

Note

Herbivory impacts *Vallisneria americana* recovery in the lower St. Johns River, Florida

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INTRODUCTION

Tape grass (*Vallisneria americana*) once formed large, dense meadows of long (up to 1 m) plants in the littoral zones of Lower St. Johns River (LSJR) and its associated lakes and tributaries (Sagan 2007). Tape grass and most other nonalgal submerged aquatic vegetation (SAV) vanished from much of the river basin after an extended period of high, tannin-stained water and increased turbidity due to flooding from Hurricane Irma in 2017 (Goldberg and Trent 2020, Lundy et al. 2022, K.J., unpub. data). Flood events in the LSJR commonly cause temporary SAV die-offs (Lacoul and Freedman 2006, Bornette and Puijalon 2011). In 2004 prolonged conditions of low light availability caused by strikes from three major hurricanes (Charley, Frances, and Jeanne) were followed by extensive SAV loss throughout the river basin. Tape grass and other SAV re-emerged within 3 yr as the river returned to baseline hydrologic and water quality conditions. By contrast, SAV in the LSJR did not fully recover in the 5 yr between when Hurricane Irma made landfall in 2017 and 2022, despite a return to background water conditions. The tape grass plants that remain as of 2022 when data were collected for this study are sparse and have canopy heights below 10 cm (Goldberg and Trent 2020, Lundy et al. 2022, K.J., unpub. data).

Herbivory commonly limits tape grass recovery in freshwater and estuarine habitats, including Kings Bay and other Florida waterways, but the extent to which it impacts SAV in the LSJR is unknown (Carter and Rybicki 1985, Hauxwell et al. 2004b, Johnson et al., 2019). Recent efforts to restore tape grass upstream of the LSJR in Lake George and Silver Glen Spring by using wire fenced enclosures to prevent grazing by herbivores yielded canopy heights approximately 10-fold higher than surrounding unenclosed plants. When these protective fences were removed or breached the plants were grazed by cooters (*Pseudemys* spp.) within days to canopy heights equal to the surrounding SAV (< 10 cm). Additionally, blue tilapia (*Oreochromis aureus*) were observed uprooting

unprotected plants near the restoration area (D.K., unpub. data). The Florida Fish and Wildlife Conservation Commission (FWC) has received multiple reports indicating that the tape grass beginning to re-establish areas of the LSJR appear similar to the heavily grazed plants in Lake George and Silver Glen Spring. This study was conducted to determine the effect of herbivory on the growth of tape grass in the Lower St. Johns River.

METHODS

Four littoral sites in the LSJR were selected based on current presence and consistent historical presence of tape grass (*Vallisneria americana*). To account for differing salinity regimes in the river, sites were established at varying distances to the river mouth while prioritizing site accessibility for monitoring. The four sites were, in order from north to south, Shand's Bridge (SHAN), Bayard Point Conservation Area (BAY), Palatka (PAL), and San Mateo (MAT; Figure 1). These sites range from approximately 100 to 50 km downriver from the FWC restoration sites in Lake George and Silver Glen Spring. The northernmost sites, SHAN and BAY, are near the edge of the oligohaline zone of the LSJR and are commonly exposed to salinities that approximately range from 0 to 5, whereas PAL and MAT are in the freshwater zone where salinities range from 0 to 0.75 (R.T., unpub. data).

In March of 2022, three 1 by 1-m wire enclosures and three 1 by 1-m control plots were installed by St Johns River Water Management District (SJRWMD) and FWC staff over existing tape grass beds at equal (where possible) water depths at each study site. Enclosures were open at the top and consisted of four steel T-posts covered with PVC pipe then wrapped with galvanized steel mesh (1.3-cm mesh size) secured by plastic cable ties. PVC stakes were placed directly adjacent to each enclosure to demark the control plots. Galvanized steel, though not suitable for long-term enclosures, was selected over PVC-coated mesh because of the short duration of the study.

Longest leaf length of three haphazardly selected shoots were recorded within a 0.5 by 0.5-m section at the center of the plots monthly from March to July by SJRWMD staff ($n = 12$). Damage to cages, evidence of grazing, and presence of grazers within enclosures were also recorded.

Data analyses was performed using R Statistical Programming Language (R Development Core Team 2010). Linear

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DOI: 10.57257/JAPM-D-23-00003

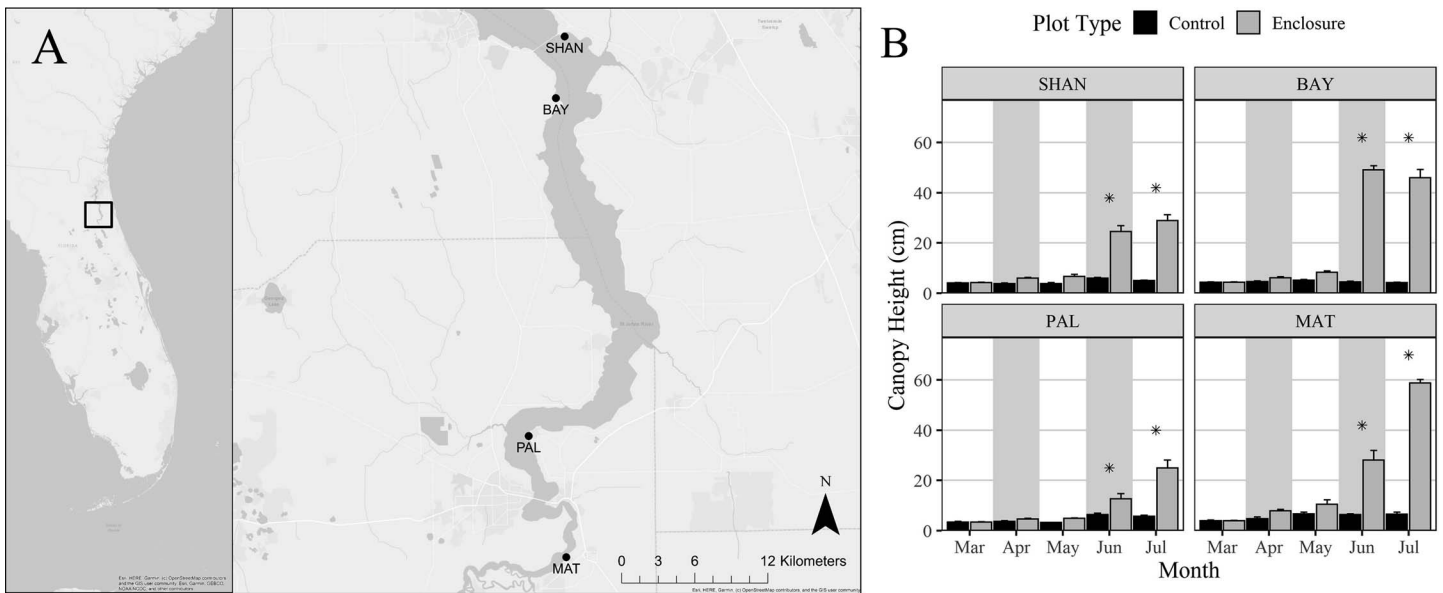


Figure 1. (A) Locations of the study sites at Shand's Bridge (SHAN), J. P. Hall Bayard Point Conservation Area (BAY), Palatka (PAL), and San Mateo (MAT) in the Lower St. Johns River. (B) Bar graphs of mean *Vallisneria americana* leaf length in control and enclosed plots at each site from deployment (March) to the end of monitoring (July). Error bars depict standard error and asterisks indicate Bonferroni-corrected Dunn's tests of enclosures vs. controls with P values below 0.05.

mixed-effect models were created with the lme4 package to determine the effect of plot type (enclosed or control) on tape grass leaf length (Bates et al. 2015). Plot type, month, and site were included in the model as fixed effects with interaction terms and individual plot was inputted as a random intercept effect. A P value for the overall effect of plot type was calculated by comparing this model to a model without the plot type variable via analyses of variance (ANOVA). Model residuals were plotted and visually inspected to assess fit. P values for pairwise comparisons of leaf lengths within and among sites during each month were subsequently obtained by Bonferroni-corrected Dunn tests. An alpha of $P < 0.05$ was used to determine statistical significance. Though variance in residuals was largely consistent across fitted values, it differed between enclosed and control plots. Because of the large effect size of plot type (LRT = 727.2, DF = 20, $P < 0.001$), we determined that data transformation or additional model terms were unnecessary.

RESULTS AND DISCUSSION

Plot type had a significant overall effect on tape grass leaf length (ANOVA, $P < 0.001$). Control and enclosed plots leaf lengths were not different among any sites during deployment in March (mean \pm SE: 3.9 cm \pm 0.1, 3.9 cm \pm 0.1, Dunn $P = 0.99$) through May (4.7 cm \pm 0.3, 7.5 cm \pm 0.6, Dunn $P = 0.32$). By the third month after deployment (June) leaf lengths within enclosed plots ranged from 2-fold to 10-fold longer than those in control plots at all sites (5.9 cm \pm 0.2, 28.6 cm \pm 2.6, Dunn $P < 0.001$). The discrepancy in leaf length further increased during July, the final month of deployment (5.4 cm \pm 0.3, 39.7 cm \pm 2.6, Dunn $P < 0.001$; Figure 1).

Control plot leaf lengths did not vary from March to July (3.9 cm \pm 0.1, 5.4 cm \pm 0.3, Dunn $P = 0.73$). July enclosed

plot leaf lengths at San Mateo (MAT) were the longest of all sites, and Bayard Conservation Area (BAY) were second longest (58.8 cm \pm 1.4, 46.0 cm \pm 3.3, Dunn $P < 0.002$). Shand's Bridge (SHAN) and Palatka (PAL) were both shorter than BAY (Dunn $P < 0.001$, Dunn $P < 0.001$) and MAT (Dunn $P < 0.001$, Dunn $P < 0.001$), but not different from each other (28.9 cm \pm 2.3, 25.0 \pm 3.2, Dunn $P = 0.99$). July control plot leaf lengths did not vary among sites.

Our results demonstrate a clear, positive effect of grazer exclusion on the growth of tape grass and that herbivory may be a substantial barrier to tape grass recovery in the Lower St. Johns River. Further, in the absence of grazing pressure, tape grass biomass recovers without transplants or seeding.

Cooters (*Pseudemys* spp.) graze heavily on tape grass at restoration sites in Lake George and Silver Glen Spring, but it is unclear which herbivores are the primary grazers in the LSJR and whether this varies among regions within the river drainage. Other possible candidates include invasive non-native species, such as blue tilapia (*Oreochromis aureus*), grass carp (*Ctenopharyngodon idella*), and armored catfish (*Loricariidae* spp.), as well as native herbivores, such as blue crabs (*Callinectes sapidus*), mullet (*Mugil* spp.), and manatees (Hauxwell et al. 2004a, Scopettone et al. 2005, Cohen 2008, Adler et al. 2018, Johnson et al. 2019, Schad et al. 2021). Blue crabs contribute to SAV recovery bottlenecks in the James River and Chesapeake Bay and were found inside our study enclosures during July, likely having entered through a gap between the wire mesh and river bottom created by sediment erosion (Harwell and Havens 2003, Adler et al. 2018, Johnson et al. 2019). Both cooters and blue crabs are present in large numbers throughout the St. Johns River and have feeding strategies that leave tape grass blades with the clipped appearance that is common to unenclosed plants in

the LSJR (D.K., unpub. data). The identity of the primary species, if any, responsible for SAV herbivory in the LSJR should be the subject of future research.

Water clarity returned to background levels prior to the 2022 Hurricanes Ian and Nicole, but the relative intensity of grazing pressure on SAV during this time is unknown. Herbivory is a limiting factor for SAV in the Lower St. Johns, and atypically high grazing pressure may ultimately be limiting recovery amid typical water clarity conditions. However, there are a number of alternative scenarios for which grazing is only a proximate limiting factor: Absent additional stressors, atypically low water (drought) and high water clarity may be required to enable rapid growth to overcome losses from background levels of grazing pressure after a die-off. Elevated salinities and epiphyte loads increase light requirements for SAV (Sand-Jensen 1977, Kraemer et al. 1999, French and Moore 2003, Dobberfuhl 2007). Either stressor, or a combination of the two, may slow plant growth enough such that background grazing pressure is enough to limit recovery.

The size of plot required to withstand grazing pressure after enclosures have been removed or compromised is unknown. Additionally, substantial effort may be required to maintain the integrity of large-scale enclosures as SAV is targeted by grazers after enclosure breach or removal and quickly loses biomass, even after months of protected growth (Hauxwell et al. 2004b, D.K., unpub. data). Chances of postexposure success may increase if sufficiently large plots can be sheltered for multiple growing seasons to establish robust beds in areas with surrounding SAV that may diffuse grazing pressure after enclosure removal (Moore et al. 2010). Based on these criteria, our results can inform decisions about future large-scale SAV enclosure restoration efforts in the Lower St. Johns River. This study demonstrates that protected tape grass can grow in the LSJR at least as far south as San Mateo and as far north as Shand's Bridge, 100 km downriver of the Silver Glen Springs restoration sites. Plants at MAT and BAY grew larger than those at PAL and SHAN, indicating that enclosure restoration may have the greatest chance of succeeding near MAT and BAY. However, the southern section of the river surrounding MAT (and PAL) has narrow littoral zones and provides little habitat with water shallow enough to support SAV growth, often only 10 to 20 m perpendicular to shore. Additionally, this area is highly developed, with many docks and obstructions that may interfere with large SAV enclosure construction. BAY is adjacent to the J.P. Hall Bayard Point Conservation Area, a large undeveloped area owned by the SJRWMD. The shallow sloping banks of this section of the river create a large area of habitable benthos where expansive SAV beds have historically grown and continue to persist along most of the shoreline in 50 to 100-m-wide beds of closely cropped tape grass. Of the four study sites, BAY is the best candidate for large SAV restoration enclosures.

ACKNOWLEDGEMENTS

The project was made possible by materials supplied through FWC's Aquatic Habitat Restoration/Enhancement

subsection, and data collection efforts and mapmaking of Randy Fink and Anabelle Baggs of the St. Johns River Water Management District. We also thank Erich Marzolf and Tim Houghtaling for their stewardship of the project enclosures and generously allowing us to use their land for site access.

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