Seagrass and epiphyte seasonality in a biogeographic transition zone

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Abstract

North Carolina, USA is an ecotone that includes two seagrass species located at the edge of their distributional ranges: *Zostera marina*, a temperate species, and *Halodule wrightii*, a tropical species. Both support dynamic epiphyte communities, yet seagrass and epiphyte species composition and biomass relationships are not well documented in mixed-species transition zones. This study investigates the seagrass and epiphyte biomass and epiphyte community composition by seagrass species by using monthly collections over one year from Topsail Sound, NC. *H. wrightii* biomass peaked in the fall and declined to seasonal minimums in winter. *Z. marina* biomass peaked in the spring and was lowest in fall. Maximum epiphyte biomass per leaf area occurred during periods of thermal stress for both species, summer for *Z. marina* and winter for *H. wrightii*. Epiphyte community composition differed between seagrass species within all seasons except for spring, which is a period of concurrent growth for both species, while there was no difference in community across the entire year. Variation in epiphyte communities within NC can be explained by divergent periods of thermal stress, leaf growth, and staggered periods of peak biomass between *H. wrightii* and *Z. marina.* Mixed temperate and tropical species meadows ensured continuous substrate for macroalgal epiphytes throughout the year with the seasonality of the epiphyte community closely tied to the growth cycles of their seagrass hosts. This research contributes to our understanding of mixed-species seagrass meadows in biogeographic transition zones and informs conservation and management strategies needed for a rapidly changing climate.

1. INTRODUCTION

Seagrasses are marine angiosperms found globally in subtropical, tropical, and temperate coastal waters forming highly productive meadows (Short et al. 2007). These meadows act as ecological indicators, especially in regions like North Carolina, USA, which serves as an ecological transition zone between temperate and tropical bioregions located along the Western North Atlantic Ocean (Short et al. 2007). The interaction between the warm Gulf Stream and the cold Labrador current creates a dynamic range of water temperatures spanning 5°C – 30°C (Shearman and Lentz 2010, Jarvis et al. 2012), setting the stage for complex interplay of biodiversity. This transition zone harbors the temperate *Zostera marina*, tropical *Halodule wrightii*, and eurythermal *Ruppia maritima* (Thayer et al. 1984) all within the same meadow, a phenomenon unique to this part of the Western Atlantic (Short et al. 2007). The coexistence of these species within this ecotone provides an opportunity to study the seasonal dynamics of seagrass-epiphyte interactions between a tropical and temperate species, an area that has received relatively little attention.

Seagrasses are foundational species that underpin the marine food web and coastal communities by providing vital substrate and nursery habitat for economically important organisms and fisheries (Phillips and Meñez 1988, Beck et al. 2001, Barbier et al. 2011, Unsworth et al. 2019) including many benthic invertebrates, juvenile fish, and early life-history stages of a myriad of organisms (Phillips and Meñez 1988). These natural engineers produce leaves that reduce wave and current energy (Larkum et al. 2006b), provide a food source for numerous invertebrates, fish, and mega-herbivores (Thayer et al. 1984, Lavery et al. 2013), and act as substrate for a diverse array of epiphytic organisms including amphipods (Bologna

and Heck 2002), snails (Voigt and Hovel 2019), polychaetes (Nelson and Capone 1990), numerous species of bacteria, micro- (Campbell and Fourqurean 2014) and macroalgae (Brauner 1975, Wium-Anderson 1984, Hoffmann et al. 2020).

The micro- and macroalgal epiphytes found on seagrass leaves are a community of fast-growing primary producers, which can account for a significant portion of the biomass in the seagrass ecosystem (Borowitzka et al. 2006, Ruesink 2016). Studying these epiphytes is crucial as they can serve as an indicator of changing environmental or stress conditions (Nelson 2017), particularly during a period of shifting temperature regime (Hansen et al. 2022). A fast-recruiting biofilm of bacteria and unicellular microalgae provides additional substrate for larger macroalgal epiphytes, which can increase in abundance with light, nutrient availability, and warm water temperatures (Larkum et al. 2006a, Pillay and Waspe 2019). Micro- and macroalgae outcompete seagrasses for nutrients and reduce the quantity and quality of light the plants receive through shading (Bulthuis and Woelkerling 1983, Brodersen et al. 2015, Ruesink 2016), which can directly influence the physiological and reproductive success of their host (Sand-Jensen 1977, Ow et al. 2020). This results in reduced leaf growth/turnover rate, shoot density, and increased non-structural carbohydrate content (Cimon et al. 2021). Epiphytes can also increase oxidative stress, reduce chlorophyll *b* levels (Costa et al. 2015), and alter plant metabolism (Ow et al. 2020). Epiphyte species have varied morphologies and growth patterns, which can influence the quality of light that reaches the plant. The biomass of these epiphytes determines the degree of light attenuation and its subsequent negative effects on seagrass photosynthesis (Brush and Nixon 2002).

Epiphyte biomass varies spatially and temporally among seagrass meadows (Larkum et al. 2006a) and is influenced by a myriad of factors including seagrass leaf turnover rate (Hemminga 1998, Douglass et al. 2010), herbivory (Hoffmann et al. 2020), epiphyte accumulation rate (Bulthuis and Woelkerling 1983), diversity of both seagrass and grazer (Duffy et al. 2015), as well as environmental conditions such as nutrient availability (Jaschinski and Sommer 2011) and irradiance (Burnell et al. 2014). Top-down factors such as species richness of grazers and herbivory are important in mediating epiphyte abundance (Hughes et al. 2004, Pillay and Waspe 2019, Cimon et al. 2021). Notably, the biodiversity of grazers has a stronger influence on epiphyte biomass than the grazer biomass itself, and a reduction in grazers stimulates epiphytic algae growth more significantly than nutrient addition (Reynolds et al. 2014). In this context, a more diverse seagrass ecosystem can harbor a more diverse grazer community (Reynolds et al. 2014, Duffy et al. 2015). Therefore, a reduction in seagrass diversity might lead to a decline in grazer diversity, which may potentially lead to a surge in epiphytic biomass.

Despite the recognized importance of epiphytes, their dynamics in transition zone seagrass meadows with unique species combinations (e.g., *Z. marina* and *H. wrightii*) remain unexplored (but see Brauner 1975). Given the existence of an ecological transition zone in North Carolina, understanding the patterns, interactions, and health of its seagrasses is of importance as these meadows are currently being negatively affected by climate change (Jarvis et al. 2012, Bartenfelder et al. 2022). In the North Carolina ecotone, marked by the coexistence of temperate and tropical seagrass species, we aim to quantify the seasonal biomass of seagrass and epiphytes and characterize the annual and seasonal macroalgal epiphyte community between seagrass species, shedding light on interspecies interactions, ecological

dynamics, and implications for edge-of-range species. This will provide insight into the resilience and adaptability of transitional zone seagrass habitats as water temperatures continue to rise and temperate habitats become tropicalized (Hyndes et al. 2016), with implications for conservation and management strategies in similar biogeographic transition zones worldwide.

2. MATERIALS AND METHODS

2.1. *In situ* sampling

Seagrass and epiphyte samples were collected from a site located along the intracoastal waterway in Topsail Sound, NC (34°23'53.2"N 77°36'55.1"W). This site is located adjacent to salt marshes, oyster reefs, and mudflats with a tidal range of 1.0-1.5m; landward portions of the meadow are intertidal, and seaward are subtidal, with a total area roughly 10,000m^2. This meadow contains *Zostera marina, Halodule wrightii*, and *Ruppia maritima*; is habitat for numerous invertebrate and fish species including blue crabs and scallops; exhibits seasonal water quality fluctuations (water clarity is greater in winter and worsens in summer; Jarvis et al. 2023), and has been monitored for changes in seagrass biomass and density throughout the seagrass growing season since 2017 (Jarvis et al. 2022). Given that this project focused on edge-of-range species experiencing seasonal thermal stress in this transition zone, only data from *H. wrightii* and *Z. marina* are reported.

Sampling events occurred monthly from January – December 2021. During each sampling event, four biomass cores (22 cm in diameter, 15 cm depth) were collected throughout the meadow to obtain aboveground, belowground, and epiphyte biomass for *Z. marina* and *H. wrightii*. Ten shoots per seagrass species were collected to identify macroalgal epiphyte species and assess differences in epiphyte assemblage. All samples were collected with a stratified random sampling technique between 0.5m – 1.5m depth to ensure representation of the meadow's heterogeneity. Once collected, samples were taken back to UNCW's Center for Marine Science and stored in a -20°C freezer until analysis.

2.2 Seagrass and epiphyte biomass

Seagrass biomass cores were separated by species in the laboratory; shoots were counted, and aboveground and belowground biomass was separated at the meristem. Flowering shoots were counted and weighed separately when found. A subset of three *Z. marina* and *H. wrightii* shoots were further analyzed for the number of leaves (leaves $shoot^{-1}$), leaf length and width to obtain leaf area (cm^{-2}), and epiphyte biomass standardized to leaf area (g DW cm^{-2}). To quantify epiphyte biomass, all epiphytes from the subset of measured shoots were scraped into 500 ml of 1µm filtered seawater, vacuum filtered onto pre-weighed 47 mm glass fiber filters (GF/F), then placed in a 60°C drying oven until a constant dry weight was reached. After removing epiphytes and sediment, all remaining seagrass aboveground and belowground biomass was placed into pre-weighed aluminum foil packets and dried in a drying oven at 60°C until a constant dry weight was reached. The GF/F filters with epiphyte biomass were then placed in a combustion oven at 500°C for 4 hours to obtain the ash free dry weight. All samples are reported as mean monthly or seasonal biomass (g DW m^{-2}) values ± SE.

2.3 Epiphyte Identification

Ten shoots of *Z. marina* and *H. wrightii* per monthly collection were thawed and visible epiphytes were identified to the lowest taxonomic level possible using Schneider and Searles (1991). The top 3–5 cm of the two oldest leaves were examined microscopically (40x, 100x, 400x magnification) to identify minute and microscopic epiphytes to genus or species if possible. Microalgae were not identified but noted when found. The tips of the oldest leaves were selected as this is where epiphytes are most likely to have settled and grown (Burnell et al. 2014). Pictures of common epiphytes were taken for reference. Epiphyte species were reported as presence/absence per shoot.

2.4 Statistical Analyses

All statistical analyses were run in R (R-Core-Team 2020) with R Studio (RStudio Team 2020) using packages 'vegan' (Oksanen et al. 2020), 'glmmTMB' (Brooks et al. 2017), and 'multcomp' (Hothorn et al. 2008). Data analysis and visualization were done using the package 'tidyr' and 'ggplot2' (Girlich 2022). Seasonal changes in seagrass biomass and epiphyte biomass were analyzed using general linear models with a gamma distribution due to the positive and continuous nature of the data. Months were grouped into seasons based on local water temperatures; January-March defined as 'winter' (8–15°C), April-June as 'spring' (15–25°C), July-September as 'summer' (25–31°C), and October-December as 'fall' (17–25°C). We began with a full model including all possible factor combinations, all non-relevant covariates were removed, and the model was refined until only relevant covariates remained (Zuur et al. 2007). Fixed effects included seagrass species, season, and their interaction. Residuals were also inspected visually for patterns by plotting the fitted versus response variables. The best-fit model was considered to be the simplest model with the lowest Akaike information criterion (AIC) score (Zuur et al. 2007), which was calculated using the 'bbmle' package (Brooks et al. 2017). Overall effects of categorical variables were quantified via analysis of deviance for all model parameters using a type II ANOVA for models with no interaction terms and a type III ANOVA when interactions were present (car' package; Fox and Weisberg 2019). During post hoc analysis all pairwise comparisons were computed from the contrasts between factors with a 'tukey' adjustment using 'lsmeans' package (Lenth 2016).

Multivariate patterns of epiphyte species assemblage were visualized using non-metric multidimensional scaling (R 'vegan' package) to obtain seasonal differences in the epiphyte community between seagrass species. Data were recorded as presence/absence of epiphyte per seagrass shoot grouped into seasons (same groupings as field data) to quantify seasonality. A distance matrix using Bray-Curtis dissimilarity was created using package 'vegan' to run a pairwise analysis, analysis of similarity (ANOSIM), and permutational multivariate ANOVA (PERMANOVA) to obtain statistical significance of epiphyte community between and among seasons or seagrass species. A pairwise analysis was run on the distance matrix to determine during which seasons the seagrass epiphyte communities differ. A similarity percentages breakdown (SIMPER) was then run to determine which epiphytes were the main contributors to dissimilarity between species and season.

3. RESULTS

3.1 Biomass

An interaction between species and season significantly influenced both aboveground ($p < 0.001$, $c^2 = 40.042$, df = 3, Table 1a, 1b) and belowground ($p < 0.001$, $c^2 = 30.606$, df = 3, Table 2a, 2b) biomass. *Halodule wrightii* aboveground biomass exceeded that of *Z. marina* in the fall by a significant margin ($p < 0.001$, t-ratio = 6.297, df = 71, Supplemental A), with no significant differences between species within the other seasons (Figure 1, Supplemental A). The same was true for *H. wrightii* belowground biomass, which exceeded that of *Z. marina* in the fall ($p < 0.001$, t-ratio = 7.248, df = 72, Supplemental A) with no significant differences between species in the other seasons (Figure 1).

3.2 Epiphyte biomass standardized to leaf area

An interaction between species and season significantly influenced epiphyte biomass when standardized to leaf area ($p < 0.001$, $c^2 = 55.088$, df = 3, Table 3a, 3b). *H. wrightii* epiphyte biomass was significantly greater than that of *Z. marina* in spring ($p = 0.0001$, t-ratio = 4.961, df = 71), fall ($p < 0.0001$, t-ratio = 6.349, df = 71), and winter ($p < 0.0001$, t-ratio = 10.363, df = 71, Supplemental A). There was no difference in epiphyte biomass between the species in summer (Figure 2).

3.3 Aboveground to belowground ratio

H. wrightii aboveground to belowground ratio (AG:BG) was significantly influenced by an interaction between species and season ($p < 0.001$, $c^2 = 22.006$, df = 3, Table 4a, 4b). AG:BG of *H. wrightii* differed significantly from *Z. marina*, with *H. wrightii* showing a lower ratio in winter ($p = 0.0003$, t-ratio = -4.705, df = 64) and spring ($p = 0.0002$, t-ratio = -4.915, df = 64), a greater ratio in summer ($p = 0.0397$, t-ratio = 3.208, df = 64), with no difference between the species in fall (Supplemental A, Figure 3).

3.4 Epiphyte Community

We identified thirty-one distinct epiphyte taxa spanning various phyla and life history stages. Analysis of similarities (ANOSIM) revealed seasonal variation in epiphyte communities when comparing the two seagrass species ($R = 0.428$, $p = 0.001$), however, there was no significant annual variation in epiphyte communities when comparing the two ($R = 0.026$, $p = 0.008$). Permutational Multivariate Analysis of Variance (PERMANOVA) highlighted a significant interaction between seagrass species and season ($p = 0.001$, $R^2 = 0.0395$, df = 3, Table 5). Further pairwise comparisons showed significant differences between the epiphyte communities of *H. wrightii* and *Z. marina* in winter, summer, and fall ($p = 0.001$ for all), whereas there was no difference in the spring ($p = 0.214$, Table 6). Non-metric Multidimensional Scaling (NMDS) ordination (Figure 4a) revealed that fall and winter communities were related, summer formed a distinct group, and spring spanned across all seasons in multivariate space. Examining the data within each season individually (Figure 4b), there was little difference between seagrass species in the spring epiphyte community, however, fall, summer, and winter exhibited distinct clustering for *Z. marina* and *H. wrightii.*

SIMPER analysis revealed *Acanthosiphonia echinata* as the dominant winter epiphyte, found on 96% of *H. wrightii* shoots but only 10% of *Z. marina* shoots. This species alone accounted for 15% of the dissimilarity between the two seagrass epiphyte communities (Figure 5, Supplemental B). Winter epiphytes were primarily *Acanthosiphonia echinata, Hummia onusta*, and filamentous brown algae in the genera *Ectocarpus*, *Hinksia* and *Acinetospora* (Figure 6). *Ectocarpus* spp. were present on 70% of *H. wrightii* and 15% of *Z. marina* shoots during fall, accounting for 12.5% of the dissimilarity (Supplemental B). The fall *Z. marina* community shares similarity with the winter *H. wrightii* community (Figure 5); both are relatively abundant in *Hummia onusta* and *Acanthosiphonia echinata,* however filamentous brown species were not as prevalent on *Z. marina* in the fall. During summer, the cyanobacteria *Lyngbya* was present on 73% of *Z. marina* shoots but only 6% of *H. wrightii* shoots accounting for 11% of the dissimilarity (Supplemental B). An increase in the relative abundance of crustose coralline algae, non-macroalgal epiphytes such as *Lyngbya*, and hydroids was seen in the summer (Figure 6). Spring and summer were the most diverse communities (Figure 6). Species in the Acrochaetiaceae were found throughout the year on both seagrasses.

To highlight the primary contributors of the observed variations in the epiphyte communities across seasons, we focused on the top 18 species that accounted for 80% of the dissimilarity between seagrass epiphyte communities within summer, fall, and winter (Figures 5 and 7). Overall, the epiphyte composition was generally shared between the two seagrass hosts, apart from 5 rare species: *Anotrichium* sp., *Hooperia divaricata*, and *Phaeostroma pusillum* were associated with *Z. marina,* while *Botrytella micromora* and *Hypnea cryptica* were unique to *H. wrightii*, none of which were included in the SIMPER results due to their infrequent occurrence.

4. DISCUSSION

This study focuses on the seasonal changes of edge-of-range seagrasses and their associated epiphyte communities within one of many vulnerable biogeographic transition zones, which are already experiencing impacts of climate change (Fraser et al. 2014, Bartenfelder et al. 2022). The dynamics of macroalgal epiphyte communities and fluctuations in biomass in mixed-species seagrass meadows – specifically at the interface of temperate and tropical regions in the North Atlantic – offer insight into the complex relationships between plant phenology, environmental stress, and productivity. In this transition zone where seagrasses exhibit contrasting biomass peaks, the macroalgal epiphytes increase productivity during periods of minimal seagrass biomass. This minimal seagrass biomass during winter is associated with high macroalgal epiphyte biomass, suggesting macroalgal epiphytes play an important role in seasonal production within transition zone seagrass meadows, but more research is needed to investigate the nuances of this relationship. Interestingly, the period of maximum epiphyte biomass (standardized to seagrass leaf area) coincided with periods of thermal stress and contrasting fluctuations in water quality for both *Halodule wrightii* (winter cold stress, greater water quality) and *Zostera marina* (summer heat stress, lower water quality); however, it is unclear if epiphyte impacts on thermal thresholds are similar for both high and low temperature seagrass physiological responses.

The cumulative annual epiphyte communities did not differ between the studied temperate and tropical seagrass species, but their seasonal epiphyte communities significantly differed in every season except for spring, a period of concurrent growth for both species. Winter months were characterized by the prevalence of larger foliose epiphytes, contrasting to the predominance of non-macroalgal and non-foliose epiphytes observed during the summer months. Additionally, the transition of *Z. marina* from a perennial to annual life cycle (Jarvis et al. 2012), where biomass is lost from August to December and potentially reducing the availability of substrate for epiphytes, does not result in diminished epiphyte diversity. This is likely due to the presence of *H. wrightii*, which supports epiphyte communities during *Z. marina* gap periods. Observing no overall yearly difference in epiphyte community highlights the importance of mixed temperate/tropical meadows in maintaining ecological function in biogeographic transition zones. Given these results at a local scale, there may be significant variability in epiphyte community structure in seagrasses at broader spatial scales limiting the ability to generalize the overall impacts of epiphytes on seagrass dynamics.

4.1 Seagrass and epiphyte seasonal biomass

Seagrass metrics proved to be species specific and seasonal, reflecting substantial interspecies variation in seasonal productivity cycles, suggesting *H. wrightii* and *Z. marina* allocate their resources differently across seasons. This is likely due to the different growth patterns and seasonal temperature ranges for *H. wrightii* and *Z. marina* in North Carolina (Bartenfelder et al. 2022). *H. wrightii* experiences cold stress during winter but persists by reducing metabolic activity resulting in its lowest biomass, a phenomenon that has been documented in other locations such as Texas (Kowalski et al. 2009) and Brazil (Sordo et al. 2011). Growth during suboptimal winter conditions is fueled mainly by carbohydrate reserves in the belowground biomass (Dawes and Lawrence 1980). The reduced growth and leaf turnover, along with reduced grazer activity during this season, allows for prolonged epiphyte accumulation on *H. wrightii* (Ruesink 2016, Pillay and Waspe 2019). Notably, the increased epiphyte biomass during this period reduces light availability to the seagrasses. This suggests that macroalgal epiphytes, while playing an integral role in seasonal productivity cycles within this ecosystem, may intensify stress effects on the seagrasses by further reducing available light. Unlike *H. wrightii*, winter marks a phase of establishment and growth for *Z. marina*, which germinates from seeds to recover from its fall senescence. The newly produced leaves of *Z. marina* must be colonized by epiphytes, which, coupled with the plant's growth patterns, explains the low epiphyte biomass observed per leaf area during this period.

Spring marks a period of growth for both *H. wrightii* and *Z. marina*, with *H. wrightii* recovering from winter cold stress and *Z. marina* seedlings benefiting from conducive growth conditions. *H. wrightii* total biomass increases to 44.2 ± 7.39 g m^{-2} in spring, values that are lower than have been found in tropical areas such as Laguna Madre, TX, which averages ~ 125 g m^{-2} (Kowalski et al. 2009) and Baja California Sur, Mexico at 56.8 ± 8.39 g m^{-2} (Perez-Estrada et al. 2021), but exceed the biomass recorded in Brazil, located at the species southern geographic distribution limit in the Western Atlantic, which had a maximum of 35.6 g m^{-2} (Sordo et al. 2011) during the same season. As *H. wrightii* experiences a resurgence in spring, there is a decline in epiphyte biomass from winter suggesting that older leaves with higher epiphyte biomass are

being replaced by new leaves that are just beginning to be colonized by epiphytes. In spring, *Z. marina* seedlings have established, grown, and begun to flower causing an increase in total biomass from winter (54.3 ± 7.62 g m^{-2}). Comparing these to observed values from Chesapeake Bay, which average ~ 150 g m^{-2} during the same season (Orth and Moore 1986), suggests that regional environmental variables such as greater thermal fluctuations in lower latitudes (Bartenfelder et al. 2022) could influence biomass accumulation. The higher AG:BG for *Z. marina* in spring can be attributed to the production of flowering shoots, which make up 33% of the aboveground biomass during this period. *Z. marina* epiphyte biomass does not change significantly from winter to spring.

Z. marina flowering shoots reduce activity and senesce during summer resulting in a decline in biomass (38.1 ± 6.33 g m^{-2}) and AG:BG ratio. These seagrass biomass values are lower than found in temperate perennial meadows including Denmark, which averages 354 g m^{-2} (Olesen and Sand-Jensen 1994) and the Chesapeake Bay, at ~ 125 g m^{-2} during the same season (Orth and Moore 1986). In summer, *Z. marina* experiences heat stress, which can lead to reduced growth and leaf turnover rate (Marsh et al. 1986) resulting in higher (but not significantly greater) epiphyte biomass observed per leaf area than during spring. Like *H. wrightii* in winter, *Z. marina* reaches its peak annual epiphyte biomass per leaf area during summer, a period characterized by thermal stress, reduced growth, and coinciding with reduced water quality in these meadows. Low light stress, known to slow down leaf turnover rates, has been linked to increased epiphyte biomass (Hemminga 1998). This increase in epiphyte biomass can further exacerbate the light limitation the seagrass is already experiencing. When water temperatures become warmer in summer, *H. wrightii* shoots allot resources into production of leaves to increase photosynthetic output resulting in an increase in AG:BG ratio. This increase in aboveground production allows less time for epiphytes to accumulate (Bulthuis and Woelkerling 1983, Ruesink 2016), along with increased activity of grazers during summer (Pillay and Waspe 2019), resulting low epiphyte biomass observed per leaf area on *H. wrightii* during this time.

In the fall, *H. wrightii* has significantly increased belowground biomass compared to the other seasons, reflected by a decrease in AG:BG ratio. This accumulation of biomass surpasses recorded values at its southernmost range in Brazil (Sordo et al. 2011). Interestingly, seasonal trends in belowground (and total) biomass align closely to what was found in a perennial monospecific meadow in Baja California Sur, Mexico (Perez-Estrada et al. 2021), suggesting a convergent adaptation across populations to environmental stress through funneling biomass into carbohydrate storage tissues in the roots (Dawes and Lawrence 1980, Perez-Estrada et al. 2021). In contrast, *Z. marina* exhibits its lowest biomass during the fall (10.1 ± 2.46 g m^{-2}), which results from a period of senescence following summer heat stress (Bartenfelder et al. 2022). *Z. marina* is nearly absent at this time but is able to recover over the winter months via germination of seeds from previous flowering events (Jarvis et al. 2012).

Our findings reveal that seagrass biomass diminishes during winter while macroalgal epiphyte biomass increases. Consequently, macroalgal epiphytes make up a larger portion of the primary producer biomass in winter compared to the other seasons. This increase in macroalgal epiphyte biomass has implications for seagrass survival, particularly through reduction of available light (Ow Yan et al. 2020). In the summer,

these meadows experience a decline in water quality and reduction of light availability, in contrast to winter when the water quality is greater, and light is less limiting (Jarvis et al. 2023). The morphology of the epiphyte species, especially those that grow larger and denser structures, can exacerbate light attenuation, which is critical during periods of stress when seagrasses need light for photosynthesis and growth (Borowitzka et al. 2006).

4.2 Epiphyte community

This diverse assemblage of identified epiphytes indicates a rich seasonal epiphyte community associated with these seagrass species. Seagrass epiphyte communities are ephemeral, dynamic, and vary with environmental conditions (Borowitzka et al. 2006). Over the span of the entire year, there was no significant difference in epiphyte community between *H. wrightii* and *Z. marina*. However, a seasonal breakdown reveals a difference in the epiphyte community between seagrass species within winter, summer, and fall, with spring the exception.

During winter, the primary contributors to the difference in epiphyte communities between *Z. marina* and *H. wrightii* were *Acanthosiphonia echinata*, a red alga, and sporophytes of *Hummia onusta*, a brown alga. These are two foliose species that were found commonly during the winter months on *H. wrightii*. Z. *marina* plants during this season are primarily seedlings that have recently germinated (Jarvis et al. 2012), which is reflected in their mostly juvenile epiphyte community. Very little *Acanthosiphonia echinata* was found on *Z. marina* during this time, but juvenile *Polysiphonia* spp. were relatively abundant and unrecognized juvenile *Acanthosiphonia* could have been included within this latter group.

Spring marks a period of growth for both seagrasses, resulting in a similar epiphyte community distribution on both species. This may be a product of concurrent growth periods reducing epiphyte retention, rather than a period of stress associated with reduced leaf turnover rate increasing epiphyte accumulation (Bulthuis and Woelkerling 1983, Hemminga 1998). Summer brings a shift, with species of the cyanobacteria genera *Lyngbya*, and a bryozoan, *Bulgula* sp., being more commonly found on *Z. marina*, while juvenile *Polysiphonia* spp. were found more commonly on *H. wrightii.* Spring and summer had the most diverse epiphyte communities and saw an increase in crustose coralline algae and *Lyngbya*, and a decrease in species such as *Acanthosiphonia echinata* and *Hummia onusta*.

The fall shows a distinction in the two seagrass epiphyte communities that is likely due to the difference in growth and stress responses affecting leaf retention and longevity. In an inverse pattern to winter, *Z. marina* supports a greater abundance of adult *Acanthosiphonia echinata* and *Hummia onusta* sporophytes than *H. wrightii* during fall. However, *Hummia* gametophytes were found more commonly on *H. wrightii*. *Ectocarpus* and *Hincksia* were more prevalent on *H. wrightii* than *Z. marina* during the fall and winter, but the relationship was swapped during the spring and summer, suggesting that seasonal growth cycles of these seagrasses influence epiphyte diversity and abundance in this transition zone.

5. CONCLUSIONS

Biogeographic transition zones, such as in North Carolina, are critical areas of study due to the diverse and dynamic seagrass ecosystems currently being affected by climate change (Fraser et al. 2014, Bartenfelder et al. 2022). The interactions between water temperatures, seagrass species, life history strategies, and epiphyte recruitment allows for seasonal shifts of productivity (Bartenfelder et al. 2022). It is important to understand local and regional seasonal dynamics of epiphyte composition and biomass when assessing climate impacts on seagrass growth and survival, as they may interact with abiotic factors that impact health and resilience of seagrasses.

As water temperatures rise, temperate meadows may become tropicalized with the potential introduction of tropical seagrass species (Hyndes et al. 2016, Wilson and Lotze 2019). Such a shift may induce changes in epiphyte community structure and biomass.

As research continues in transition zone seagrass meadows and their epiphyte communities, there is need to contextualize the findings presented here within a broader ecological narrative. The seasonal rhythm of biomass distribution, coupled with the heightened epiphyte biomass during periods of thermal stress and the potential to exacerbate light limitation, offers insights into the ecological resilience of these seagrass meadows, a resilience that is increasingly vital in the face of climate change. Further research should aim to deepen our understanding of the complex interplay between seagrasses, epiphytes, and their environment, focusing on the survivability and sustainability of these ecologically and environmentally critical ecosystems.

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Tables

Table 1a Analysis of deviance table of the effects of species and season on aboveground biomass. Significant values denoted with an asterisk (*)

Parameter	LR Chisq	Df	Pr(>Chisq)
Season	**10.6693**	**3**	**0.0136 ***
Sp	**0.9123**	**1**	**0.3395**
Season:Sp	**40.0422**	**3**	**1.0438e-08 *****

Table 1b Gamma regression summary table for the effects of species and season on aboveground biomass. Significant values denoted with an asterisk (*).

Parameter	Estimate	Std. Error	T value	Pr(>|t|)
(Intercept)	1.3243	0.2748	4.820	7.91e-06 ***
SEASONSpring	0.7856	0.3515	2.235	0.0286 *
SEASONSummer	1.0519	0.3515	2.993	0.0038 **
SEASONFall	1.1789	0.3515	3.354	0.0013 **
SPZM	0.3856	0.4045	0.953	0.3436
SEASONSpring:SPZM	0.3685	0.5056	0.729	0.4686
SEASONSummer:SPZM	-0.2995	0.5096	-0.588	0.5586
SEASONFall:SPZM	-2.3858	0.5143	-4.639	1.55e-05 ***

Table 2a Analysis of deviance table of the effects of species and season on belowground biomass. Significant values denoted with an asterisk (*)

Parameter	LR Chisq	Df	Pr(>Chisq)
Season	7.940	3	0.0473 *
Sp	4.6858	1	0.0304 *
Season:Sp	30.6059	3	1.0290e-06 ***

Table 2b Gamma regression summary table for the effects of species and season on belowground biomass. Significant values are denoted with an asterisk (*).

Parameter	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.5363	0.2609	13.553	< 2e-16 ***
SEASONSpring	0.0458	0.3338	0.137	0.8911
SEASONSummer	-0.0307	0.3338	-0.092	0.9268
SEASONFall	0.6636	0.3338	1.988	0.0506
SPZM	-0.8525	0.3840	-2.220	0.0296 *
SEASONSpring:SPZM	0.87578	0.4802	1.824	0.0723
SEASONSummer:SPZM	0.61991	0.4839	1.281	0.2043
SEASONFall:SPZM	-1.28109	0.4839	-2.647	0.0100 **

Table 3a Analysis of deviance table of the effects of species and season on epiphyte biomass per leaf area. Significant values denoted with an asterisk (*)

Parameter	LR Chisq	Df	Pr(>Chisq)
Season	170.3217	3	1.0844e-36 ***
Sp	85.4417	1	2.3863e-20 ***
Season:Sp	56.2462	3	3.7222e-12 ***

Table 3b Gamma regression summary table for the effects of species and season on epiphyte biomass per leaf area. Significant values are denoted with an asterisk (*).

Parameter	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.0750	0.1953	-5.505	6.97e-07 ***
SEASONSpring	-2.5831	0.2633	-9.811	2.22e-14 ***
SEASONSummer	-3.0917	0.2761	-11.196	< 2e-16 ***
SEASONFall	-2.3491	0.3087	-7.609	1.58e-10 ***
SPZm	-2.9089	0.2761	-10.534	1.30e-15 ***
SEASONSpring:SPZm	1.6757	0.3688	4.543	2.51e-05 ***
SEASONSummer:SPZm	2.9329	0.3856	7.606	1.60e-10 ***
SEASONFall:SPZm	0.8949	0.4366	2.050	0.0445 *

Table 4a Analysis of deviance table of the effects of species and season on aboveground to belowground ratio (AG:BG). Significant values denoted with an asterisk (*)

Parameter	LR Chisq	Df	Pr(>Chisq)
Season	26.9324	3	6.0826e-06 ***
Sp	20.5817	1	5.7138e-06 ***
Season:Sp	22.0060	3	6.5044e-05 ***

Table 4b Gamma regression summary table for the effects of species and season on aboveground to belowground ratio (AG:BG). Significant values are denoted with an asterisk (*).

Parameter	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-2.2950	0.1869	-12.277	<2e-16 ***
SEASONSpring	0.7922	0.2391	3.313	0.0015 **
SEASONSummer	1.2818	0.2391	5.360	1.04e-06 ***
SEASONFall	0.6829	0.2391	2.856	0.0057 **
SPZM	1.2686	0.2752	4.610	1.79e-05 ***
SEASONSpring:SPZM	-0.3061	0.3467	-0.883	0.3804
SEASONSummer:SPZM	-1.3620	0.3499	-3.893	0.0002 ***
SEASONFall:SPZM	-1.0856	0.3499	-3.103	0.0028 **

Table 5 PERMANOVA on Bray-Curtis distance matrix to see the effects of species and season on the epiphyte community. Significant values are denoted with asterisks (*).

Parameter	Df	SumOfSqs	R2	F	Pr(>F)
SP:SEASON	3	1.780	0.0395	4.0146	0.001 ***
Residual	222	32.802	0.7284		
Total	229	45.033	1.0000		

Table 6 Pairwise comparison of species and season on the Bray-Curtis distance matrix of epiphyte community.

	Fall_Hw	Fall_Zm	Spring_Hw	Spring_Zm	Sum_Hw	Sum_Zm	Winter_Hw
Fall_Zm	0.001	-	-	-	-	-	-
Spring_Hw	0.001	0.001	-	-	-	-	-
Spring_Zm	0.001	0.001	0.214	-	-	-	-
Summer_Hw	0.001	0.001	0.001	0.001	-	-	-
Summer_Zm	0.001	0.001	0.001	0.001	0.001	-	-
Winter_Hw	0.001	0.001	0.001	0.001	0.001	0.001	-
Winter_Zm	0.001	0.001	0.001	0.001	0.001	0.001	0.001

Figures

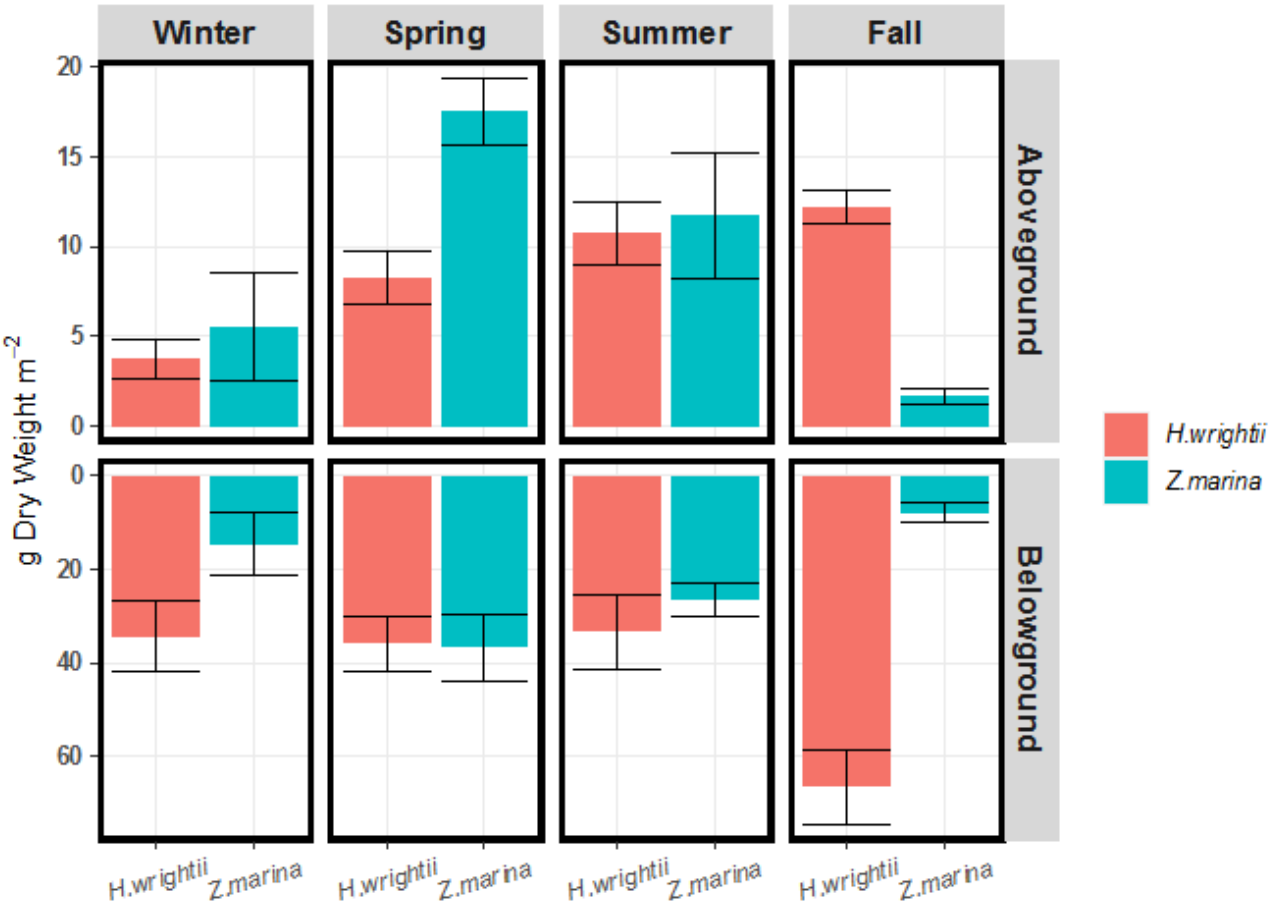

Figure 1

Mean (+/- se) aboveground and belowground biomass (g m^{-2}) by season and seagrass species from Topsail Sound, NC. Species are represented by color, aboveground biomass the top four frames, and belowground the bottom four. The interaction between species and season is significant ($p < 0.001$)

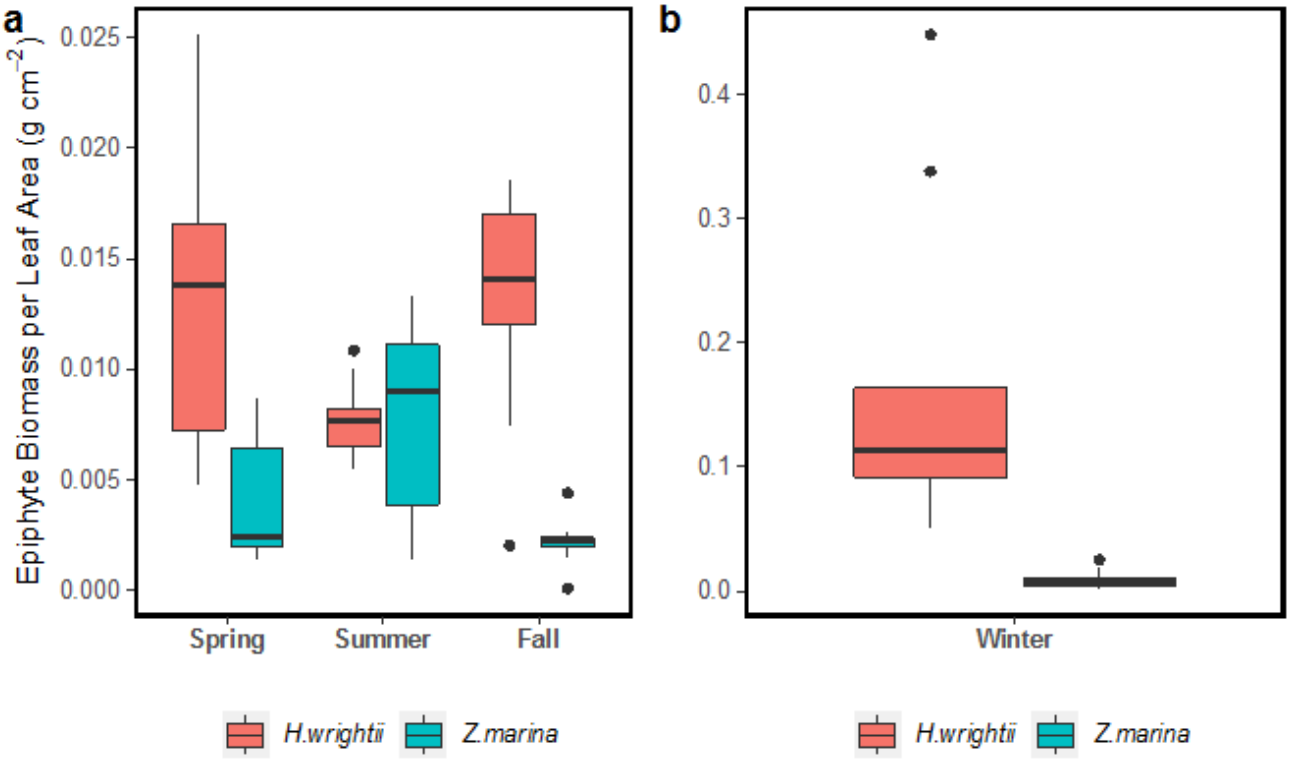

Figure 2

Mean (+/- se) epiphyte biomass per leaf area (g cm^{-2}) during spring, summer, fall, and winter 2021 from Topsail Sound (a). Winter is shown separately due to extremely high epiphyte biomass causing trends in other seasons to not be seen (b)

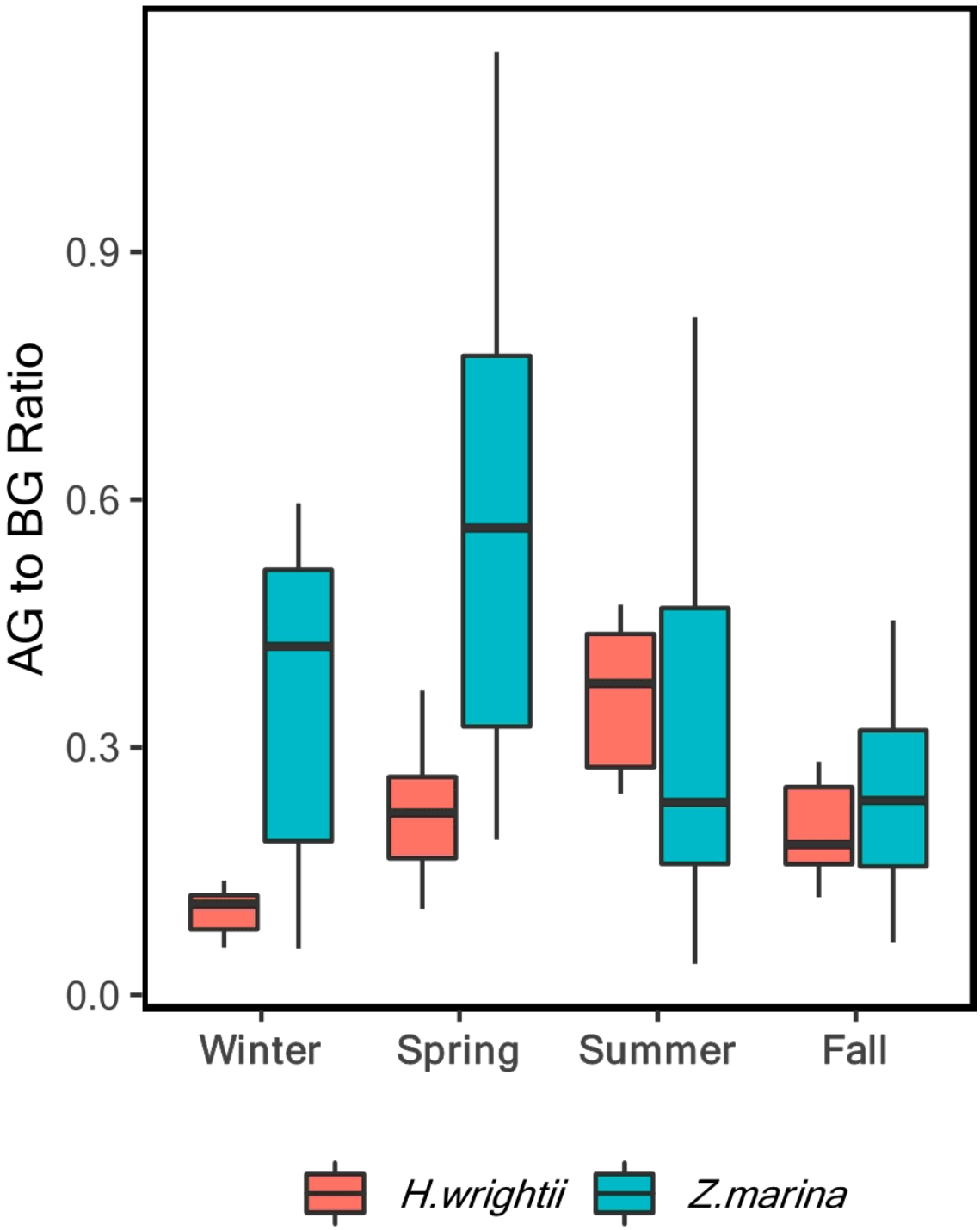

Figure 3

Seasonal aboveground to belowground ratio from Topsail Sound 2021. Higher values correspond to more resources allocated into aboveground than belowground biomass

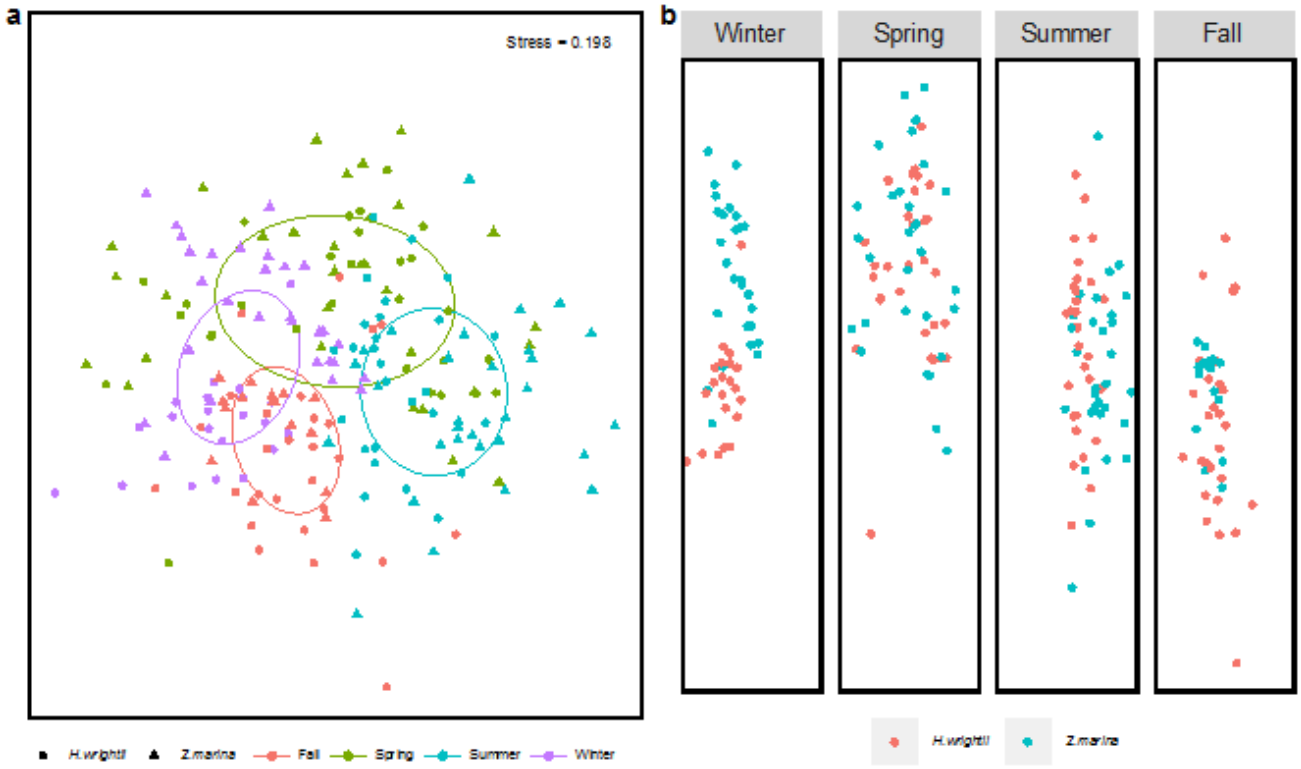

Figure 4

Non-metric multidimensional scaling ordination of epiphyte community from Topsail Sound. Color corresponds to season; shape corresponds to seagrass species (a). Non-metric multidimensional scaling plots of epiphyte community separated by season (b). Color corresponds to seagrass species

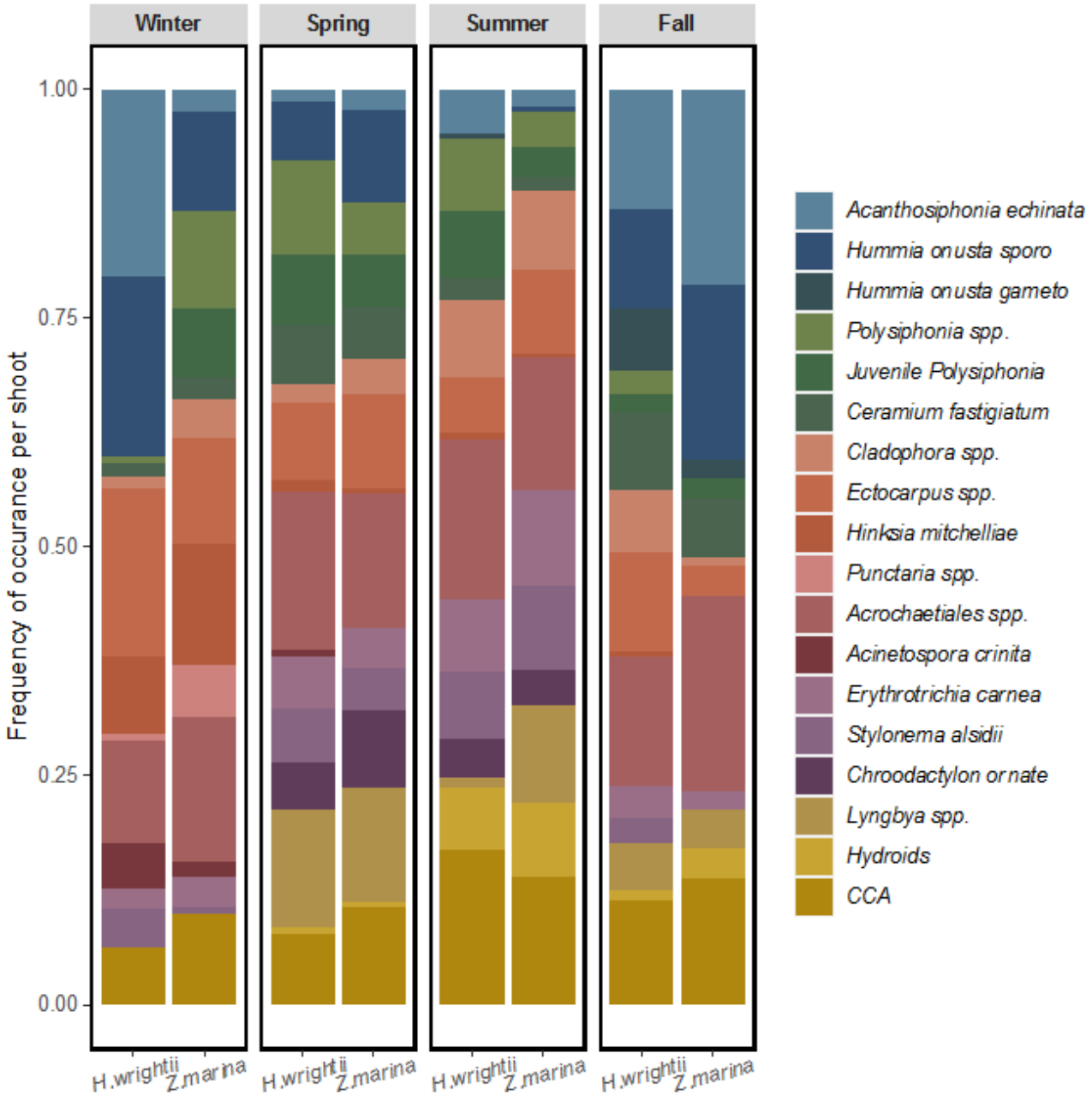

Figure 5

Relative frequency of occurrence of the top 18 most influential epiphytes in the difference between seagrass species within winter, summer, and fall communities. CCA is an abbreviation for crustose coralline algae

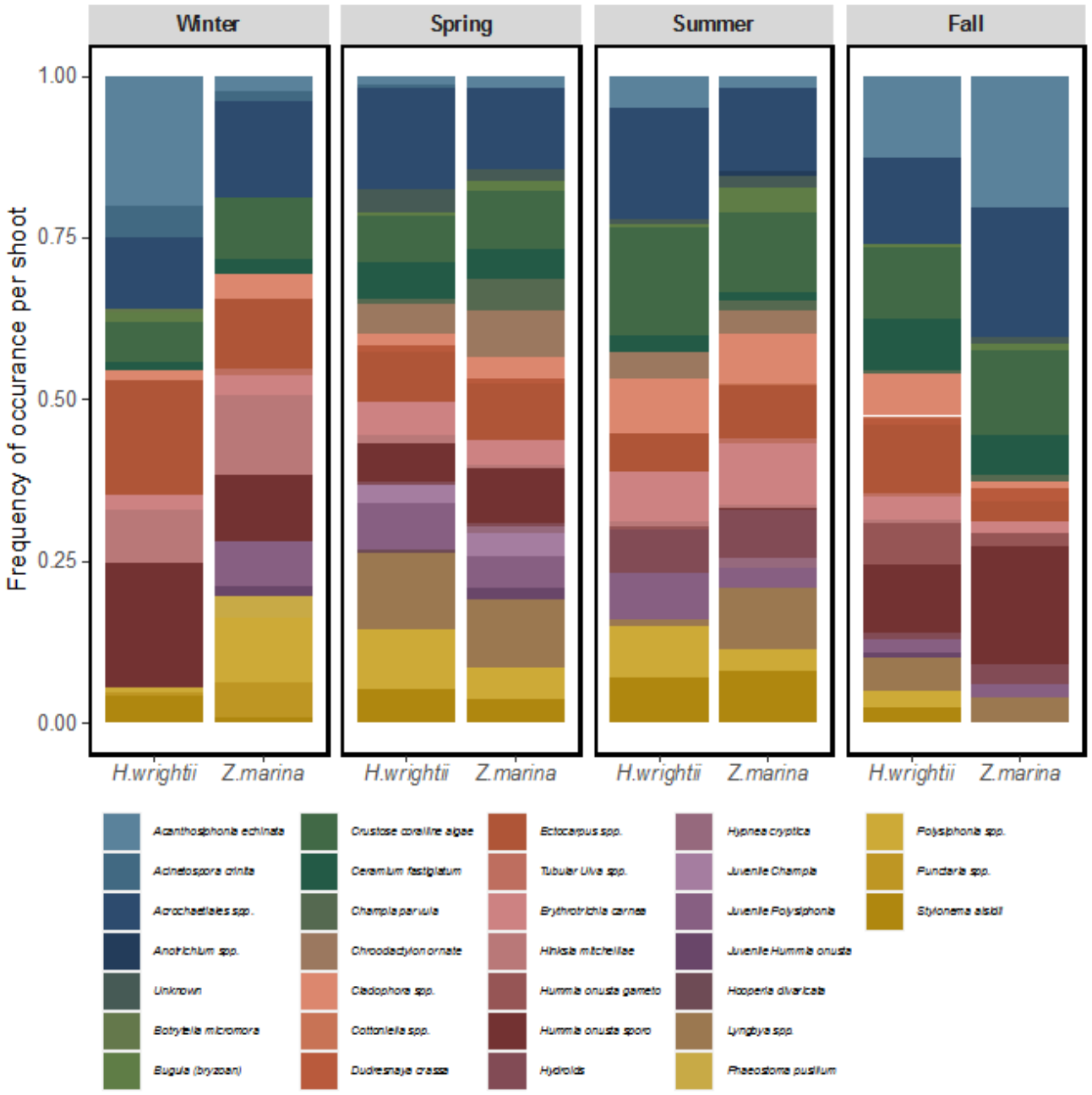

Figure 6

Seasonal epiphyte community (31 unique epiphytes total) and relative frequency of occurrence between seagrass species

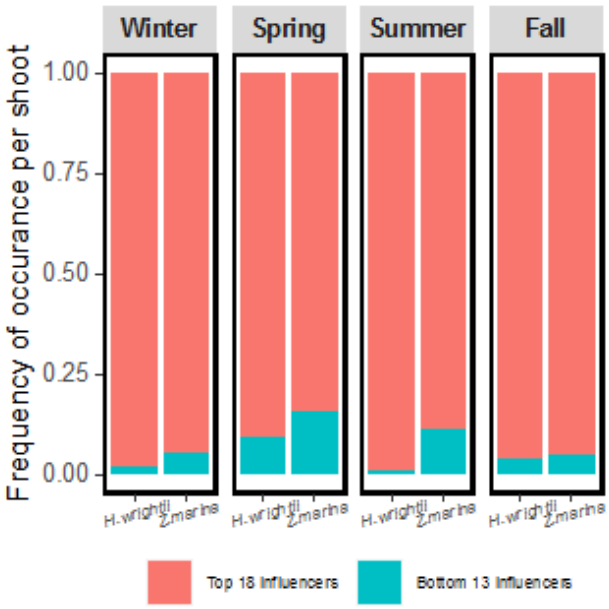

Figure 7

Relative abundance of the top 18 most influential epiphytes (red) vs the bottom 13 (blue) least influential epiphytes between seagrass species and seasons

Supplementary Files

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