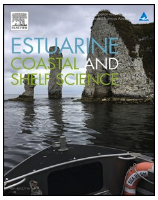
Estuarine, Coastal and Shelf Science 291 (2023) 108414

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Characterizing potential resource use of sargasso-dominant sea wrack by terrestrial invertebrate fauna during sargasso influxes in South Florida

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ARTICLE INFO

Keywords:
Sea wrack
Invertebrates
Pelagic sargasso
Microhabitat
Stable isotopes
Caribbean

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 discernible 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 of sargasso would likely be attributed to generalist resource use rather than a specific preference to sargasso. The potential uses of sargasso depend on the amount of biomass accumulated on the beach surface and the habitat requirements of specific invertebrate species.

1. 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).

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https://doi.org/10.1016/j.ecss.2023.108414
Received 15 March 2023; Received in revised form 14 June 2023; Accepted 15 June 2023
Available online 23 June 2023

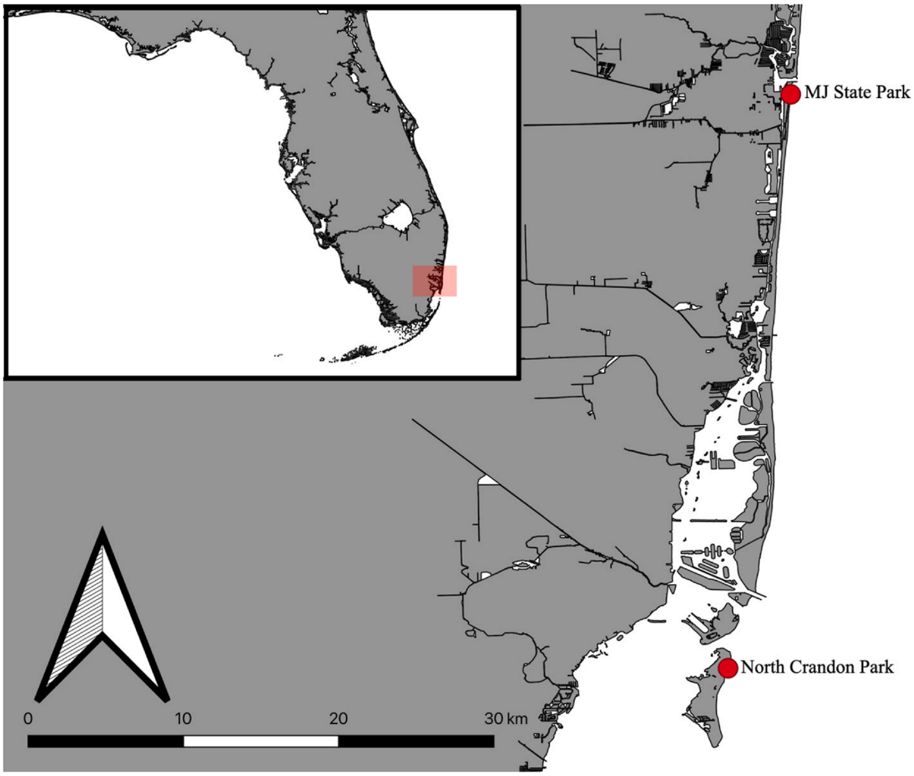

Fig. 1. Map of southeastern Florida study sites. Insert with red box shows relative location of study sites within Florida, USA. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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.

2. Methods

2.1. 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

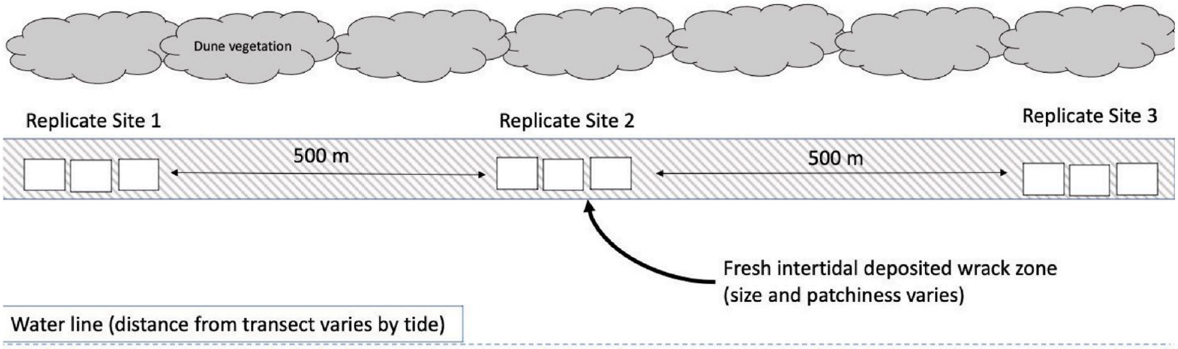

Fig. 2. Conceptual illustration of field sampling. Drawings are not to scale. Each replicated site per location was separated 500 m apart from each other. Each replicated site involved percent cover measurements and collection of habitat samples along fresh wrack at the intertidal zone.

separate by longitudinal distance (Fig. 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).

2.2. 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. 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 × 18.0 × 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 °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 (Supplementary Fig. 1). To estimate the total number of individuals during those situations, the collected amphipods were evenly distributed in a 20.0 × 20.0 × 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.

2.3. 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 5 min. 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 × 1.0 m^2, with sufficient space approximately 0.50 m between treatments. Each trial started at 10:00 a.m. and finished at 2:00 p.m. 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.

2.4. Stable isotope sample collection and analyses

During each of the HOBO trial days, samples of macrophytes and

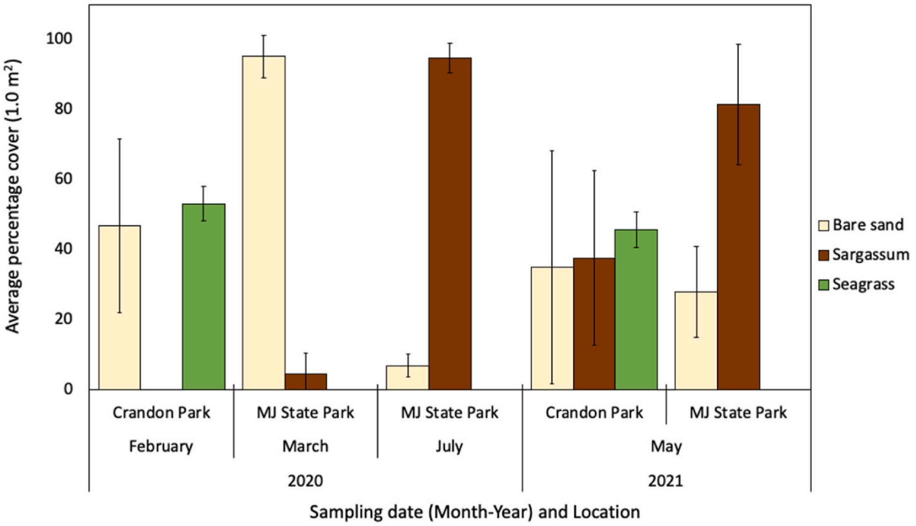

Fig. 3. Average percentage cover of macrophytes per series of quadrats in Crandon Park and MJ State Park per sampling dates in 2020 and 2021. Error bars represent standard deviation. Empty bars represent a true zero value.

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 4 h 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 65 °C 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).

2.5. 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

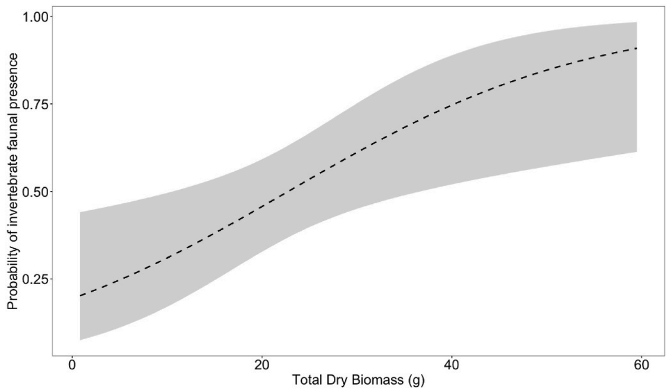

Fig. 4. Logistical regression model of probability of finding invertebrate fauna present per total dry biomass amount collected. Grey shading represents the 95% confidence interval.

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).

3. Results

3.1. Field sampling

Field sampling at 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. 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 (Supplementary Fig. 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 to 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. A breakdown of samples with the number of invertebrates collected can be found on Supplementary Table 1. 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%–75.0% (Fig. 4).

A total of 7427 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 ($p = 0.048$) 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. 5A, stress = 0.07, k = 2) or dominant taxa (Fig. 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 1A). However, when examining dissimilarities in presence-absence of fauna, those dissimilarities were contributed by dipterans, beetles, and arachnids (Table 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. 5C, stress = 0.08, k = 2, and Fig. 5D, stress = 0.07, k = 2). SIMPER analyses showed amphipods and dipteran larvae contributing to dissimilarities in abundance (Table 1C), while dipterans and beetles

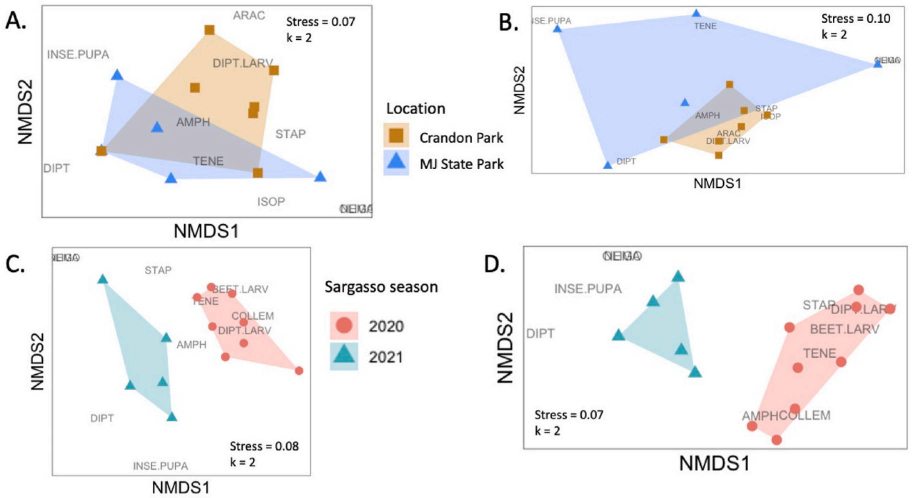

Fig. 5. Series of non-metric multidimensional scaling of associated invertebrate faunal communities via abundance or presence data. Visualizations include the following: (A.) invertebrate presence-absence between Crandon and MJ State park during the 2021 sargasso season, (B.) invertebrate densities (per 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).

Table 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.

A.	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

B.	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

C.	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

D.	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

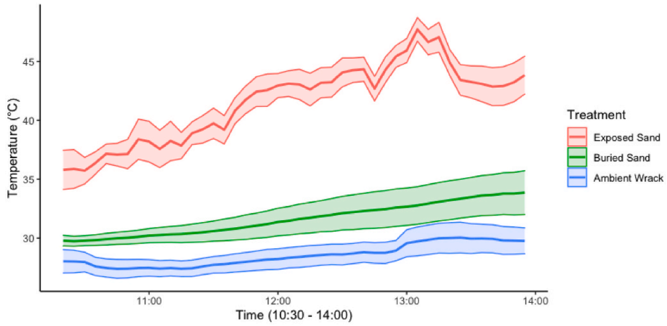

Fig. 6. Overall changes in temperature based on treatments of the HOBO logger microhabitat experiment. Data was compiled using all four trials during the sargasso season 2021. Bold line represents average value compiled for all four trials. Error ribbon represents standard error.

(staphylinid and tenebrionid) of both life stages contribute to dissimilarities in frequency (Table 1D).

3.2. Microhabitat experiment

Temperature was statistically discernible 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 reached 1 p.m. 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 reached 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. 6). Each individual trial demonstrated differences in temperature between month and day of trial ($p > 0.001$) and location ($p > 0.001$).

3.3. 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 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. 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 to 70% sourced from other marine subsidies than pelagic sargasso, depending on location (Supplementary Table 2).

4. 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

Table 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.

	Crandon Park			MJ State Park		
	Number of samples	δ15N (vs Air) (Average ± Std.Dev if applicable)	δ13C (vs PDB) (Average ± Std.Dev if applicable)	Number of samples	δ15N (vs Air) (Average ± Std.Dev if applicable)	δ13C (vs PDB) (Average ± Std.Dev if applicable)
Fauna						
Annelid						
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			
Syringodium filiforme (rhizome)	5	4.32 ± 0.47	−10.264			
Terrestrial Plants						
Cocoloba uvifera (leaves)	5	−1.07 ± 1.11	−27.836	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

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

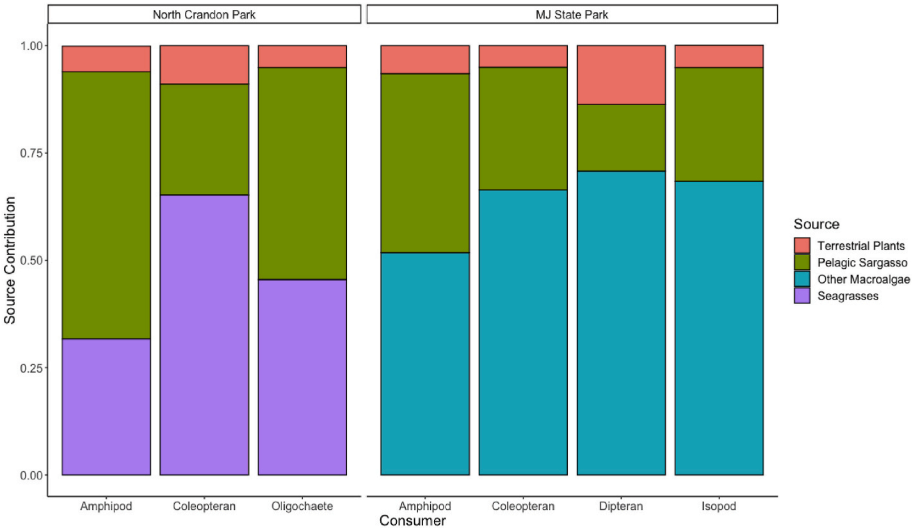

Fig. 7. Average source contribution by proportion to consumer resource use between locations during the 2021 sargasso season.

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 δ^{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 and 65% of their resource use from pelagic sargasso, suggesting a trophic link between sargasso and amphipod consumers. 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-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 δ^{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 pelagic sargasso, as a seasonal and dynamic resource especially during inundation events, was used extensively by terrestrial invertebrate fauna.

CRediT authorship contribution statement

Lowell Andrew R. Iporac: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **W. Ryan James:** Writing – review & editing, Software, Resources, Formal analysis, Conceptualization. **Ligia Collado-Vides:** Writing – review & editing, Supervision, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Lowell Andrew Iporac reports financial support was provided by National Science Foundation.

Data availability

Most data will be available on request. Suppl. Table 1 has raw data of invertebrate fauna associated with wrack samples.

Acknowledgments

We would like to thank lab volunteers Nancy Ayala, Marydelis Lugo, Gabriela Rodriguez, Deepak Rapolu, Kimberly Gonzalez, Marielys Gutierrez, Vanessa Mendoza, and many others for their lab and field assistance throughout many semesters. We would also like to thank Carlos Varela Perez for talitrid amphipod identification, and the volunteers at BugGuide.Net for dipteran identification. Collection of samples was permitted by Miami-Dade County Department of Environmental Resources Management (No. 318) and the Florida Department of Environmental Protection (#12261915). This material is based upon work supported by the National Science Foundation under Grant No. HRD-1547798 and Grant No. HRD-2111661. These NSF Grants were awarded to Florida International University as part of the Centers of Research Excellence in Science and Technology (CREST) Program. This is contribution number #1587 from the Institute of Environment, a Preeminent Program at Florida International University. Additional support was provided by the Stable Isotope Laboratory at FIU and the Dissertation Year Fellowship from Florida International University.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108414.

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