FLORIDA INTERNATIONAL UNIVERSITY

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INTERACTIONS BETWEEN MARINE MACROPHYTE HABITATS, SMALL INVERTEBRATE FAUNA, AND PELAGIC SARGASSO INUNDATIONS IN TROPICAL SHALLOW COASTAL SYSTEMS

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Lowell Andrew R. Iporac

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To: Dean Michael R. Heithaus
College of Arts, Sciences, and Education

This dissertation, written by Lowell Andrew R. Iporac and entitled Interactions between Marine Macrophyte Habitats, Small Invertebrate Fauna, and Pelagic Sargasso Inundations in Tropical Shallow Coastal Systems, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Charles Amsler

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The dissertation of Lowell Andrew R. Iporac is approved.

Dean Michael R. Heithaus
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CHAPTER V

Iporac LAR, Hatt DC, Bally NK, Castro A, Cardet E, Mesidor R, Olszak S, Duran A, Burkholder D, and Collado-Vides L. Community-based monitoring reveals spatiotemporal variation of sargasso inundation levels and morphotype dominance across the Caribbean and South Florida. Aquatic Botany 182: 10.1016/j.aquabot.2022.103546.

DEDICATION

I dedicate this dissertation to my family, my partner, and to all the comrades and kasamas
I met, loved, and learned from over the years.

When we struggle, we win. When we fight, we overcome.

Makibaka, Huwag Matakot.

Venceremos.

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ABSTRACT OF THE DISSERTATION

INTERACTIONS BETWEEN MARINE MACROPHYTE HABITATS, SMALL INVERTEBRATE FAUNA, AND PELAGIC SARGASSO INUNDATIONS IN TROPICAL SHALLOW COASTAL SYSTEMS

by

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Marine macrophytes form biogenic habitats that maintain the biodiversity of coastal systems such as seagrass beds and sandy beaches. These habitats are used by small invertebrate fauna that provide ecosystem functions and trophic links between macrophytes and secondary consumers. These systems were also challenged with periodic influxes of pelagic sargasso, a region-wide issue affecting the Caribbean since 2011. Very little is known about how these sargasso influxes affected the macrophyte and invertebrate faunal communities. This research investigated the macrophyte habitat characteristics that drive invertebrate faunal communities and how those communities were affected by pelagic sargasso inundations.

Initial assessments of habitat types were conducted in South Florida to characterize assemblages of macrophytes composing these habitats and associated fauna. Six unique habitat types were compared, of which red macroalgal mats contained higher faunal richness and abundance than other habitats. This variation of faunal diversity was further investigated by quantifying macrophyte diversity, biomass, and architecture as habitat metrics. These three metrics were further synthesized into a structural complexity index. However, biomass itself explained variation in faunal diversity as well as the structural complexity index. This finding interrogated the use of an index as an accurate predictor of species diversity patterns.

These macrophytes can be transported onto intertidal zones and used by terrestrial invertebrate fauna. Thus, seasonal sargasso influxes was hypothesized to be a major contributor to invertebrate faunal resource use. Temperature in sargasso-dominant wrack was lower and more stable than the surrounding beach. There also was evidence of trophic resource use of sargasso by invertebrates, particularly with terrestrial amphipods. The regional scope of pelagic sargasso inundations called for monitoring efforts to investigate spatiotemporal variation in sargasso accumulation levels and species composition. This was accomplished using community-contributed data, where seasonality in sargasso accumulations between 2019 and 2021 was detected, and the Mexican Caribbean had longer seasons and higher accumulation levels than South Florida.

This research synthesizes the role of macrophytes providing resources for invertebrate faunal communities in coastal systems that encompassed submerged benthic vegetation and intertidal sandy beaches. These findings could be applicable to investigate further changes of these systems under periodic sargasso inundations.

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

TABLE PAGE

CHAPTER II

CHAPTER III

CHAPTER IV

CHAPTER V

LIST OF FIGURES

FIGURE PAGE

CHAPTER I

CHAPTER II

CHAPTER III

CHAPTER IV

CHAPTER V

CHAPTER VI

CHAPTER I

INTRODUCTION

Shallow coastal systems, such as seagrass beds, red mangrove forests, and intertidal sandy beach systems, could maintain high species diversity with the provision of biogenic habitats by habitat-forming organisms (Heck Jr. and Orth 1980, Sheridan 1992, Tuya et al. 2014, Duarte et al. 2020). The provision of biogenic habitats in coastal systems were provided by marine macrophytes, namely seagrasses and macroalgae, and especially benefit small invertebrate fauna such as peracarid crustaceans, mollusks, and polychaetes (Marx and Herrnkind 1985, Lewis 1987, Virnstein and Howard 1987, Knowles and Bell 1998). These faunal communities could be composed of detritivores or epiphyte herbivores that can benefit the primary contributors of macrophyte habitat through recycling of organic matter or reduction of epiphytic loads attached to macrophytes (Woodin 1977, Zimmerman et al. 1979, Ferreira Barbosa et al. 2019).

The provision of these biogenic habitats by marine macrophytes could occur at different yet interconnected contexts. In submerged systems such as seagrass beds or mangrove prop roots, macrophytes were largely influenced by environmental factors in the water column, such as salinity, substrate and nutrient availability, and water current activity (Hay 1981, Fourqurean et al. 1992, Collado-Vides et al. 1994, 2011, Biber 2007, Lirman et al. 2014). Marine macrophytes however could senesce and be transported from the submerged system to intertidal zones of sandy beaches as ‘sea wrack.’ Unlike the living seagrasses and macroalgae of the submerged system from where they originate, sea wrack habitats have different properties as habitat that resulted from their senescence, desiccation, and decomposition. While submerged macrophyte habitats serve as food and habitat for one community of invertebrate epifauna, the transportation and decomposition of macrophytes to sandy beaches would provide food and habitat to a completely different community of invertebrate fauna (Figure 1.1, Stenton-Dozey and Griffiths 1983, Jaramillo et al. 2006, Ince et al. 2007, Ruiz-Delgado et al. 2015).

Influxes of pelagic sargasso that have periodically occurred since 2011 have demonstrated profound impacts on shallow coastal systems at a local level. Pelagic sargasso (*Sargassum natans* I Parr, *Sargassum natans* VII Parr, and *Sargassum fluitans* III Parr) would usually compose sea wrack in Florida and Caribbean coastal areas, originating offshore from sources such as the Sargasso Sea (Ardron et al. 2011). The low accumulation of sargasso-dominated wrack nourishes the sandy beach by inputting allochthonous sources of energy for invertebrate fauna, which then could be foraged by migratory seabirds, decapods, or other larger fauna (Dugan et al. 2003, Moser and Lee 2012, Morrow et al. 2014, Schlacher et al. 2017). High accumulations however would form anoxic conditions in the water column, driven by the decomposition of decaying biomass. The development of a ‘sargasso-brown tide’ would alter the benthic vegetation from seagrass-dominant to macroalgae dominant, suffocate marine fauna from a lack of oxygen, and alter trophic dynamics of nearshore submerged systems (Figure 1.2, van Tussenbroek et al. 2017, Cabanillas-Terán et al. 2019, Rodríguez-Martínez et al. 2019). However, not much is known about how these influxes of sargasso would affect terrestrial or nearshore submerged epifaunal communities.

Chapter II titled “Assessment of macrophyte habitats and epifaunal communities in two shallow coastal areas of Southeast Florida” characterized different habitat types formed by assemblages of marine macrophytes and compared epifaunal communities between these habitat types. Southeast Florida’s shallow coastal bays, namely Biscayne Bay and Florida Bay, were dominated by a matrix of seagrass beds and mangrove ridges that were highly developed. Among the research capacity and conceptualization of how the benthic vegetation and habitats function in these bays, there was surprisingly little on epifaunal communities associated with macrophyte habitats in Biscayne and Florida Bay. The last major advancement of epifaunal-macrophyte habitat assessments in Biscayne Bay was driven by the development of a power plant at Turkey Point during the 1970s (Thorhaug et al. 1973, Josselyn 1977, Thorhaug and Roessler 1977, McLaughlin et al. 1983). Epifaunal-habitat studies done on Florida Bay were even less available, with recent advancements focusing on amphipods (Sweatman 2016) or sacoglossan slugs (Middlebrooks et al. 2020). The holistic approach to assessing both macrophyte assemblages and epifaunal communities was an ambitious attempt to investigate associations among macrophytes and between these two communities. The multiple habitat types sampled on two sites, Deering Estate in Biscayne Bay and Sunset Cove in Florida Bay, also brings to question the role of utilizing generalized operational names such as ‘drift algae,’ ‘seagrass,’ or ‘algal turfs’ to describe a habitat (Biber 2007, Connell et al. 2014, Tano et al. 2016).

Chapter III titled “Synthesizing composition, quantity, and architecture as structural components of macrophyte habitats for epifauna” examined multiple aspects of structural complexity of the macrophyte habitats for epifaunal communities. This directly builds from chapter II, where the focus of the article was on species assemblages and associations between macrophyte species composing habitats. In contrast, chapter III investigates macrophyte diversity, quantity, and architecture as metrics of habitat complexity. Many studies of these metrics of habitat complexity focus on only one of these three categories, but hardly any studies incorporate all three of these aspects. The few that attempt to do so synthesizes these three aspects into a quantitative index of structural complexity that produces a calculated value that can be compared among habitats (Kovalenko et al. 2009, Ferreira Barbosa et al. 2019, Duarte et al. 2020). Using measurements of diversity (richness and diversity index), quantity (biomass availability), and architecture (degrees of branching and fractal dimensions), we developed an index of structural complexity to compare between habitat types found in nearshore submerged areas from the first chapter. These index values, as well as measurements of macrophyte diversity and quantity, were correlated with epifaunal diversity metrics to determine what habitat metrics best explain epifaunal diversity patterns.

While chapters II and III were situated in the submerged shallow mangrove-seagrass-macroalgae system, chapters IV and V transition over to the sandy intertidal beach system. Chapter IV titled “Characterization and potential resource use of sargasso-dominant sea wrack by terrestrial invertebrate fauna during sargasso influxes in South Florida” investigated how beach-cast macrophytes compose a new resource as ‘sea wrack’ that can be used by terrestrial invertebrate fauna. “Sea wrack” can be composed of any number or species of submerged marine macrophytes that were moved from their original location underwater to the intertidal zone of coastal areas where they then desiccate and decompose (Orr et al. 2005). The composition and quantity of sea wrack in South Florida is especially of interest when inundations of pelagic sargasso dominated the composition and quantity of sea wrack. Very little has been studied of the effects of pelagic sargasso-dominated wrack on the terrestrial invertebrate faunal communities. Previous studies conducted in other areas with different species of macrophytes producing wrack demonstrated sea wrack as a food source or stable microhabitat conditions for invertebrate fauna on otherwise unvegetated beach systems (Stenton-Dozey and Griffiths 1983, Ince et al. 2007, Ruiz-Delgado et al. 2015). This study tested the hypothesis that these inundations of landed pelagic sargasso could provide some subsidy to these invertebrates.

Chapter V investigated the spatiotemporal distribution of pelagic sargasso inundations across South Florida and the Caribbean using community-contributed data. The periodic influxes of pelagic sargasso persisted over the years such that efforts to monitor and forecast their arrival and quantity of accumulations were conducted extensively (Frazier et al. 2013, Wang and Hu 2016, Maréchal et al. 2017, Rodríguez-Martínez et al. 2022). Satellite imagery and remote sensing were the primary methods of forecasting and modelling sargasso arrivals and influxes throughout the Caribbean. While these satellite imagery models cover a large area of the region, they are limited by the amount of resolution provided, especially on a local level (Trinanes et al. 2021). Ground-truthing the arrivals of sargasso through *in situ* monitoring could help refine the predictive models of sargasso, and compare the severity of sargasso accumulation and species composition that would dominate wrack communities on a local level. Using the Epicollect5 app (Gupta et al. 2021), the “Sargassum Watch” community science program was developed and distributed to many volunteer groups in Florida and the Caribbean. Volunteers were asked to take photos of the monitored coastal area, regardless of sargasso inundations or not, and the species of sargasso present within the area. Using the data gathered from volunteers over multiple years, we investigated the spatial and temporal variation in sargasso inundations and species composition of sargasso associated with those inundations. This program and data collected can especially be useful to investigate other ecological questions related to sargasso inundations, refine satellite imagery models (Trinanes et al. 2021), and guide decision-makers in the management of sargasso on coastal areas with ecological or economic significance (Degia et al. 2022).

Each of these chapters provide some contribution to macrophyte or faunal ecology in shallow coastal systems in Florida. While the first two data chapters were conducted in the absence of pelagic sargasso inundations, it would be likely that such inundations would alter the local habitat types found in Deering Estate and Sunset Cove and their use as habitat for local epifauna communities. Conversely, the accumulation of sargasso as a dominant component of sea wrack also questions the role of sargasso as a provider of food and habitat for one, intertidal community and as a disturbance on another adjacent, submerged coastal community (van Tussenbroek et al. 2017, Cabanillas-Terán et al. 2019, Rodríguez-Martínez et al. 2019). These findings can also influence management and conservation decisions of nearshore coastal systems when considering the role of macrophyte habitats for epifaunal communities that contribute to biodiversity, and pelagic sargasso inundations as a complex factor affecting these coastal communities.

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APPENDIX

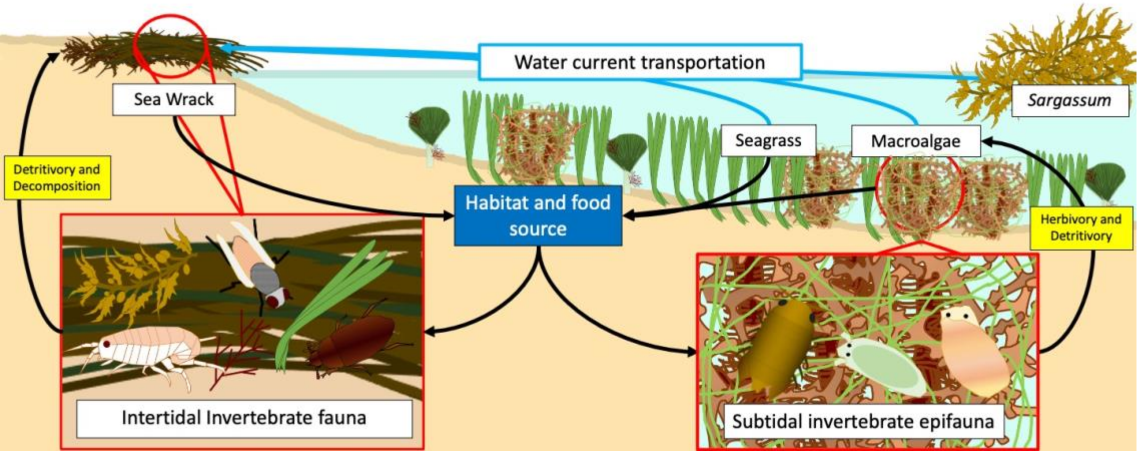

Figure 1.1: Conceptual diagram of a shallow coastal system that includes submerged aquatic habitat types and beach-cast sea wrack along intertidal zones of sandy beaches. The following interactions were depicted: 1. Various species of macrophytes provide habitat structure for invertebrate epifauna. 2. The epifauna could provide herbivory and detritivory functions that could benefit the primary contributors of macrophyte habitat. 3. Senesced macrophytes from submerged systems could get transported onto land where they decompose and provide similar resources to a completely different community of invertebrates, with similar interactions at play from the submerged system.

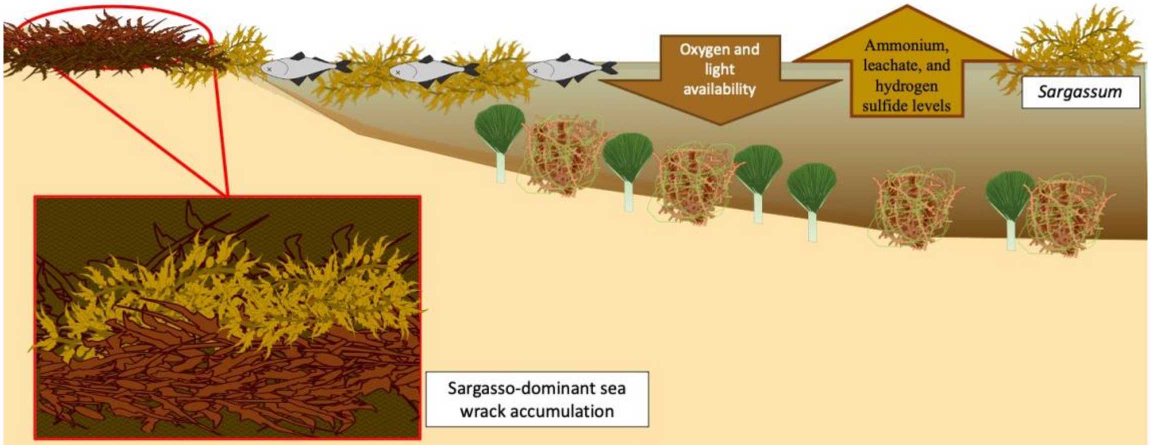

Figure 1.2: Conceptual diagram of major effects of sargasso inundations on shallow coastal systems. Depicted are the following effects: Accumulation of sargasso on-shore and along the nearshore water column lead to subsequent decomposition, submerged benthic vegetation shifted from seagrass-dominant vegetation to macroalgal-dominant vegetation resulting from decreased oxygen and light availability (van Tussenbroek et al. 2017), and faunal mortality from lack of oxygen (Rodríguez-Martínez et al. 2019).

CHAPTER II

ASSESSMENT OF MACROPHYTE HABITATS AND EPIFAUNAL COMMUNITIES IN TWO SHALLOW COASTAL AREAS OF SOUTHEAST FLORIDA

Abstract

Habitat-forming organisms contribute physical structure and maintain high species diversity in South Florida’s nearshore systems dominated by seagrasses, macroalgae, and mangroves. Habitat types for invertebrate epifauna are characterized by a single macrophyte species or an operational name such as ‘drift macroalgae.’ However, the composition of species forming these habitats vary by location and associated environmental conditions, implying infinite permutations of assemblages per set of habitat types. Macrophyte composition at two prominent bay areas in South Florida, Biscayne Bay and Florida Bay, were historically studied, yet very few studies examining both macrophyte habitats and associated epifauna were conducted in recent years. This study examined different habitat types formed by assemblages of macrophytes and diversity of associated epifauna. Habitat samples were collected at Deering Estate in Biscayne Bay, and Sunset Cove in Florida Bay. Six habitat types were identified and varied in macrophyte composition. Epifaunal richness, abundance, and diversity was higher in red macroalgal mat habitats than other seagrass or algal habitat types. While no distinct epifaunal assemblage was detected between habitat types, multiple habitat types would aid in maintaining high species diversity in nearshore coastal systems.

Introduction

Assessment of biodiversity requires understanding characteristics of the community’s habitat, defined as the necessary resources and conditions needed for organisms to survive and reproduce (Hall et al., 1997; Krausman and Morrison, 2016). In shallow coastal and marine systems, an assemblage of macrophytes can collectively form a distinct habitat unit. Each species within that assemblage could either provide primary structure or provide secondary support that enhances the complexity of that habitat (Collado-Vides et al., 1994).

Habitats could either be categorized based on a single species that provided that primary structure, or as a generalized operational name based on the overall physiognomy, or appearance, of that habitat unit. One example of the latter would be "drift macroalgae" that describes any combination of green, brown, or red macroalgae with the unifying trait of detachment and floatation from the shallow benthos (Biber and Irlandi, 2006; Kopecky and Dunton, 2006; Rudershausen et al., 2003; Virnstein and Howard, 1987b). Operational names of habitat would be useful to compare different assemblages of macrophytes that have similar traits and functions (Connell et al., 2014).

Macrophyte diversity within an ecosystem can diversify habitat types for associated epifauna. While species-specific variation can occur in epifaunal habitat preference, higher richness and abundance of epifauna are shown in red macroalgal habitats than seagrass habitats, even though these two habitat types can be found within the same vegetation (Knowles and Bell, 1998; Virnstein and Howard, 1987b). Southeast Florida's coastal nearshore vegetation are diverse, characterized by intertidal red mangrove prop roots covered in epiphytic algae, and intermixed seagrass and macroalgal benthos. Additionally, similar habitat units could be composed of different macrophyte compositions, which can imply potentially infinite permutations of macrophyte assemblages within a habitat type (Fig. 2.1) (Biber, 2007; Collado-Vides et al., 1994; Lapointe and Bedford, 2007).

The diversity of species contributing to these habitat units would be dependent on environmental and physical conditions in a given area. Salinity gradients determine the dominance of seagrasses and macroalgae composing any coastal seagrass system (Biber and Irlandi, 2006; Lirman et al., 2014). In Biscayne Bay for example, salinity gradients can be delineated between brackish nearshore areas susceptible to freshwater inputs from upland (Brook, 1982; Collado-Vides et al., 2011) and oceanic areas with less variability in salinity (Caccia and Boyer, 2005; Wang et al., 2003). This salinity gradient drives much of the species composition of shallow seagrass vegetation (Biber et al., 2004; Lirman and Cropper, 2003). Historically, development of a power plant near Turkey Point drove temperature changes in surrounding seagrass bed communities, including the associated epifauna (Roessler and Zieman, 1970; Thorhaug et al., 1973). Florida Bay's nearshore areas, located south to Biscayne Bay, is comparatively more marine in environmental conditions. Salinity gradients in Florida Bay vary spatially, attributing to precipitation as a major source of salinity fluctuations than surface runoff (Kelble et al., 2007; Swart and Price, 2002). Salinity fluctuations can affect in plant biomass in vegetation and densities of animals living among the vegetation (Montague and Ley, 1993). Florida Bay also has a history of stressors and disturbances such as development of canals and railroads near the northeastern area, episodes of seagrass die-offs, and hurricanes that affect nearshore vegetation composition and habitat availability for fauna (Robblee et al., 1991; Wachnicka et al., 2013; Wilson et al., 2019; Zieman et al., 1999).

To our knowledge, there has not been any recent small-scale, local surveying of epifauna-habitat associations in South Florida (Tab. 2.1). In Biscayne Bay, there has not been any sampling of epifauna and macrophyte habitats since the development of a power plant near Turkey Point and subsequent seagrass restoration in the 1970s (Brook, 1982; McLaughlin et al., 1983; Thorhaug and Roessler, 1977). Sampling of epifauna in

Florida Bay from the last decade focused on specific taxa such as amphipods (Sweatman, 2016) and sacoglossan slugs (Middlebrooks et al., 2020) rather than entire epifaunal communities. The daunting task of identifying both macrophyte and invertebrate communities would prevent more recent efforts to survey these associated communities. This study aims to characterize habitat types formed by assemblages of marine macrophytes among nearshore coastal vegetation and compare epifauna assemblages and diversity patterns among habitat types.

Materials and Methods

Study Sites. Deering Estate's coastal bay (noted as "Deering" from here on, 25° 36' 50.5224" N, 80° 18' 2.862" W) and Sunset Cove in Key Largo ("Sunset Cove", 25° 5' 20.2452" N, 80° 27' 2.556" W) were selected areas for this study due to their similar vegetation. Deering Estate's coastal bay is representative of Biscayne Bay's dynamic environmental conditions marked by periodic freshwater input from canals such as the C-100 canal and the mangrove sheet flow pump (Tarr, 2011; Turtletaub, 2013). Sunset Cove in Key Largo has less variation in environmental conditions, although the 1988-1989 seagrass die-off, marked by prior low salinity and temperature, led to accumulation of sediment sulfide in that site (Carlson et al., 1994). Both Deering and Sunset Cove bay areas included sites that were adjacent to a mangrove island or a mangrove ridge, and subtidal seagrass beds. In Deering, one site was selected for mangrove epiphyte collection, two sites for benthic vegetation collection, and one for both vegetation given proximity to mangrove and benthic vegetation. In Sunset Cove, two sites were selected for mangrove epiphyte collection while two sites for benthic vegetation collection (Fig. 2.2).

Habitat sample collections. A literature review and observational survey was conducted prior to any field collection to determine the possible habitat types, based on operational names or common macrophyte species, that could be encountered for this study (Collado-Vides et al., 1994; Knowles and Bell, 1998; Lewis, 1987; Lirman et al., 2014; Stoner, 1985; Virnstein and Howard, 1987b). Observational surveys were conducted between October 2019 and February 2020, leading to the identification of six macrophyte habitats (Fig. 2.3):

1. Seagrass habitats formed by multiple stands of flat leaves containing small epiphytic algae on the leaf surface.
2. Benthic green macroalgal mats ("benthic green mats") dominated by green algae and collected on the soft sediment benthic floor.
3. Red macroalgal mats formed by corticated red macroalgae and also found among the benthic floor.
4. Floating green macroalgal mats ("Floating green mats") composed of loose-lying filamentous green algae.
5. Mangrove prop root epiphytes ("mangrove epiphytes") composed of macroalgae directly attached to the mangrove prop roots.
6. Rhizophytic calcareous green macroalgae forming entire algal units through siphons that compose branches.

Macroalgal mat samples were collected in June 2020 at both sites by enclosing the sample with a zip-lock bag to prevent epifauna from escaping. The amount of biomass collected varied per replicate, but the total volume is limited to 365.76 cm^3, which is the standard volume of a quart-sized zip-lock bag. Multiple seagrass leaves (10-

15 blades in close proximity to each other) were enclosed with a Uline polystyrene bag (548.64 cm^3 volume) and cut of all aboveground biomass using shears prior to being sealed with a zip tie. Samples of mangrove prop root epiphytes were collected using a scraper blade and stored in a quart-sized zip-lock bag. Due to the low biomass of the epiphytes, multiple prop roots were scraped until a sufficient amount (two to three prop roots approximating $\geq$1.0 g wet biomass) was collected per sample. Upon initial collection underwater, excess water in the zip-lock bag was drained through a 0.5 mm mesh sieve while retaining the epifauna before returning contents to the bag. All samples were stored frozen at -20 ^oC for later processing.

Samples were drenched wet with tap water inside a 0.5 mm mesh sieve to retain epifauna and macrophytes while removing sediment and detritus. Macrophytes were cleaned, identified to the lowest possible taxonomic level, and weighed for wet biomass to the nearest 0.01 g prior to drying in an 65^{o}C oven for a week before being re-weighed for dry biomass. Macroalgae were identified using morphological characteristics at the lowest taxonomic level using taxonomic field guides (Littler et al., 2008; Littler and Littler, 2000). The AlgaeBase taxonomic database was used to check that the taxonomic name of the macroalga was currently used (https://www.algaebase.org/).

Epifauna were identified to lowest possible taxonomic level. Most invertebrates were identified to the phylum and order level and counted for abundance. Additional identification was conducted for peracarid crustaceans (amphipods, isopods, and tanaids) given their abundance in other areas of Florida and the Caribbean (Lewis, 1987; Stoner, 1985; Virnstein and Howard, 1987b). Only adult specimens however were identified to species level. Peracarid crustaceans were identified to the genus or species level, were only marked for presence per sample (Heard et al., 2004; Kensley and Schotte, 1989; LeCroy, 2000). Names of peracarid crustaceans were also checked for current name use via the World Register of Marine Species (WoRMS) database (https://www.marinespecies.org/).

Data analyses. The number of samples per habitat type was dependent on their availability collected per study site. To test for sufficient number of habitat samples, a rarefaction curve was created per combination of site and habitat type. Based on these analyses, three to five replicates per combination of habitat and sample site was sufficient (Fig. S2.1).

Community-scaled dissimilarities of macrophyte assemblages among habitat types were visualized using non-metric multidimensional scaling (nMDS). Matrices used were calculated using a square root-transformed Bray-Curtis similarity matrix (Bray and Curtis, 1957) with dry biomass values of macrophytes composing a habitat sample. A similarity percentages procedure (SIMPER) was used to compare taxon composition and relative abundance of equivalent assemblages between localities. Dissimilarity contribution (δ_i) was ranked from highest to lowest, and only major ranked taxa that contributed up to ~70% of cumulative dissimilarity was reported. An exception was made for mangrove epiphyte habitat, since there was much biomass composed of drifting algae and senescent seagrass leaves (e.g. *Sargassum*, *T. testudinum*, *H. wrightii*, etc.) that were entangled among the prop roots. All species that were directly attached to the mangrove prop roots were listed for that analysis.

Diversity of epifauna per sample of habitat was calculated using the Shannon-Weiner Index, *H*:

$$H = -\Sigma p_i * ln(p_i)$$

Where p is the proportion of epifaunal species i composing the entire community of epifauna per habitat sample.

Comparative analyses of epifaunal communities were conducted among habitats within each location to standardize for differences in presence of habitat types per location. To test for normality of distributions, a Shapiro—wilks test was applied to the dataset. Since epifaunal data was not normally distributed, comparisons of taxon richness, abundance, and H of epifauna among habitats within each location were tested using a Kruskal-Wallis Test. Statistically discernable differences were evaluated using a Dunn post-hoc test with Benjamini-Hochberg adjustment method to outline differences in epifaunal metrics among habitats within each location. Dissimilarities among epifaunal assemblages among habitat types per location were visualized using a nMDS, using abundance values of each epifaunal taxon per habitat sample. PERMANOVA was used to determine the amount of variation attributed to habitat types on epifaunal assemblages per location. SIMPER was used to determine the most dominant epifaunal taxa contributing to the dissimilarities in assemblages among equivalent habitat types between localities. Only major taxa contributing ~70% of dissimilarity were reported.

All statistical analyses were conducted using R and RStudio (R Core Team, 2020) with the vegan package for nMDS calculations (Oksanan et al., 2019), FSA package for Dunn test post-hoc analyses (Ogle et al., 2022), agricolae package for Tukey HSD post-hoc analyses (de Mendiburu and Yaseen, 2022), and ggplot2 package for data visualization (Wickham, 2016).

Results

Macrophyte Assemblages Composing Habitat Types. A total of 52 samples was collected and processed for this study. The number of samples for each habitat type per location depended on its availability during field collections. Twenty-eight genera and species of macrophytes were identified. Two macrophyte taxa were seagrasses, *T. testudinum* and *H. wrightii*, 11 taxa belonged to the phylum Chlorophyta, 13 to the phylum Rhodophyta, and two taxa to the phylum Ochrophyta, including one macroalga and one supergroup of "diatom-detritus" epiphytes. One category of macrophytes is also designated for "terrestrial materials" that include fallen leaves, branches, and bark that got entangled with marine macrophytes. Terrestrial materials were not included among the 28 taxa and were considered a separate group (Tab. 2.2).

Non-metric multidimensional scaling visualization per location showed each habitat type composed of a distinct assemblage of macrophytes (Fig. 2.4). The contribution of each macrophyte per habitat type depends on its biomass relative to the entire sample collected (Tab. 2.2). In Deering, red macroalgal mats were composed of primarily *Digenea mexicana* G. H. Boo & D. Robledo or species of the genus *Laurencia.* Other, epiphytic macroalgae within red macroalgal mats include *Jania*, *Acetabularia*, *Batophora*, *Ulva*, and *Chondria*, among others. Seagrass habitats were composed of either *T. testudinum* or *H. wrightii,* of which the latter can include diatom epiphytes. No macrophytes collected as part of the mangrove epiphyte habitat surpassed average dry weight values of 1.0 g. Mangrove epiphytes were dominated by entangled thalli of *Cladophora liniformis* (O.F. Müller) Kützing and *Sargassum.* Mangrove epiphytes directly attached to prop roots were composed of Bostrychietum complex algae that included *Bostrychia*, *Catenella*, or *Caloglossa* in Deering, or *Polysiphonia* or *Caulerpa verticillata* J. Agardh in Sunset Cove. The following three habitat types were unique to either Deering or Sunset Cove. Floating green mats in Deering were composed of *Cladophora liniformis* Kützing, Benthic green mats in Sunset Cove were composed of *Ulva* spp. and *Chaetomorpha linum*, and rhizophytic calcareous green algae in Sunset Cove were composed of *Penicillus* spp., mostly *Penicillus capitatus* Lamarck (Tab. 2.2).

Dissimilarities in macrophyte composition were found in equivalent habitat types between locations. Red macroalgal mats between Deering and Sunset Cove were composed of *Laurencia*, though Deering Estate included both *Laurencia* spp. and *D. mexicana* as essential components of red macroalgal mats, compared to Sunset Cove where *Laurencia* spp. was the main component. Seagrass in both locations were composed of *H. wrightii* and *T. testudinum*, though proportions differ in Deering's seagrass habitat having more *T. testudinum* than *H. wrightii* than Sunset Cove with more *H. wrightii* than *T. testudinum*. Mangrove epiphytes between Deering and Sunset Cove were the most dissimilar; Deering's mangrove epiphyte habitats were dominated by *Bostrychia*, *Catenella*, and *Caloglossa*, versus Sunset Cove mangrove epiphyte composition dominated by *Polysiphonia*, *Spyridia*, and *Caulerpa verticillata* J. Agardh (Tab. 2.3).

Epifaunal Diversity and Assemblages. A total of 33,959 epifaunal individuals was collected for this study, representing 28 taxonomic groups that varied in resolution from phylum to family (Tab. 2.4). In Deering Estate, red macroalgal mats showed higher taxon richness ($H(3) = 21.259$, $p < 0.0001$) and abundance ($H(3) = 20.069$, $p < 0.05$) than other habitat types, but have comparable Shannon index to other habitat types except for floating green mats ($H(3) = 10.375$, $p < 0.05$). In Sunset Cove, rhizophytic calcareous green algae has the lowest taxon richness ($H(4) = 15.072$, $p < 0.01$) and Shannon index ($H(4) = 12.362$, $p < 0.05$), while red macroalgal mats were comparatively higher. Although a statistically discernable effect of habitat type on epifaunal abundance was detected ($H(4) = 10.518$, $p < 0.05$), the Dunn test did not detect any pairwise differences. However, the benthic green mats and red macroalgal mats seem to have comparatively higher epifaunal abundance than rhizophytic calcareous green algal habitats (Fig. 2.5, Tab. 2.5).

Deering's epifaunal composition nMDS model showed floating green mats having a separate epifaunal community from the other three habitat types. The epifaunal composition of red macroalgal mat habitats overlaps with seagrass and mangrove epiphyte habitats that also overlap slightly. Many epifauna cluster on the center of the nMDS model, suggesting that these taxa are shared between the three overlapping habitats (Fig. 2.6). Sunset Cove's epifaunal composition showed red macroalgal mats and benthic green mats slightly overlapping in epifaunal composition. The epifaunal composition of mangrove epiphyte habitats were enclosed within the composition of the rhizophytic calcareous green algal habitat. PERMANOVA analysis showed habitat type explained 45% of variation in epifaunal composition in Deering ($p < 0.001$) and 42% of variation in epifaunal composition in Sunset Cove ($p < 0.001$) (Tab. 2.6).

SIMPER analyses of equivalent habitat types between locations revealed eight taxa of epifauna composing dissimilarities of assemblages. Amphipods were detected as significant contributors to dissimilarities to all three pairwise comparisons of habitat types between locations, while gastropods, serpulid polychaetes, and tanaids were detected on only two pairwise comparisons. The dissimilarities in epifaunal assemblages were most apparent with red macroalgal mat habitat in Deering showing a four-fold higher amphipod abundance and three-fold higher gastropod abundance than red macroalgal mat habitat in Sunset Cove (Tab. 2.7).

Nineteen taxa of peracarid crustaceans were found in Deering and Sunset Cove during June 2020, including five amphipods, ten isopods, and four tanaids. Red macroalgal mats in Sunset Cove had the highest total richness of 12 peracarid crustaceans, as opposed to floating green mats in Deering with only one species found. Common peracarids identified across locations and habitat types included the amphipod *Cymadusa compta* Smith, isopods *Erichsonella attenuata* Harger and *Harrieta faxoni* Richardson, and tanaid *Leptochelia* spp. (Tab. 2.8).

Discussion

Habitat characteristics are important for understanding biodiversity patterns on a fine spatial scale. In this study, we characterized assemblages of macrophytes composing different habitat types and the associated diversity of epifauna between those habitats. The low taxonomic resolution of epifaunal identification or the sampling methods involving zip-lock bag collection could be sources of error that would prevent elucidating differences in epifaunal composition among habitats. Our analyses of epifaunal communities using broad groups and specific peracarid species provided comparisons between taxonomic resolutions. Despite taxonomic resolution, broad patterns of habitat use could still be identified, with red macroalgal mats containing higher epifaunal richness and abundance. Alternatively, the zip-lock bags have a limited volume for biomass collections and the possibility of epifauna escaping during collection while underwater. However, that source of error was remedied by draining the bag of excess water using a sieve to collect epifauna from escaping prior to final collection.

The two habitat types found in Sunset Cove, benthic green mats and rhizophytic calcareous green algae, included macroalgae that were previously studied as contributors of primary structure in other areas. *Penicillus* was previously studied as a habitat provider for invertebrate fauna (Stoner 1985), as was *Chaetomorpha* (Bolam and Fernandes 2002) and *Ulva* (Balducci et al. 2001, Cardoso et al. 2004, Ba-Akdah et al. 2016, Zaabar et al. 2017), albeit separately. To our knowledge, there has been no recorded instance of an *Ulva-Chaetomorpha* association in South Florida that forms mixed-mat habitat for faunal communities. Both *Ulva* and *Chaetomorpha* are non-calcareous green algae that increase in abundance from nutrient enrichment (Taylor et al. 2005, Zhang et al. 2014). *Chaetomorpha* was observed to produce filaments that extend beneath the soft sediment surface, anchoring the algal mat to the benthos (Raffaelli, 2000)(Fig. 2.7D). *Penicillus* lives in calcium carbonate sediments, consistent with its characterization as a calcifying alga, and the rhizome also anchors the thallus to the calcareous sediment (Bedinger 2012). While both were found in Sunset Cove, nutrient and substrate availability and capability of algae to attach themselves among the benthos allows these two green algal habitats to co-occur yet have distinct characteristics.

Red macroalgal mat and floating green mat habitats could be classified as “drift” macroalgae, though their species compositions are distinct from each other, translating to differences in their potential to drift along the water column. Fragmented branches of *Laurencia* can develop rhizoids once they come into contact with compatible substrate, including of other macrophytes (Frankovich and Fourqurean, 1997; Herren et al., 2013;

Humm, 1964). This phenomenon could explain small *Laurencia* epiphytes found on seagrass leaves, while senescent seagrass leaves were found as a minor component of red macroalgal mat habitats (Fig. 2.7A). However, there were many recorded occurrences where *Laurencia* was observed to be entangled with seagrass leaves yet were not seagrass epiphytes (Biber, 2007; Hamm and Humm, 1976; Phillips, 1960). Large red macroalgal biomass and current flow could enable *Laurencia*-dominated red mats to drift along the water column with their senescent seagrass leaves (Biber, 2007; Kopecky and Dunton, 2006) or tumble along the seagrass bed (Holmquist, 1994). On the other hand, red mats dominated by *D. mexicana* would be more likely to be directly attached to rocky substrate through their holdfast, unless conditions enable physical detachment (Fig. 2.7B). Floating green mats dominated by *C. liniformis* float and drift until they get entangled by seagrass leaves or mangrove prop roots, hence their presence in mangrove epiphyte assemblages (Fig, 2.7C). These differences in macrophyte species composition could allow differences in habitat traits such as drifting potential that would allow epifaunal dispersal over long distances (Holmquist, 1994).

Red mat and seagrass habitats were often found intermixed with each other among the benthos and demonstrated similar epifaunal composition and diversity. However, red mats have higher epifaunal richness and abundance than seagrass habitats. Our results seem consistent with previous diversity assessments in Tampa Bay (Knowles and Bell, 1998) and Indian River Lagoon (Virnstein and Howard, 1987b), but differed slightly with findings from Apalachee Bay (Lewis, 1987). In Apalachee Bay, crustacean richness was higher in *T. testudinum* than any of five other dominant macroalgae, including *D. mexicana* (formerly *D. simplex*), *Laurencia*, and *Penicillus*. However, some crustaceans were found in higher abundances of one macroalgal habitat compared to other species. In Tampa Bay and Indian River Lagoon, drift macroalgal habitats generally had higher epifaunal abundance than seagrass. For our study, the three most abundant epifaunal taxa (amphipods, gastropods, and bivalves) were found in higher abundances on red macroalgal mats than seagrasses. The high abundance of epifauna in shallow benthic macroalgal habitats could be due to the three-dimensional architecture and large availability of biomass from macroalgae providing interstitial spaces between branches as possible refuge from surrounding predation pressures. Caribbean Pipefish (*Syngnathus caribbaeus* Dawson) were found among the benthic green mats in Sunset Cove. Pipefish were noted to be sit-and-wait invertivores on seagrass beds feeding on amphipods and copepods (Howard and Koehn, 1985). Other invertivorous fish, such as pinfish, were visual predators and would find prey fauna more efficiently among branching macroalgae than foliose macroalgae (Holmlund et al., 1990). The architecture of the different macrophytes composing habitats could either provide refuge from predation through provision of small interstitial spaces between branches or increase the visual contrast for predators to forage on epifauna.

Life histories, feeding ecology, tolerance to environmental conditions, or active habitat selection of particular invertebrate species could also influence the composition and abundance of the epifauna community. Though the life stages of epifaunal species were not quantified, many of the bivalves collected were juveniles of *Brachidontes exustus* L., which previously demonstrated high abundance in areas with hard substrate availability, low wave exposure, and high salinity (Dugan and Livingston, 1982; Hoese, 1960; Murray and Wingard, 2006; Whorff et al., 1995). Many peracarids collected were also at the juvenile or subadult stages, hence their ubiquity throughout multiple habitats and both locations. However, identification of juveniles at a species level was ambiguous given the underdeveloped morphological traits needed for identification. Common peracarid species, such as *C. compta*, *E. attenuata*, and *H. faxoni*, were shown to have broad diets that include algae, epiphytes, and seagrass debris (Boström and Mattila, 2005; Zimmerman et al., 1979). The isopod *E. attenuata* demonstrated active habitat selection for food value in the absence of predation pressure; however, under predation pressure by fish, *E. attenuata* showed habitat selection for refuge value (Boström and Mattila, 1999). Given the broad comparisons of epifaunal composition among habitat types in this study, common species of epifauna found could be identified and used as representative species to test further hypotheses of habitat selection.

Macrophyte assemblages were shown on multiple studies to be driven by temperature, salinity, and nutrient availability, which is especially applicable to South Florida's geographic and floristic history (Browder et al., 2005). Previous monitoring of macrophyte communities found macroalgal assemblages in Biscayne Bay were dominated by estuarine-tolerant species (Biber and Irlandi, 2006; Collado-Vides et al., 2011). Deering's coastal area vegetation was dominated by *H. wrightii* more than *T. testudinum*, which was driven by salinity tolerance and nutrient availability (Lirman et al., 2014). However, our sampling efforts found more *T. testudinum* biomass collected than *H. wrightii* in Deering, and vice versa at Sunset Cove. All macroalgae and seagrasses examined had some relationship with salinity, with *T. testudinum* and *Penicillus* having a positive relationship with salinity, while *H. wrightii*, *Batophora*, *Laurencia*, and *Acetabularia* having a negative relationship (Lirman et al., 2014).

Mangrove epiphyte assemblages were very different between Deering and Sunset Cove. Deering's mangrove epiphyte assemblage was dominated by an assemblage of *Bostrychia, Caloglossa,* and *Catenella* which were low in biomass yet can tolerate intertidal conditions (Coppejans and Gallin, 1989; Post, 1936). This contrasts with Sunset Cove's mangrove epiphyte assemblage dominated by *Spyridia*, *Polysiphonia*, and *Caulerpa* that preferred subtidal, marine conditions (Burkholder and Almodóvar, 1973; Ortegón-Aznar and González-González, 2000). However, it was possible to have macroalgal assemblages containing both marine-tolerant and estuarine-tolerant species (Collado-Vides et al., 2011), and drift algal mats could be transported from other locations, such as *Laurencia* that could exist in a wide range of salinities (Biber et al., 2004). Florida Bay's salinity was more marine, although salinity fluctuations do occur from hurricanes or drought periods (Kelble et al., 2007; Montague and Ley, 1993). Kelble et al. (2007) assessed the salinity of Florida over a seven-year period from 1998-2005, and found that the northeastern area, which included our site, had the lowest mean salinities compared to other areas.

Biodiversity assessments are an essential component for effective management of shallow coastal systems, as these systems provide ecological and economic benefits. The shallow coastal systems in Biscayne and Florida Bays especially have an intricate history that includes anthropogenic development, seagrass die-offs, salinity fluctuations, and macroalgal blooms, among other events (Collado-Vides et al., 2013; Montague and Ley, 1993; Wachnicka et al., 2013; Zieman et al., 1999). Species-specific changes in communities were also noted, such as the recent disappearance of a sacoglossan slug following Hurricane Irma, despite recovery of associated algal communities

(Middlebrooks et al., 2020). Examining both macrophyte and epifaunal communities would provide a more holistic assessment of coastal biodiversity.

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TABLES

Table 2.1: Literature review of all studies done in Florida that collected samples of macrophyte habitats and epifaunal communities.

Bay area in Florida	Sampling dates (years)	Epifaunal habitats assessed	Source
Apalachee Bay	1979-1980	Seagrasses, green algae, red algae	Lewis (1987)
Apalachiola Bay	1975-1976	Seagrasses	Sheridan and Livingston (1983)
Biscayne Bay	1953	Seagrasses	Voss and Voss (1955)
	1973	Seagrasses	Brook (1978)
	1971-1974	Seagrasses, red algae, green algae	Thorhaug and Roessler (1977)
	1973-1977	Seagrasses	McLaughlin et al. (1983)
	1979-1980	Seagrasses, red algae, green algae	Brook (1982)
Florida Bay	1975	Red mangrove prop roots	Nickelsen (1976)
	1986-1987	Seagrasses	Montague and Ley (1993)
	2014	Seagrasses, red algae, green algae	Sweatman (2016)
	2018-2019	Green algae	Middlebrooks et al. (2020)
Indian River Lagoon	1982	Seagrasses, red algae	Virnstein and Howard (1987a, 1987b)
	1987-1988	Seagrasses, green algae	Nelson et al. (2022)
Rookery Bay	1988-1989	Red mangrove prop roots	Sheridan (1992)
Tampa Bay	1992	Seagrasses, red algae	Knowles and Bell (1994)
	2004	Seagrasses, green algae	Gibson (2007)
Tarpon Bay	1999-2000	Seagrasses, red algae	Rudershausen et al. (2003)

Table 2.2: List of macrophyte species and average dry biomass (± SD) per set of habitat samples per location. Asterisks (*) represent average dry biomass values below 0.01 g. Plus signs (+) note taxa that were found in only one sample per each set of location – habitat samples.

		Deering Estate				Sunset Cove				
Phylum	Macrophyte	Floating green mats	Mangrove epiphytes	Red macroalgal mats	Seagrass	Benthic green mats	Rhizophytic calcareous green algae	Mangrove epiphytes	Red macroalgal mats	Seagrass
Chlorophyta	*Acetabularia*			0.11 ± 0.10					0.06 ± 0.07	+
	Anadyomene			0.10 ± 0.15	+					
	Batophora	0.023 ± 0.03		0.03 ±0.04		+			0.014 ± 0.02	+
	Caulerpa verticillata							0.03 ± 0.045		
	Chaetomorpha linum	*		+		2.65 ± 3.19			0.08 ± 0.12	0.03 ± 0.04
	Cladophora			0.23 ± 0.26	+				0.02 ± 0.03	
	Cladophora liniformis	1.32 ± 0.62	0.55 ± 0.95	0.22 ± 0.30						
	Cladophoropsis			0.19 ± 0.31		0.08 ± 0.11			*	+
	Penicillus capitatus						0.29 ± 0.09			
	Ulva	+		0.02 ± 0.02		1.92 ± 1.15				
	Ulva (*Enteromorpha*)	*								
Ochrophyta	Diatom-detritus mix				0.78 ± 0.04					
	Sargassum		0.38 ± 0.54	0.08 ± 0.07	0.07 ± 0.06					
Rhodophyta	*Acanthophora*	*		+		0.04 ± 0.004			+	
	Bostrychia		0.72 ± 0.90							
	Caloglossa		0.08 ± 0.05							
	Catenella		0.22 ± 0.10							
	Centroceras					+				
	Ceramium			+			*	+	+	
	Chondria	*		0.01 ± 0.02	+			+	0.04 ± 0.04	
	Digenea mexicana			4.20 ± 3.63	0.07 ± 0.07					
	Hypnea					0.037 ± 0.072				
	Jania			0.03 ± 0.05	*				0.31 ± 0.56	0.01 ± 0.01
	Laurencia	0.07 ± 0.07		3.30 ± 3.89	0.09 ± 0.15	+			3.83 ± 3.14	0.029 ± 0.03
	Polysiphonia	0.01 ± 0.01	+	0.02 ± 0.03	0.03 ± 0.004	*	*	0.02 ± 0.02	0.05 ± 0.05	
	Spyridia	*		+				0.07 ± 0.06	+	
Tracheophyta	*Halodule wrightii*	0.02 ± 0.016	0.11 ± 0.17	0.11 ± 0.13	0.61 ± 0.68	*			0.08 ± 0.08	1.82 ± 1.41
	Thalassia testudinum	+	+	0.12 ± 0.13	2.90 ± 0.72	0.06 ± 0.10			0.17 ± 0.12	0.45 ± 0.31
Other	Terrestrial materials		0.12 ± 0.07	+						

Table 2.3: Results of Similarity Percentages Procedures (SIMPER) analyses showing macrophytes contributing to dissimilarity of equivalent habitat types between locations.

	Average Dry Biomass				
Taxon	Deering Estate	Sunset Cove	δi	δi/SD(δi)	cum.δi%
Red macroalgal mats					
Digenea mexicana	4.20	0.00	0.35	1.31	0.46
Laurencia complex	3.30	3.83	0.32	1.40	0.89
Seagrass					
Thalassia testudinum	2.17	0.30	0.39	1.95	0.52
Halodule wrightii	0.53	1.82	0.29	1.62	0.91
Mangrove epiphytes					
Bostrychia spp.	0.60	0.00	0.46	1.41	0.46
Cladophora liniformis	0.36	0.00	0.23	0.65	0.69
Catenella spp.	0.11	0.00	0.12	0.73	0.81
Caloglossa spp.	0.05	0.00	0.09	0.84	0.91
Spyridia spp.	0.00	0.04	0.05	0.65	0.95
Polysiphonia spp.	0.00	0.02	0.02	0.75	0.98
Caulerpa verticillata	0.00	0.01	0.02	0.42	0.99

Table 2.4: List of epifaunal taxa and presence among habitat types per location.

	Deering Estate				Sunset Cove				
Taxon	Mangrove epiphytes	Red macroalgal mats	Seagrass	Floating green mats	Mangrove epiphytes	Red macroalgal mats	Seagrass	Benthic green mats	Rhizophytic calcareous green algae
Arthropoda									
Amphipoda	X	X	X	X	X	X	X	X	X
Tanaidacea	X	X	X		X	X	X	X	X
Idoteidae		X	X	X		X	X	X	
Janiridae					X	X	X	X	X
Sphaeromatidae	X	X	X		X	X	X	X	
Isopoda (Other)	X	X			X	X			
Brachyura		X							
Caridea		X				X		X	
Anomura		X							
Cirripedea	X								
Copepoda		X			X			X	
Ostracoda						X			X
Insecta (Adult)	X								
Insecta (Larva)	X	X	X						
Annelida									
Nereididae		X	X	X	X	X	X	X	X
Serpulidae	X	X	X		X	X	X	X	
Terebellidae						X			
Polychaeta (Other)		X						X	
Mollusca									
Bivalvia	X	X	X		X	X	X	X	
Gastropoda	X	X	X	X	X	X	X	X	X
Polyplacophora		X	X			X	X	X	X
Echinodermata									
Asteracea							X		
Holothuroidea						X	X	X	X
Ophiuroidea						X	X	X	
Cnidaria									
Anthozoa								X	
Hydrozoa						X			
Nematoda		X				X	X	X	
Collembola		X							
Sipunculida			X				X		

Table 2.5: Results of Kruskal-Wallis test for comparisons of taxon richness, abundance, and Shannon-Weiner diversity index between habitat types per location. Asterisks denote significant effects at a 0.05 (*), 0.01 (**), or 0.001 (***) level.

Factor		Kruskal Chi-square H	df	p-value	
Deering					
	Richness	21.26	3	0.0001	***
	Abundance	20.07	3	0.0001	***
	Shannon Index	10.38	3	0.015	*
Sunset Cove					
	Richness	15.07	4	0.004	***
	Abundance	10.52	4	0.03	*
	Shannon Index	12.36	4	0.01	*

Table 2.6: Results of Permutational Multivariate Analysis of Variance (PERMANOVA) epifaunal composition among habitat types per location. Asterisks denote significant effects at a 0.05 (*), 0.01 (**), or 0.001 (***) level.

Source of Variation	Df	Sum of squares	R^2	F-Model	P-value
Deering					
Habitat Type	3	2.15	0.45	6.63	0.001^{***}
Residual	24	2.60	0.54		
Total	27	4.73	1		
Sunset Cove					
Habitat Type	4	1.87	0.42	4.09	0.001^{***}
Residual	22	2.50	0.57		
Total	26	4.37	1		

Table 2.7: Results of Similarity Percentages Procedures (SIMPER) analyses showing epifaunal contributing to dissimilarity of similarly-designated habitat types between locations.

Habitat Type	Average Abundance				
	Deering	Sunset Cove	δi	δi/SD(δi)	cum.δi%
Mangrove epiphytes					
Nereid Worms	0.00	14.60	0.20	0.98	0.23
Cirripeds	12.00	0.00	0.16	0.87	0.42
Tanaids	0.67	13.40	0.16	0.99	0.60
Amphipods	2.67	12.40	0.13	1.27	0.75
Red macroalgal mats					
Amphipods	155.90	38.17	0.20	1.45	0.29
Gastropods	132.30	40.33	0.19	1.13	0.56
Bivalves	65.60	20.17	0.08	1.24	0.69
Serpulid Worms	5.90	40.33	0.06	0.98	0.78
Seagrass					
Serpulid Worms	1.67	11.00	0.14	0.99	0.20
Tanaids	1.67	12.00	0.12	1.08	0.36
Idoteid Isopods	0.67	9.17	0.09	1.29	0.49
Gastropods	9.22	4.67	0.08	1.03	0.61
Amphipods	6.11	7.00	0.08	1.48	0.71

Table 2.8: List of peracarid crustacean species and their presence among habitats per location. Note that only adult specimens were identified to species level.

				Deering				Sunset Cove				
Order	Family	Species	Authority	Floating green mats	Mangrove epiphytes	Red macroalgal mats	Seagrass	Benthic green mats	Rhizophytic calcareous green algae	Mangrove epiphytes	Red macroalgal mats	Seagrass
Amphipoda	Ampithoidae	*Cymadusa compta*	(Smith, 1873)			X		X	X		X	X
	Bateidae	*Batea cuspidata*	(Shoemaker, 1926)								X	X
	Ischyroceridae	*Cerapus* spp.								X		
	Lysianassidae	*Lysianopsis alba*	Holmes, 1903					X		X	X	
	Melitidae	*Dulichiella lecroyae*	Lowry & Springthorpe, 2007					X	X		X	X
Isopoda	Holognathidae	*Cleantioides verecundus*	Kensley and Clark, 1998			X	X					
	Idoteidae	*Erichsonella attenuatta*	(Harger, 1873)	X		X	X	X			X	X
	Ischyroceridae	*Ericthonius brasiliensis*	(Dana, 1853)						X	X	X	
	Janiridae	*Carpias* spp.						X	X	X	X	X
	Maeridae	*Elasmopus pocillimanus*	(Bate, 1862)							X	X	X
	Munnidae	*Uromunna*			X	X	X					
	Sphaeromatidae	*Harrieta faxoni*	(Richardson, 1905)			X	X	X		X	X	X
		Paracerceis caudata	(Say, 1818)					X			X	X
		Sphaeroma terebrans	Bate, 1866		X							
		Sphaeroma walkeri	Stebbing, 1905		X							
Tanaidacea	Leptocheliidae	*Chondrochelia savigny*	(Kroyer, 1842)							X	X	
		Leptochelia forresti	(Stebbing, 1896)							X		X
		Leptochelia spp.						X	X	X	X	X
	Metapseudidae	*Hoplopolemius propinquus*	(Richardson, 1902)							X		

FIGURES

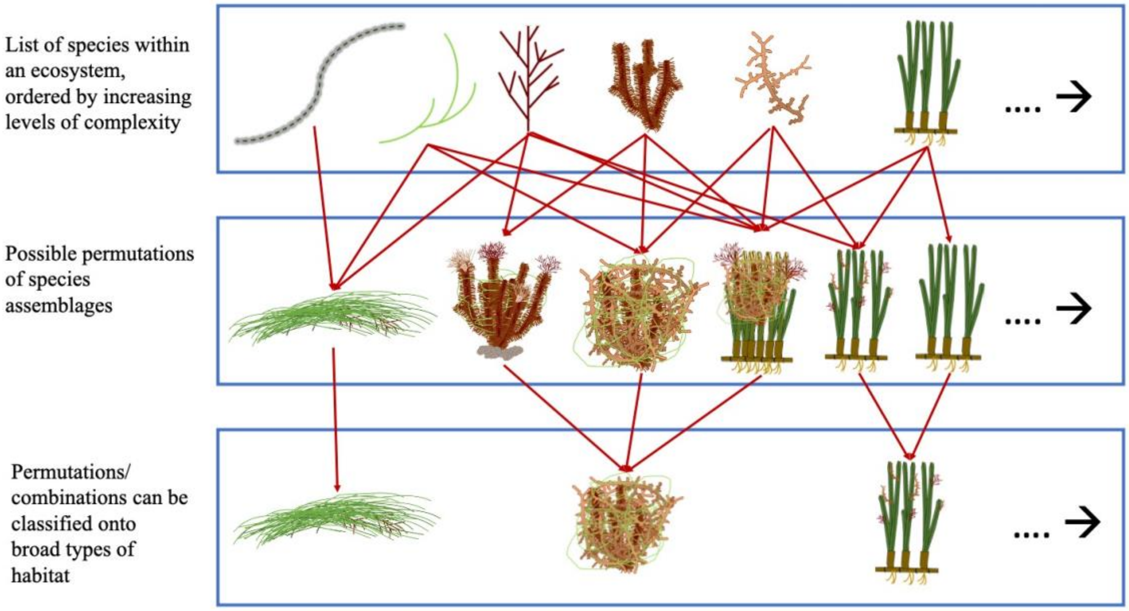

Figure 2.1: Conceptual model demonstrating the relationship between habitat types and the assemblages of macrophytes composing these habitats. The top portion represents the list of species whose total number depends on the study system and their environmental conditions. These macrophytes, depending on their available biomass, architecture, and substrate use, could form into different permutations of associations with each other. These different permutations of associations then can be grouped into broad categories of habitat types.

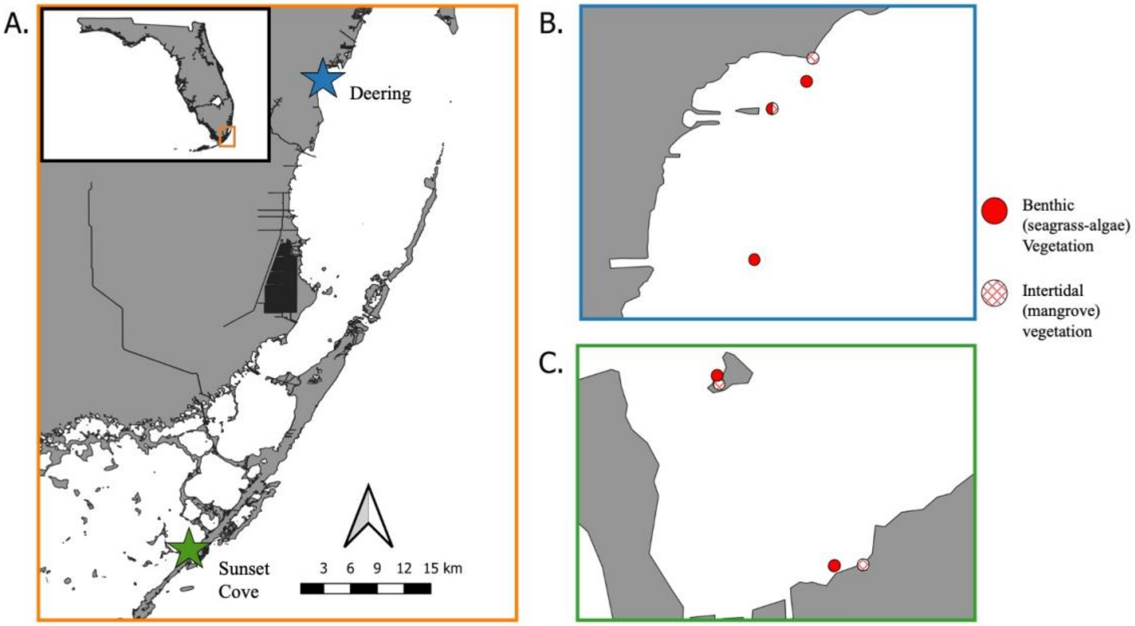

Figure 2.2: Map of study area, including an insert of South Florida (A), showing relative location of Deering and Sunset Cove in both Biscayne Bay and Northeast Florida Bay. Inserts show closeup of collection sites in Deering (B) and Sunset Cove (C). Key on the right denotes sites where samples of benthic seagrass-algae or intertidal mangrove habitat samples were collected based on broad vegetation type.

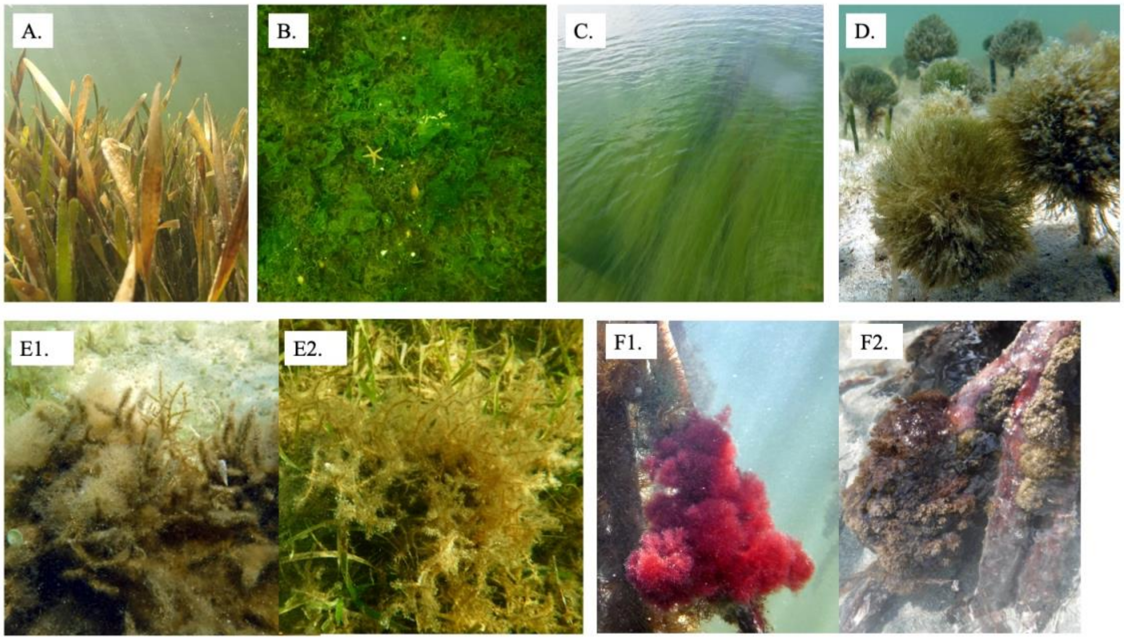

Figure 2.3: Representative habitat types found in South Florida for this study, including (A) seagrass habitat dominated by *T. testudinum* (B) benthic green algal mats dominated by *C. linum* and *Ulva* spp., (C), floating green algal mats dominated by *C. liniformis*, (D) rhizophytic calcareous green algae represented as *Penicillus* spp., (E1), red macroalgal mats in rocky substrate composed of *D. mexicana*, *Laurencia*, spp., and *Jania* spp., (E2) red macroalgal mats composed of *Laurencia* spp. found entangled with *T. testudinum* leaves, (F1) mangrove prop root epiphytes, dominated by filamentous red algae (probably *Ceramium*), and (F2) mangrove epiphytes dominated by Bostrychietum complex algae.

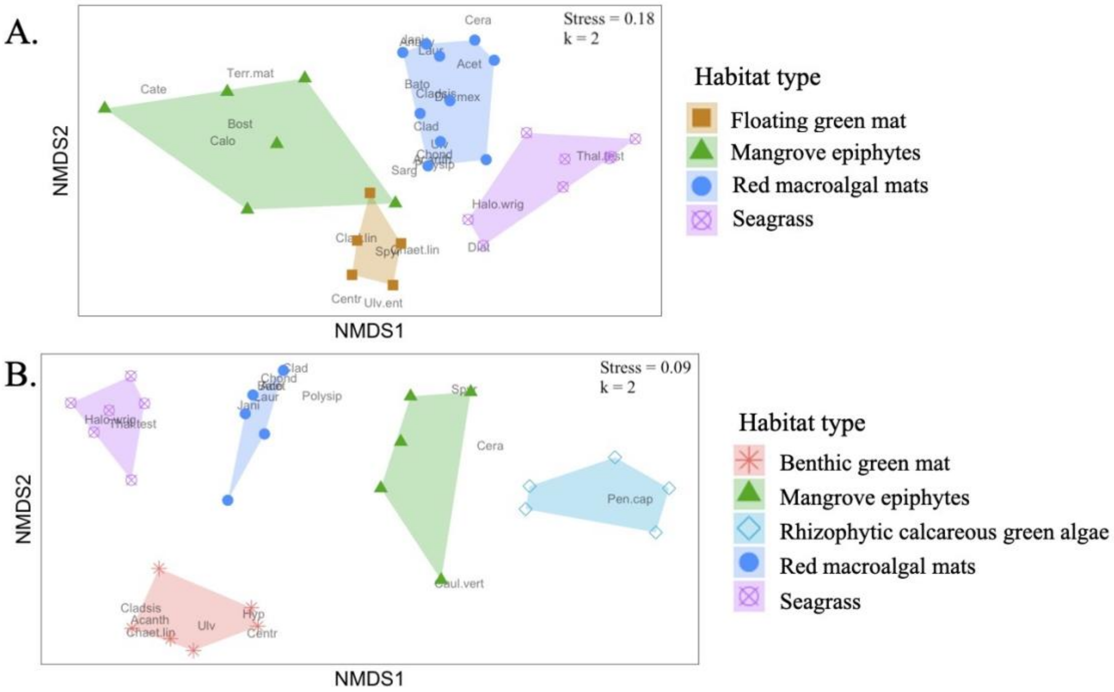

Figure 2.4: Non-metric multidimensional scaling (nMDS) plot displaying macrophyte assemblages and samples classified by habitat type in Deering (A) and Sunset Cove (B).

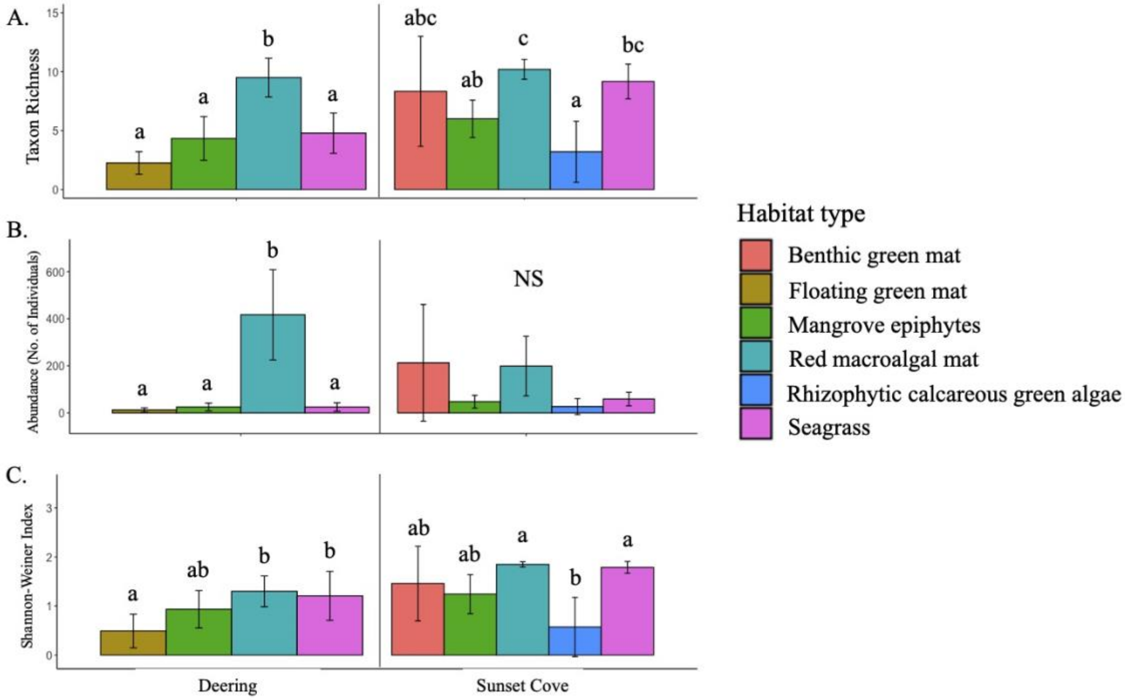

Figure 2.5: Comparison of (A) taxa richness, (B) abundance, and (C) Shannon-Weiner diversity index among habitats per location. Letters mark non-significant results of Dunn post-hoc tests. Error bars represent standard deviation.

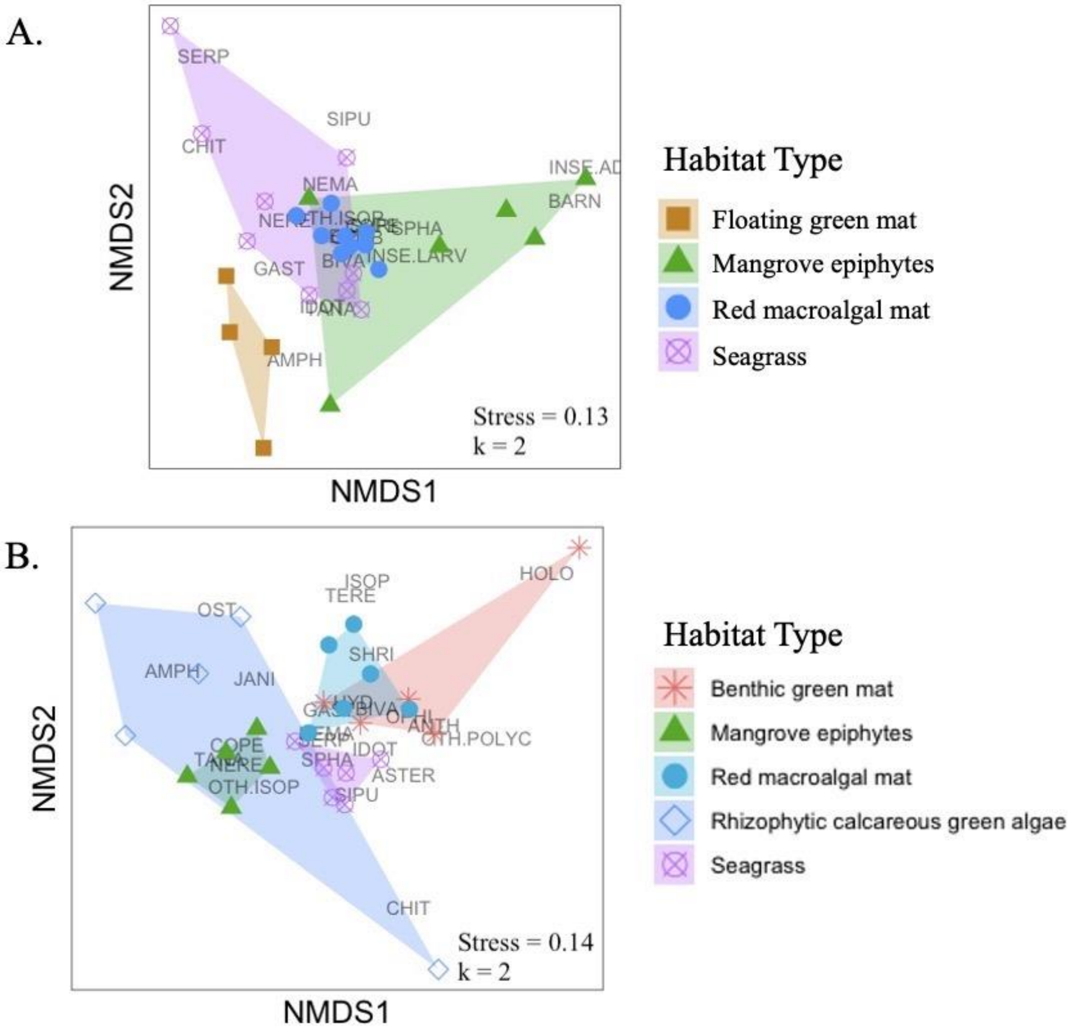

Figure 2.6: Non-metric multidimensional scaling (NMDS) plot of epifaunal assemblages per samples of habitat types in Deering (A) and Sunset Cove (B).

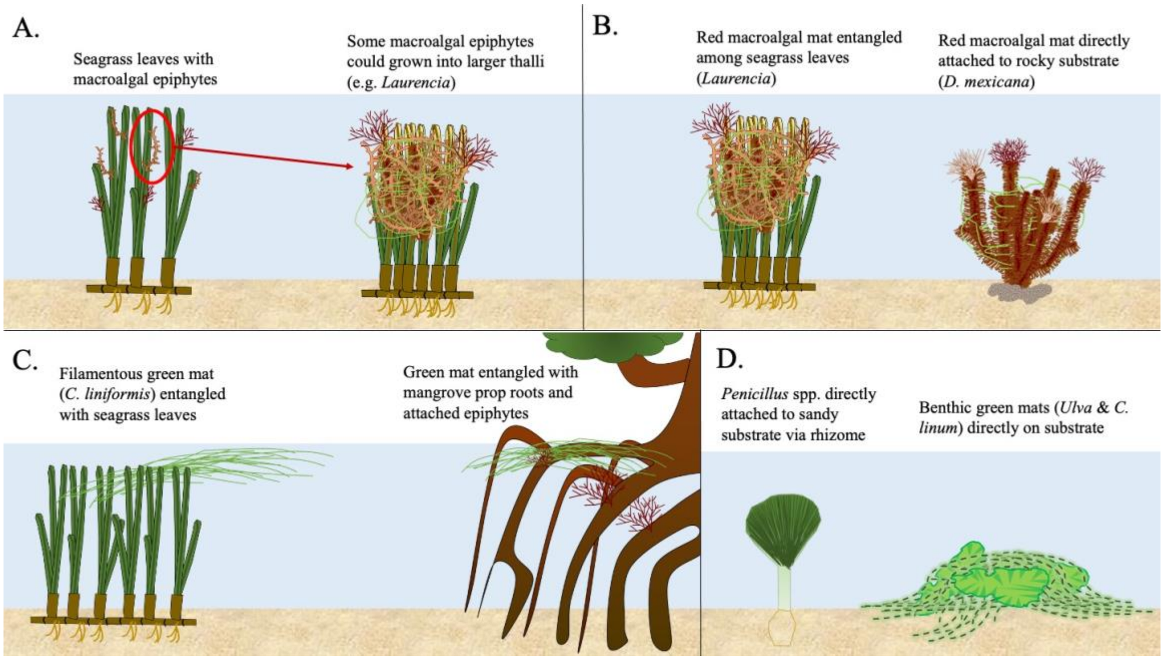

Figure 2.7: The different habitat types collected in this study and their potential properties resulting from associations among macrophyte species. The different properties are as follows: (A.) Seagrass leaves can include epiphytic macroalgae such as *Laurencia* that could grow into red macroalgal mats with entangled senescent seagrass leaves. (B.) Substrate use of red macroalgal mats could depend on the species composition of the mats, with *Laurencia* more likely to entangle with seagrass leaves while *D. mexicana* would more likely be attached to rocky substrate through their holdfast. (C.) Floating filamentous green mats formed by *C. liniformis* would get entangled onto seagrass leaves or mangrove prop roots; whether these mats would get exchanged between vegetation types is unknown. (D.) *Penicillus* spp. as the primary rhizophytic calcareous green algal habitat would form solitary units through their rhizome buried under the substrate, while benthic green macroalgal mats characterized by an association of *Ulva* and *C. linum* were directly attached to the benthos by the anchoring of *C. linum* filaments into the benthic surface. Figures of macrophytes displayed are not to scale.

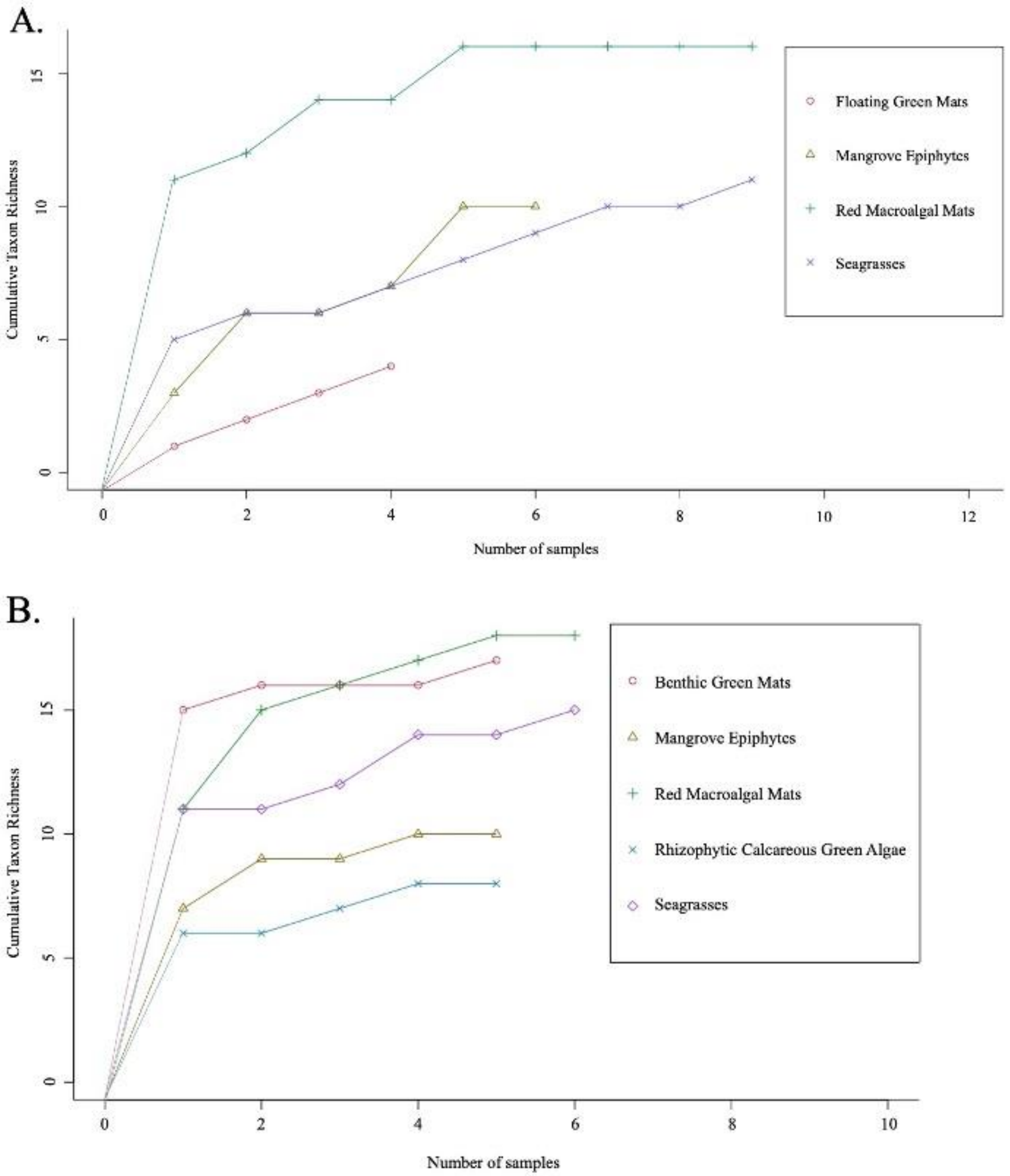

Figure S2.1: Sample rarefaction curves of cumulative epifaunal taxon per set of habitat samples collected from Deering (A) and Sunset Cove (B). Number of samples collected varied by availability of habitat type samples per sampled site and overall location.

CHAPTER III

SYNTHESIZING COMPOSITION, QUANTITY, AND ARCHITECTURE AS STRUCTURAL COMPONENTS OF MACROPHYTE HABITATS FOR EPIFAUNA

ABSTRACT

Structural complexity of habitat is often investigated as a driver of species diversity in communities. This can be even more complex when considering biogenic habitat sources such as seagrasses and macroalgae in coastal systems. Quantifying structural complexity can be multifaceted, and can include the species composition of the habitat and their associations, quantity of habitat, and differences in architecture from habitat-forming organisms. Measurements of structural complexity is often reduced to a single metric, such as biomass, or synthesized as an index that would incorporate multiple metrics. However, these approaches would exclude biogenic habitats formed by multiple species with various levels of associations and contribution to habitat complexity. This study examined structural complexity of five different macrophyte habitats for epifauna in South Florida. A total of 49 samples of habitat were collected, which included 28 macrophyte species. Additional samples of individual macrophytes were collected to quantify architecture per macrophyte species. A structural complexity index was created that incorporates species composition, habitat quantity, and architecture of each species present. However, calculation of this index was primarily influenced by biomass. Red macroalgal mats, with branching corticated algae as primary components, demonstrated high variation of index values compared to other habitat types. Epifaunal diversity patterns could be explained by multiple factors, such as macrophyte richness, total biomass, and the complexity index. With shortcoming in our approach, we compared our methodology to other studies with a complexity index. Justification of our methods and recommendations for future studies were outlined as such.

INTRODUCTION

Structural complexity can be defined as an emergent property from the culmination of all involved, interconnected components that contribute to physical structure (Carvalho and Barros, 2017). The summation of components from biogenic habitats could be represented as an assemblage of habitat-forming species that contributed to the development of physical structures and interstitial spaces (Bates and DeWreede, 2007). Characterizing structural complexity is often multifaceted and therefore debated (Carvalho and Barros, 2017), and quantifying complexity either resulted in a single variable or an index that incorporated multiple variables per unit habitat (Gee and Warwick, 1994). For biogenic habitats, indices were used to incorporate diversity, quantity, and architecture of all habitat-forming organisms involved in a habitat unit (Figure 3.1) (Bartholomew et al., 2000; Kovalenko et al., 2009). In many previous studies that attempt to assess habitat complexity effects were measured by any of the three components, often reduced to a single variable such as biomass, with varying results (Attrill et al., 2000; Desmond et al., 2018; Virnstein and Howard, 1987).

The composition of habitat-forming species can be measured through various classification systems. Traditional taxonomic identity denotes species present at an assemblage by its name and presence, which at an assemblage level can be quantified into species richness and derived indices. Habitat types would either labeled by the most dominant, structural ‘host’ species providing primary habitat (Ba-Akdah et al., 2016; Christie et al., 2009) or through an operational name such as ‘drift algae’ or ‘algal turfs’ (Biber, 2007; Connell et al., 2014). Alternatively, classification can depend on a species’ function, either through form-functional groups classified by morphology (Bates, 2009; Steneck and Dethier, 1994) or based on the relative ecological role (Collado-Vides et al., 1994).

Metrics of habitat quantity for a biological community, such as biomass, height, or surface area, consider the totality of the habitat rather than its individual components. Many studies have associated higher habitat quantity with higher diversity of associated communities (Attrill et al., 2000; Heck and Wetstone, 1977; Veiga et al., 2014). These metrics however are often conflated as measurements of entire habitat complexity, often omitting assemblage effects from epiphytes or architecture between macrophyte species within a habitat type. This conflation often leads to misleading results, as biomass and surface area as predictors of increased epifaunal diversity and assemblages were met with mixed results. For instance, Attrill et al. (2000) noted that seagrass-epifaunal relationships can be explained by biomass availability rather than an index of structural complexity. Virnstein and Howard (1987) compared epifaunal communities between macroalgal and seagrass habitats and found surface area and biomass to be inconsistent predictors of epifaunal abundances. However, macroalgal habitat, compared to seagrass habitats, usually demonstrate higher biomass translating to higher abundances of epifauna (Knowles and Bell, 1998; Lewis, 1987). The magnitude of habitat quantity as a reliable indicator of high species diversity remains to be contested.

Architecture of a structure is synonymous with design, including the number, shape, size, and arrangement of its components (Hacker and Madin, 1991). For habitat architecture, the ‘design’ of habitat can be attributed to the gross morphology and interactions of components within a biogenic habitat unit (Collado-Vides et al., 1994;

Hacker and Steneck, 1990). Measurements of habitat architecture are also varied, including the number of branches, degree of branching, and fractal dimensions (Chemello and Milazzo, 2002; Dibble and Thomaz, 2009; Holmlund et al., 1990; Huang et al., 2007). Previous studies showed macrophytes with more complex branching patterns are indicative of higher architecture than linear or planar-shaped algae, and would be more conducive habitat for epifauna as refuge from predators (Dibble and Thomaz, 2009; Gee and Warwick, 1994; Hooper and Davenport, 2006; Jeffries, 1993; McAbendroth et al., 2005). However, the effectiveness of increased refuge from interstitial spaces depends on the characteristics of both epifauna and their predators (Crowder and Cooper, 1982; Hacker and Steneck, 1990; Holmlund et al., 1990).

The fractal method of measuring habitat architecture was useful as a mathematical method of measuring architecture independent of macrophyte identity or quantity through biomass (Gee and Warwick, 1994). A fractal dimension could be defined as a ratio of two-dimensional space occupied by an object relative to a given space (Fernández-Martínez and Sánchez-Granero, 2014; Kinsner, 2008), and has been used as an independent measurement of strucutral complexity (Duarte et al., 2020; Ferreira Barbosa et al., 2019; Kovalenko et al., 2009). Fractal approaches to quantifying architecture of habitat-forming organisms have been used for marine macroalgae (Martínez-Laiz et al., 2018; Pérez-García et al., 2015; Torres et al., 2015; Veiga et al., 2014) and freshwater plants (Dibble and Thomaz, 2009; McAbendroth et al., 2005) of various complexities. However, the usage of fractal dimensions would emphasize dominant, primary structural species and not secondary or epiphytic macrophytes, which could risk omission of minor yet essential components of biogenic habitat.

The purpose of this study was to determine habitat characteristics brought by marine macrophytes that bets explained diversity patterns of associated invertebrate epifauna. We pursued the following objectives: 1. Characterize different habitat types based on composition following descriptors from different classification systems, 2. Compare diversity, quantity, and architecture of macrophytes between habitat types, and 3. Assess characteristics of macrophytes that best correlate with epifauna diversity.

METHODS

Sample collection: Samples of macroalgal habitat and epifauna were collected from Deering Estate's coastal bay (25° 36' 50.5224" N, 80° 18' 2.862" W) and Sunset Cove in Key Largo (25° 5' 20.2452" N, 80° 27' 2.556" W). These two study areas were composed of a mix of seagrass-macroalgal benthic vegetation that included various assemblages of macrophytes forming into habitat types. From initial surveys, five unique habitat types were identified with an assemblage of structural and supportive species contribution to habitat complexity (Figure 3.2). Details on each habitat type, including species composition, relative biomass contribution, and comparisons between sites were elaborated on chapter 2:

1. Seagrass habitats formed by multiple stands of flat leaves containing small epiphytic algae on the leaf surface.
2. Benthic green macroalgal mats ("benthic green mats") dominated by green algae and collected on the soft sediment benthic floor.
3. Red macroalgal mats formed by corticated red macroalgae and also found among the benthic floor.

4. Floating green macroalgal mats ("Floating green mats") composed of loose-lying filamentous green algae.
5. Mangrove prop root epiphytes ("mangrove epiphytes") composed of macroalgae directly attached to the mangrove prop roots.

Samples of macrophyte habitats were collected by enclosing the mat with a zip-lock bag to prevent epifauna from escaping, while seagrass habitats were collected by enclosing a stand of seagrass leaves with a Uline polystyrene bag and sealing the contents with a zip tie after cutting the leaves from the benthic floor. Mangrove epiphyte habitats were collected by scraping the epiphytes off the prop roots of *Rhizophora mangle* L. onto a zip-lock bag. Given the low biomass yield of mangrove epiphyte collection, multiple prop roots were scraped of epiphytes per one unit of habitat. Samples were then returned to the lab, cleaned of sediment and detritus.

Macrophyte components of each habitat sample were identified to lowest possible taxonomic level using field guides (Littler et al., 2008; Littler and Littler, 2000) and checked for the current use of the name using the AlgaeBase taxonomic database (Guiry et al., 2014), while invertebrates were identified at class and order level. Sorted macrophytes were weighed of wet and dry biomass after drying in a 65°C oven, while sorted invertebrates were counted for abundance and preserved in 70% ethanol. Additional classification of macrophytes were conducted using various previous literature, including of relative structural role of macrophytes (Collado-Vides et al., 1994), and form-functional groups (Ortegon-Aznar et al., 2008; Steneck and Dethier, 1994).

Structural complexity analyses: Additional specimens of macrophytes were collected to quantify the structural architecture at the genus or species level, though the sample of macrophyte branches per species varied depending on what was available in the field. To conduct fractal analyses as a proxy of macrophyte architecture, each branch was placed on a shallow polystyrene tray with water. The branch was arranged to expose all branches without overlapping as a two-dimensional structure, which would then be flattened using a glass pane. Some algae with many filaments, such as *Digenea mexicana*, would be altered to reduce filament overlap by cutting off structures that would overestimate thallus width that may contribute to fractal dimension calculations. The sample was placed onto a scanner to be scanned with the software WinRHIZO. Images were cropped to center the macrophyte branch as a visible object to standardize for pixel length and size. The image was also cleaned of any blemishes and separated from overlapped branches using pixel image manipulation tools.

The images were analyzed to obtain each replicate fractal dimension using the FracLac plugin tool of ImageJ (Karperien, 1999). The ImageJ plugin tool used a box-counting method that implemented a grid over the image and counted the number of grid boxes that included any part of the macrophyte branch over the total number of boxes. This was then graphed as a regression line, where the slope of the line represents the ratio of grid boxes and box sizes used for all trials (Morse et al., 1985; Sugihara and May, 1990). The FracLac plugin converts the scanned image to a binary image and models a bounding box around the foreground object to calculate the calibers of grid box sizes per series of trials (Karperien, 1999). Three box-counting trials were conducted using 12, 64, and 240 box placements per replicate, with each number of box placements inversely proportional to the box grid size. Each trial calculated an average fractal dimension, F per macrophyte branch. The three values from the trial were then averaged into a single F representing the final average per replicate. Macrophytes that have a linear or planar branching pattern were given F value of 1. Macrophytes that were highly branched such that they form a planar object when compressed into a two-dimensional figure, such as *Bostrychia*, were given a F value of 1.5. Fractal dimensions of each set of replicates per species were averaged to represent the final fractal dimension per species, F_i, for subsequent analyses (Table 3.1).

Degree of branching values of macrophytes were also collected from separate herbarium specimens from the Marine Macroalgae Research Lab at Florida International University (MMRL-FIU). The herbarium collection included various macrophyte species collected across South Florida since 2006 until 2022. Calculating degrees of branching was determined by the procedure outlined by Chemello and Milazzi (2002): Starting from the most distal branch as a value of 1, one value is added whenever two branches of the same degree meet at a branching point.

Data analyses: Diversity of macrophytes within a habitat type was calculated using the Shannon-Weiner index, H, using the following equation below:

$$H = -\Sigma p_i * ln(p_i)$$

Where p is the proportion of macrophyte species i composing the entire community represented as a habitat type per sample. H was also calculated for associated epifaunal communities per habitat sample.

Calculating the habitat complexity index (C_d) of each habitat sample using fractal dimensions and biomass was calculated using the following equation:

$$C_d = \sum_{i=1}^{n} B_i * e^{(D_i - 1)(F_i - 1)}$$

Where B_i is the wet biomass of the macrophyte species within a habitat unit (a measurement of habitat quantity), D_i is the average degree of branching for a macrophyte species i, F_i is the average fractal dimension of the macrophyte species i, and n as the number of macrophyte species composing that habitat. The degree of branching and fractals are multiplied as an exponent to natural number e, and was structured such that unbranched macrophytes, whether D or F are 1, are calculated as an architectural value of $e^0 = 1$.

Principal component analysis (PCA) was used to test for variation among diversity and assemblage variables per habitat type, including H, C_d, taxon richness, and total wet biomass and discerning which variables provide the highest differentiation among habitats. One-way ANOVA models were conducted to compare average richness, H, total wet biomass, and C_d of macrophytes among habitats. Significant differences between groups were further assessed using a Tukey Honest Significance Differences (HSD) test between paired groups.

Multiple regression models were conducted to explore correlations between epifaunal response variables (taxon richness, log-transformed total abundance, and Shannon-Weiner Index) and habitat predictor variables (richness, total wet biomass, H', C_d, PC1 and PC2). Regression analyses were conducted per paired predictor and response variable. All statistical analyses were conducted using R and RStudio and functions in the package vegan (Oksanan et al., 2019; R Core Team, 2020).

RESULTS

A total of 49 habitat samples were collected for this study. From these 49 samples, 28 species of macrophytes were identified, including two seagrasses, 11 chlorophytes, 13 rhodophytes, and two phaeophytes. These species vary by biomass contribution towards the habitat unit and details can be found on chapter one. Six form-functional groups were identified among all macroalgal species, with an additional ‘seagrass’ functional group added to distinguish from macroalgal form-functional groups. All habitat types have at least one species that functions as the provider of primary structure (either as ‘structural’ or ‘structural-intertwining’). *Laurencia* spp. and *Digenea mexicana*, both of which were corticated branching rhodophytes, were providing the primary structure of red macroalgal mat habitats. The primary structural algae of benthic green mats were foliose *Ulva* spp. and the uniseriate, unbranched, filamentous algae *Chaetomorpha linum*. Mangrove epiphytes were site-dependent (details on chapter 1), with Deering Estate’s mangrove epiphytes dominated by the ‘Bostrychietum’ complex of *Bostrychia*, *Catenella*, and *Caloglossa*, all of which were epiphytes and used each other’s thalli as a substrate for attachment and growth. Sunset Cove’s mangrove epiphytes were dominated by *Caulerpa verticillata* and *Polysiphonia* spp., both of which were usually considered intertwining species but contributed to mangrove epiphyte primary structure. Floating green mats were composed of the green branching filamentous algae *Cladophora*, and seagrasses collected include *Thalassia testudinum* and *Halodule wrightii*.

A total of 67 macrophyte herbarium specimens from nine different taxa were measured for degrees of branching. An additional 12 taxa were assigned a degree of branching number for later structural complexity analyses. The highest degree of branching was assigned to *Bostrychia* spp. which is a branching red macroalga composing mangrove epiphyte habitats. The highest degree of branching calculated averaged to 6.50 (± 2.12) for *Polysiphonia*. *Laurencia* (4.13 ± 0.87) and *D. mexicana* (4.28 ± 0.82) degree of branching values were roughly similar to each other (table 3.1).

A total of 177 macrophyte branches from ten different taxa were collected for scans for later fractal dimension calculations. An additional 11 taxa were assigned a fractal value. *D. mexicana* had the highest average fractal value (1.55 ± 0.06), although most macrophyte F_i ranged from 1.0 - 1.5. Other branching rhodophytes have fractal values ranging from 1.30 - 1.40. In contrast, most chlorophytes have fractal values between 1.00 - 1.18, with the exception of *C. verticillata* assigned to a fractal value of 1.5 owing to the high degree of branching (table 3.1).

Macrophyte habitat samples distributed within the PCA showed large overlap, with the exception of mangrove epiphyte habitats and red macroalgal mat habitats (figure 3.3). The first two main axes of PCA explained 86.01% of variation in macrophyte habitat complexity (table 3.2). PCA1 accounted for 60.97% of variation in habitat characteristics and was highly correlated with the structural complexity index (0.587), total dry biomass (0.575), and total macrophyte richness (0.528). PCA2 accounted for 25.04% of variation and was highly correlated with the Shannon-Weiner index for macrophyte diversity (0.897).

Mangrove epiphytes and seagrass habitats have lower richness than other macrophyte habitats ($p < 0.0001$), with only two to three species, compared to five to seven species in other habitats. Shannon-Weiner diversity from macrophytes did not differ among habitats ($p = 0.09$). H ranged from 0.54 in benthic green mat habitats to 0.32 in floating green mat habitats. Total wet biomass was higher in red macroalgal mat and benthic green mat habitats than other habitat types ($p < 0.0001$). Red macroalgal mats have higher C_d than other habitat types ($p < 0.0001$), attributing to the primary structure from branching rhodophytes. Average C_d of red macroalgal mats was 193.24 ± 125.57, six times higher in structural complexity than the next highest average C_d of 30.65 ± 19.23 from benthic green mats (Figure 3.4).

Epifaunal Shannon-Weiner Index did not correlate with any of the macrophyte habitat metrics. Macrophyte Shannon-Weiner Index did not correlate with any of the epifaunal diversity metrics. Total dry biomass and PC1 were roughly equal in contributing to variation in epifaunal taxon richness ($R^2 = 0.24$, $p > 0.001$). PC1 demonstrated the highest explanation in variation of epifaunal abundance ($R^2 = 0.48$, $p < 0.001$). Among specific macrophyte components, taxon richness, total dry biomass, and C_d were roughly equal in contributing to variation in epifaunal abundance ($R^2 = 0.36$ – 0.37, table 3.3). Visualization of linear regressions reveal red macroalgal mat habitats showed the highest variation in C_d among replicates compared to other habitat types (Figure S3.1).

DISCUSSION

Categorizing species based on broad classification systems would be useful to characterize diversity patterns and identify species that were primary composers of habitat (Collado-Vides et al., 1994; Steneck and Dethier, 1994). This was evident in our descriptors of macrophytes providing habitat, as each habitat type can be described by one to three macrophyte species forming associations with each other. There was however an inherent risk in losing resolution when using broad classification systems in describing species composition (Bates, 2009; Dethier, 1994). Bates (2009) noted that taxonomic relatedness of macrophyte habitats were better predictors of epifaunal diversity patterns than functional groups, which would obscure the diversity patterns of epifauna. The primary structural providers of red macroalgal habitats in our study, *Laurencia* and *D. mexicana*, were both corticated rhodophytes. However, these two macroalgae have very different morphologies in branch width, which was not calculated in this study, and filament arrangement; *D. mexicana* has more filaments than *Laurencia* that contributed to differences in fractal dimension. Conversely, the benthic green mat habitats were formed by an association of two chlorophytes, with one species a uniseriate, unbranched filamentous species (*C. linum*) and a one-layered foliose species (*Ulva* spp.). These algae, although widely different in architecture and morphology, were considered to have lower complexity than branching macroalgae, as assigned in branching degree and fractal dimension in our study.

The structural complexity of a macrophyte habitat was previously shown to exponentially provide interstitial spaces for fauna to utilize (Hacker and Steneck, 1990). This provided the basis of adjusting our structural complexity index that differed from similar indices used previously (table 3.4). Of all the habitat types, red macroalgal mats only seemed to respond to the index calculation with their sizeable biomass contribution and higher degrees of branching and fractal dimension from red branching algal species. Other habitat types, either with low total biomass or with unbranching macrophytes as primary components, seemed to respond poorly to the structural complexity index calculation (Figure S3.2). This seemed to be a notable weakness in our study, as C_d

benthic green mats dominated by *Ulva* and *C. linum* were similar in structural complexity to seagrass and mangrove epiphyte habitats with very different physiognomies (Figure S3.4). From the PCA, total wet biomass and C_d were very closely correlated to each other. While wet biomass was a component of the index equation, input from degree of branching or fractal values seems to have limited influence on the final calculations. Therefore, C_d values seemed to be dependent on total wet biomass and could be considered a redundant value that added minimal information in explaining structural complexity than biomass availability.

Many studies of macrophyte structural complexity using fractal dimensions utilized the entire thallus or shoot to calculate the fractal dimensions of said macrophyte (Dibble and Thomaz, 2009; Duarte et al., 2020; Kovalenko et al., 2009; McAbendroth et al., 2005). The box-counting method used to calculate the fractal dimension relied on two assumptions during the methodology: 1. The three-dimensional macrophyte would have to be converted onto a two-dimensional, binary-colored plane, and 2. Branches or other structures composing the individual macrophyte sample should not overlap with each other. Overlapping of structures onto a two-dimensional plane would lead to the binary image appearing as a large planar object than as a branching object. While previous studies did not address that shortcoming, our study attempted to address that by sampling small branches representing iterations of the macrophyte species. While macrophytes could not be considered truly fractal objects, they resemble such that fractal dimensions can be utilized as a tool regardless (Collado-Vides et al., 1997; Halley et al., 2004). Our approach to this fractal may have addressed that issue of methodology, but fell short in reducing the range of fractal dimension (the largest being *D. mexicana* with a fractal value of 1.55) and our inability to compare our data to previous studies that used the whole-individual approach to fractal dimensions. One future consideration in utilizing fractal dimensions as a measurement of architecture would be to gain fractal values using the entire individual and a small branch representing an iteration of that individual. However, many macroalgal-composed habitats were composed of more than one thallus, could be composed of multiple species, and therefore the primary contributor of structure would not be easily discerned. Our use of fractal dimension, regardless, did provide comparisons to macrophyte species providing primary structure to a mixed-macrophyte habitat.

There seemed to be high correlation between most epifaunal diversity (richness and abundance) and macrophyte habitat metrics (richness, total wet biomass, and C_d). Therefore, there wasn't a clear distinction on what macrophyte habitat metrics could best explain variation in epifaunal diversity, and multiple explanations based on complexity alone could be warranted. The total habitat biomass providing the best explanation in variation of epifaunal richness is very akin to a classical species-area relationship (Attrill et al., 2000). Macrophyte richness, total biomass, and C_d all have relatively equal contributions in explaining epifaunal abundance (Table 3.4), suggesting that there could be multiple explanations to the variation in epifaunal abundance. However, red macroalgal mats, and benthic green mats to a lesser extent, seemed to be the habitat types that responded well to the best-fit line than other habitat types (Figure S3.1). The variation in epifaunal abundance could very well be explained by multiple factors outside of structural complexity. Furthermore, epifaunal abundance could be habitat-dependent, and not one metric of habitat complexity, outside of quantity, could conform for hypothesis-testing to all the possibly infinite permutations of habitat types composed by many different species (for details on epifaunal abundance between habitat types, see chapter 1).

Approaches to quantifying biogenic habitats formed by habitat-forming species and their associations can be very complex and multifaceted. This study relied on assuming that structural contributions of epiphytes could also be of value to structural macrophytes providing primary structure, which has been seldom approached in that direction when assessing habitat complexity. This study explored possibilities in assessing habitats formed by more than one species of macrophytes, which differed from many studies that would use the primary species name as the habitat itself (Ba-Akdah et al., 2016; El-Khaled et al., 2022; Russo, 1997). Should conventional approaches to naming habitats be used in our study, then labelling our red macroalgal mat habitats as "*Laurencia*" or "*D. mexicana*" mats could narrow the possibilities of red macroalgal mat habitats with differing amounts of biomass between these two species, or red mats with neither algal species present or in negligible amounts. In areas with a diverse array of macroalgae such as Biscayne Bay, many combinations of macroalgae could compose a generalized habitat type such as 'drift algal mats' (Biber, 2007). Alternatively, discerning effects of structural complexity and environmental conditions in contrasting ecosystems could be an interesting future avenue for examining differential effects of these two factors in epifaunal diversity patterns. This would especially be relevant to South Florida areas where environmental conditions were dynamic given their history of coastal development, and the diversity of submerged macrophytes among coastal and bay areas in South Florida. Finally, a global analysis of macrophyte complexity could also be of interest, as large kelps and intertidal macroalgae could differ just in size alone from seagrass and submerged algal mat habitats with less biomass but more diversity and possibly different architectures brought by different species. Quantifying structural complexity effects however would require different methods that were not considered in this study, such as interstitial spaces within a habitat unit, while also bearing in mind the qualitative differences in size and quantity of macrophyte habitats such as of kelps, seagrasses, and algal mats.

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APPENDIX

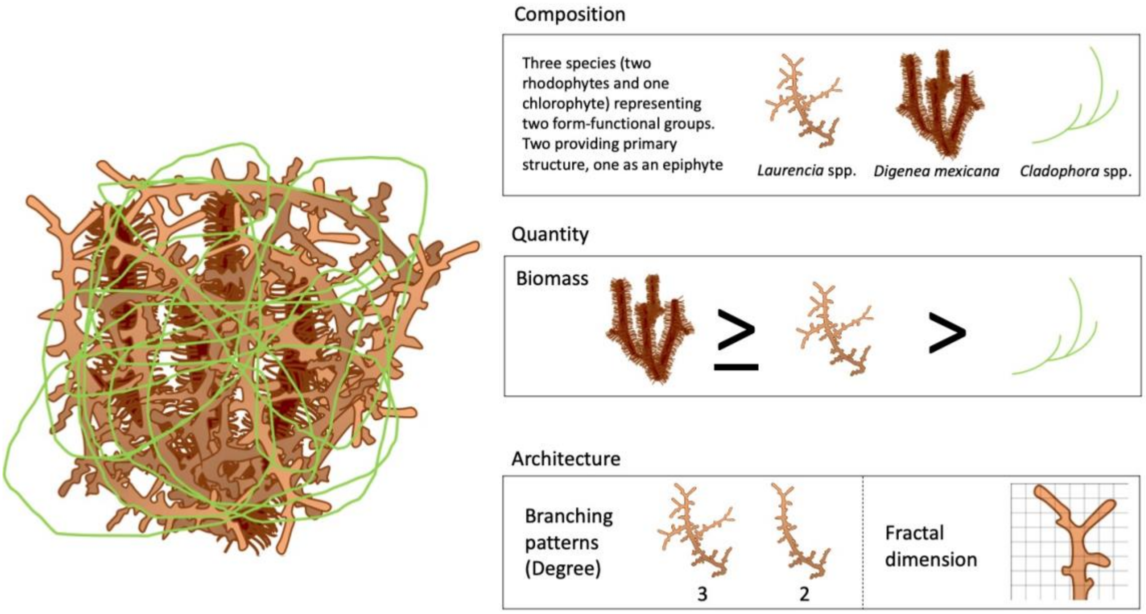

Figure 3.1: Methods of quantifying structural complexity from a macrophyte habitat unit composed of multiple species. The top box represents descriptors of macrophyte species per unit of habitat based on phylum, form-functional group, and relative ecological role. The middle box representing relative contribution of habitat quantity by biomass; in this example, *D. mexicana* contributed the highest biomass, followed by *Laurencia*, and *Cladophora* contributing the least biomass. The bottom box representing different methods of quantifying macrophyte architecture either by degrees of branching or fractal dimension.

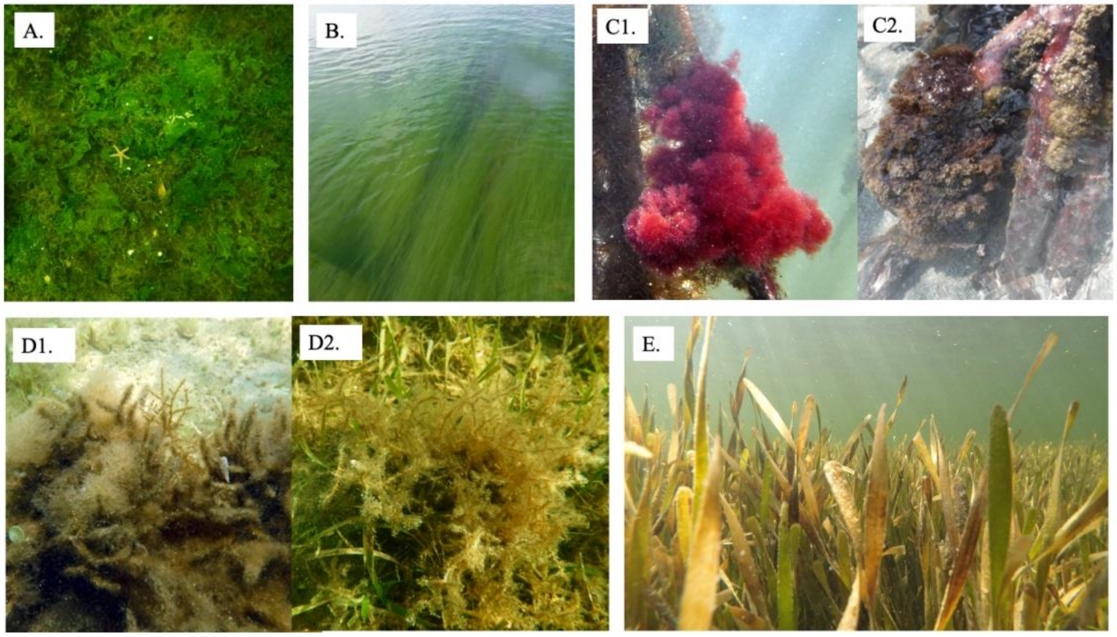

Figure 3.2: Representative habitat types found in South Florida for this study, including (A) benthic green algal mats dominated by *C. linum* and *Ulva* spp., (B) floating green algal mats dominated by *C. liniformis*, (C1) mangrove prop root epiphytes, dominated by filamentous red algae (probably *Ceramium*), (C2) mangrove epiphytes dominated by Bostrychietum complex algae, (D1), red macroalgal mats in rocky substrate composed of *D. mexicana*, *Laurencia*, spp., and *Jania* spp., (D2) red macroalgal mats composed of *Laurencia* spp. found entangled with *T. testudinum* leaves, and (E) seagrass habitat dominated by *T. testudinum.*

				Degree of Branching (D_i)			Fractal Dimension (F_i)		
	Phylum	Form-Functional Group	Role	Number of samples (herbaria)	Average ± SD (if applicable)	Method of Data Collection	Number of Samples (Scanned)	Average ± SD (if applicable)	Method of Data Collection
Acanthophora	Rhodophyta	Corticated	Structural	14	4.14 ± 0.86	Measured	22	1.31 ± 0.15	Measured
Acetabularia	Chlorophyta	Calcareous green	Epiphytic	NA	1.00	Assigned	NA	1.00	Assigned
Anadyomene	Chlorophyta	Foliose	Epiphytic	NA	1.00	Assigned	NA	1.00	Assigned
Bostrychia	Rhodophyta	Corticated Polysiphonus filamentous	Structural-Intertwining	NA	6.00	Assigned	NA	1.50	Assigned
Caloglossa	Rhodophyta	Foliose	Structural-Intertwining	1	5.00	Measured (one sample)	NA	1.00	Assigned
Catenella	Rhodophyta	Corticated	Structural-Intertwining	NA	2.00	Assigned	6	1.30 ± 0.07	Measured
Caulerpa verticillata	Chlorophyta	Coenocytic	Structural-Intertwining	1	7.00	Measured (one sample)	NA	1.50	Assigned
Chaetomorpha linum	Chlorophyta	Filamentous	Structural-Intertwining	NA	1.00	Assigned	15	1.07 ± 0.02	Measured
Chondria	Rhodophyta	Corticated	Structural	5	4.20 ± 1.30	Measured	39	1.30 ± 0.08	Measured
Cladophora	Chlorophyta	Filamentous	Intertwining	NA	2.00	Assigned	15	1.18 ± 0.08	Measured
Cladophora liniformis	Chlorophyta	Filamentous	Structural-Intertwining	NA	2.00	Assigned	NA	1.18 ± 0.08	Assigned (based on *Cladophora*)
Cladophoropsis	Chlorophyta	Filamentous	Intertwining	NA	2.00	Assigned	NA	1.18 ± 0.08	Assigned (based on *Cladophora*)
Digenea mexicana	Rhodophyta	Corticated	Structural	14	4.28 ± 0.82	Measured	21	1.55 ± 0.06	Measured
Halodule wrightii	Tracheophyta	Seagrass	Structural	NA	1.00	Assigned	NA	1.00	Assigned
Hypnea	Rhodophyta	Corticated	Structural	3	5.00 ± 1.00	Measured	14	1.40 ± 0.05	Measured
Laurencia	Rhodophyta	Corticated	Structural	23	4.13 ± 0.87	Measured	36	1.35 ± 0.12	Measured
Polysiphonia	Rhodophyta	Corticated Polysiphonus filamentous	Intertwining	2	6.50 ± 2.12	Measured	2	1.29 ± 0.05	Measured
Spyridia	Rhodophyta	Corticated Polysiphonus filamentous	Structural-Epiphytic	4	5.00 ± 0.82	Measured	7	1.49 ± 0.05	Measured
Thalassia testudinum	Tracheophyta	Seagrass	Structural	NA	1.00	Assigned	NA	1.00	Assigned
Ulva spp.	Chlorophyta	Foliose	Structural	NA	1.00	Assigned	NA	1.00	Assigned
Ulva intestinalis	Chlorophyta	Foliose	Epiphytic	NA	1.00	Assigned	NA	1.00	Assigned

Table 3.1: List of macrophytes found in habitat units used for this study. Macrophyte species were categorized by phylum, form-functional group, and relative role based on Collado-Vides et al. (1994). Each macrophyte was also either assigned or measured a value of degree of branching of fractal value. Average values (based on two or more samples), include standard deviation, if applicable. Lack of standard deviations could be for assigned values or measured values with only one replicate per species.

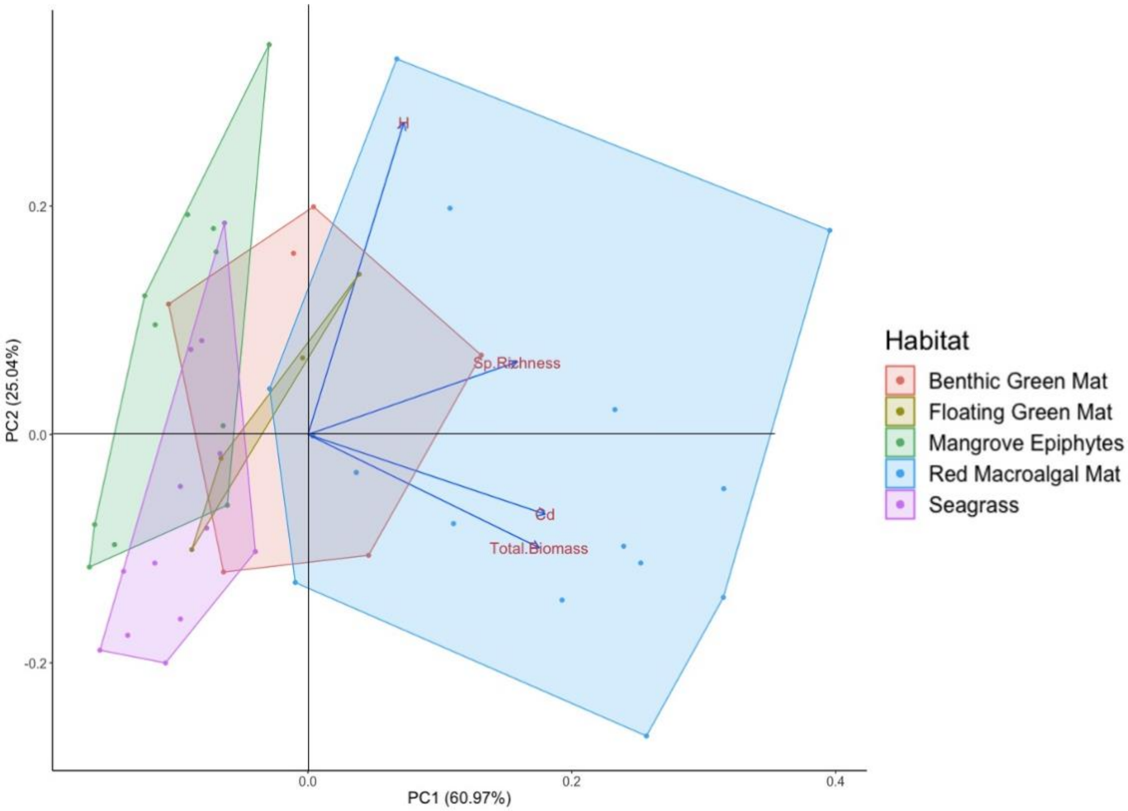

Figure 3.3: PCA plot visualizing the variation of macrophyte habitats and their relation to habitat metrics and principal components.

Macrophyte habitat metrics	PC1	PC2	PC3	PC4
Structural Complexity Index (C_d)	**0.587**	-0.201	0.383	0.684
Total Dry Biomass	**0.575**	-0.328	0.225	-0.715
Taxon Richness	**0.528**	0.217	-0.818	0.068
Shannon-Weiner Index	0.214	**0.897**	0.366	-0.125

Table 3.2: Principal components based on macrophyte habitat metrics. Bold numbers represent significant metrics that explain variation per principal component.

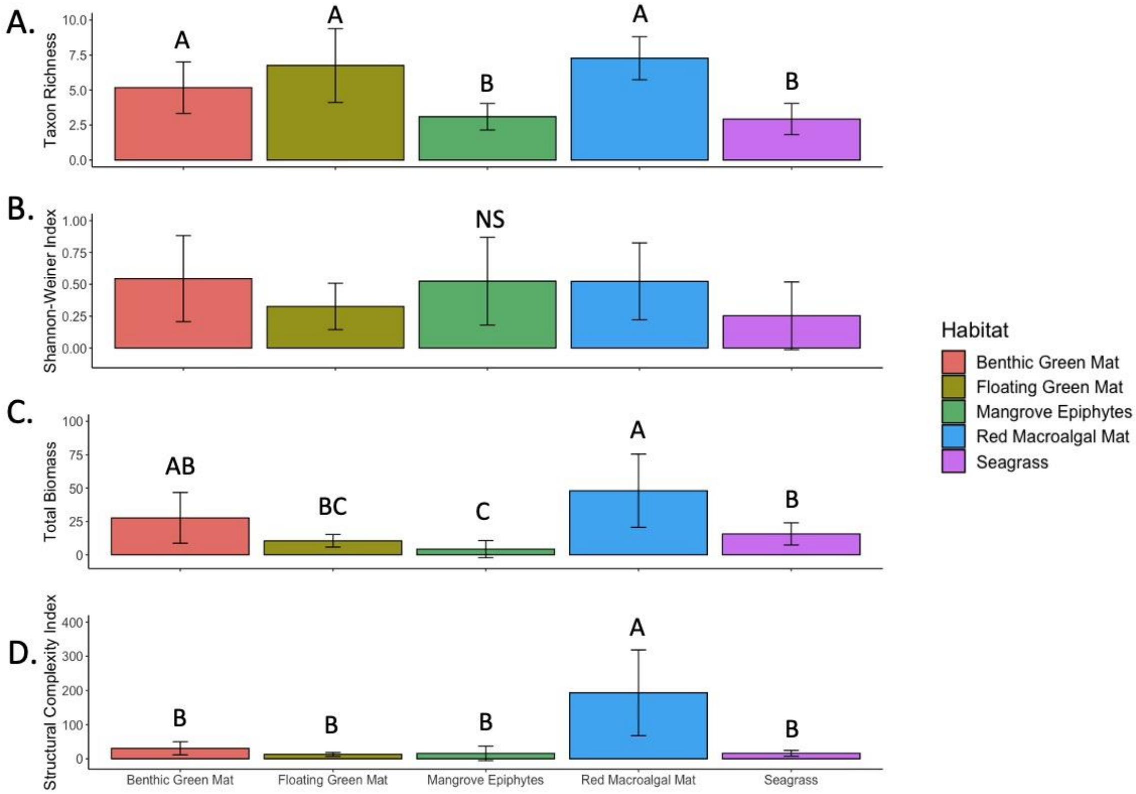

Figure 3.4: Comparisons of taxon richness (A), Shannon-Weiner indices (B), total wet biomass (C), and structural complexity (D) between habitat types. Bars represent averages per habitat type. Error bars represent standard deviation. Letters represent results of Dunn post-hoc test following results of Kruskal-Wallis test. No significant difference was detected in Shannon-Weiner indexes between habitat types.

	Epifaunal Metrics		
Macrophyte Habitat Metrics	Taxon Richness	Log-Transformed Abundance	Shannon Index
Taxon Richness	0.14**	0.37***	-0.013 NS
Shannon Index (*H*)	0.02 NS	0.03 NS	-0.005 NS
Total Wet Biomass	0.24***	0.37***	0.03 NS
Structural Complexity Index (C_d)	0.15***	0.36***	0.001 NS
PC1	0.24***	0.48***	0.01 NS
PC2	-0.02 NS	-0.02 NS	-0.02 NS

Table 3.3: Results of multiple regression analyses between macrophyte habitat metrics and epifaunal diversity metrics. Values represent R2 correlation coefficient (Pearson's), asterixis represent significance level (NS = no significance, * = < 0.05, ** = < 0.01, *** = < 0.001).

Source	Equation	Method of measuring species composition	Method of measuring quantity	Method of measuring architecture
Kovalenko et al. 2009	$C_d = \sum_{i=1}^{n} D_i \cdot N_i$	Richness as sum of species n.	N: Number of macrophyte stems counted along 1.0 m transects per species *i*	D: Fractal dimension of entire macrophyte stem per species *i*
Duarte et al. 2019	$C_d = FD \cdot W$	NA, Each macrophyte habitat was a single macroalgal species	W: Wet weight of a single algal thallus representing one species and habitat unit	FD: Fractal Dimension of entire algal thallus
Ferreira Barbosa et al. 2019	$C_d = \sum_{i=1}^{n} D_i \cdot N_i$	Richness as sum of species n.	N: Abundance of mollusk species per macrophyte habitat	D: Fractal Dimension of entire algal thallus
Our Study	$C_d = \sum_{i=1}^{n} B_i \cdot e^{(D_i-1)(F_i-1)}$	Richness as sum of species n.	B: Biomass of each macrophyte species *i* within a habitat unit	D: Degree of branching of entire thallus per macrophyte species *i* F: Fractal Dimension of small branch iteration per macrophyte species *i*

Table 3.4: Structural complexity indices used for macrophyte habitat complexity from previous studies and our study.

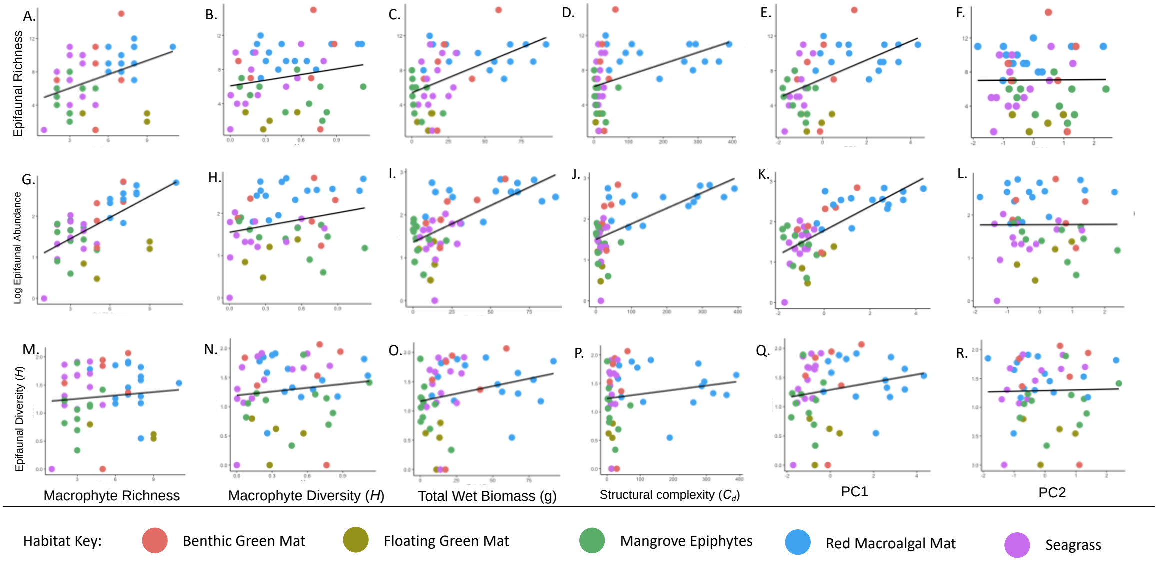

Figure S3.1: Visualized multiple regressions between macrophyte habitat complexity variables and epifaunal diversity variables. Macrophyte variables used include richness (A,G,M), Shannon-Weiner diversity *H* (B, H, N), total wet biomass (C, I, O), structural complexity index C_d (D, J, P), principal component values PC1 (E, K, Q), and principal component values PC2 (F, L, R). Epifaunal values include richness (A-F), long-transformed abundance (G –L), and Shannon-Weiner diversity *H* (M-R). Best fit lines for all analyses represent regressions using all habitat samples.

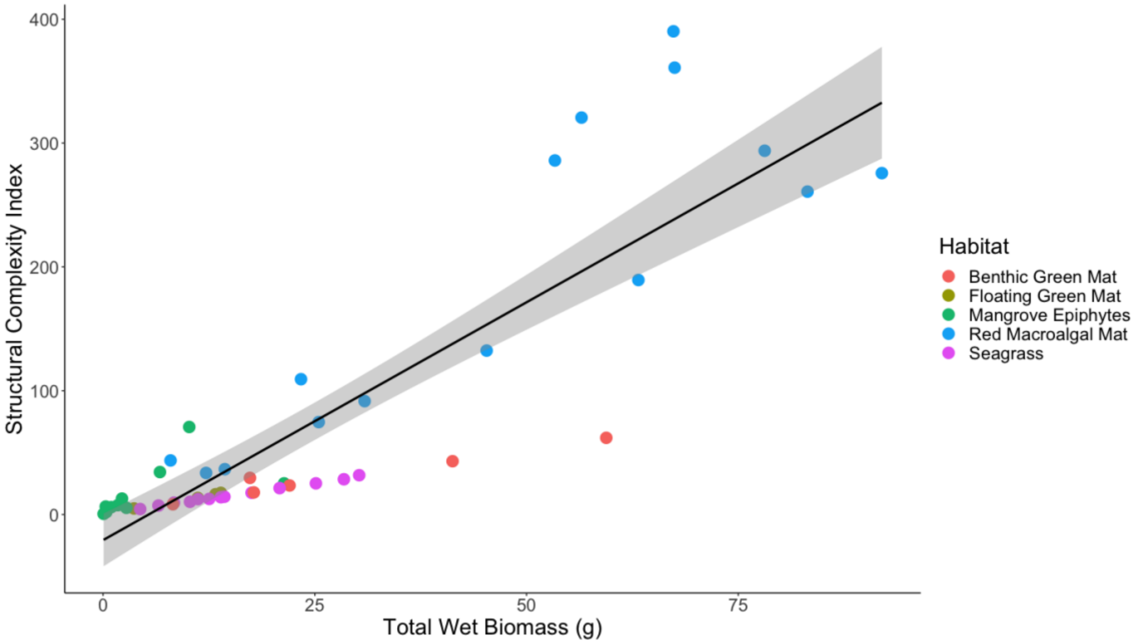

Figure S3.2: Linear Relationship between total wet biomass and the structural complexity index. Best fit line represent regression from all habitat samples.

CHAPTER IV

CHARACTERIZATION AND POTENTIAL RESOURCE USE OF SARGASSO-DOMINANT SEA WRACK BY TERRESTRIAL INVERTEBRATE FAUNA DURING SARGASSO INFLUXES IN SOUTH FLORIDA

ABSTRACT

Marine-derived macrophytes primarily compose beach-cast sea wrack that can be used by terrestrial invertebrate fauna in sandy beach system. Since 2011, the inundations of pelagic sargasso would accumulate and decompose at local, nearshore systems across the Tropical Atlantic. While ecological effects of pelagic sargasso influxes were considerably studied on tropical Atlantic nearshore coastal systems, not much has been known about their effects on the intertidal interface or terrestrial faunal communities. This study aims to investigate terrestrial invertebrate communities associated with landed sargasso and the sargasso's potential as habitat or food for these invertebrates. Surveys, sample collection of flora and fauna, and trials of a temperature experiment were conducted at Crandon Park and MJ State Park along Southeast Florida during the 2020 and 2021 sargasso seasons. Invertebrate communities were primarily composed of talitrid amphipods, coleopterans, and dipterans. The quantity of sargasso, dependent on year of sampling session, seemed to have a more discernable effect on invertebrate composition than location. HOBO logger microhabitat experiment trials showed treatments with sargasso-dominant wrack having lower temperatures than treatments with exposed or buried sand. Many invertebrate consumers showed $\delta^{13}C$ and $\delta^{15}N$ signatures closer to marine macrophytes than terrestrial plants. However, mixing models reveal amphipods and oligochaete worms having a trophic link with pelagic sargasso, while insect fauna had their resource use sourced from other marine macrophytes. However, any consumption would likely be attributed to generalist resource use rather than a specific preference to sargasso. The potential uses depend on the amount of biomass accumulated on the beach surface and the habitat requirements of specific invertebrate species.

INTRODUCTION

Sea wrack is a composition of beach-cast macrophytes from subtidal systems, such as macroalgae and seagrass, that land on intertidal beach areas and decompose. Sea wrack is used as habitat or food for coastal invertebrates in otherwise unvegetated, intertidal beach systems (Colombini and Chelazzi, 2003). Invertebrate fauna that consume sea wrack or its derived detritus subsidize carbon for predators, establishing an essential link to the beach system's trophic food web as prey or detritivores (Catenazzi and Donnelly, 2007a; Colombini et al., 2011; Griffiths et al., 1983; Schlacher et al., 2017). Sea wrack can also be suitable habitat by forming microhabitat conditions that would differ from the sandy beach system (Ince et al., 2007; Jaramillo et al., 2006). These conditions, characterized by cooler temperatures and higher moisture content, are conducive for invertebrates as refuge from excessive heat and desiccation (Colombini et al., 2009; Ruiz-Delgado et al., 2015). Resource use of wrack by invertebrate fauna depends on the species identity of the macrophytes and the amount of biomass each species contributed towards the wrack composition (Poore and Gallagher, 2013; Rodil et al., 2015).

Beach trophic systems heavily rely on macrophytes that senesce from the adjacent shallow subtidal system and are transported by surface currents onto shore. Examples of these macrophytes deposited and their sources include seagrass leaves or rhizomes from subtidal meadows (Colombini and Chelazzi, 2003; Heck et al., 2008; Ruiz-Delgado et al., 2015), or brown or red algae such as kelp from macroalgal beds (Griffiths et al., 1983; Marsden, 1991). The macrophyte composition deposited can be affected by extrinsic factors such as wave exposure, tidal patterns, beach substrate, and elevation, and intrinsic factors such as the morphologies of macrophytes deposited (Gómez et al., 2013). Factors related to the physical environment of the intertidal systems are also highly susceptible to spatiotemporal variation (Barreiro et al., 2011; Orr et al., 2005; Rutten et al., 2021). Given the variation in wrack availability, its use as a resource for coastal invertebrate fauna also varies. Overall however, many coastal invertebrates would find and use wrack as habitat over bare, exposed sand (Colombini et al., 2009; MacMillan and Quijón, 2012; Ruiz-Delgado et al., 2015).

The excessive influxes of pelagic *Sargassum* spp. (composed of *S. natans* I Parr, *S. natans* VIII Parr, and *Sargassum fluitans* III Parr) has affected tropical Atlantic shores since 2011 (Wang et al., 2019). The impact of these influxes were common in the Caribbean such that the three morphotypes were collectively referred to as 'pelagic sargasso' or 'sargasso' and would be referred to as such for the rest of this study (García-Sánchez et al., 2020; Iporac et al., 2022; Rodríguez-Martínez et al., 2021; Uribe-Martínez et al., 2022). These influxes accumulate and decompose on the coastal waters, creating a "sargasso-brown-tide" (van Tussenbroek et al., 2017) that causes mass mortality of coastal subtidal communities (Rodríguez-Martínez et al., 2019). Physical factors that affect the magnitude of sargasso landings across the Caribbean include offshore nutrient availability, seasonality, ocean current activity, and wind patterns in the Caribbean region (Brooks et al., 2018; Franks et al., 2016; García-Sánchez et al., 2020). While studies examining the effects of pelagic sargasso on subtidal communities are developing, we know little about how sargasso could change the intertidal community. Previous studies in other parts of the world showed that beach-cast benthic *Sargassum* spp. can be a source of habitat and detritus for supralittoral invertebrates (Lastra et al., 2015; Olabarria et al., 2010; Rodil et al., 2008; Rossi et al., 2010). While landings of pelagic sargasso onto beaches is not a new phenomenon, it is unclear if the large amounts of biomass associated with influxes also provide a similar source of food and habitat for terrestrial invertebrate fauna. The copious amounts of sargasso also did not originate from an adjacent, nearshore system, but rather from an offshore source, primarily the Great Atlantic Sargassum Belt (GASB) (Wang et al., 2019), and has a seasonal pattern that occurs yearly from spring to summer months (Iporac et al., 2022).

Although well-studied in context of other types of macrophytes composing wrack, the role of sargasso sea wrack as a resource for terrestrial invertebrate fauna is poorly understood. In other parts of the world, sargassum wrack was shown to be a source of food and habitat for coastal invertebrates (Olabarria et al., 2010; Poore and Gallagher, 2013; Rodil et al., 2008; Rossi et al., 2010). While there was observed foraging of migratory shorebirds on sargasso wrack in Florida beaches (Schultz Schiro et al., 2017), it is unclear whether sargasso wrack, especially during sargasso influx seasons, could be used as a habitat or food source for coastal invertebrate fauna. This study aims to characterize the composition of macrophytes composing intertidal beach-cast sea wrack and associated terrestrial invertebrates in Southeast Florida beaches, and the potential of landed pelagic sargasso as a source of food or microhabitat conditions. This was conducted by: a) field sampling before and during sargasso seasons for two years, b) a microhabitat field experiment assessing temperature differences between habitat types, and c) stable isotope collections. The following hypotheses were tested: 1. The accumulated biomass of sargasso would be associated with higher richness, abundance, and diversity of fauna, which would be consistent regardless of location or year of sargasso, 2. Temperature would be lower in wrack habitat due to shading and moisture evaporation from decomposing wrack than surrounding beach temperature without wrack, and 3. There would be possible resource use link between landed pelagic sargasso and terrestrial invertebrate fauna present.

METHODS

Study sites: North Crandon Park (called "Crandon Park" hereafter, 25° 43' 12.3132" N, 80° 8' 48.3144" W) and Dr. Von D. Mizell-Eula Johnson State Park (called "MJ State Park" hereafter, 26° 5' 16.5264" N, 80° 6' 33.264" W) were selected locations for this study as two sandy beaches separate by longitudinal distance (Fig. 4.1). Both sites were adjacent to the offshore Gulf Stream and often received sargasso during the summer months (Iporac et al., 2022). Crandon Park's slow current velocity directed toward shore and shallow benthic depth reduces water flux, enabling the site's susceptibility to accumulation of dislodged macrophytes that would facilitate microbial decomposition (Fiorentino and Reniers, 2014). MJ State Park's nearshore water currents were also susceptible to wind and tidal activity, although tidal currents flow towards an alongshore direction parallel to the shoreline (Carsey et al., 2015). Crandon Park's wrack in the absence of an influx would usually be dominated by seagrasses such as *Thalassia testudinum* and *Syringodium filiforme*. MJ State Park's wrack without pelagic sargasso would be dominated by brown macroalgae, such as *Padina* sp. and *Dictyosphaeria* sp., given the area's proximity to reef systems (Carter and Prekel, 2008; Moyer et al., 2003).

Field Sampling: Sampling was conducted before the influx of sargasso (February 2020 in Crandon and March 2020 in MJ State Park) and during the influx of sargasso (July 2020 in MJ State Park, and late April to early May 2021 in both locations).

In each location, three replicate sites were laid out 500 m apart from each other. The transect site locations were marked using a GPS device and distance between sites was measured using a distance-measuring GPS app. Within each site, three 1.0 m^2 quadrats were randomly placed directly along the sea wrack line (Fig. 4.2). Wrack percent coverage estimation to the nearest 5% was determined visually between three major categories, including ‘seagrass’, ‘sargasso’, and ‘bare sand’ that represented coverage without macrophytes (Bråkenhielm and Qinghong, 1995). These categories were determined by prior observations from both sites.

Within each quadrat, one zip-lock bag (14.0 x 18.0 x 1.0 cm^3) was used to collect one subsample of sea wrack within each quadrat, which was then returned to the lab for further analysis. Zip-lock bag subsample collection involved enclosing the bag over the sea wrack to prevent escape of any invertebrate faunae. In quadrats with heterogeneous wrack coverage, the area with the most wrack was used as a spot to collect a subsample of wrack to find invertebrate fauna. In quadrats with homogenous wrack coverage (close to 100%), especially during the sargasso season, wrack was collected at a randomly selected point within the quadrat.

Wrack macrophytes were cleaned of sand and separated from faunae by running sink water and a 0.5 mm sieve. Macrophytes were identified and placed in a 65^{o}C dry oven to gain dry biomass values. Invertebrate faunae were identified between class to family level and counted for abundance before being stored into 120 ml scintillation vials with 70% ethanol solution. Insects were photographed under a stereoscope, with the following images submitted to BugGuide.net for identification (https://bugguide.net/)(Bartlett, 2003).

Two habitat wrack samples collected during the summer contained amphipod abundance that exceeded 1000 individuals per zip-lock bag (Fig. S4.1). To estimate the total number of individuals during those situations, the collected amphipods were evenly distributed in a 20.0 x 20.0 x 5.0 cm^3 square dish with 70% ethanol solution and divided into four sections. Of those four sections two were randomly selected and counted of all amphipods before multiplying that number by two for a final calculated estimate.

Temperature microhabitat experiment: During the summer of 2021, four trials of a microhabitat experiment (two per location) were conducted. Onset HOBO® pendant temperature data loggers (UA-001-64, Onset Computer Corporation, Bourne, U.S.A., temperature accuracy: ± 0.53°C, temperature resolution: 0.14°C at 25°C) were used to continuously record temperature every five minutes. Each HOBO logger was randomly assigned one of three treatments, though the number of HOBO loggers used per treatment was at least two:

1. The treatment assigned “exposed sand’ involved a HOBO logger placed on top of the sandy beach surface exposed to the sun and other elements.
2. The treatment assigned ‘buried sand’ involved burying a HOBO logger below the sandy surface. The depth of the HOBO logger buried was approximately 18.0 cm, the length of a trowel used to dig the hole for this treatment.
3. The treatment ‘ambient wrack’ involved placing the HOBO logger on the surface of the sandy beach but was then covered with available sea wrack. Most sea wrack available was dominated by pelagic sargasso. The amount of wrack placed on top of the HOBO logger was not measured.

The first set of trials was conducted between late April – early May with only the ambient wrack (n = 2 per trial) and exposed sand (n =3) treatments, while the second round of trials was conducted in July with all three treatments (n = 2 ambient wrack, n = 2 buried sand, n = 3 exposed sand). Each trial was conducted on a single plot measured approximately 2.5 x 1.0 m^2, with sufficient space approximately 0.50 m between treatments. Each trial started at 10:00 am and finished at 2:00 pm. To prevent loss of HOBO logger equipment from tidal patterns, sand burial, or other intrusions, string was tied from each HOBO logger to an adjacent PVC pipe staked onto the ground. Calibration of HOBO loggers, including of timing at the start and end of each trial, and data retrieval were conducted by a HOBO pendant logger USB port and associated HOBOware software.

Stable isotope sample collection and analyses: During each of the HOBO trial days, samples of macrophytes and invertebrate fauna for stable isotope analyses were collected opportunistically yet simultaneously using multiple methods. The opportunistic approach to collecting samples of consumers and basal resources were necessary to account for variation in presence and dominance of macrophytes and fauna found in the field (Catenazzi and Donnelly, 2007a). Macrophytes were collected as they were available on the day of sampling, including fresh tissues of terrestrial plants and washed-up seagrasses and macroalgae on the fresh wrack line. Invertebrate faunae were collected using butterfly nets to collect flying insect fauna, pitfall funnel traps to collect crawling fauna on the surface of the sand under the wrack, and by hand and trowel to collect burrowing fauna under the sand. Butterfly net collection involved running parallel to the wrack line with the net directly above the wrack. Pitfall trap set up involved digging a hole directly underneath the wrack line where a jar with a funnel was placed and replacing the wrack on top of the trap. The pitfall traps were left for four hours minimum, during which crawling invertebrate fauna would fall through the funnel into the trap.

Samples of macrophytes and fauna were cleaned of debris, including epibionts attached to macrophytes, dried in a 65ºC dry oven, and grinded for homogenization using a Fritsch Analysette 3 Spartan Vibratory Sieve Shaker. Samples of macrophytes were readily available to form replicates given the copious availability of biomass in the field. All faunal individuals were pooled together per lowest identifiable taxonomic level to achieve a sufficient biomass yield. Replicates of each taxon were stored using 60.0 mL scintillation vial for later stable isotope analyses. Subsamples for C and N stable isotope analyses were sent to the Stable Isotope Lab at Florida International University. Samples were analyzed through a Thermo Delta C EA-IRMS (http://sil.fiu.edu/). Carbon and nitrogen isotope values are expressed in standard δ notation (Fry, 2007) with PeeDee Belemnite (PDB) and atmospheric nitrogen used as the reference standards for C and N, respectively (Coplen, 1995; Gröning, 2004).

Data analyses: From our initial processing of wrack habitat samples with associated invertebrate fauna, wrack biomass collected varied per quadrat, location, and site. Additionally, not all wrack habitat samples contained any invertebrates. The sample sizes used for multivariate analyses of wrack macrophyte and invertebrate fauna composition would therefore vary, with invertebrate-based analyses utilizing a smaller number of samples. A logistical regression model was conducted to determine the probability of invertebrate presence based on collected total dry biomass of wrack per habitat sample. For this analysis, all wrack habitat samples were used, regardless of invertebrate presence or absence.

Invertebrate composition among wrack was visualized with non-metric multidimensional scaling (nMDS) (k =2) using Bray-Curtis dissimilarity matrices (Bray and Curtis, 1957). No wrack samples collected from February 2020 at Crandon Park or MJ State Park in March 2020 were used for nMDS analyses given insufficient samples with invertebrates. Two nMDS models were visualized to evaluate invertebrate composition: One matrix was standardized to compare invertebrate composition between Crandon Park and MJ State Park during the 2021 sargasso season to visualize dissimilarities between locations. Another matrix was standardized to compare invertebrate composition only at MJ State Park between July 2020 and May 2021 to visualize dissimilarities during sargasso seasons between years. These two nMDS models were replicated twice; one model used presence-absence values to emphasize rare species, while another model used density values (abundance standardized per g dry wrack biomass collected per sample) to emphasize dominant species.

Factors affecting invertebrate composition were further assessed with a permutational multivariate analysis of variance (PERMANOVA). A PERMANOVA test that involve comparing community composition between locations during the 2021 sargasso season used location (Crandon Park and MJ State Park) as fixed factors. A PERMANOVA test that involved comparing MJ State Park community composition between the 2020 and 2021 sargasso season used year (2020 and 2021) as a fixed factor and replicate sites (three per location) as random factors. Similarity Percentages Procedure (SIMPER) analyses were conducted to assess dissimilarities in invertebrate composition only between comparisons that were significant based on the PERMANOVA test.

Generalized Linear Models (GLM) with gaussian error distributions were used to determine variables that best explain variation in temperature from the experiment. For the generalized linear model, treatment (three levels), hour (four levels), location (two levels), and trial (four levels) were treated as fixed factors.

Stable isotope values were averaged and grouped per location and major floral or faunal type, depending on taxon. Flora types included seagrasses, terrestrial plants represented as dune vegetation, pelagic sargasso algae, and other macroalgae (including *Colpomenia* and benthic *Sargassum* spp.). Faunal types include amphipods, coleopterans, dipterans, isopods, and oligochaete worms. Basal resource use was estimated using Bayesian mixing models using the MixSIAR package (Stock et al., 2018), with three chains of length 100,000, 50,000 burn-in, and 50 thin and multiplicative error (residual error x process error). Trophic enrichment of each element was 3.4 ± 1.0‰ and 0.4 ± 1.3‰ for N and C, respectively (Post, 2002). Corrections were made for the elemental difference between basal sources by average % C and % N (Phillips and Koch, 2002).

All analyses of data and visualization of non-metric multidimensional scaling (nMDS) were conducted using R and RStudio (R Core Team, 2020) with the vegan package for nMDS calculations (Oksanan et al., 2019) and ggplot2 for visualization (Wickham, 2016).

RESULTS

Field sampling: Crandon Park during February 2020 and MJ State Park during March 2020 showed wrack composition in the absence of a sargasso influx. Crandon

Park’s wrack coverage averaged to 53.11 ± 24.82% (SD), dominated by seagrasses, while wrack coverage at MJ State Park averaged to 4.67 ± 5.92% with sargasso-dominated wrack. Sargasso season 2020 sampling was conducted at MJ State Park only due to logistical constraints. During July 2020, MJ State Park wrack coverage averaged to 94.56 ± 5.92% dominated by sargasso, showing a 20-fold increase in pelagic sargasso wrack deposition. The 2021 sargasso season demonstrated sizeable sargasso representation at both locations but at different proportions (Fig. 4.3). MJ State Park showed 81.33% coverage of wrack dominated by pelagic sargasso, compared to 83.34% of wrack coverage in Crandon Park dominated by a homogeneous mix of pelagic sargasso and seagrass (Fig. S4.2). Since the sargasso-seagrass wrack seemed homogeneous at Crandon Park’s sites, coverage per quadrat would be marked as a 50:50 mix of sargasso and seagrass, leading to final percent coverage estimates at 37.67% sargasso and 45.67% coverage of seagrass, respectively.

A total of 44 wrack habitat samples were collected and processed throughout the study period. More wrack biomass was collected on sampling dates during sargasso inundation seasons than seasons without sargasso inundations. Off-season wrack habitat collections ranged from 5.0 – 20.0 g in total dry biomass collected, compared to 30.0 – 45.0 g of biomass collected during the sargasso season in both years.

Of the 44 wrack samples collected throughout the study period, 28 of those had at least one individual invertebrate. Logistical regression analysis revealed higher biomass availability increasing the probability of invertebrate faunal presence ($p < 0.01$). From 20.0 g to 40.0 g of dry biomass collected, the probability of finding invertebrate fauna increased from approximately 45.0% to 75.0% (Fig. 4.4).

A total of 7,427 invertebrates were collected throughout the study period, divided to nine groups based on taxonomic resolution and life stage. Groups of invertebrate taxa that were represented included amphipods of the family Talitridae, coelopterans of families Staphylinidae and Tenebrionidae, dipterans, and springtails from the phylum Collembola. The amphipods collected were all dominated by one species, *Insularorchestia monodi* (Mateus, Mateus & Afonso, 1986).

Among invertebrate community dissimilarities during the 2021 season, location seemed to have marginal influence on variation in invertebrate composition, regardless of density ($p = .048$ or presence-absence of invertebrates ($p = 0.051$). When comparing invertebrate communities, the polygons displaying dissimilarities clearly overlap regardless of emphasis of rare taxa (Fig. 4.5A, stress = 0.07, $k = 2$) or dominant taxa (Fig. 4.5B, stress = 0.10, $k = 2$). Abundance-based SIMPER analyses showed major dissimilarities in amphipod abundance; samples collected at MJ State Park averaged four amphipod individuals collected than Crandon Park samples with 950 amphipods (Table 4.1A). However, when examining dissimilarities in presence-absence of fauna, those dissimilarities were contributed by dipterans, beetles, and arachnids (Table 4.1B). Among MJ State Park invertebrate composition between the 2020 and 2021 sargasso seasons, year explained 43% the variation of associated invertebrate communities ($p < 0.05$). The invertebrate communities showed a clear distinction between sargasso season years (Fig. 4.5C, stress = 0.08, $k = 2$, and Fig. 4.5D, stress = 0.07, $k = 2$). SIMPER analyses showed amphipods and dipteran larvae contributing to dissimilarities in abundance (Table 4.1C), while dipterans and beetles (staphylinid and tenebrionid) of both life stages contribute to dissimilarities in frequency (Table 4.1D).

Microhabitat experiment: Temperature was statistically discernable among treatments when compiled across all four trials ($p < 0.0001$). The highest recorded temperature was during the exposed sand treatment, which can reach up to an average of 47.7 ± 1.0 °C (SE) once the experiment reaches 1 pm in the afternoon. This is 14 °C higher than HOBO loggers buried under sand (33.7 ± 1.9 °C), followed by the wrack-based treatment. Ambient wrack-based temperatures averaged around 29.0 ± 1.5 °C when the experiment reaches 1:00 PM. Exposed sand treatments also demonstrated the highest amount of variability, followed by buried sand treatments exhibiting an intermediate amount of variation, and ambient wrack treatments showing the lowest variation in temperature changes (Fig. 4.6). Each individual trial demonstrated differences in temperature between month and day of trial ($p > 0.001$) and location ($p > 0.001$).

Stable Isotope Analyses: There was a clear separation of average $\delta^{13}C$ values between terrestrial plants and marine-derived macrophytes regardless of location studied. Among marine-derived macrophytes, the $\delta^{15}N$ values of pelagic sargasso was 5.0‰ lower in $\delta^{15}N$ than other marine macrophytes, rendering sargasso a separate basal source. All invertebrate fauna collected for this study had $\delta^{13}C$ values more similar to marine-derived macrophytes than to terrestrial plants (Table 4.2).

In both sites, resource use seems to be attributed more to marine subsidies than terrestrial sources, though the resource use of invertebrates varies by contribution of these marine sources (Fig. 4.7). In Crandon Park, 62.0 ± 0.12% of amphipod resource use were contributed to pelagic sargasso, which was twice as much as seagrasses (31.0 ± 0.09%). In MJ State Park however, amphipod resource use was slightly higher in other landed macroalgae represented by benthic *Sargassum* and *Colpomenia* (51.0 ± 0.12%) than pelagic sargasso (41.7 ± 0.13%) but were roughly equal otherwise. A similar generalized distribution of resource use was shown in oligochaete worms between pelagic sargasso and seagrasses at Crandon Park. However, the trend in marine subsidies was reversed for coleopterans at both sites, as well as dipterans and isopods at MJ State Park. These invertebrates resource ranged from 65-70% sourced from other marine subsidies than pelagic sargasso, depending on location (Table 4.3).

DISCUSSION

The large percentage cover of pelagic sargasso during the summer months was consistent with other sargasso monitoring efforts in Florida and the Caribbean since 2011 (García-Sánchez et al., 2020; Iporac et al., 2022). While pelagic sargasso has traditionally been a component of local wrack composition even before 2011, wrack components of local beaches would usually depend on the species composition of adjacent nearshore systems, wave current patterns, and geomorphological characteristics of the beach (Orr et al., 2005). This was the case for Crandon Park, where the wrack composition primarily was composed of senesced seagrasses when sargasso inputs were not considered. Sargasso is a case of an offshore macrophyte composing sea wrack at many local beaches, and whose abundance is dependent on local and regional factors transporting the algae (Andrade-Canto et al., 2022; Brooks et al., 2018; Rutten et al., 2021; Skliris et al., 2022).

The increased probability of finding invertebrates with more biomass collected was consistent with the simple species-area relationship that would arise as a sampling artifact (Attrill et al., 2000). The sufficient biomass collected from the field makes it likely that the associated invertebrates and their relative abundances would be representative of what was found in nature. Furthermore, medium- and large-sized patches of sea wrack were shown to be associated with higher richness and abundance of fauna (Olabarria et al., 2007). Based on our analyses of wrack coverage, the low wrack coverage prior to an influx event would lead to high patchiness of wrack that would prevent its usage by invertebrate fauna.

However, other studies have showed that large amounts of beach-cast macrophytes could lead to compaction and anoxic conditions that would prevent establishment of an invertebrate community (Hyndes et al., 2022; McGwynne et al., 1988). Accumulated biomass and subsequent decomposition of sargasso was shown to release hydrogen sulfide as a byproduct, causing respiratory problems among beachgoers (Resiere et al., 2020). Additionally, the presence of a sargasso brown tide was also associated with faunal mortality from offshore systems (Rodríguez-Martínez et al., 2019). Given the anoxic effects of sargasso accumulation and decomposition, it was unclear if similar conditions would be considered present at a small, intertidal level and would similarly affect terrestrial invertebrate fauna. There could be an intermediate threshold of available biomass that allows invertebrates to occupy wrack; too little wrack would not be enough for habitat conditions to occur, and too much wrack could lead to compaction, anoxic conditions, and release of leachates and metals that would not be conducive for wrack resource use (Eereveld et al., 2013; McGwynne et al., 1988; Olguin-Maciel et al., 2022).

An interesting observation was the magnitude in differences of abundance among talitrid amphipods. Samples with high abundances of one talitrid amphipod species (*I. monodi*) were found in Crandon Park during the 2021 sargasso season than other sampling-dates or at MJ State Park. Talitrid amphipods generally would be very abundant among fresh wrack within the intertidal zone (Jaramillo et al., 2006; Ruiz-Delgado et al., 2015; Stenton-Dozey and Griffiths, 1983). The provision of resources wrack could allow high reproductive potential for amphipods to occur. Previous cohort studies of amphipods collected on beaches noted higher female abundances than males (Pavesi and De Matthaeis, 2009; Prato et al., 2009; Salman et al., 2018), which could increase the reproductive potential of associated amphipod populations with high amounts of wrack. While we did not examine life history stages of amphipods in this study, variation in body sizes were found, as well as eggs and juveniles observed among gravid females, suggesting high reproductive potential when provided wrack as a resource. The high abundance of amphipods among sea wrack habitat could facilitate the detritivory of sargasso wrack, which can provide foraging opportunities for shorebirds (Schultz Schiro et al., 2017)

Temperature under sargasso-dominant wrack was lower than exposed sand that lack wrack, consistent with other wrack temperature experiments. A similar study conducted in Antigua found sargasso wrack temperature differences vary by seasons, with lowered temperature than exposed sand treatments during the summer, yet increased sand temperatures during the autumn with high rain (Maurer et al., 2022). Invertebrate fauna could occupy wrack to escape desiccation and heat for more stable conditions, though their preferences for temperature vary by species. This was shown in seagrass-dominated wrack in the Mediterranean, where higher amphipod abundance was associated with higher wrack moisture content, while tenebrionid beetles preferred drier wrack with lower moisture (Colombini et al., 2009). The transpiration of sargasso wrack was not quantified in this study. However, the decomposition of wrack could include desiccation of its water contents that could provide a cooling effect. The desiccation of sargasso wrack however seemed dependent on the amount of biomass accumulated. While low amounts of sargasso wrack led to full desiccation of the thalli, high amounts of wrack showed desiccation only at the surface-exposed top layer. Sargasso under the desiccated top layer remained moist, although a multi-day experiment would be needed to quantify changes in transpiration of sargasso wrack dependent on biomass amounts.

Most invertebrate fauna have $\delta^{13}C$ values similar to wrack macrophytes than terrestrial plants. This is consistent with many other studies that compared primary-produced food sources (Catenazzi and Donnelly, 2007a, 2007b). Based on source contribution comparisons, the talitrid amphipods have between 50-65% of their resource use from pelagic sargasso, demonstrating an important trophic link between amphipods and sargasso. These amphipods were observed captive in-lab eating sargasso thalli directly (personal observation), and other species were demonstrated to feed on *Sargassum* spp. in other areas (Crawley and Hyndes, 2007; Poore and Gallagher, 2013; Rossi et al., 2010). The probability of sargasso used as a food source could however be dependent on availability of other basal resources and their potential use as a food source. In Crandon Park, there was less contribution from seagrasses, suggesting that seagrasses were unlikely a food source for these amphipods, consistent with *P. oceanica* wrack use in the Mediterranean (Colombini et al., 2009). However, amphipod source contribution was similar between pelagic sargasso and other phaeophyte species (benthic *Sargassum* and *Colpomenia* spp.) at MJ State Park. This interaction between amphipods and other macroalgae suggests amphipods having a more generalized resource use of marine macroalgal subsidies, rather than attaining a specific preference of pelagic sargasso (Rossi et al., 2010; Wildish and LeCroy, 2014). This result also contrasted with another study showing very limited resource use of a bloom-forming alga by local invertebrates (Sturbois et al., 2022). Our study has provided solid evidence for a direct trophic link between pelagic sargasso and talitrid amphipods, which can be useful for further studies on sargasso-invertebrate faunal trophic interactions.

Other invertebrate fauna, especially those from MJ State Park, seemed to show resource use from other marine subsidies than pelagic sargasso. With dipteran flies, high $\delta^{15}N$ values could be indicative of their microbivorous diet (Hyndes et al., 2022), although there was evidence of flies having similar stable isotope values to algae (Ince et al., 2007). The decomposition of landed pelagic sargasso and other marine macrophytes can provide fertile substrate for microbial communities that microbivores could utilize as a resource (Hyndes et al., 2022; Polis and Hurd, 1996; Tomenchok et al., 2021). Conversely, oligochaetes at Crandon Park showed source contribution from pelagic sargasso comparable to amphipods. Oligochaetes are infaunal detritivores that can be found in sand under wrack (Heerhartz et al., 2016; Sobocinski et al., 2010). The diet of oligochetes more likely consisted of detritus produced by the decomposition of sargasso-dominant wrack. Among all consumer taxa in this study however, most of the energy was sourced from marine subsidies than terrestrial plants.

Sandy beaches are very dynamic systems that involve ephemeral, allochthonous sources of resources. There are many opportunities for further research in trophic and habitat ecology involving interactions between sargasso-dominated wrack and associated invertebrates. The addition of larger fauna such as shorebirds or introduced reptile fauna (for Crandon Park) onto stable isotope analyses could be explored to determine the amount of energy transfer from pelagic sargasso to invertebrate faunal prey for these carnivores. Shorebirds heavily rely on sea wrack as foraging sites for invertebrate prey (Dugan et al., 2003; Schlacher et al., 2017). Examining the depth of sargasso during the peak season and its habitat usage by invertebrate fauna should also be explored (Colombini et al., 2000), as only a small fraction of often large amounts of wrack were collected for invertebrate faunal composition for this study. Regardless, this study demonstrated how landed pelagic sargasso, as a seasonal and dynamic resource especially during sargasso inundation events, was used extensively by terrestrial invertebrate fauna.

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APPENDIX

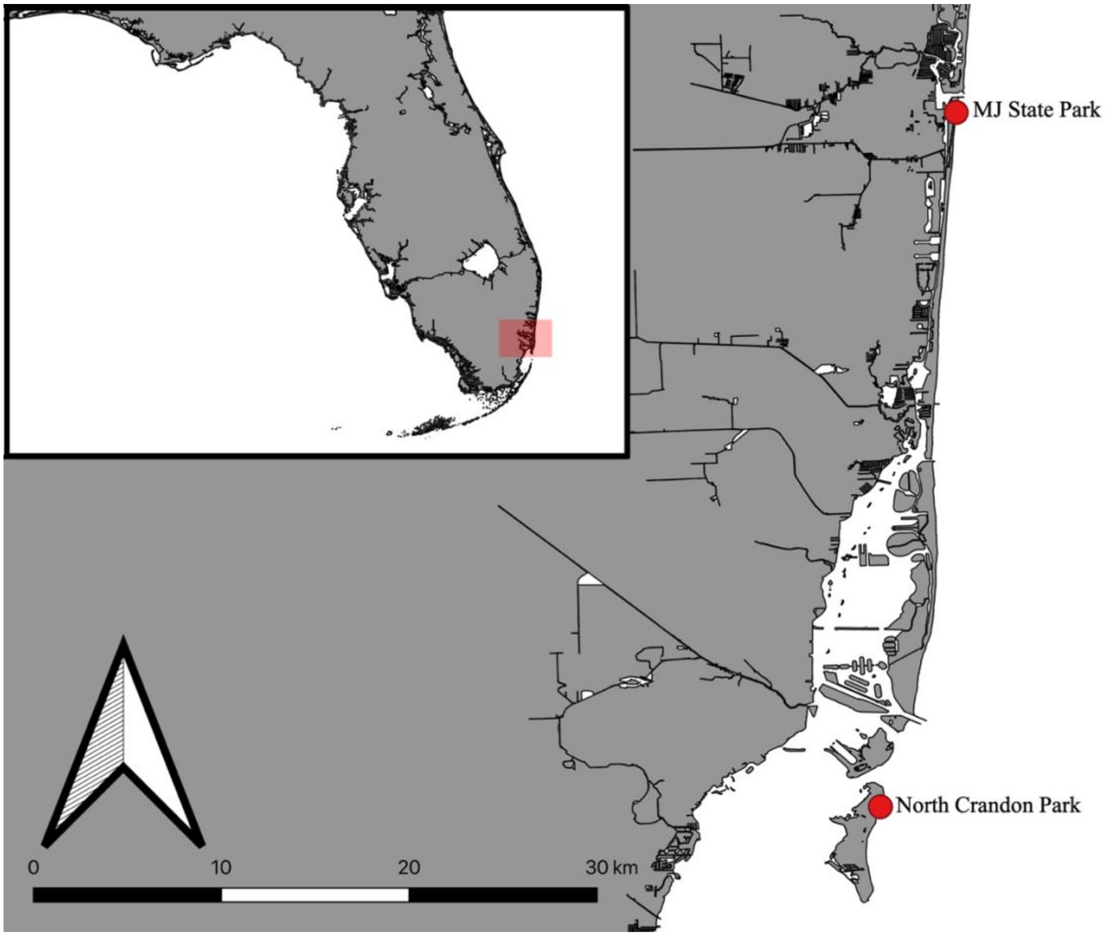

Fig. 4.1. Map of southeastern Florida study sites. Insert with red box shows relative location of study sites within Florida, USA.

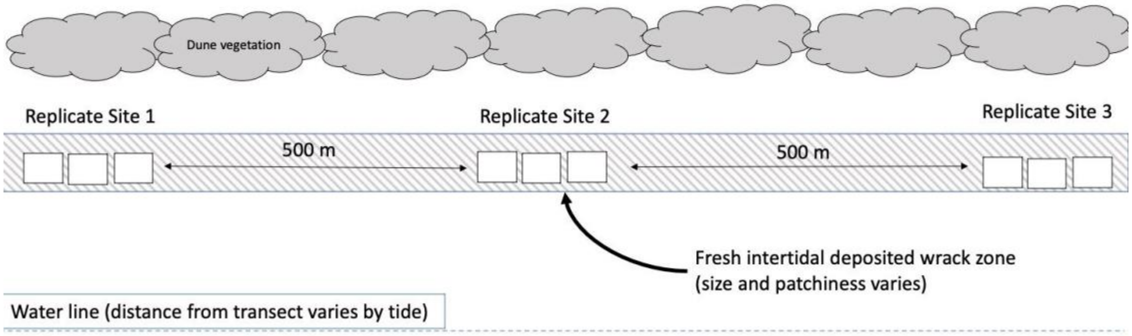

Fig. 4.2. Conceptual illustration of field sampling. Drawings are not to scale. Each replicated site per location was separated 500 m apart from each other. Each replicated site involved percent cover measurements and collection of habitat samples along fresh wrack at the intertidal zone.

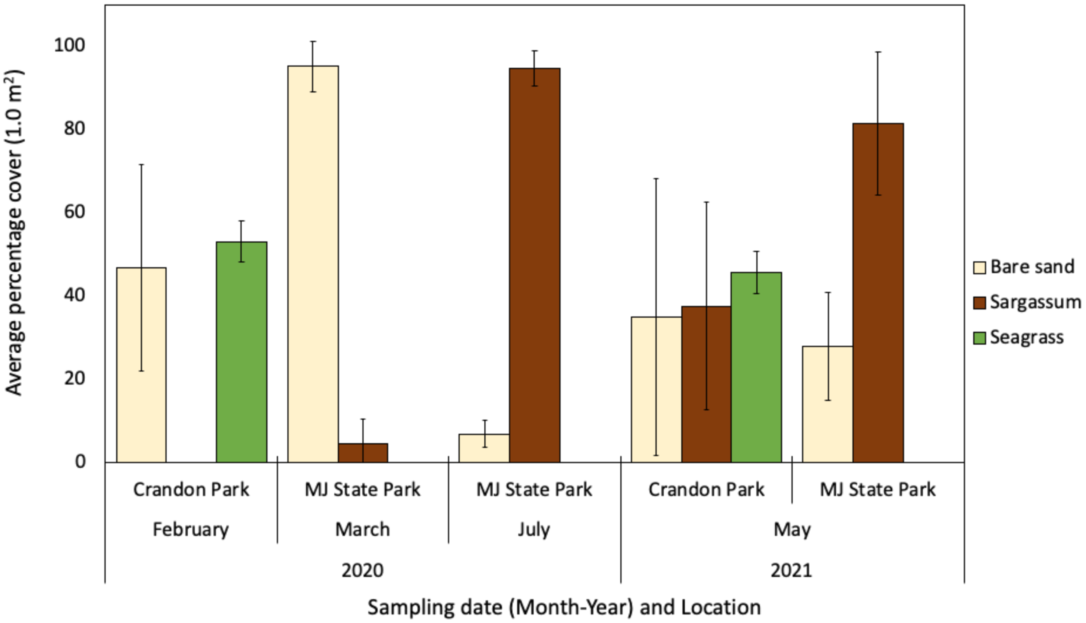

Fig. 4.3. Average percentage cover of macrophytes per series of quadrats in Crandon Park and MJ State Park per sampling dates in 2020 and 2021. Error bars represent standard deviation. Empty bars represent a true zero value.

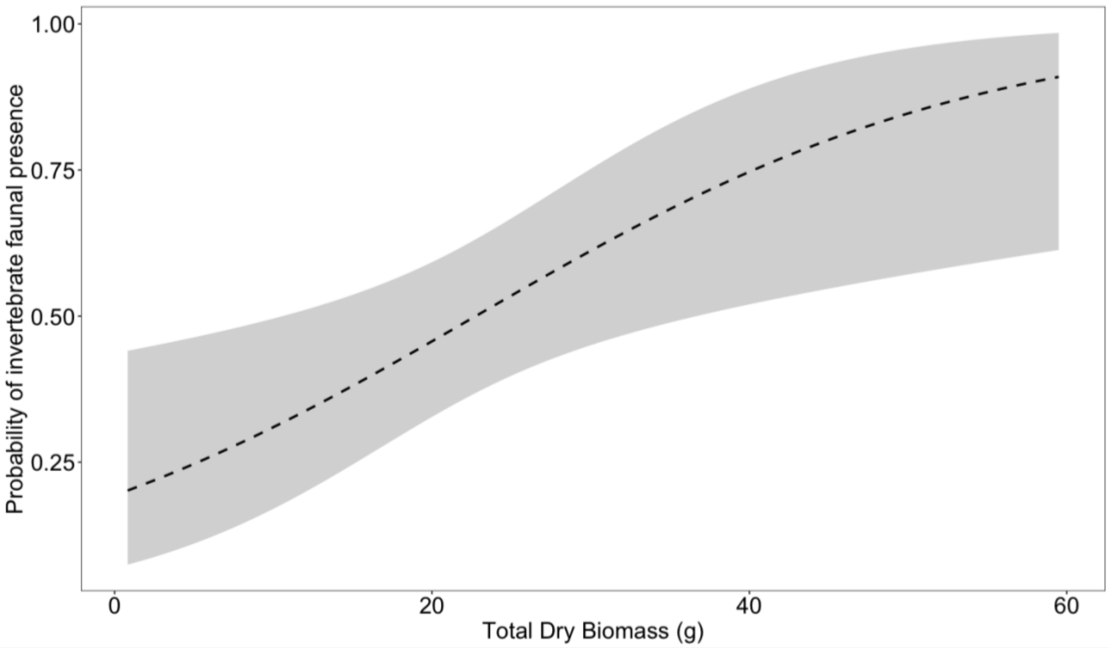

Fig. 4.4. Logistical regression model of probability of finding invertebrate fauna present per total dry biomass amount collected. Grey shading represents the 95% confidence interval.

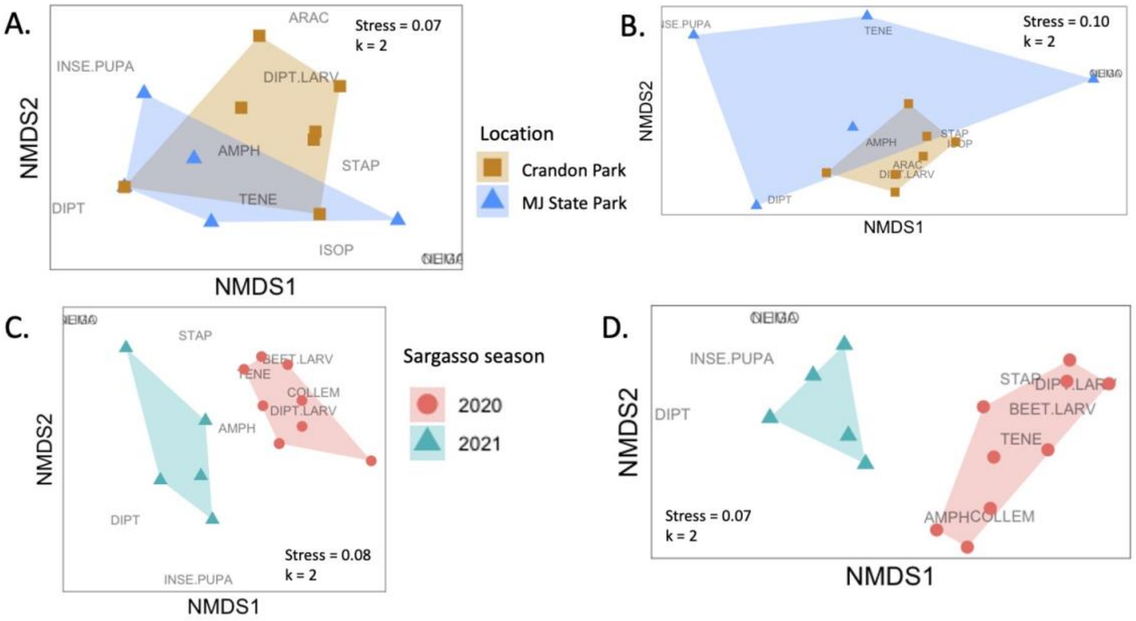

Fig. 4.5. Series of non-metric multidimensional scaling of associated invertebrate faunal communities via abundance or presence data. Visualizations include the following: (A.) invertebrate presence-absence between Crandon and MJ State park during the 2021 sargasso season, (B.) invertebrate densities (per g dry wrack biomass) between Crandon and MJ State Park during the 2021 season, (C.) invertebrate presence-absence between 2020 and 2021 sargasso season at MJ State Park, and (D.) invertebrate densities between the 2020 and 2021 sargasso season at MJ State Park. Invertebrate fauna abbreviated for nMDS visualizations include amphipods (AMPH), insect pupae (INSE.PUPA), Dipterans (DIPT), dipteran larvae (DIPT.LARV), Isopods (ISOP), Arachnids (ARAC), Staphylinid beetles (STAP), tenebrionid beetles (TENE), Beetle larvae (BEET.LARV), collembolan springtails (COLLEM), Oligochaete worms (OLIGO), and Nematodes (NEMA).

	Average Density				
	MJ State Park	North Crandon Park	δi	δi/SD(δi)	cum.δi%
Amphipods	0.08	34.99	0.98	67.37	0.99

	Frequency				
	MJ State Park	North Crandon Park	δi	δi/SD(δi)	cum.δi%
Dipterans (Larvae)	0.00	0.71	0.14	1.42	0.26
Staphylinid Beetles	0.20	0.57	0.10	1.05	0.45
Dipteran (Adult)	0.20	0.14	0.06	0.60	0.57
Tenebrionid Beetles	0.20	0.14	0.06	0.61	0.67
Arachnids	0.00	0.29	0.05	0.61	0.76

	Average Density				
	2021	2020	δi	δi/SD(δi)	cum.δi%
Dipterans (Larvae)	0.00	1.29	0.50	1.41	0.55
Amphipods	0.08	0.48	0.26	0.92	0.84

	Frequency				
	2021	2020	δi	δi/SD(δi)	cum.δi%
Dipterans (Larvae)	0.00	1.00	0.21	2.74	0.34
Tenebrionid Beetles	0.20	0.44	0.08	0.86	0.48
Beetle Larvae	0.00	0.33	0.05	0.67	0.56
Staphylinid Beetles	0.20	0.22	0.05	0.69	0.65
Dipterans (Adults)	0.20	0.00	0.04	0.47	0.72

Table 4.1: Results of SIMPER analyses with invertebrate composition. Dissimilarity comparisons include the following: (A.) invertebrate densities (per g dry wrack biomass) between Crandon and MJ State park during the 2021 sargasso season, (B.) invertebrate frequencies between Crandon and MJ State Park during the 2021 season, (C.) invertebrate densities between 2020 and 2021 sargasso season at MJ State Park, and (D.) invertebrate frequencies between the 2020 and 2021 sargasso season at MJ State Park.

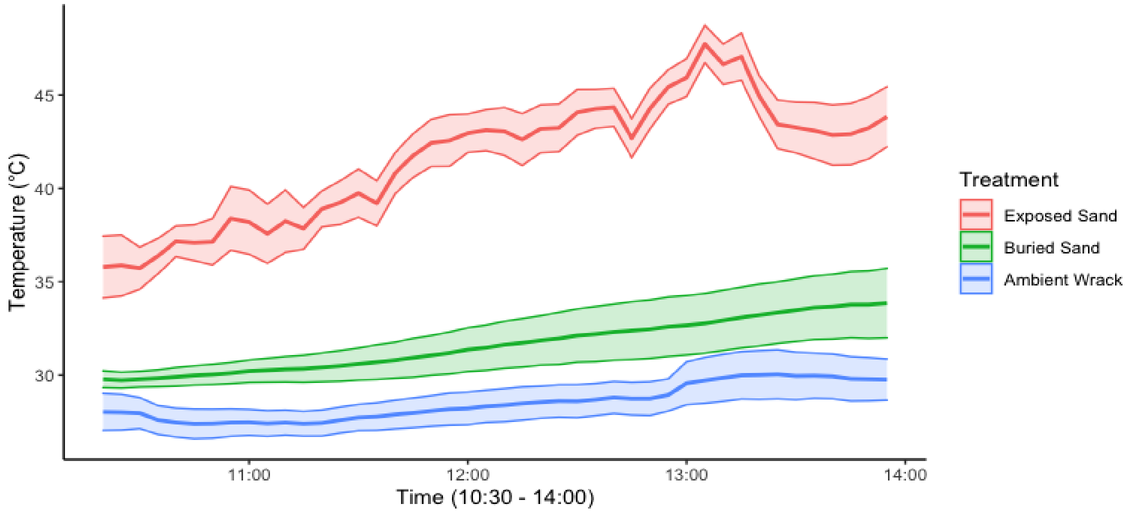

Fig. 4.6. Overall changes in temperature based on treatments of the HOBO logger microhabitat experiment. Data was compiled using all four trials during the sargasso season 2021. Bold line represents average value compiled for all four trials. Error ribbon represents standard error.

	Crandon Park			MJ State Park		
	Number of samples	δ^{15}N Avg ± SD (if applicable)	δ^{13}C Avg ± SD (if applicable)	Number of samples	δ^{15}N Avg ± SD (if applicable)	δ^{13}C Avg ± SD (if applicable)
Fauna						
Annelida						
Oligochaete (pink)	3	5.02 ± 0.32	-14.64 ± 0.25			
Oligochaete (white)	1	4.70	-14.79			
Coleoptera						
Beetle larvae				1	6.65	-15.86
Phaleria testacea (Tenebrionidae)	1	8.31	-13.42	3	5.36 ± 0.06	-14.41 ± 0.18
Cafius spp. (Staphylinidae)	1	6.03	-14.42	1	5.89	-15.11
Ellipsoptera spp.	1	5.19	-19.5			
Diptera						
Ephydridae spp. 1 (black fly)				1	8.94	-22.37
Asyndetus interruptus				1	7.73	-17.43
Dipteran (Stratiomyidae) larvae				1	3.145	-13.93
Limosininae flies				1	5.33	-15.1
Ephydridae spp. 2 (grey fly)				2	5.04 ± 0.27	-19.27 ± 0.61
Empididae spp.				1	8.61	-15.5
Peracarida						
Insularorchestia monodi (Amphipoda)	3	3.05 ± 0.16	-14.74 ± 0.03	3	3.31 ± 0.28	-15.07 ± 0.20
Littorophiloscia culebrae				1	5.86	-13.64
Flora						
Other Phaeophyceae						
Benthic *Sargassum* spp.				2	3.23 ± 0.04	-20.59 ± 0.87
Colpomenia spp.				4	4.01 ± 0.40	-12.85 ± 1.20
Pelagic sargasso						
Sargassum fluitans III	3	-2.37 ± 0.46	-18.87 ± 0.71	5	-2.62 ± 0.46	-18.51 ± 0.26
Sargassum natans I	3	-2.45 ± 0.20	-17.05 ± 0.42	3	-3.46 ± 0.27	-17.01 ± 0.71
Sargassum natans VIII	5	-2.34 ± 0.14	-17.07 ± 0.38	4	-1.71 ± 0.41	-16.78 ± 0.26
Seagrasses						
Halodule wrightii (leaves)	5	5.53 ± 0.23	-13.39 ± 0.18			
Halodule wrightii (rhizome)	5	4.85 ± 0.11	-13.807 ± 0.19			
Syringodium filiforme (leaves)	5	4.89 ± 0.53	-9.678 ± 0.10			
Syringodium filiforme (rhizome)	5	4.32 ± 0.47	-10.26 ± 0.33			
Terrestrial Plants						
Cocoloba uvifera (leaves)	5	-1.07 ± 1.11	-27.84 ± 0.34	6	1.23 ± 0.57	-28.75 ± 0.78
Sesuvium portulacastrum	6	3.59 ± 0.04	-28.26 ± 0.18	3	5.54 ± 0.12	-25.76 ± 0.12

Table 4.2: List of flora and fauna collected for stable isotope analyses, including number of samples per location, and average δ^{13}C and δ^{15}N values (± SE). Values are presented without calculation by trophic enrichment factors. Blank cells imply no samples collected of organism per location.

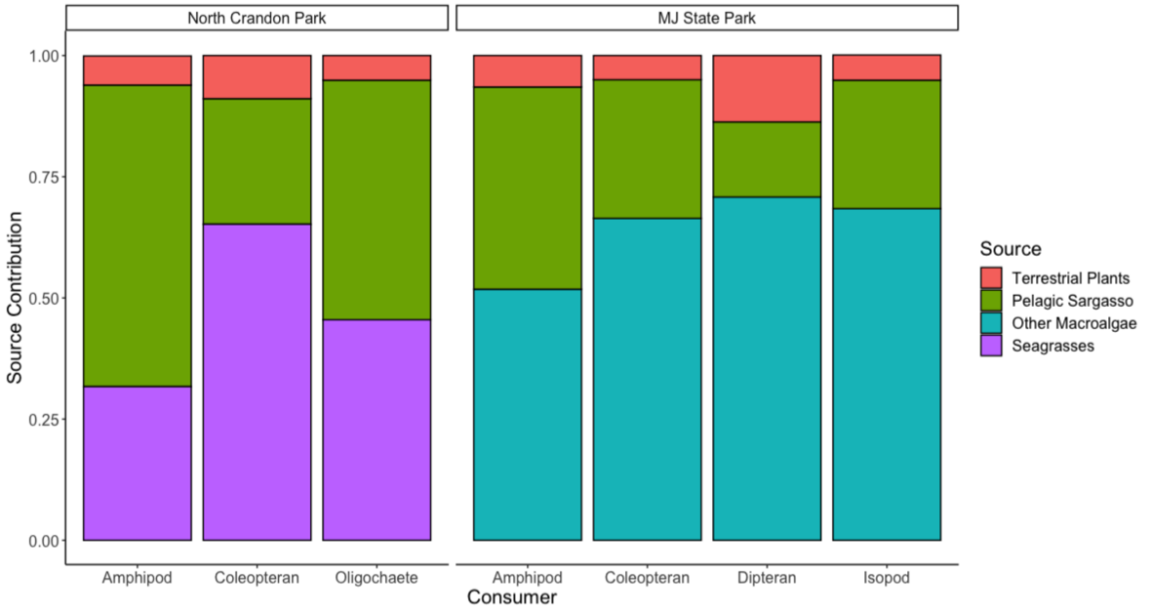

Fig. 4.7. Average source contribution by proportion to consumer resource use between locations during the 2021 sargasso season.

		Wrack Sources			
Site	Consumer	Terrestrial plants	Pelagic Sargasso	Seagrasses	Other Macroalgae
Crandon Park	Amphipod	0.06 ± 0.05	0.622 ± 0.12	0.317 ± 0.099	
	Oligochaete	0.051 ± 0.046	0.494 ± 0.1	0.455 ± 0.085	
	Coleopteran	0.089 ± 0.081	0.259 ± 0.13	0.652 ± 0.122	
MJ State Park	Amphipod	0.065 ± 0.05	0.417 ± 0.13		0.518 ± 0.122
	Coleopteran	0.05 ± 0.048	0.286 ± 0.113		0.664 ± 0.115
	Dipteran	0.137 ± 0.107	0.155 ± 0.088		0.708 ± 0.128
	Isopod	0.052 ± 0.055	0.265 ± 0.166		0.684 ± 0.17

Table 4.3: Summary of average source contributions (± SD) by proportion to consumer resource use between locations during the 2021 sargasso season.

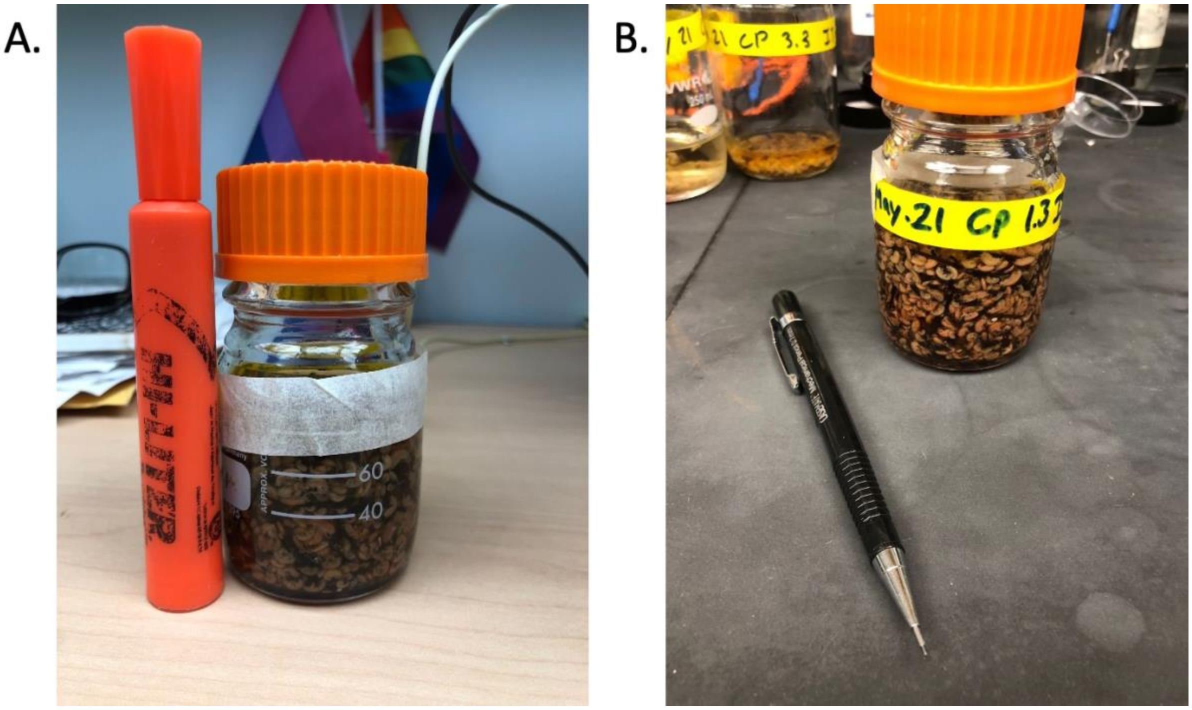

Fig. S4.1. Two samples (A. and B.) of amphipod-dominant faunal communities collected from a sample of sargasso-dominant wrack in Crandon Park on 2021. Samples were enclosed with 100 ml vials with 70% ethanol. Highlighter marker and pencil were used for size comparison.

Fig. S4.2. A well-mixed wrack pile of pelagic sargasso and seagrasses *T. testudinum* and *S. filiforme* at North Crandon Park during the May 2021 sampling season. US size 9.0 sandals placed on pile for size comparisons.

CHAPTER V

COMMUNITY-BASED MONITORING REVEALS SPATIOTEMPORAL VARIATION OF SARGASSO INUNDATION LEVELS AND MORPHOTYPE DOMINANCE ACROSS THE CARIBBEAN AND SOUTH FLORIDA

Abstract

During the past decade, massive inundations of holopelagic *Sargassum* spp. (*S. natans* I, *S. natans* VIII, and *S. fluitans* III), commonly known as sargasso, have drastically affected beaches and coasts throughout the tropical Atlantic, leading to strong forecasting and monitoring efforts. This study aimed to characterize spatiotemporal variation in accumulation levels and morphotype composition of sargasso inundations. Community science initiatives can aid in monitoring sargasso regionally by locally collecting data on morphotype composition and accumulation level. A volunteer network compiled community-contributed photos from the "Sargassum Watch" Epicollect5 digital application. Florida and the Gulf coast showed less susceptibility to high accumulations than other subregions of the tropical Atlantic. *S. fluitans* III was the most frequently encountered morphotype, though the probability of encountering any of the three morphotypes depended on accumulation level. Despite differences in latitude, the 2021 season demonstrated similar 'peak' sargasso months between South Florida and Mexican Caribbean (May–July), though the intensity and duration of high-accumulation months differed. Much of these composition patterns and accumulation levels were likely related to the proximity of both regions to the Great Atlantic Sargassum Belt and dispersal through wind and water currents. Using community-collected data to outline quantitative trends and patterns in sargasso accumulation levels and composition, this study can be useful for future collaborations and syntheses with other forecasting and monitoring programs.

1. Introduction

Regional influxes of holopelagic *Sargassum* spp. (*S. natans* I Parr, *S. natans* VIII Parr, and *S. fluitans* III Parr) during the past decade have led to drastic ecological and economic effects on coastal systems (Wang et al., 2019). To harmonize terms used in this paper relevant to other published research done on *Sargassum* spp., we'll be referring to 'sargasso' as a common term to include only holopelagic *Sargassum* species to avoid confusion with other benthic species of the genus *Sargassum*. Excessive biomass of sargasso decomposes in the water column or on the beach, producing a 'Sargassum-brown tide' that results in anoxic conditions that kill marine fauna and shift benthic communities (Cruz-Rivera et al., 2015; van Tussenbroek et al., 2017; Rodríguez-Martínez et al., 2019). These environmental impacts of sargasso inundations can have long-term effects, and recovery of these coastal systems requires effective and proactive management (van Tussenbroek et al., 2017).

Prior to initial inundation events of 2011, the most prominent source of sargasso was the Sargasso Sea in the North Atlantic region (Parr, 1939; Sissini et al., 2017). This sargasso assemblage was composed of two species, *S. natans* and *S. fluitans*, each with their representative morphotypes (Parr 1939, Wrinn et al., 2016). This area was reputed as a "golden rainforest," harboring endemic biodiversity in a largely pelagic ecosystem and essential to fisheries in the Gulf of Mexico (Butler et al., 1983). However, recent observational studies and oceanographic models suggest that the bloom-forming sargasso most likely originated from the North Equatorial Recirculation Region (NERR), between the eastern coast of Brazil and West Africa, where the Great Atlantic Sargassum Belt (GASB) formed (Franks et al., 2016; Wang et al., 2019). Previous monitoring efforts showed the span of sargasso influxes to be vast, stretching from the western Gulf of Mexico (Tabone, 2011; Webster and Linton, 2013) to West Africa (Smetacek and Zingone, 2013; Oyesiku and Egunyomi, 2014), though the intensity of sargasso was strongest in the lower Caribbean (Franks et al., 2011; García-Sánchez et al., 2020; Trinanes et al., 2021). The factors that led to the development and dispersal of the GASB are multifactorial, and could be caused, among others, by wind patterns, North Atlantic Oscillations in water currents, changes in sea surface temperature (SST), and nutrient availability, though the contribution of these factors towards the bloom is unclear (Lapointe, 1995; Sanchez-Rubio et al., 2017; Broman, 2019; Johns et al., 2020; Andrade-Canto et al., 2022, Skliris et al. 2022). Analyzing the spatiotemporal distribution of sargasso inundations along the Caribbean can provide a baseline for understanding the origins, mechanisms, and fate of sargasso.

This phenomena's ambiguous origin and sizable impacts have led to strong development of forecasting and monitoring efforts. Regional monitoring efforts focused on satellite imagery modeling using various tools such as Moderate Resolution Imaging Spectroradiometer (MODIS) and Sentinel-2 (Wang and Hu, 2016, Maréchal et al., 2017, Putman et al., 2018). Data collected from these tools are often calculated to indices such as the maximum chlorophyll index (MCI), the floating algal index (FAI), and the alternative floating algal index (AFAI) to name a few (Trinanes et al., 2021). Satellite imagery modeling effectively forecasts sargasso movements based on water and wind current dynamics (Brooks et al., 2018; Andrade-Canto et al., 2022). However, these models are often limited by the resolution of these predictions, which is inversely related to the large, regional-scale these models encompass (Arellano-Verdejo and Lazcano-

Hernandez, 2020). Fine-scale satellite imagery resolution for local, nearshore areas are often lacking, and the frequency of model outputs is also slower than the real-time movement of large rafts (Trinanes et al., 2021). Finally, anomalies in wind and water currents, such as from eddies, can render the fine-scale movement of sargasso to be more unpredictable (Andrade-Canto et al., 2022). The large geographic scale and the unpredictability of landings results in high variability that cannot be detected in regular monitoring sites. Multiple and integrative approaches to estimate the inundations of sargasso are needed; shortcomings from satellite imagery methods can be overcome by integrating ground-truthing methods providing many observations. Those observation should also consider the morphological plasticity of sargasso that was outlined and documented before these periodic inundations (Parr, 1939). Many studies report sargasso as either one genus without mentioning species diversity (*Sargassum* spp.) or between the two species, *S. natans* and *S. fluitans*, without further classification of morphotypes (Fidai et al., 2020). Using morphological traits, this taxonomic resolution of sargasso morphotypes proved useful in previous studies examining assemblage composition (Schell et al., 2015; Govindarajan et al., 2019).

Community science initiatives, synonymous with 'participatory science,' 'volunteer monitoring,' 'crowdsourcing', or 'citizen science', can aid in monitoring ecological phenomena at a large spatial scale (Trainer and Hardy, 2015; Gillis et al., 2018). Many initiatives monitor sargasso using community-contributed photos and observations (Franks et al., 2011; Iporac et al., 2019; Arellano-Verdejo and Lazcano-Hernandez, 2020; Valentini and Balouin, 2020). *In situ* photo data is adequate for collecting less than a meter in resolution observations, and can produce large amounts of data over a long period (Forrester et al., 2015; Chandler et al., 2017), suitable for long-term biogeographic analyses. This collection of data can then be forwarded to be deposited onto a larger database for more accessibility, facilitating more collaborations and expanding spatial and temporal scope (“OceanViewer,” 2021; “Sargassum Monitoring,” 2021). In May 2019, during the 39th Association of Marine Laboratories in the Caribbean (AMLC) meeting, a workshop was held that developed the International Sargassum Network Listserv (SargNet) and the “Sargassum Watch" citizen science program, both established at Florida International University, and is ongoing.

The goal of this study is to characterize spatiotemporal accumulation levels and morphotype composition of sargasso inundations within the tropical Atlantic region that includes South Florida, the Caribbean, and the Gulf of Mexico. This is pursued by addressing the following objectives: 1. Detect spatial variability of sargasso across biogeographic zones by comparing sargasso accumulation levels across the Caribbean, 2. Compare morphotype dominance in inundation-associated areas, and 3. Detect seasonal variation of sargasso accumulations from select locations consistently monitored. This study is useful as a baseline to detect the potential origin of influx-causing sargasso and the severity of impacts associated with these inundations.

2. Methods

2.1 Study species and area

Five subregions were drawn out within the tropical Atlantic region based on surface current patterns in the Caribbean area (Roberts, 1997; Robertson and Cramer, 2014). The "Greater Caribbean" (GC) subregion spans from the eastern Caribbean islands to Nicaragua, "Western Caribbean" (WC) spanning from Honduras to the east coast of the Yucatán peninsula of Mexico, the "Gulf of Mexico" (GoM) subregion encompassing the rest of Mexico and US coasts aside from Southern Florida, "Floridian" (FL) subregion based mostly on Florida, and the "Bahamian" (BH) subregion encompassing the Bahamas and Turks and Caicos (figure 5.1).

We have identified five data-sufficient sites that were monitored anywhere from daily to bi-weekly strictly for seasonality analyses based on the cumulative amount of data collected ($n \geq 60$, figure 5.1). Two sites in South Florida were identified, including Dr. Von D. Mizell-Eula Johnson State Park (MJSP, N 26^{o} 3' 37", W 80^{o} 06' 41.126") and Key Colony, Key Biscayne (KCKB, N 25^{o} 41' 48.98", W 80^{o} 09' 21.236"). Two sites in Quintana Roo, Mexico were also identified, including Reef Systems Unit, Institute of Marine Sciences and Limnology, National Autonomous University of Mexico (UNAM, N 20^{o} 52' 07.82", W 86^{o} 52' 5.485") and Playa del Carmen (PdC, N 20^{o} 38' 40.016", W 87^{o} 03' 19.81"). Sufficient data was also available for the general Boddentown area in Grand Cayman, Cayman Islands, and was compiled together as the "Boddentown" site (Bdt, N 19^{o} 16' 50.52", W 81^{o} 14' 59.24"). MJSP and KCKB are separated by latitude and intensity of the shoreline cleanup, with MJSP having minimal cleanup of the beach and KCKB cleaned daily. Similar characteristics distinguish UNAM and PdC, with UNAM being rarely cleaned and PdC cleaned daily with an additional floating barrier utilized during the sargasso peak season.

2.2 Community science photo collection

Community-contributed photos were compiled by a volunteer network using the application (called "app" hereafter) Epicollect5 (Gupta et al., 2021). Epicollect5 is a free and easy-to-use app platform that allows form-based data collection to be distributed among volunteers to collect photo data. Using this app method, we made five publicly-available versions of the "Sargassum Watch" community science program that varied in length of the form and language used (Iporac et al., 2020). Volunteers were identified and recruited using SargNet and personal/professional networks and retained through email or personal communication if data collection had paused from the group or individual.

Volunteers were given protocols and training sessions in-person or online to use the app if the volunteer or group requested. Required information from volunteers included date and time, GPS coordinates, site and region name, three angled photos of the site, evidence of sargasso management (if applicable), and one photo containing all morphotypes present. Evidence of sargasso management can include, but not limited to, large tire tracks, appearance of cleanup machinery such as trucks or tractors, sargasso cleanup crews, and sargasso buried in sand after cleanup. Volunteers then uploaded their observations onto the open-source database for later analyses.

Accounting for this study's biogeographical scope being limited by the availability of volunteers per geographic area, additional data from the iNaturalist database was downloaded to supplement the biogeographical scope of this study. Unlike Epicollect5, which utilizes networks of committed volunteers to consistently monitor selected sites, iNaturalist data collection is more occasional and opportunistic in frequency of encountering sargasso but does so at a much larger geographical scale.

Keywords used to retrieve iNaturalist data included “Sargassum,” “Sargassum natans,” and “Sargassum fluitans,” and were restricted to the Gulf, Florida, and Caribbean areas. Morphotype names could not be used as keywords on the iNaturalist search engine.

2.3 Data processing and analyses

Multiple criteria were used to determine the usability of observations collected for analyses. At minimum, all observations needed to have photos of a site (beach, dock, etc.), regardless of whether there was sargasso present or not. If sargasso was present, the accumulation shown must be comparable to the rest of the site where it was present (beach, dock, cliff, etc., Table S5.1). Observations collected were either classified as “opportunistic” if collected less than once a month on average anywhere within the five subregions, or “monitored” if collected at the same-named site on a more frequent basis (bi-weekly to daily). Observations with low-quality photos or only close-up specimens were removed from further analyses.

Each observation was categorized into an accumulation level based on a modified table by Collado-Vides et al. (2018) (table 5.1). To minimize the subjectivity of classifying an accumulation level depending on the analyzer's perception, at least two processors examined a photo to calibrate our perception of an accumulation level prior to finalizing an accumulation level. However, multiple processors often lead to disagreements on an assigned accumulation level of an observed landing. Any unresolved consensus of an observed accumulation level was determined by the discretion of the most experienced processor present or by majority vote (mode). Morphotype photos were also examined for the presence or absence of sargasso morphotypes per observation as outlined by Parr (1939) and Wrinn (2016).

Given the more opportunistic modality of data collection by iNaturalist contrasting the more consistent monitoring of volunteers using Epicollect5, a linear regression analysis was conducted to determine the usability of iNaturalist data. This analysis accounts for observation bias by testing the hypothesis that the number of observations would increase as a function of the increased accumulation level encountered (Geldmann et al., 2016). The regression analysis involves using accumulation level as a predictor and the number of observations as the response variable.

Observations were grouped onto a contingency table by accumulation level and subregion. Relative proportions of observed accumulations were plotted onto the map of the subdivided Caribbean region to visualize the variability of sargasso inundation levels. Pearson's chi-square test was used on the frequency of observations associated with accumulation levels and subregions to detect the susceptibility and intensity of observed sargasso accumulations between subregions, regardless of time.

Presence-absence data of morphotypes were converted into normalized relative frequency per number of observations per subregion. Observations with no sargasso present were removed for this analysis. Relative frequency of each sargasso morphotype per subregion (R_{mr}) was calculated using this equation:

$$R_{mr} = F_{mr} / N_r$$

Where F_{mr} is the total frequency of a sargasso morphotype m per subregion r, and N_r is the total number of observations per subregion r. Relative frequency values for each morphotype and subregion combination were calculated separately because many observations display more than one morphotype present. Normalized relative frequency data of morphotypes per total observations per subregion was graphed to visualize the dominance of morphotypes in inundation-associated areas. Pearson's chi-square analysis was used on the total frequency of morphotypes per subregion to determine the variability of sargasso morphotype composition found per subregion in inundation-associated areas. Using all morphotype data, including those with an absence of morphotypes, logistic regression curves were compiled using the ggplot package of RStudio to determine the probability of encountering a morphotype per subregion based on accumulation level. For each curve, binomial logistic regression analysis was conducted to assess the likelihood of encountering a morphotype depending on the accumulation level.

Accumulation levels between the five monitored sites were summarized using a contingency table and bar plots showing the relative proportion of observations per month during the 2021 season. A similar plot was formed showing the relative proportion of accumulation levels in MJSP for 2019–2021 sargasso seasons to examine temporal variability in accumulation levels in one site. Pearson's chi-square test was used on the frequency of observations associated with accumulation levels and month to detect the susceptibility and intensity of observed sargasso accumulations between months per year in both analyses.

To compare the probability of encountering an observed accumulation level per month during the 2021 season, density plots were compiled using the ggplot2::geom_density function in RStudio using the total frequency of accumulation levels per month. Monitored site data was compiled to represent subregions; the FL density plot was constructed using the MJSP and KCKB datasets, and the WC density plot was constructed using the UNAM and PdC datasets. Bdt dataset was too restricted in sampling months for density plots, and no monitored sites were identified in the GoM or BH subregions.

3. Results

A total of 1756 observations were collected from the Epicollect5 program and used for this study. An additional 146 observations of *Sargassum* spp. (based on keywords used from the app search engine) were retrieved from the iNaturalist database after quality-checking that included the identification of pelagic species. Most of the data available were from 2019 onwards due to the implementation of Epicollect5 (figure S5.1), although few observations from iNaturalist were available before 2019 (figure S5.2). No statistically significant relationship was found between accumulation level and number of observations on either iNaturalist data (R^2 = 0.21, p = 0.54) or Epicollect5 (R^2 = 0.81, p = 0.09) (figure S5.3). With no evidence to suggest observational bias as a lurking factor, both iNaturalist and Epicollect5 data were combined for the following analyses.

The sample size of each subregion varied from n = 31 in GoM to n = 1093 in FL. The observed accumulation levels varied over different regions X^2 (15, N = 1901) = 310.46, $p < 0.0001$. FL showed less susceptibility for moderate to high sargasso inundations, noted by a higher-than-expected amount of level 1 observations and lower-than-expected amount of level 3-4 observations. WC showed a lower than expected amount of level 1 observations and a higher than expected amount of levels 2-4 observations. GC showed similar trends as WC, with a more than expected amount of level 4 observations and a lower than expected amount of level 1 observations, demonstrating that GC and WC showed higher susceptibility to sargasso inundations relative to other subregions in the Caribbean (figure 5.2).

The number of observations with sargasso morphotypes identifiable ranged from n = 15 in GoM to n = 503 in FL, and included both observations collected by monitoring groups ("monitored") and "opportunistic" observations (figure S5.4). Observations with no identifiable sargasso present were excluded from normalized relative frequency calculation. There was considerable variation in morphotypes found throughout the subregions associated with the inundations X^2 (8, N = 921) = 29.704, $p < 0.01$. Throughout the Caribbean, *S. fluitans* III was the most commonly encountered morphotype. Relative frequencies of *S. fluitans* III ranged from 0.73 in the GoM to 0.95 in GC and WC. In four out of five subregions, *S. natans* VIII was the second most commonly encountered morphotype, except in GC, where the relative frequencies of *S. natans* VIII and *S. natans* I were roughly equal. The lowest relative frequency of *S. natans* VIII was 0.41 in GC, while the highest relative frequency was 0.80 in WC. *S. natans* I was the least commonly encountered morphotype; the lowest relative frequency of *S. natans* I was 0.14 in BH, while the highest relative frequency was 0.38 in GC (figure 5.3).

Logistic regression analyses shows that the probability of finding any of the three morphotypes is dependent on subregion and accumulation level (figure 5.4). All *S. fluitans* III subregional regression models showed that the probability of encountering that morphotype increases as accumulation levels increase ($p > 0.0001$). Similar trends were found for most subregional models of *S. natans* I ($p > 0.001$) except for the WC subregion ($R^2 = 0.033$, $p = 0.59$), and *S. natans* VIII ($p > 0.0001$) except for WC ($R^2 = 0.11$, $p = 0.071$ NS) and BH subregions ($R^2 = 0.12$, $p = 0.11$ NS). Table S5.2 summarizes the results of logistic regression models associated with the probability curves.

Seasonal variation of accumulation levels was examined between the five data-sufficient sites during 2021 (figure 5.5). No data was collected outside of June–August in Bdt. MJSP and KCKB in Florida have similar proportional accumulation levels observed between UNAM and PdC in Mexico. Both Florida and Mexico sites showed a gradual increase in accumulation levels in May (though PdC observed high accumulation levels in March). Sargasso accumulation levels peaked in June at MJSP, UNAM, and PdC. Accumulation levels in KCKB during June and July are roughly similar, though there were slightly higher proportions of observations during July. Bdt showed increased accumulation between June and July before slightly decreasing in August. July showed the highest proportion of accumulation levels observed between these three data-available months.

MJSP has the largest sample size of all other sites (N = 452) spanning three years (2019-2021); this site was used for interannual comparisons of accumulation levels between months and years (figure 5.6). No observations were collected from November to February each year. Considerable variation occurred between 2019 and 2021 $X^2(105, N = 372) = 336.05$, $p < 0.0001$. In 2019, the sargasso season started in April and continued until July, when accumulation levels decreased from August to October. In 2020 the sargasso season started in May and peaked between June and July before decreasing in August. The 2021 sargasso season showed a similar trend to the 2020 season, though the intensity of accumulation levels was higher that year.

Density curve models between FL and WC subregions showed similar trends in dominant accumulation levels observed between months during the 2021 season (figure 5.7). Higher accumulation levels coincided with a more restricted time frame when those observations were present. Level 1 and 2 observations were present in most months of the season but had the highest density before and after the peak season, depending on the subregion. FL level 3 observations were concentrated from May to June and WC in May and August, months adjacent to the peak season. Level 4 observations were mostly present in June–July in FL and May–July in WC, representing the peak season.

4. Discussion

This study utilizing collaborations between individual and groups of volunteers was fundamental to garner a region-wide perspective on sargasso inundations between large-scale satellite imagery and small-scale *in situ* monitoring approaches such as quadrats. Using community-contributed data, our results showed spatial variability in sargasso inundations levels, demonstrating that Florida and the Gulf were less susceptible to high accumulation levels than the rest of the tropical Atlantic region during the studied period. Morphotype composition and accumulation levels varied within the tropical Atlantic independent of wherever sargasso landed. Finally, seasonal variation was detected between years of one site and between sites during one season. Though the 2021 season showed similar peak seasons between the Florida and Western Caribbean subregions, the duration and intensity of these peak months differed.

Overall biogeographic trends were consistent with the satellite imagery models at a regional level. The intensity and frequency of sargasso depend on an area's proximity to the GASB and dispersal of sargasso biomass through wind and water currents (Brooks et al., 2018; Johns et al., 2020). Putman et al. (2018) simulated sargasso transport and found that the Equatorial Atlantic (east of EC) would eventually export sargasso through the Caribbean Sea within a year. Johns et al. (2020) noted that windage patterns could form long mats of sargasso and transport them from the Inter-Tropical Convergence Zone (ITCZ), where the GASB is sourced, to the Central Atlantic across the Caribbean. Remnant populations of sargasso can still exist during the off-season before recovering the following year (Johns et al., 2020). Recent oceanographic models also suggested mesoscale eddies can collect and disperse sargasso to trajectories that would differ from initial, main current patterns (Andrade-Canto et al., 2022). While this study did not examine the transport of sargasso, emphasis was placed on the fate of sargasso from the GASB to landed areas across the Caribbean. Subregions that did not report as high a frequency of high-accumulation levels as others can still be susceptible to lasting impacts from sargasso, as was the case in seagrass beds in Turks and Caicos in the BH subregion. In that area, stakeholders noted that sargasso accumulations have always been observed but were noted to be a problem in 2018 (Bartlett and Elmer, 2021). Though our Sargassum Watch Epicollect5 Program could not get observations from before 2019, consistent monitoring and opportunistic, single observations can be valuable to show the extent of these massive inundations.

Our results examining morphotype composition associated with landed sargasso can be a useful baseline to compare future monitoring programs and previous baselines associated with morphotype composition onshore or offshore. Other studies that monitor sargasso morphotype composition across the Eastern Atlantic region have found considerable temporal and spatial variation. Offshore surveys from 2015 revealed a dominance of *S. natans* VIII across the Caribbean, contrasting with *S. natans* I dominance in the Sargasso Sea (Schell et al., 2015). Another shipboard survey from 2015–2016 showed *S. fluitans* III and *S. natans* VIII dominant in the Tropical Atlantic, Greater Caribbean, and Gulf of Mexico regions, while the Gulf Stream region is dominated by *S. natans* I and *S. natans* VIII. Only in the Sargasso Sea was there a sizeable representation of all three morphotypes, with *S. fluitans* III occurring in 33% of dip net collections, *S. natans* VIII occurring in 23% of collections, and *S. natans* I occurring in 43% of collections (Martin et al., 2021). Interestingly, these post-2011 surveys differed from earlier surveys where *S. fluitans* III and *S. natans* I were previously the most dominant species, with little detection of *S. natans* VIII (Parr, 1939). It seems that *S. natans* VIII became an increasingly integral morphotype composing these inundations after 2011, along with the other morphotypes. From a regional perspective, our results are consistent with previous post-2011 surveys as *S. fluitans* III was the most commonly encountered morphotype. At the same time, *S. natans* VIII and *S. natans* I can also be present depending on subregion and accumulation level.

Our seasonal approach comparing morphotype composition using frequency contrasted with results that monitored biomass. Concurrent monthly monitoring of MJSP showed that *S. natans* I dominated in biomass during months without an inundation, while *S. fluitans* III dominated in biomass during influx seasons. *S. natans* VIII showed the least biomass throughout that study (Hatt et al., unpublished data). Previous monitoring programs of sargasso in the Mexican Caribbean from 2016 to 2020 found largely *S. fluitans* III dominance throughout, though dominance of *S. natans* I and VIII varied by sampling month (García-Sánchez et al., 2020). Other single-day sampling efforts in Jamaica and Mexican Caribbean also outlined *S. fluitans* III dominance, with a limited abundance of *S. natans* I and VIII (Machado et al., 2022; Vázquez-Delfín et al., 2021). Though *S. natans* I occurred in much less frequency than the other morphotypes, the absence of *S. natans* I on observed landings could not imply absence (Altman and Bland, 1995). Given morphological differences, *S. natans* VIII is often a readily identifiable morphotype than the more inconspicuous *S. natans* I. However, discerning differences in morphotypes requires identifying minute traits within the algal thallus (Parr, 1939), which could not be readily identifiable with photos often low in resolution. Marking the presence of a morphotype requires examining and identifying the overall thalli based on the rough level of structural complexity.

Seasonal comparisons of accumulation levels were mostly consistent with the satellite imagery models that would regionally predict an increase or decrease of sargasso, although the Floridian subregion would receive less accumulation than the Greater Caribbean. Peak seasons of sargasso also tend to vary yearly, but usually fall between April to September (García-Sánchez et al., 2020; Bartlett and Elmer, 2021; Vázquez-Delfín et al., 2021; Machado et al., 2022). Sargassum Inundation reports (SIR) during the 2019-2020 year noted Florida’s southeast coast as having primarily low to medium susceptibility of sargasso inundations (Trinanes et al., 2021), which was largely similar to on-ground monitoring results of MJSP during those same years. Our analyses further support this before and during the 2021 season that showed a gradual transition of observations primarily of low accumulation to high accumulation that were characteristic of peak months from May to July. This transition and intensity of peak months also varied with subregion, with WC having more high accumulation events than FL, consistent with previous years' monitoring (Trinanes et al., 2021).

When comparing our results to previous biomass monitoring programs, Florida monitoring previously reported upwards of 4.0 wet kg m^{-2} during April 2019 (Hatt et al., unpublished data), contrasting 17.3 wet kg m^{-2} in the Mexican Caribbean during the summer of 2018 (García-Sánchez et al., 2020). Based on these previous biomass monitoring efforts, the severity of sargasso accumulations can greatly differ between these two subregions. The Mexican Caribbean can receive at least four times the biomass landed in Florida. Given the proximity of these two subregions to the GASB and the trajectory of the water currents from the Caribbean Current, to Loop Current, to Gulf Stream, it could be that the Floridian subregion is receiving the residual biomass that did not land in the Mexican Caribbean, where much more of that biomass has landed (Putman et al., 2018; Johns et al., 2020). Alternatively, sargasso from the GASB can be transported to Florida via the Antilles Current (Putman et al., 2020). However, given the comparatively lower accumulation levels observed in the Bahamian subregion, it is difficult to tell how often that occurs.

The frequency and intensity of sargasso landings can also be influenced by small-scale coastal factors that occur daily and locally; and local managerial strategies. In areas with adjacent fringing reefs, lower wave and wind activity gradually increased sargasso accumulation. In contrast, high wave and wind activity would inundate the landed sargasso and flush it back into the water column. Depending on subsequent wind and wave activity, re-suspended sargasso can re-land on beaches or get flushed entirely (Rutten et al., 2021). Observations at the Reef Systems unit of UNAM in Quintana Roo, Mexico have somewhat detected this phenomenon; observations with high accumulation often coincided with high tide that inundates landed and floating sargasso (Rutten et al., 2021). Sargasso accumulations at UNAM would mostly have between level 2–4 accumulation levels, depending on the month of the sargasso season. Conversely, consistent management of local beaches through removal or displacement can also mediate otherwise high accumulations of sargasso. In our study, KCKB in Florida was cleaned daily through machinery. In contrast, PdC in Mexico was cleaned daily with machinery with an additional nearshore barrier set up during the peak season. Proportions of observed accumulation levels in cleaned sites were largely similar to sites that lack consistent cleaning, albeit fewer observations showing moderate and high accumulations were noted in cleaned sites.

This study also led to results related to conducting community science programs. Community science programs require rigorous data quality control, which can be maintained through protocols, active training, and feedback (Fore et al., 2001; Nerbonne and Vondracek, 2003). The uneven distribution of available volunteers in the Greater Caribbean region also leaves many impacted areas unmonitored, which can be a source of sampling bias that would prevent holistic assessment of sargasso landings (Nerbonne et al., 2008; Iporac et al., 2020). Our study attempted to mitigate sampling bias by utilizing supplemental iNaturalist data and testing for observational bias, which our regression results suggested was minimal.

The sheer potential of using photo observations for quantitative analyses is developing rapidly. Previous tools have been proposed for use, such as an accumulation table for manual classification (this study, Collado-Vides et al., 2018), to computerized neural networks for automated detection of sargasso landings in photos (Valentini and Balouin, 2020; Arellano-Verdejo and Lazcano-Hernández, 2021). The manual classification method was limited by the number of images to categorize and subjectivity of classifying an accumulation level per photo(s). The automated method can process large amounts of photos, quickly detecting the presence or absence of sargasso with over 90% accuracy but currently does not translate to more comparative data beyond that (Arellano-Verdejo and Lazcano-Hernández, 2021). Both quantification methods were also limited by the quality of photos sent by volunteers for later processing. For monitored data to be useful, volunteers' frequency of photo collection must be maintained by constant communication and developed trust and commitment between volunteers and program managers. Opportunistic data from other sources, such as iNaturalist, can also be bolstered through outreach efforts, although data quality varies by available protocols associated with data collection.

This study is among the first known that attempts to use the collected citizen science data to outline quantitative trends and patterns in sargasso accumulation levels and morphotype dominance. Recent publications have used the Epicollect5 database for qualitative presence of sargasso landings with satellite imagery models, and these comparisons were effective in ground-truthing and detecting concordance (Trinanes et al., 2021). Other previous works acknowledged the effectiveness of the Epicollect5 program in data collection yet criticized the accessibility of app usage and limited usage of presence/absence data rather than the abundance of sargasso (Arellano-Verdejo and Lazcano-Hernandez, 2020). The United Nations Environmental Programme (UNEP) noted the quantity per volume of sargasso that landed as a major gap in monitoring sargasso (United Nations Environment Programme- Caribbean Environment Programme, 2021), especially given the heterogeneity of biomass landing within the tropical Atlantic region. Synthesizing photographic data with other methods such as *in situ* monitoring of biomass can be used to re-examine photographs to estimate biomass on a higher frequency. Estimating biomass through photos can then be recalculated to estimate inputs associated with sargasso, such as nutrient availability, metal concentrations, and foraging grounds for shorebirds feeding on terrestrial invertebrates. There is also potential for automated approaches to quantify the sheer amount of photos to quantitative data, as was done with presence-absence conversion (Arellano-Verdejo and Lazcano-Hernández, 2021). However, there is the challenge of calculating meaningful data from low-resolution images. Finally, these photos and associated biomass estimates can further be synthesized by satellite or aircraft images to validate the amount of biomass arriving, of which similar efforts are already developing recently (Baldwin et al., 2019; Degia et al., 2022; Hernández et al., 2022; Optical Oceanography Laboratory, 2018; Trinanes et al., 2021). This synthesis of data from different scales can be combined with other hazard, exposure, and vulnerability data to estimate the impact forecasting of sargasso on coastal environments and affected local communities (Degia et al. 2022).

Detection of accumulation levels largely relies on sampling efforts by volunteers, which may not always be available. Much of our currently collected data concentrated on a few areas with sufficient resources and collaborative research capacity to include citizen science as a monitoring strategy. Many of these under- or non-monitored areas may not have adequate support and simultaneously could be areas that experience highly impactful sargasso inundations. Many of these countries associated with sargasso inundations also have histories of colonial and neocolonial exploitation and imperialism that still manifest today through contemporary geopolitical situations. When collaborating via community science, we advocate for open use of our data and collaborations between community groups and nations to study and manage a regional issue, especially in data-insufficient areas of this study. However, we also highlight the need to ensure that practices of science and policy in this field lead to equitable and just science and policy for peoples in the global south, including Central America, West Africa, and the Caribbean that often gets impacted by sargasso (Edwards et al., 2021; Stefanoudis et al., 2021).

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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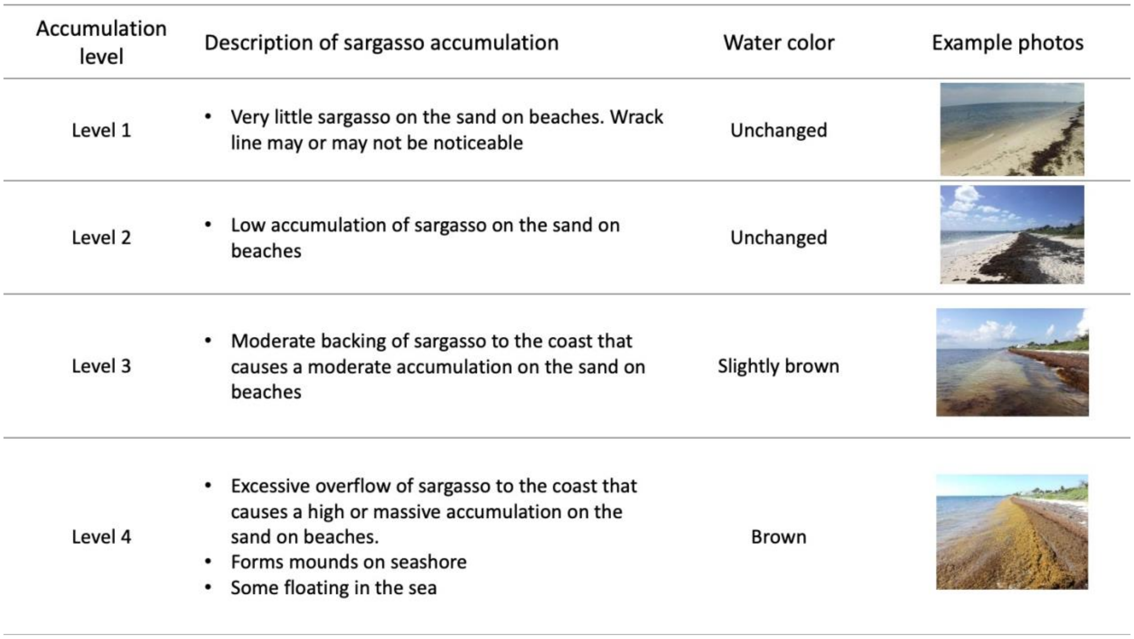
Appendix



Accumulation level	Description of sargasso accumulation	Water color	Example photos
Level 1	- Very little sargasso on the sand on beaches. Wrack line may or may not be noticeable	Unchanged	
Level 2	- Low accumulation of sargasso on the sand on beaches	Unchanged	
Level 3	- Moderate backing of sargasso to the coast that causes a moderate accumulation on the sand on beaches	Slightly brown	
Level 4	- Excessive overflow of sargasso to the coast that causes a high or massive accumulation on the sand on beaches. - Forms mounds on seashore - Some floating in the sea	Brown	

Table 5.1. Accumulation table for photo classification slightly modified by Collado-Vides et al. (2018)

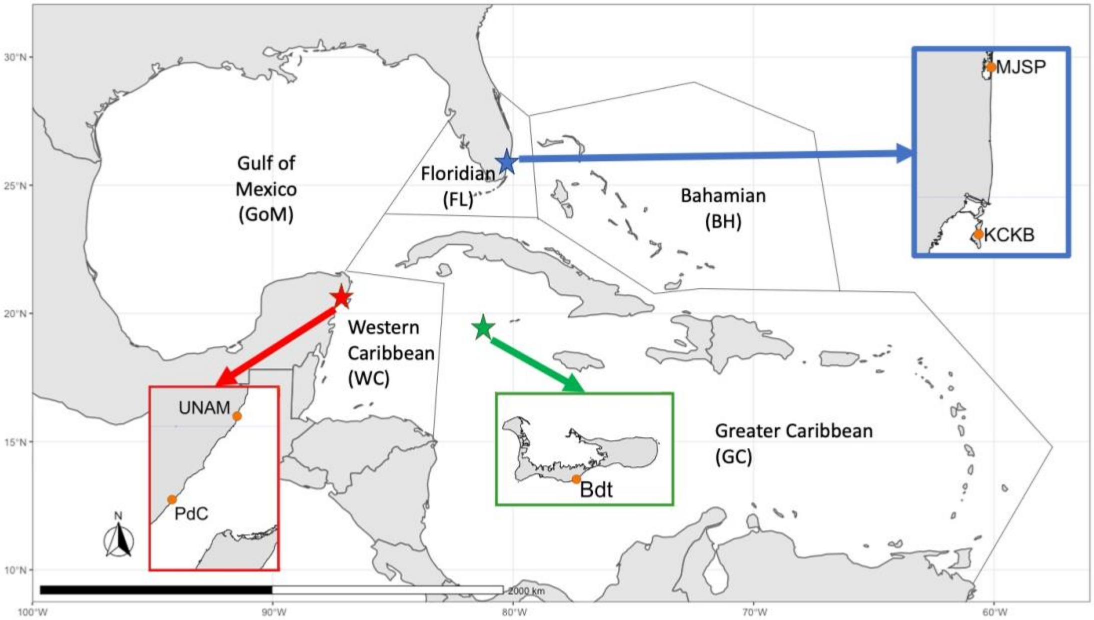


Figure 5.1. Map showing the five subregions and locations of the five data-sufficient monitored sites. Two sites, Dr. Von D. Mizell-Eula Johnson State Park ((MJSP, N 26° 3' 37", W 80° 06' 41.126")) and Key Colony, Key Biscayne (KCKB, N 25° 41' 48.98", W 80° 09' 21.236") are shown in the blue inset in Florida. Two sites inside the red inset representing the Western Caribbean include the Reef Systems Unit, Institute of Marine Sciences and Limnology, National Autonomous University of Mexico (UNAM, N 20° 52' 07.82", W 86° 52' 5.485"), and Playa del Carmen (PdC, N 20° 38' 40.016", W 87° 03' 19.81"), both in Mexico. Boddentown (Bdt, N 19° 16' 50.52", W 81° 14' 59.24") site is also shown up-close in the green Grand Cayman inset.

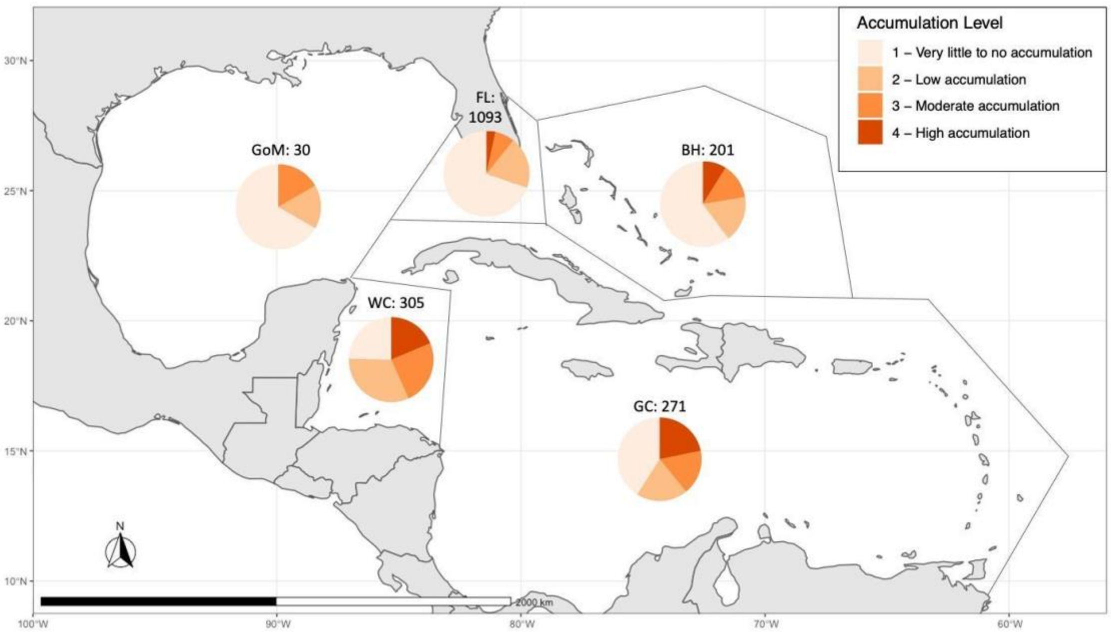


Figure 5.2. Number of observations and proportion of observed accumulation levels of sargasso compiled from 2011-2021 for "Greater Caribbean" (GC), "Western Caribbean" (WC), "Gulf of Mexico" (GoM), "Floridian" (FL) and "Bahamian" (BH) subregions. Numbers represent sample size per subregion. The size of pie charts is not proportional to the sample size of the subregion.

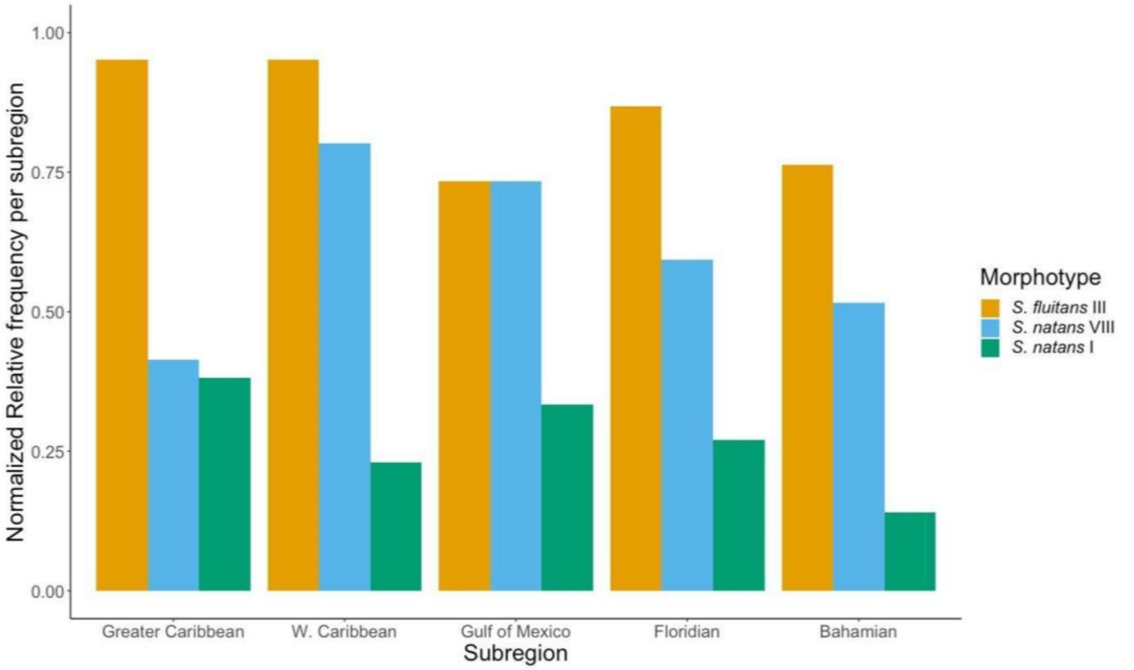


Figure 5.3. Normalized relative frequency of sargasso morphotypes present in an observed inundation per subregion.

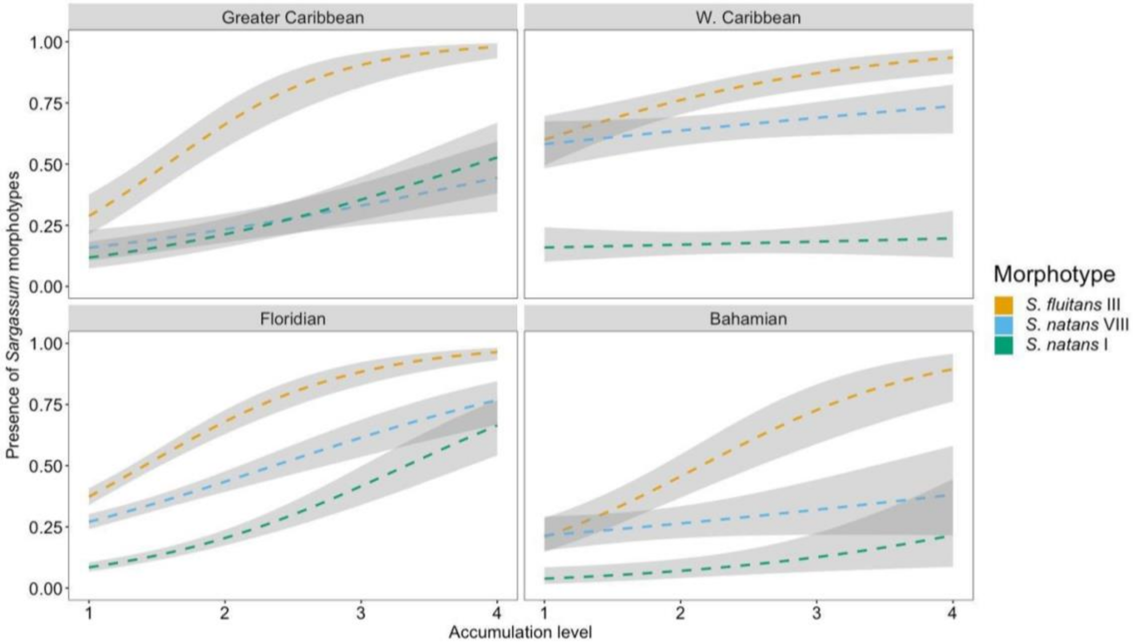


Figure 5.4. Logistic probability models of *Sargassum* spp. morphotypes presence as a function of accumulation level per subregion. No probability models were made for GoM with lack of sufficient data.

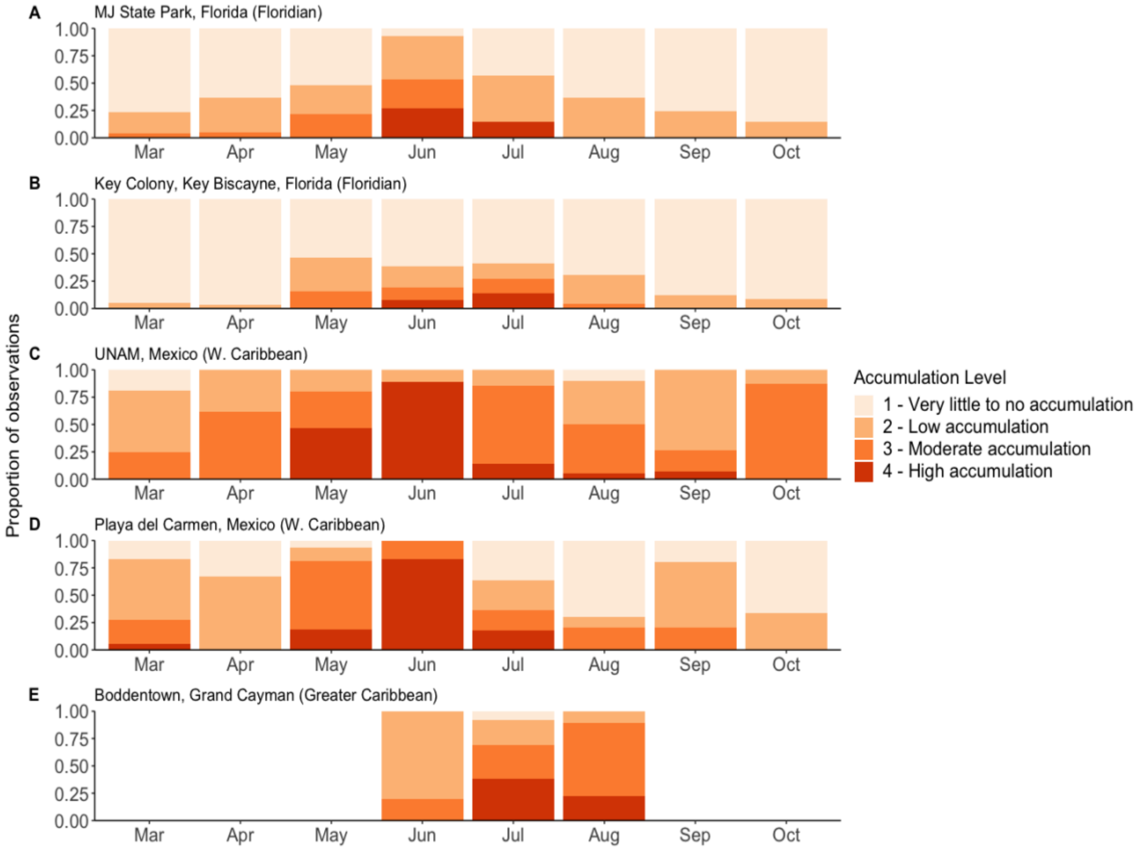


Figure 5.5. Proportion of observed accumulation levels per month from March to October 2021 across the five study areas (A) MJSP, Florida, (B) Key Colony, Key Biscayne, Florida, (C) UNAM, Mexico, (D) Playa del Carmen, Mexico, and (E) Boddentown, Grand Cayman. No data was available from March-May and September-October in Boddentown, Grand Cayman, Cayman Islands.

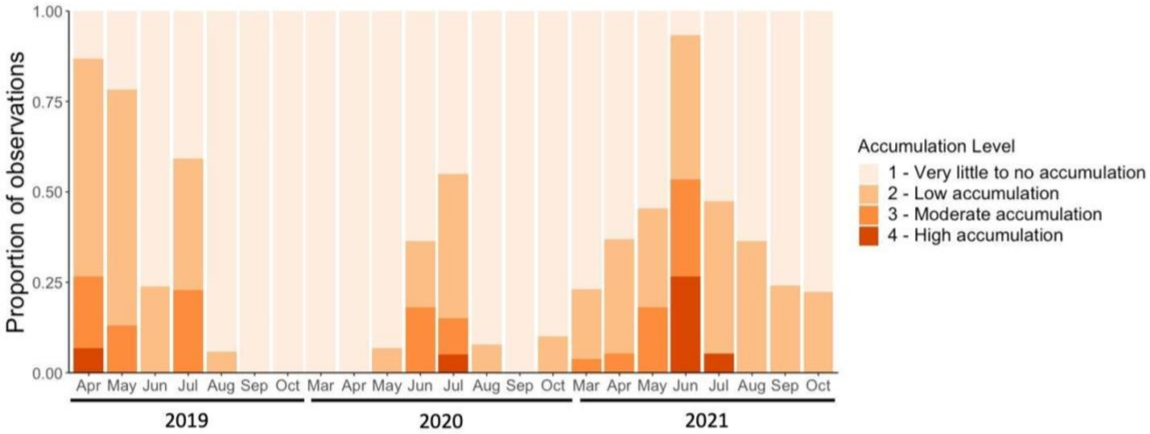


Figure 5.6. Proportion of observed accumulation levels per month from 2019-2021 in MJ State Park, Fort Lauderdale, Florida, USA. No data was available from November-February in all three years and March 2019.

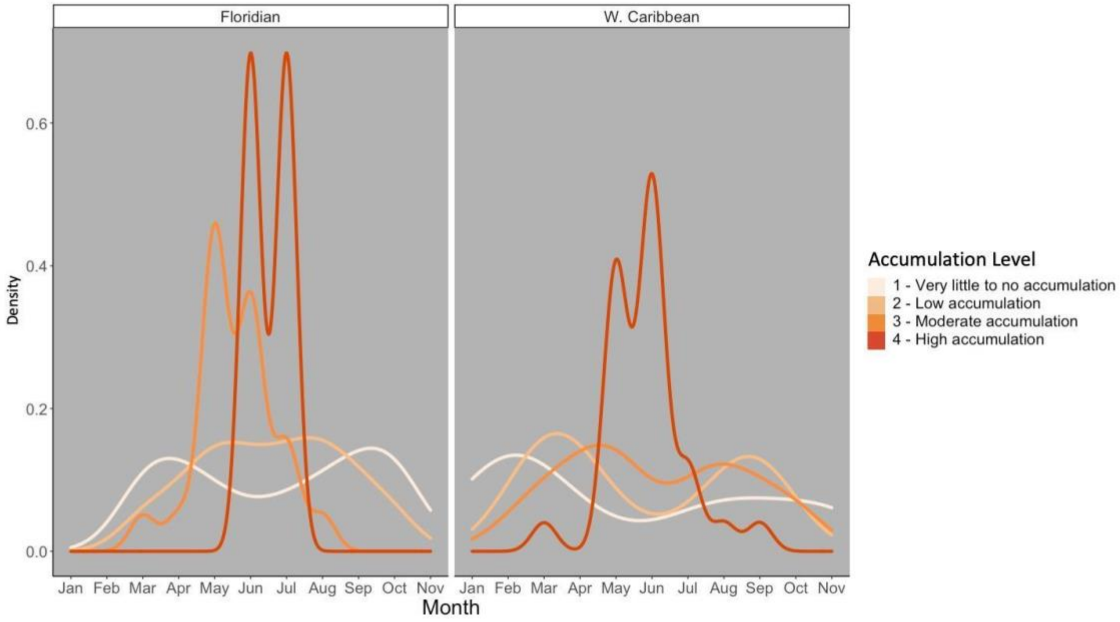


Figure 5.7. Kernel density plots of observed accumulation levels between FL and WC subregions during the 2021 sargasso season.

Subregion	Accumulation Level			
	Level 1	Level 2	Level 3	Level 4
Bahamian (BH)				
Floridian (FL)				
Gulf of Mexico (GoM)				No observations found
Western Caribbean (WC)				
Greater Caribbean (GC)				

Table S5.1. Example observations organized by subregion and accumulation level. Each photo's origin is outlined from left to right, top to bottom as follows: (A) North Caicos (N 21° 57' 13.061", W 71° 56' 37.773"), 15 July, 2020, (B) Long Bay, South Caicos (N 21° 31" 45.746", W 71° 29' 46.503"), 29 April, 2021, (C) Conch Farm, Grand Turk, Turks and Caicos (N 21° 26' 57.26",W 71° 7' 35.648"), 27 August, 2021, (D) Conch Farm, 22 September, 2021, (E) MJSP, Florida, USA (N 26° 3' 37", W 80° 06' 41.126"), 27 July, 2021, (F) MJSP, 29 April 2021, (G) MJSP, 3 June, 2021, (H) MJSP, 11 June 2021, (I) Grass Island, Alabama, USA (N 30° 13' 51.54", W 87° 55" 16.421"),12 June, 2021, (J) Galveston Island Texas, USA (N 29° 13' 38.448", W 94° 53' 40.92"), 21 July, 2020, (K) Bryan Beach, Texas, USA (N 28° 54' 26.065", W 95° 20' 31.028"), 31 May, 2013, (L) UNAM, Quintana Roo, Mexico (N 20° 52' 07.82", W 86° 52' 5.485"), 8 October, 2020, (M) UNAM, 22 April 2021, (N) UNAM, 28 April 2021, (O) UNAM, 1 June 2021, (P) Boddentown, Grand Cayman (N 19° 16' 50.52", W 81° 14' 59.24"), 23 July 2021, (Q) Boddentown, 13 July 2021, (R) Boddentown, 12 July 2021, and (S) Boddentown, 23 July 2020. No known observations of level 4 accumulations were collected within the GoM subregion.

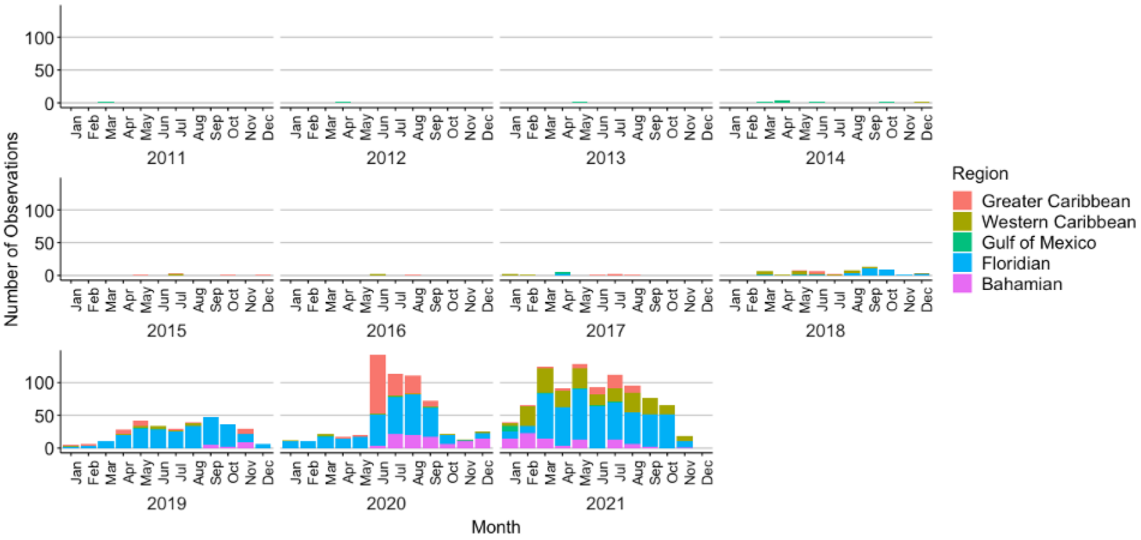


Figure S5.1. Number of observations per subregion by month within and between years. Empty columns imply no observations collected from either citizen science app.

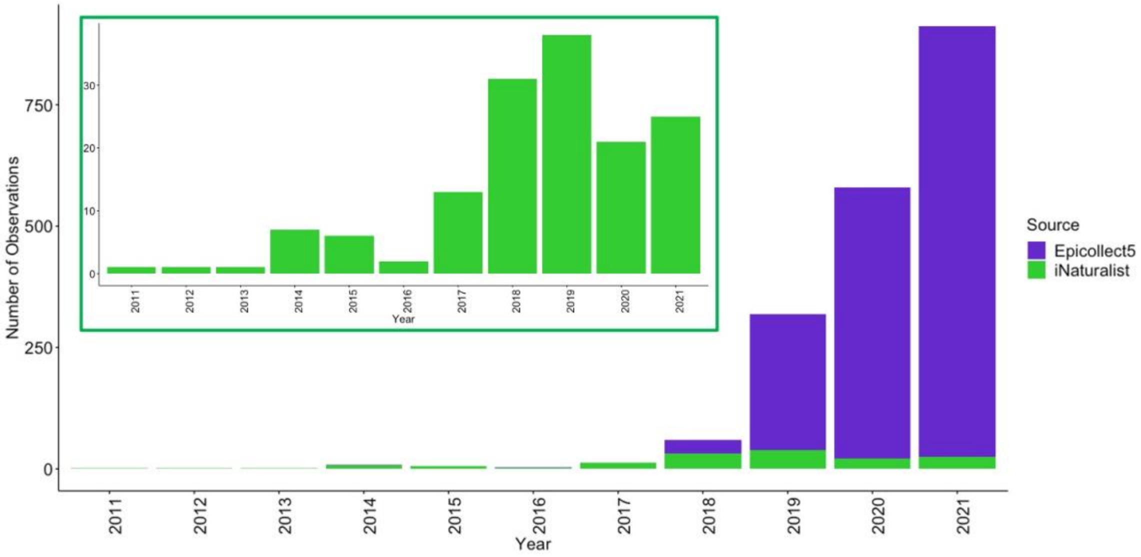


Figure S5.2. Number of observations of sargasso landings per citizen science app and year. Green-outlined insert magnifies iNaturalist-collected observations otherwise indiscernible below the Epicollect5 bars. Note the differences in scale of axes.

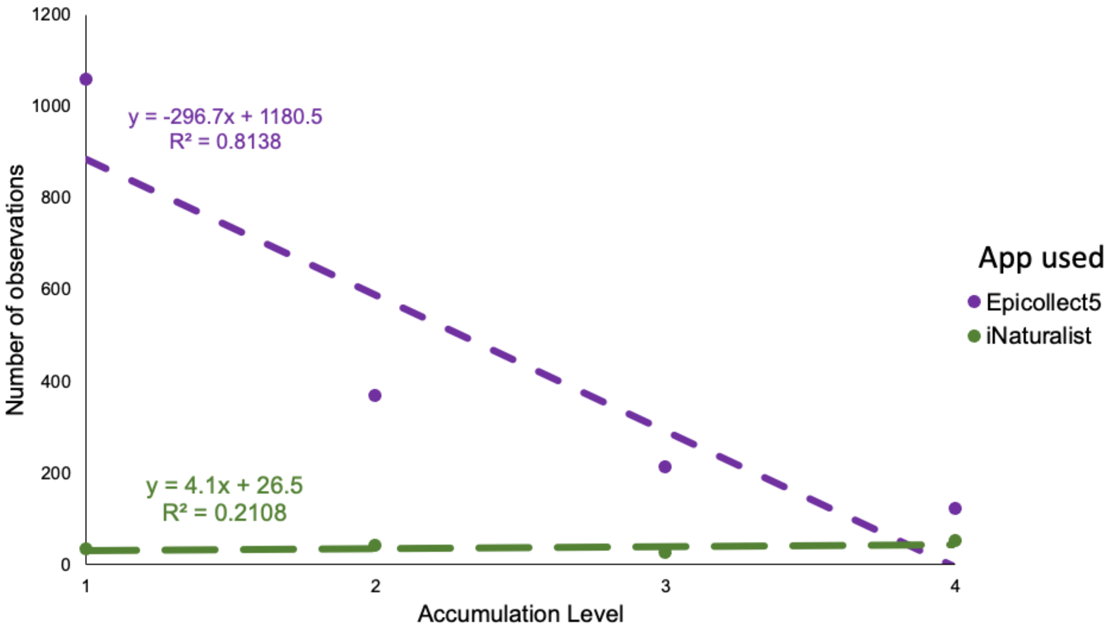


Figure S5.3. Linear regression analysis showing number of observations collected as a function of accumulation level encountered per citizen science application used.

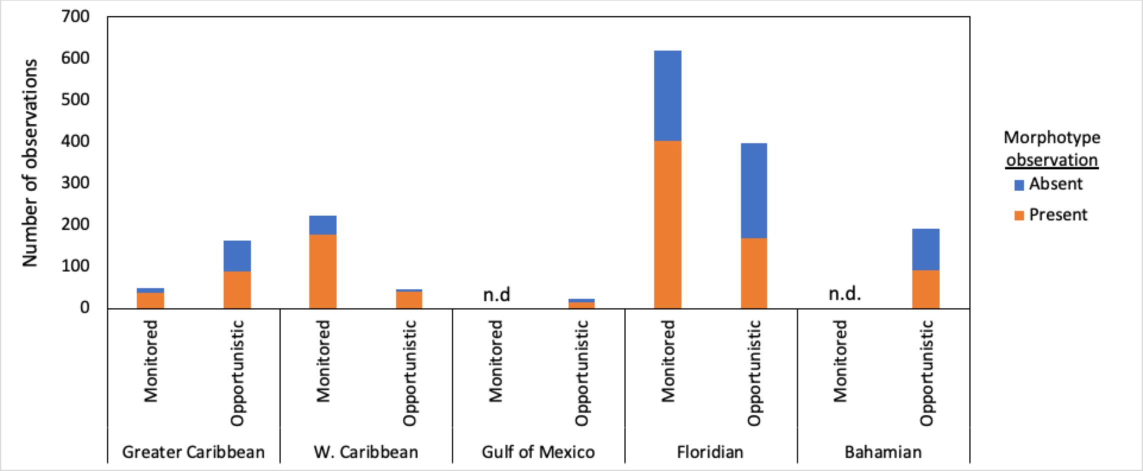


Figure S5.4. Absolute contribution of observations that have sargasso present or absent based on availability of closeup photos of morphotypes grouped by modality and subregion. Observations that do not have any closeup photo and did not confirm the absence of sargasso were removed from this analysis. No monitored observations were available for the Bahamian or Gulf of Mexico subregions.

	Morphotype		
Subregion	*S. fluitans* III	*S. natans* I	*S. natans* VIII
BH	0.47****	0.19**	0.12 NS
FL	0.35****	0.34****	0.25****
WC	0.28****	0.033 NS	0.11 NS
GC	0.56****	0.34****	0.24****
Caribbean Region	0.42****	0.26****	0.25****

Table S5.2. Results of logistic regression mode. Values represent R^2 value, and asterixis represent significance levels: * > 0.05, ** > 0.01, *** > 0.001, **** > 0.0001, NS: No significance.

Organization	Type	Location	Subregion	No. Trained Volunteers	No. Monitored Sites	Start date
FIU Marine Macroalgae Research Lab	Academic	Miami, Florida, USA	FL	≥ 10	3	October 2018
Broward County Sea Turtle Conservation Program	Conservation	Broward, Florida, USA	FL	> 30	7	March 2019
Department of Environmental and Coastal Resources	Governmental	Turks and Caicos	BH	4	19	August 2019
Miami Waterkeeper	Non-profit organization	Miami and Broward, Florida, USA	FL	8	22	September 2019
Deering Estate	Conservation	Miami, Florida, USA	FL	5	1	January 2020
Department of Environmental Resources Management	Governmental	Miami, Florida, USA	FL	15	5	June 2020
Marine Turtle Monitoring Programme, Cayman Islands Department of Environment	Governmental	Grand Cayman, Cayman Islands	GC	≥ 20	14	June 2020
Miscellaneous volunteers	Public	Miami, Florida, USA	FL	1	1	January 2021
Miscellaneous volunteers	Public	Quintana Roo, Mexico	WC	1	1	January 2021
Reef Systems Unit, Institute of Marine Sciences and Limnology, National Autonomous University of Mexico	Academic	Puerto Morelos, Mexico	WC	1	1	February 2021
			Total	≥ 95	73	

Table S5.3. List of volunteer organizations, with type of organization, location relative to subregion, number of trained volunteers, number of monitored sites, and date (month-year) data collection started. Order of rows on table organized chronologically.

CHAPTER VI

CONCLUSIONS AND FUTURE DIRECTIONS

Macroalgal habitats and associated epifaunal communities are an often overlooked aspect of shallow coastal and marine systems in tropical areas. Despite this, macroalgae and invertebrates are often upheld as indicators of environmental change and disturbances (Jones 1971, Thomas 1993). The trophic link and ecosystem functions between macrophytes as primary producers, epifauna as herbivores and detritivores, and predators of epifauna still needs to be investigated in future studies, especially in south Florida that has a high degree of coastal development (Browder et al. 2005, Rudnick et al. 2005). This research provides a recent foundation that can investigate these questions, with a changing ecological context and conditions from earlier studies of invertebrate fauna and macrophyte habitats in south Florida.

Chapter II examined multiple macrophyte habitats and associated epifaunal communities at two shallow coastal areas in southeast Florida. The approach to assessing these habitats formed by macrophyte assemblages showed associations of macrophytes, including between primary structural providers and secondary epiphytes, that would not be noticed had the habitat be deduced to a single species' name or generalized operational name. Additionally, different coastal, estuarine, and marine areas worldwide would entail possibly infinite permutations of macrophyte assemblages composing habitat for fauna, largely limited by the number of macrophyte species present in that area. A habitat type such as 'drifting macroalgal mat' could differ in species composition between bays and coastal areas in Florida and elsewhere (Norkko and Bonsdorff 1996, Biber 2007, El-Khaled et al. 2022). A global analysis of macrophyte habitats, which are not restricted to dominant species such as kelp or seagrass, but also formed by red and green macroalgae, could help generalize or specify contexts on macrophyte species would provide habitats for epifaunal communities. The consideration of multiple macrophyte habitats, including macroalgae that have different resource needs from seagrasses, could entail investigating additional factors that could be expanded on a much larger scale. Examples of these factors could include nutrient and light availability, differences in temperature and salinity, and level of upland or coastal development.

Chapter III investigated multiple aspects of habitat complexity from macrophytes and their relationship to epifaunal diversity. We hypothesized that they synthesis of multiple aspects of habitat onto a calculable index would best explain variation in epifaunal diversity rather than individual aspects of macrophyte diversity, quantity, and architecture. From our approach, the structural complexity index and biomass availability are roughly equal in explaining variation in epifaunal diversity. Therefore, biomass as a single metric describes most of the epifaunal diversity patterns, with minimally added explanation in variation when incorporating architectural effects of macrophyte habitat. Part of the issue for this discrepancy was the prominent influence that biomass had on our complexity index, and how our approaches to measuring architecture might have minimal effect on adding variation between habitat types and describing that variation as was observed in the field. The small size of these habitats and the vast diversity of macroalgae composing these habitats as an assemblage prevented previously-used approaches to measuring architecture and habitat, as was done in similar studies involving much larger macroalgae (Hacker and Steneck 1990, Huang et al. 2007). Between our study and previous studies, the scale and approaches were different, as was the morphological complexity of different macrophyte species forming different habitat types.

The shortcomings of our approach in measuring fractal dimensions using small branch iterations could have been complemented with measuring fractal dimensions of the whole thallus prior to subsampling the branches. The effect size of differences between individual branches and entire thalli would help determine the integrity of utilizing fractal dimension as a measurement of architecture or if it is size-dependent. Additionally, the diverse approaches to measuring habitat architecture as outlined by (Chemello and Milazzo 2002) also could be considered in the construction of an index. Finally, the comparisons of structural complexity should also consider differences in structure between planar objects, such as seagrass leaves or foliose algae, and uniseriate filamentous algae. The *Ulva-Chaetomorpha* association composing benthic green mat habitats was a notable case of two macroalgae that differ in morphology and both considered to have less structural complexity than branching red algae. However, benthic green mats made of these macroalgae were comparable in epifaunal diversity to red macroalgal mat habitats (see figure 2.5 in chapter II for epifaunal diversity comparisons). A method that measures interstitial spaces in small-sized (low biomass compared to kelp) macrophyte habitats would be essential to investigate structural complexity between these habitats in a subtropical shallow coastal setting.

Chapter IV investigated resource use of sargasso-dominated wrack in intertidal sandy beach systems during sargasso inundation seasons. The presence and abundance of terrestrial fauna, lower temperature conditions under wrack, and stable isotope analyses all point to sargasso being a prominent resource for terrestrial fauna. However, the resource use of sargasso might differ among invertebrate faunal species. Of all invertebrate fauna collected, terrestrial amphipods and oligochaete worms seem to have the strongest link to pelagic sargasso. However, it is unknown if direct consumption of sargasso was the mechanism of resource use, or if a derived substance such as microbes on the sargasso or detritus from decomposition was the more likely mechanism. Feeding assays with invertebrate fauna and macrophytes composing wrack would be essential to understanding trophic dynamics, as well as incorporating detritus and microbes, if at all possible, to stable isotope mixing models. The resource use of sargasso by fauna also depends on the location and level of sargasso accumulation, of which higher sargasso accumulation would entail higher invertebrate abundance up to a certain threshold of biomass. Invertebrate faunal collections would have to differentiate between levels of accumulation, as previous studies of invertebrate fauna incorporated depth of the wrack during collections (Colombini et al. 2000). Finally, higher trophic levels as represented by decapods, shorebirds, and introduced reptiles as was the case in Crandon Park, were also recommended as further avenues of investigations, as some of these fauna were observed foraging along the sargasso-dominated sea wrack (Figure 6.1).

Chapter V utilized community-contributed data to monitor spatial and temporal variation in accumulation levels and species composition of sargasso in the Caribbean region. Using this data, we were able to demonstrate the variability of sargasso accumulations among subregions of the Caribbean. The accumulation of sargasso on these coastal areas would imply a multitude of ecological effects where there would be high accumulation levels and subsequent decomposition. The development of this community science program opens up many opportunities for collaboration and synthesis in monitoring sargasso accumulations and their effects on tropical coastal systems. Efforts were underway to synthesize community-contributed photos as a source of ground-truthing to validate the accuracy of satellite imagery models (Trinanes et al. 2021). The use of photograph data and derived data such as accumulation level could be further used to estimate inputs of sargasso and associated resources into shallow coastal system. Aside from resource use from terrestrial fauna and their consumers, decomposing sargasso could also grow fecal enterococci bacteria and release nutrient and metal leachates to the coastal area (Collado-Vides et al. 2019, Antonio-Martínez et al. 2020, Tomenchok et al. 2021). By estimating the accumulation level of sargasso, it would be possible to translate that estimation to estimated inputs of substances that may reach harmful levels for coastal area management.

The processing and dissemination of the community-contributed photos require enormous effort where a project should be under a program that is conducive to research and outreach. The dissemination of community-contributed data as a summary bulletin would aid in the retention of volunteers collecting the data (Cigliano et al. 2015, Chandler et al. 2017, Iporac et al. 2020). The processing of data is especially needed, since the “Sargassum Watch” community science program accumulated over 6300 observations from 2019 until this time of writing this dissertation. Artificial intelligence methods can expedite the processing of data, although the algorithm of detecting sargasso as the primary component of sea wrack is a limitation that requires effort to overcome (Arellano-Verdejo et al. 2019). Alternatively, other citizen science applications, such as “Zooniverse”, can aid in the processing of data through ‘gamification’ of categorizing sargasso observations and identification of species present (Borne and Zooniverse Team 2011). This latter method would especially be preferable to educate and engage community members on the region-wide issue of sargasso across Florida, the Gulf, and the Caribbean, fostering collaborations between scientists and the local community (Reed et al. 2013, Bracey 2018).

These findings and approaches of this research are applicable in the management and conservation of shallow coastal communities in Florida and the Caribbean. Increased collaboration between scientists of different disciplines and community members can further facilitate our understanding of coastal systems and their susceptibility to environmental changes, including from macroalgal blooms and influxes such as those from pelagic sargasso. Pelagic sargasso influxes seems to be persistent in Florida and the Caribbean, and multiple approaches would be needed to examine effects of pelagic sargasso inundations on local macrophyte habitats and associated invertebrate faunal communities in seagrass beds and sandy beaches.

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APPENDIX

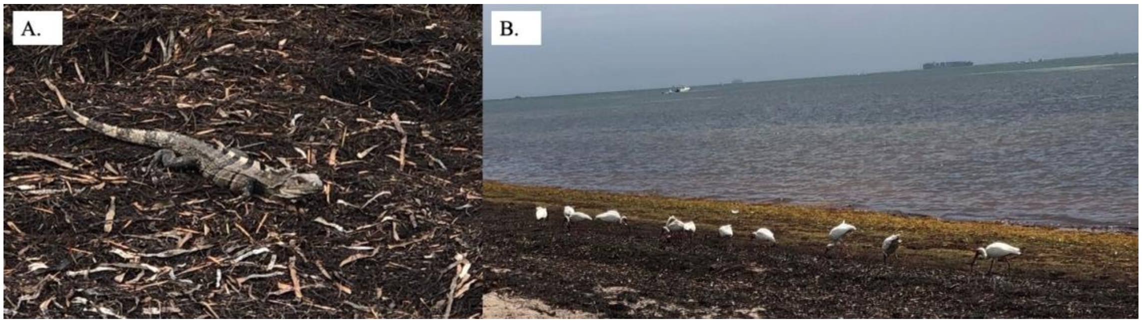

Figure 1: Observed vertebrate fauna found among sargasso-dominant sea wrack at Crandon Park during the sargasso season (July) 2021. Fauna depicted include the Black Spiny-Tailed Iguana (*Ctenosaura similis*) non-native to Florida (A) and a group of American White Ibis (*Eudocimus albus*) native to Florida and found in many parts of the Caribbean (B).

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