = 0.203$; Tables 2 and 3). Canopy length was also not significantly different among river sections ($P = 0.122$; Table 2).

Awlleaf arrowhead, *Micrantheum* sp., and coontail showed no significant temporal or spatial patterns in depth present and canopy length. During the study period, awlleaf arrowhead was present in every river section except RKM 144 and all years (Figures 5C and 6C), was the fourth most common taxon with 138 records, and showed no significant patterns in growing depths or canopy lengths ($P > 0.220$; Tables 2 and 3). *Micranthemum* sp. was the seventh most common taxon with 62 records. Depth present and canopy length were not significantly different among river sections or among years ($P > 0.070$; Tables 2 and 3). Surprisingly, the freshwater coontail (Patrick et al. 2018) was not present in the river sections farthest from the river mouth or in 2001 and 2010 (Figures 5C and 6C). This species was present in only 29 records. Likely due to the fewest number of records, no patterns in growing depths or canopy lengths were observed, which may be a function of taking up nutrients in the water column rather than from the sediments. Depth present and canopy length were not significantly different among river sections or among years ($P > 0.220$; Tables 2 and 3). Merino et al. (2009) had reported coontail in turbidity values as high as 65.6 NTU, depths of 0.90 m, and salinity values of 7 ppt. The fewer records may be indicative of greater susceptibility to disturbance than growing conditions.

CONCLUSION

Globally, SAV beds are declining due to reduced water quality from eutrophic conditions and suspended sediments (Dennison et al. 1993, Cho and May 2008), increased salinity from episodic droughts and storm surge, and reduced habitat on account of hardened shorelines (Patrick et al. 2018). The tannic waters, plankton blooms, and suspended sediments in the LSJR may have contributed to reduced light penetration, resulting in shallower SAV growing depths < 0.75 m as compared to 1.20 m in the Gulf of Mexico estuaries (Merino et al. 2019). The presence of the nine SAV taxa throughout the study period indicated resiliency of the populations due to persistent patches and propagule availability. Although not the focus of this study, the different depth distributions of the two common species wild celery and southern naiad may indicate competition for space and warrant further investigation. Unlike in Chesapeake Bay (Orth et al. 2010), SAV distribution and abundance in 2019 did not return to levels measured before 2015. Hydrilla, with its limited recovery, did not act as a facilitator for the recovery of other species, indicating that a different combination of stressors may prevent successful recruitment and growth with distance from the river mouth. The decadal study period highlights the importance of long-term monitoring. Site-specific variability in canopy lengths and growing depths suggests that localized conditions impact SAV assemblages differently, a finding that could not be identified with a one-to-two-year study. Patrick et al. (2018) underscore the importance of local management strategies given the temporal and spatial variability among the SAV assemblages. Hurricanes may thin or remove beds, but broad scale reduction in SAV coverage is likely due to persistent eutrophic conditions (Carter et al. 1996, Doering et al. 2001, Orth et al. 2010, Poirrier et al. 2017), lack of available habitat due to hardened shorelines (Patrick et al. 2018) in the upper reaches of the LSJR, increased flow regimes that contribute to thinning of the sediment layer for SAV establishment, and salinity changes (Estevez et al. 2000, Frankovich et al. 2011). The findings from this study provide valuable distributional patterns of less-studied SAV taxa and associated environmental conditions to compare with likely changes due to sea-level rise and deepening of the LSJR.

ACKNOWLEDGEMENTS

We thank J. Heine and two anonymous reviewers for their astute comments that significantly improved the paper and M. Watkins for quality control of the original data set. This project was made possible by the cooperative data collection efforts of the St. Johns River Water Management District, Palatka, FL; Sagan Biological LLC, Gainesville, FL; and Wood Environmental & Infrastructure Solutions (formerly BCI), Gainesville, FL.

LITERATURE CITED

Blanch SJ, Ganf GG, Walker KF. 1998. Growth and recruitment in *Vallisneria americana* as related to average irradiance in the water column. Aquat. Bot. 61:181–205.

Boustany RG, Michot TC, Moss RF. 2010. Effects of salinity and light on biomass and growth of *Vallisneria americana* from the lower St. Johns River, FL, USA. Wetl. Ecol. Manage. 18:203–217.

Carter V, Rybicki NB. 1985. The effects of grazers and light penetration on the survival of transplants of *Vallisneria americana* Michs in the tidal Potomac River, Maryland. Aquat. Bot. 23:197–213.

Carter VJ, Rybicki NB, Turtora M. 1996. Effect of increasing photon irradiance on the growth of *Vallisneria americana* in the tidal Potomac River. Aquat. Bot. 54:337–345.

Cho HJ, Biber P, Nica, C. 2009. The rise of *Ruppia* in seagrass beds: Changes in coastal environment and research needs, pp. 1–15. In: Handbook on environmental quality. Nova Science, New York.

Cho HJ, Biber P, Poirrier M, Garner, J. 2010. Aquatic plants of Mississippi coastal river systems. Miss. Acad. Sci. 55:211–222.

Cho HJ, May CA. 2008. Short-term spatial variations in the beds of *Ruppia maritima* (Ruppiaceae) and *Halodule wrightii* (Cymodoceaceae) at Grand Bay National Estuarine Research Reserve, Mississippi, USA. J. Miss. Acad. Sciences 53:133–145.

Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA. 1993. Assessing water quality with submersed aquatic vegetation. BioScience 43:86–94.

Dobberfuhl DR. 2007. Light limiting thresholds for submerged aquatic vegetation in a blackwater river. J. Aquat. Bot. 86:346–352.

Doering PH, Chamberlain RH, McMunigal JM. 2001. Effects of simulated saltwater intrusions on the growth and survival of wild celery, *Vallisneria americana*, from the Caloosahatchee Estuary (South Florida). Estuar. Coasts 24:894–903.

Estevez ED, Sprinkel J, Mattson RA. 2000. Responses of Suwannee River tidal SAV to ENSO-controlled climate variability, pp. 133–143. In: Seagrass management: It's not just nutrients! Proceedings of a Symposium, St. Petersburg, Florida.

[FDOT] Florida Department of Environment Protection. 2019. STORET public access. Available online at http://prodenv.dep.state.fl.us/DearSpa/public/welcome. Accessed September 7, 2019.

Frankovich TA, Morrison D, Fourqurean JW. 2011. Benthic macrophyte distribution and abundance in estuarine mangrove lakes and estuaries: Relationships to environmental variables. Estuar. Coasts 34:20–31.

Frazer TK, Notestein SK, Jacoby CA, Littles CJ, Keller SR, Swett RA. 2006. Effects of storm-induced salinity changes on submersed aquatic vegetation in Kings Bay, Florida. Estuar. Coasts 29:943–953.

Gallegos CL. 2005. Optical water quality of a blackwater river estuary: The lower St. Johns River, Florida, USA. Estuar. Coast. Shelf Sci. 63:57–72.

Goldberg NA, Trent T, Hendrickson J. 2018. Temporal and spatial changes in *Vallisneria americana* Michaux (Tape-grass) beds in the lower St. Johns River, Florida, from 2002–2011. Southeast. Nat. 17:396–410.

Gurbisz C, Kemp WM, Sanford LP, Orth RJ. 2016. Mechanisms of storm-related loss and resilience in a large submersed plant bed. Estuar. Coasts 39:951–966.

Hauxwell J, Frazer TK, Osenberg CW. 2004. Grazing by manatees excludes both new and established wild celery transplants: Implications for restoration in Kings Bay, FL, USA. J. Aquat. Plant Manage. 42:49–53.

Hillmann ER, DeMarco K, La Peyre MK. 2019. Salinity and water clarity dictate seasonal variability in coastal submerged aquatic vegetation in subtropical estuarine environments. Aquat. Biol. 28:175–186.

Izzati M. 2016. Salt tolerance of several aquatic plants, 6:154–157. In: AIP Publishing LLC, Malang, Indonesia.

Joanen T, Glasgow LL. 1965. Factors influencing the establishment of wigeongrass stands in Louisiana. In: Southeastern Association of Game and Fish Commissioners, Frankfort, Kentucky. 19:78–92.

Koch EW. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries 24:1–17.

Kreiling RM, Yin Y, Gerber DT. 2007. Abiotic influences on the biomass of *Vallisneria americana* Michx. in the upper Mississippi River. River Res. Appl. 23:343–349.

Lores EM, Sprecht DT. 2001. Drought-induced decline of submerged aquatic vegetation in Escambia Bay, Florida. Gulf Mex. Sci. 19:162–164.

Merino JH, Carter J, Merino SL. 2009. Mesohaline submerged aquatic vegetation survey along the US Gulf of Mexico coast, 2001 and 2002: A salinity gradient approach. Gulf Mex. Sci. 27:9–20.

Morris L, Dobberfuhl DR. 2012. St. Johns River Water Management District 9-1. Appendix 9.A. Submerged aquatic vegetation patterns in the lower St. Johns River Basin. St. Johns River Water Supply Impact Study. St. Johns River Water Management District, Palatka, FL. https://www.sjrwmd.com/documents/water-supply. Accessed September 7, 2019.

Orth RJ, Williams MR, Marion SR, Wilcox DJ, Carruthers TJ, Moore KA, Kemp WM, Dennison WC, Rybicki N, Bergstrom P, Batiuk RA. 2010. Long-term trends in submersed aquatic vegetation (SAV) in Chesapeake Bay, USA, related to water quality. Estuar. Coasts 33:1144–1163.

Patrick, CJ, Weller DE, Orth RJ, Wilcox DJ, Hannam, MP. 2018. Land use and salinity drive changes in SAV abundance and community composition. Estuar. Coasts 41:85–100.

Poirrier MA, Burt-Utley K, Utley JF, Spalding EA. 2010. Submersed aquatic vegetation of the Jean Lafitte National Historical Park and Preserve. Southeast. Nat. 9:477–487.

Poirrier MA, Caputo CE, Franze CD. 2017. Biogeography of submerged aquatic vegetation (SAV) in the Pontchartrain Basin: Species salinity zonation and 1953–2016 Lake Pontchartrain trends. Southeast. Geogr. 57:273–293.

Sagan JJ. 2001. Lower St. Johns River Basin submerged aquatic vegetation (SAV) monitoring. Final Report to the St. Johns River Water Management District, Palatka, FL.

Sagan JJ. 2007. SAV Monitoring Project: Interim Reports I–V. Interim reports associated with quarterly sampling and groundtruth surveys for the St. Johns River Water Management District, Palatka, FL.

Spencer DF, Ksander GG. 2002. Sedimentation disrupts natural regeneration of *Zannichellia palustris* in Fall River, California. Aquat. Bot. 73:137–147.

[SRR] St. Johns River Report. 2019. State of the river report for the lower St. Johns River basin, Florida: Water quality, fisheries, aquatic life, contaminants, and aquatic toxicology. Jacksonville, FL. http://sjrr.domains.unf.edu. Accessed 13 October 2019.

Twilley RR, Barko JW. 1990. The growth of submersed macrophytes under experimental salinity and light conditions. Estuar. Coasts 13:311–321.