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***SHORT COMMUNICATION***

# BENTHIC AND EPIBENTHIC INVERTEBRATE ASSEMBLAGES ASSOCIATED WITH ESTUARINE SUBMERGED AQUATIC VEGETATION DIFFER BETWEEN NATIVE AND INVASIVE PLANTS[§]

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## INTRODUCTION

Estuarine submerged aquatic vegetation (SAV) plays a crucial role in maintaining coastal ecosystem health and stability. These underwater plants provide habitat and food for a diverse mix of freshwater, estuarine, and marine organisms, including fish (Rozas and Odom 1988, Martin and Valentine 2019), invertebrates (Alford and Rozas 2019), and waterfowl (Zhou et al. 2020). SAV serves as nursery habitat for many commercially important species (Chesney et al. 2000, Castellanos and Rozas 2001, Martin et al. 2021), supporting biodiversity and fisheries (Lazzari et al. 2006, Brzozowski and Pełechaty 2025), and aids in improving water quality by stabilizing sediments (Han et al. 2024), reducing turbidity (Hestir et al. 2016), and mitigating excess nutrients (Zhou et al. 2018). However, many estuaries now contain non–native and invasive SAV (McDonald et al. 2023), known to cause negative ecological and economic impacts, primarily due to their rapid growth (Brundu 2015), high reproduction (Engelhardt 2011), and ability to outcompete native species (Stiers et al. 2011), leading to altered ecosystem structure and function (Lloret et al. 2004).

Eurasian milfoil, *Myriophyllum spicatum* L., is a problematic invasive species in freshwater and brackish systems across North America, with documented ecological, economic, and recreational issues (Frodge et al. 1990, Boylen et al. 1999). *Myriophyllum spicatum* has now successfully established and proliferated in many estuaries in the northern Gulf of Mexico (Frazer et al. 2006, Valinoti et al. 2011, Alford and Rozas 2019), including the Mobile–Tensaw Delta (hereafter MTD) in coastal Alabama (Chaplin and Valentine 2009, Martin and Valentine 2014). First discovered in the area in the 1950s (Beshears 1982), *M. spicatum* is now the most abundant SAV, covering up to 80–85% of surveyed locations (USACE 2019). Studies in freshwater systems indicate that *M. spicatum* outcompetes native macrophytes by developing an extensive canopy, impacting adjacent plants by out–shading (Bruce et al. 2018, Verhoeven et al. 2020), and thus poses a direct threat to the most abundant native SAV in the MTD, wild celery *Vallisneria americana* Michx. (often referred to as *V. neotropicalis*) (Kauth and Biber 2014, Lawrence et al. 2024).

Different macrophyte species are known to support different associated biological communities, particularly when their morphology (i.e., structural complexity) differs (Kovalenko et al. 2010). *Myriophyllum spicatum* has highly dissected leaflets that grow in a whorl pattern at 2 cm increments along long, flexible branching stems. This species therefore has greater structural complexity compared to the other abundant and native species, *V. americana* (Chaplin and Valentine 2009) which has simple, non–branching ribbon–like leaves that grow towards the water surface from a basal rosette. The distinct structures of these SAVs may support different biological assemblages and food webs via differences in surface area for epiphyte growth and interstitial spaces for organisms to occupy (Martin and Valentine 2011, 2019). The displacement of *V. americana* by *M. spicatum*, therefore, may result in differential macroinvertebrate communities, which could have ecosystem–wide consequences.

While previous studies have documented differences in above–ground macroinvertebrate assemblage between SAV habitats in the MTD (e.g., Chaplin and Valentine 2009, Kauffman et al. 2018, Alford and Rozas 2019), to date, belowground assemblages are often overlooked. Investigating the composition of both above and belowground macroinvertebrates is essential for gaining a complete understanding of the consequences of the *M. spicatum* invasion of the MTD and wider ecological impacts. Here, we investigate differences in above– and belowground macroinvertebrate assemblages between native *V. americana* and invasive *M. spicatum*. We hypothesized that there would be significant differences in the macroinvertebrate assemblages between the SAV, with *M. spicatum* supporting greater abundances and diversity of associated species, while *V. americana* would support more even communities.

## MATERIALS AND METHODS

### Study Site

The Mobile–Tensaw Delta is the second largest river delta in the contiguous United States (Szabo et al. 1988), and due to its

[§] *The first author conducted this research as part of the Dauphin Island Sea Lab's Research Experience for Undergraduates in the coastal and nearshore marine science program.*

rich diversity of wildlife, has been referred to as "America's Amazon." The lower reaches are comprised of several oligohaline bays, bayous, marshes, and beds of SAV resulting from the input of 5 major rivers (Chaplin and Valentine 2009). Our sampling occurred in Chocolatta Bay (30°41'15.342", –87°58'44.277"), one of the larger bays in the lower MTD.

**Experimental Design and Sampling Procedure**

To investigate differences in macroinvertebrate communities associated with native and invasive SAV within the MTD, epifaunal and infaunal samples were collected from monospecific beds of *V. americana* and *M. spicatum* in Chocolatta Bay during June 2024. A total of 12 paired epifauna and infauna samples were collected haphazardly >5 m from each other, for a total of 24 samples of each SAV species. Epifauna samples were collected by placing a 0.5–μm mesh bag over individual plants, which were severed at the sediment surface (Sullivan et al. 2021). Infauna samples were collected using a 7 cm inner diameter core inserted approximately 10 cm into the sediment and then removed, retaining sediment and fauna contained within by hand and then sieved in the field using a 0.5 mm sieve. While there was potential to capture fauna residing on the sediment surface, and as such may not reflect solely the infauna assemblage, we applied this method consistently across both SAV beds. In the laboratory, organisms were removed from SAV and transferred to vials containing 70% ethanol for identification at the lowest identifiable taxonomic level. For epifauna, dry weights of plants per sample were obtained to standardize for plant biomass (i.e., counts of organisms per gram of plant) by drying plants in a drying oven at 60°C for 72 h, at which time they were removed and weighed.

**Statistical Analyses**

To test the hypothesis that *V. americana* and *M. spicatum* habitat would support different macroinvertebrate communities, we ran a one–way permutational multivariate analysis of variance test (PERMANOVA) evaluating the effects of habitat (fixed, 2 levels: *V. americana*, *M. spicatum*) for epifauna (standardized for count per gram of plant) and infauna (percent relative abundance) separately after Bray–Curtis similarity matrices were computed (using square root transformed data on both datasets). Additionally, using a series of one–way analysis of variance (ANOVA) tests, we analyzed differences in species richness, abundance, Shannon–Weiner Diversity Index (H') and Pielou's Evenness (J', where J' ranges from 0–1 with greater values indicating higher levels of evenness), and abundances of major taxonomic groups (based on taxa contributions) between habitats.

All statistical tests were conducted in PRIMER v7 with the PERMANOVA + add–on (PRIMER–E Ltd, Anderson et al. 2008). Transformations were chosen with the aid of the Draftsman Plot function and PERMANOVAs were based on unrestricted permutation of raw data using 9999 permutations. Multivariate data were visualized using non–metric multidimensional scaling plots, and percent contributions of individual organisms to differences between SAV habitats were assessed using the similarity percentage (SIMPER) routine (Clarke and Gorley 2015). Species richness, Shannon–Weiner diversity (H'), and Pielou's Evenness (J') indices were calculated using the DIVERSE routine, compared using PERMANOVAs, and visualized in SigmaPlot v10. Treatments were considered significant at $p \leq 0.05$.

## Results

Temperature (29.0–29.3°C) and salinity (2.2–2.4) were consistent among vegetation at the time of sampling. A total of 16 macroinvertebrate taxa were recorded across the 2 species of SAV, with 12 taxa associated with *M. spicatum* and 13 taxa in *V. americana* (Supplemental Table S1). Two species were unique to *M. spicatum* (bivalves and mysid shrimp) and 3 unique to *V. americana* (*Corophium* species, Annelids, and the isopod *Cyathura polita*). *Vallisneria americana* supported more epifaunal (n = 12) and infaunal (n = 10) species compared to *M. spicatum* (epifauna, n = 11; infauna, n = 7).

One–way PERMANOVAs detected significant differences in macroinvertebrate assemblages between SAV habitats for both epifauna ($F_{1,22}$ = 14.057, $p$ < 0.001) and infauna ($F_{1,21}$ = 3.1429, $p$ =

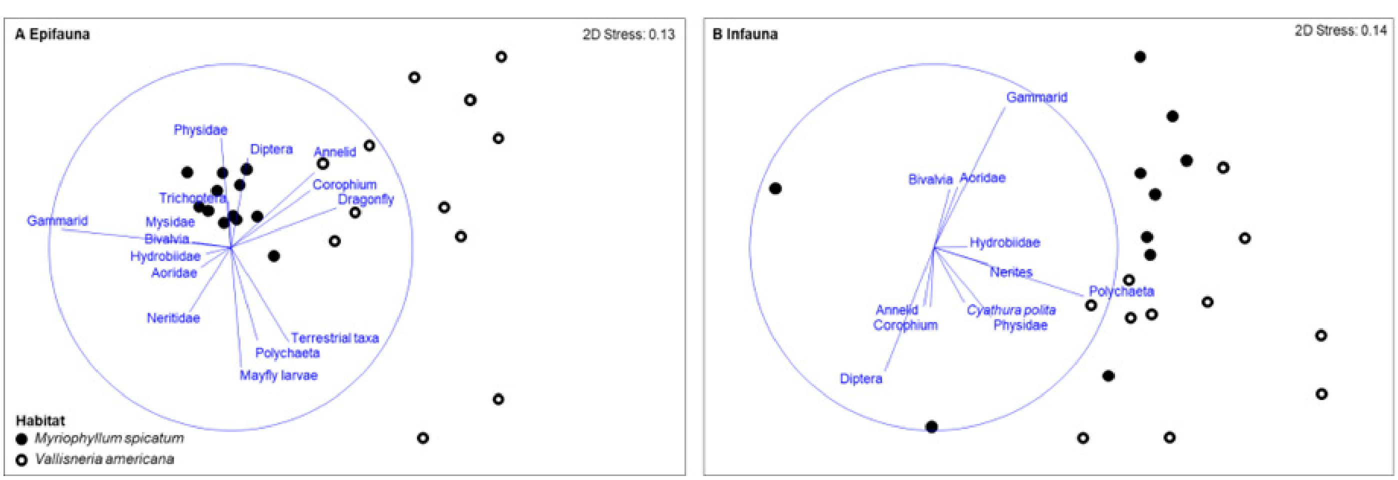


***FIGURE 1.*** *Non–metric multidimensional scaling (nMDS) plots of communities associated with* Myriophyllum spicatum *and* Vallisneria americana *in the Mobile Tensaw Delta, AL with a Spearman's Rank Correlation vector overlaid. The length and direction of the lines on the vector overlay indicate the strength and sign of the relationship between the SAV habitats and their associated species. Only vectors longer than 0.5 are shown. A. Epifauna communities. B. Infaunal communities.*

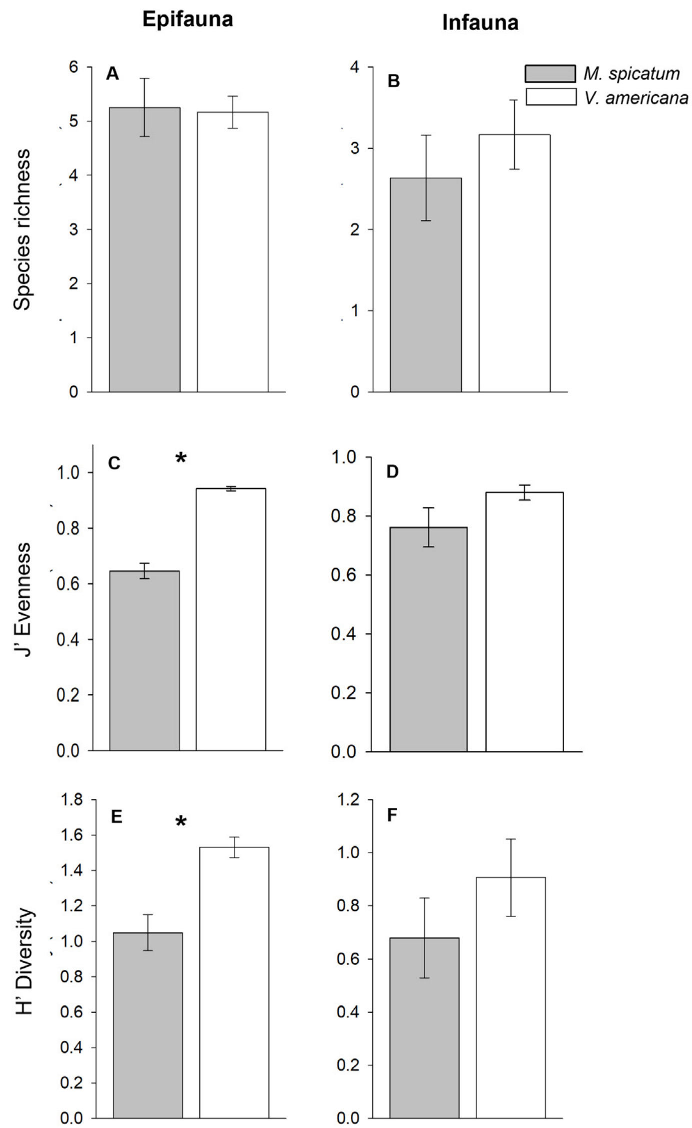


***FIGURE 2.*** *Community difference measurements for macroinvertebrates associated with* Myriophyllum spicatum *and* Vallisneria americana *in the Mobile Tensaw Delta, AL. A. Mean (± se) epifauna species richness. B. Mean (± se) infauna species richness. C. Mean (± se) epifauna Pielou's Evenness (J'). D. Mean (± se) infauna Pielou's Evenness (J'). E. Mean (± se) epifauna Shannon–Weiner Diversity Index (H'). F. Mean (± se) infauna Shannon–Weiner Diversity Index (H'). Asterisk (*) denotes significant difference between SAV species.*

0.014) (Figure 1). An analysis of the contribution from individual taxa (SIMPER) showed that about 54% of the dissimilarity observed between *M. spicatum* and *V. americana* for epifauna was due to contributions from Gammarid amphipods, which were 11.85 times more abundant in *M. spicatum*. For infauna, 24% of the dissimilarity between habitats was attributed to polychaete species, which were 3.16 times more abundant in *V. americana* (Supplemental Table S2).

Mean species richness in *M. spicatum* and *V. americana* did not differ significantly for epifauna (*M. spicatum*, 5.25 ± 0.54; *V. americana*, 5.17 ± 030; mean ± se; Figure 2A; $F_{1,22}$ = 0.268, $p$ = 0.729) nor infauna (*M. spicatum*, 2.64 ± 0.53; *V. americana*, 3.17 ± 0.42; Figure 2B; $F_{1,22}$ = 0.901, $p$ = 0.371). For Pielou's Evenness (J'), epifaunal communities significantly differed between SAV species, with communities in *V. americana* more even than *M. spicatum* (Figure 2C; $F_{1,22}$ = 65.103, $p < 0.001$); however, no significant differences were detected in the infaunal communities (Figure 2D; $F_{1,22}$ = 3.064, $p$ = 0.060). Shannon–Wiener Index (H') showed that *V. americana* supported significantly greater epifaunal (Figure 2E; $F_{1,22}$ = 11.37, $p < 0.001$) but not infaunal (Figure 2F; $F_{1,22}$ = 0.948, $p$ = 0.343) diversity compared to *M. spicatum*. *Myriophyllum spicatum* supported significantly higher abundance of epifaunal individuals (n = 4.51 ± 0.92) compared to *V. americana* (n = 2.65 ± 0.93; $F_{1,22}$ = 22.235, $p < 0.001$).

Analysis of abundances of major taxonomic groups within the epifauna community showed that *M. spicatum* supported significantly greater numbers of Gammarid amphipods (Figure 3A; $F_{1,22}$ = 51.868, $p < 0.001$). No significant differences,

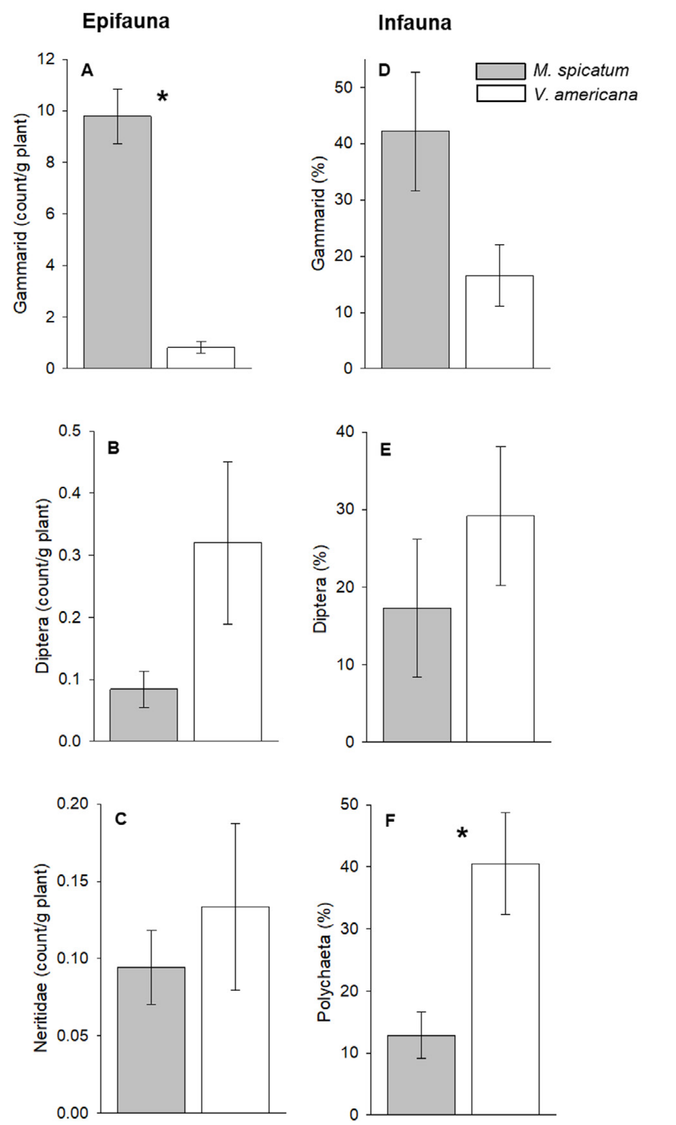


***FIGURE 3.*** *Abundance of major taxonomic groups present on* Myriophyllum spicatum *and* Vallisneria americana *in the Mobile Tensaw Delta, AL. Presence based on % contribution from SIMPER analysis. A. Mean (± se) count/g plant of Gammaridae on epifauna. B. Mean (± se) count/g plant of Diptera on epifauna. C. Mean (± se) count/g plant of Nertiidae on epifauna. D. Mean (± se) percent of Gammaridae on infauna. E. Mean (± se) percent of Diptera on infauna. F. Mean (± se) percent of polycheates on infauna. Asterisk (*) denotes significant difference between SAV types.*

however, were detected between SAV types for Diptera (Figure 3B; $F_{1,22}$ = 2.150, $p$ = 0.152) nor Neritidae (Figure 3C; $F_{1,22}$ = 0.051, $p$ = 0.868). For infaunal communities, no significant differences in abundances were found between SAV types for Gammarids (Figure 3D; $F_{1,22}$ = 0.789, $p$ = 0.410) nor Diptera (Figure 3E; $F_{1,22}$ = 0.709, $p$ = 0.4241), but there were significantly higher abundances of polychaetes in *V. americana* compared to *M. spicatum* (Figure 3F; $F_{1,22}$ = 4.615, $p$ = 0.036).

## Discussion

Results supported our hypotheses that epifaunal and infaunal macroinvertebrate assemblages would vary significantly between the native *V. americana* and the invasive *M. spicatum*, where *V. americana* would support a more even community (epifauna only), and *M. spicatum* would support a greater abundance of individuals (epifauna only). However, contrary to our hypotheses, Shannon–Weiner Diversity Index showed that *V. americana* supported significantly greater diversity compared to *M. spicatum* for epifauna.

Analysis of the epifaunal communities found that *Gammarus* species drove the difference between SAV assemblages, with this group significantly more abundant in *M. spicatum*. This result is not surprising given that Gammarids have been shown to preferentially choose more complex macrophyte habitats (Hansen et al. 2011). Furthermore, Gammarids and other taxa utilize the interstitial space of structurally complex plants to avoid encounters with predators (Martin and Valentine 2011, Valinoti et al. 2011) and Gammarids, specifically *G. mucronatus*, have been previously documented in very high abundances in *M. spicatum* (Chaplin and Valentine 2009, Kauffman et al. 2018). The ultimate impact of this enhanced Gammarid abundance on landscape–level food webs, however, remains uncertain but we speculate that, given their 11 times greater abundance in *M. spicatum* than *V. americana*, some alteration of ecosystem services (e.g., organic matter and/or nutrient cycling) are likely to occur.

Differences in infaunal communities were driven by the polychaetes, with this group significantly more abundant in *V. americana*. This result may be attributed to enhanced recruitment of polychaetes to *V. americana* beds, differential survivorship, or differences in food quantity/quality between these SAV species. The role of belowground SAV biomass in providing structural complexity and sediment oxygenation, and the corresponding effects on infaunal community structure is a topic requiring additional study. Gaining a better understanding of mechanisms driving infaunal assemblages and concomitant effects on plants may have utility for habitat restoration and conservation (Heck 2019). Polychaetes provide essential ecosystem services through aeration of sediment and provision of food for higher trophic levels, and their burrowing depths may be limited by root morphology (Pawlikowski and Kornijow 2023). A loss or reduction in this group of species through decreases in *V. americana* may thus have wider ecological effects in the MTD.

With the continued decline in coverage of native species such as *V. americana*, an ecologically vital species in the MTD, our results provide baseline data to investigate potential wider ecological consequences of the invasion of *M. spicatum* across the MTD, especially given that *V. americana* supports a more diverse and even community compared to *M. spicatum*. Additionally, the substantially higher abundance of Gammarids in *M. spicatum* (>10 times, on average) could represent greater recruitment, higher survival rates, or merely concentration of these amphipods in a preferred habitat. Since these species are often preferred prey for higher trophic level species (MacNeil et al., 1999), determining whether this abundance is transferred to higher trophic levels could clarify further functional distinctions between the two macrophyte species (Martin and Valentine, 2019).

We acknowledge temporal and spatial limitations to this study, with only one month sampled (June 2024); thus, the results may not fully represent ecological impacts throughout the year, and potential effects on ecosystem services can only be considered within the context of this specific time point. Additionally, we focused on assemblage differences between two monospecific SAV beds at a single site (Chocolatta Bay). A more comprehensive understanding of ecosystem impacts would benefit from sampling additional monospecific beds and bare sediment areas within Chocolatta Bay and the wider Mobile Bay system, as natural variations across habitats are likely due to factors such as water flow, salinity, and turbidity. Additionally, macroinvertebrate identification to a lower taxonomic level may show additional differences between the 2 SAV species. Thus, further investigations in space and time are needed to clarify the impacts of *M. spicatum* on resident biological assemblages and associated ecosystem services and will contribute to a better understanding of external sources of variation. Nevertheless, we provide important baseline data on the ecological structure of epifaunal and infaunal communities to support future research aimed at developing a mechanistic understanding of the processes influencing SAV assemblages. Specifically, future studies should aim to better understand food web alterations by invasive species and the broader implications of additional anthropogenic factors (e.g., hydrology, climate change, eutrophication) that may alter SAV composition and affect faunal communities.

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