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Nutrient Dynamics of Floating Seagrass Wracks in Greater Florida Bay

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Nutrient Dynamics of Floating Seagrass Wracks in Greater Florida Bay

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B.S., University of Connecticut, 2013

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Nutrient Dynamics of Floating Seagrass Wracks in Greater Florida Bay

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Abstract

Floating aggregations of seagrass wrack (i.e., leaves shed from seagrass beds) can serve as an ecological “hot spot” contributing to the survival of many species in the form of habitat and food source. Considerable research has been done on assessing trophic transfer of nutrients from seagrass wrack that is washed ashore, but little is known about nutrient dynamics in floating seagrass wrack. Here, drifters were deployed to track the location of floating wracks created in Greater Florida Bay and mesocosm experiments were conducted on two different of floating macrophytes (*Syringodium filiforme*, *Thalassia testudinum*, and *Sargassum sp.*) to estimate the sinking rate and the contribution of particulate and dissolved carbon and nitrogen released from the floating wracks. Floating wracks were tracked and carried through channels from Greater Florida Bay *S. filiforme* beds to near the Gulf Stream 15 km offshore. A large fraction of seagrass leaves remained buoyant for over 14 days in the mesocosms with daily shedding rates of individual leaves statistically decreasing over time from 10-15% initially to less than 5% after 6 days. When individual leaves became aggregated into whorled structures, as found offshore, the shedding rate became negligible at $<2\% \text{ d}^{-1}$ and wracks can persist for extended times. As the floating wrack ages it contributes to nutrient pools, especially total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and colored dissolved organic material pools. TDN was composed of approximately 80% dissolved organic nitrogen, with remainder dissolved inorganic nitrogen largely composed of ammonium. Both TDN and DOC showed variable rates of change but ultimately increased concentration from initial to final days of incubation. With the duration of wracks and the amount of nutrients produced, seagrass wrack can serve as an important resource for organisms living in oligotrophic waters.

1.0 Introduction

Seagrass ecosystems serve to interconnect marine and terrestrial ecosystems through passive and active transport of nutrients, detritus, prey and consumers (Heck et al. 2008). An important element of this interconnection is through the production and transport of seagrass detritus from one habitat to another. As seagrass meadows age, senesce, and interact physically with the environment around them, leaves may break off from the beds and either sink to the seafloor surrounding the plants, or float to the surface. Due to the high primary productivity and turnover rates of seagrass leaves (Zieman, Fourqurean & Iverson 1989), considerable amounts of leaves are shed from the meadows and can be transported away from the beds by currents and waves (Mateo et al. 2006). Large aggregations of floating vegetation called “seagrass wrack” can be formed (Dierssen et al. 2015) and the biomass is ultimately exported to the seafloor or washed ashore on beaches. Many studies have quantified nutrient subsidies from wrack to beach communities (Coupland, et al. 2007, Dugan et al. 2011) and the deep sea (Menzies et al. 1967, Vetter 1994, 1998), but less is known about the habitat structure and nutrient dynamics of floating seagrass wrack, particularly in surface waters devoid of nutrients.

Although reports are few, different species of seagrass appear to export different amounts of biomass ranging from 0 to 100% of total production (Mateo et al. 2006). The morphology and buoyancy of the leaves can determine the duration of the floating wrack with long, bulky leaves sinking soon after shedding and light, thin leaves staying afloat for longer period of time (Mateo et al. 2006). For example, a study on adjacent beds of broad flat-leafed *Thalassia testudinum* Banks & Sol. ex Koenig (turtle grass) and thin cylindrical-leafed *Syringodium filiforme* Kuetz (manatee grass) from a site in the U.S. Virgin Islands found that *T. testudinum* exported only 1%

of its leaf production, while *S. filiforme* exported 60-100% of its biomass (Zieman et al. 1979). In addition to differences in leaf morphology, the root structure also plays a role in export. *T. testudinum* is more sturdily rooted in the sediment and is known to be highly recycled within the beds whereas *S. filiforme* has a fragile root system and is largely advected from beds (Hemminga & Duarte, 2000). Our study evaluates floating wrack produced in Greater Florida Bay which is home to large seagrass meadows of both *T. testudinum* and *S. filiforme* (Fourqurean et al., 1999, 2001; McPherson, 2011).

Weather, tides, and the degree of bed exposure can determine the intensity of the physical forces that serve to export seagrass leaves from the beds to distant locations offshore (Thomas et al. 1961; Menzies et al. 1967; Mateo et al. 2006). Dierssen et al. (2015) found that strong southerly winter winds in Greater Florida bay advected considerable amounts of seagrass wrack comprised predominantly of *S. filiforme* from the dense meadows in Greater Florida Bay to oligotrophic Atlantic Ocean waters of the Atlantic. Over time, the leaves became more aggregated into patches and could be found in long windrows produced by downwelling lobes of Langmuir circulation. In addition, the wrack observed floating over the continental shelf contained aggregates of leaves occurring in whorled structures. Off the Tasmanian coast, Thresher et al. (1992) similarly found offshore transport of seagrass detritus coincided with strong winterly storms. Winds and turbulence associated with the 1960 Hurricane Donna produced over 1 million kg of *T. testudinum* wrack washed ashore along the beaches in Biscayne Bay (Thomas et al. 1961).

Floating at the sea surface, seagrass wrack can serve as a habitat or a metabolic “hot spot” similar to other floating vegetation such as floating macroalgae *Sargassum sp.* In tropical waters, pelagic *Sargassum sp.* wrack is an important home to many species of organisms, including juvenile fish species, many invertebrate species including shrimp, crabs, and nudibranchs, and epiphytic organisms like hydroids, bryozoans, and algae (Kingsford and Choate, 1985; Mason & Manooch, 1985; Morgan et al., 1985; Moser et al., 1997; Cho et al., 2001; Dempster and Kingsford, 2004; Jobe & Brooks, 2009), as well as recreationally and commercially important fish species like mahi, snapper, and grouper (Coston-Clements & Center, 1991). Thresher et al. (1992) is one of the only studies to report on the trophic impacts of floating seagrass wrack. Through indirect lines of evidence, they report that microbial decomposition of floating seagrass played a pivotal role in the coastal planktonic food chain. This study aims to bridge this gap by examining the degradation rate and capacity for nutrient regeneration of Florida Bay wracks composed of a variety of primary producers. Travel time of wracks and the shedding rate of seagrass beds were also examined to inform understanding of the life cycle of a floating seagrass wrack.

2.0 Methods

2.1 Study Region

This study was conducted in Greater Florida Bay during January 2014, with experimental work conducted at the Keys Marine Laboratory on Long Key, Florida, United States. Greater Florida Bay is a shallow estuary grading into a tropical lagoon, influenced by the Gulf of Mexico and the Everglades. The south Florida region, which includes Greater Florida Bay and the Atlantic

Ocean side of the Florida Keys, is covered by ~14,000 km² of seagrass. *T. testudinum* has an estimated area of 6,400 km² and *S. filiforme* of 4,400 km² (Fourqurean et al., 2001).

Winds in Greater Florida Bay during the winter are higher than during the rest of the year, and usually blow from the northeast (Schomer and Drew, 1992). During the study period in January 2014, high wind speeds over 10 m s⁻¹ created likely conditions for forming wrack. Thus, these data will represent the higher end of wrack-mediated transport of nutrients.

2.2 Seagrass Bed Leaf Loss

Periods of high leaf loss in seagrass beds are assumed to be heavily influence by current speed, often associated with surface winds in these shallow environments. To observe this phenomenon during January, a period in Greater Florida Bay with high winds, a bed was monitored to find leaf loss with and without flow.

Three units were installed over a dense *S. filiforme* bed in Greater Florida Bay, west of Long Key, at (24.900266° N, -80.920293° W). Two of the units blocked the flow of the current from reaching the bed and a larger, flow-through unit was open to the current. Two translucent plastic bins (96 L Sterilite tote) with solid sides and top were secured with rebar into the bed, approximately 1 m apart. Each covered an area of 0.6 m x 0.473 m and were placed in similar areas of high *S. filiforme* density within the bed. The unit open to the flow of the water was constructed of PVC pipe (2.5 m x 2.5 m) secured with rebar into the bed, and covered with a fine screen mesh (1mm) supported by a coarser mesh on the frame. The flow-through unit covered an area of 6.25 m² and was placed in an area of high *S. filiforme* density within the bed, similar to

the solid bins. The flow-through unit was located approximately 3 m from the solid bins. For all experiments, seagrass detritus was cleared from within the bin.

For the solid bins, shed leaf litter was collected one day after installation, to more accurately obtain a per-day loss of leaf litter. For the flow-through unit, shed leaves were collected on days 2, 4, 8, and 11 following deployment. All collections were conducted between 1000 and 1500 hours on each sampling date. Buoyant leaves were observed floating on the surface of the water above the seagrass beds in Greater Florida Bay during collection days. The leaves generally were floating individually, not aggregated.

2.3 GPS drifters

Three drifters were deployed simultaneously over the dense *S. filiforme* bed used to estimate leaf loss from the bed in order to see where seagrass shed from that particular bed may travel. The drifters also served to track the flow of drifting vegetation for use in with the PRISM overflights.

Three passive Lagrangian surface drifters were deployed simultaneously over the dense *S. filiforme* bed in Greater Florida Bay, west of Long Key, at (24.900266° N, -80.920293° W) to track flow of drifting vegetation during the PRISM overflights. Drifters were released at this position after the cage was erected, in order to see where seagrass shed from that particular bed may travel. Once deployed the drifters were allowed to float freely until collection, either when they ran aground or advected from Greater Florida Bay out to the Atlantic Ocean (Figure 3). The neutrally buoyant GPS drifters were constructed of plastic buckets, foam, and dive weights, and outfitted with NOAA GPS trackers as part of the Northeastern Regional Association of Coastal

and Ocean Observing Systems (NERACOOS) program. The drifters tracked the upper meter of the water column including wind drag, and contained GPS transmitters that broadcast their position every half hour (<http://www.neracoos.org/drifters>).

2.4 Temporal Loss of Biomass from Wracks

Leaf shedding by wrack removes biomass from the wrack and provides an external source of nutrients to the seafloor as the wrack travels. To observe the average shedding rate by various types of wrack, experimental bins were created to monitor biomass loss over time.

Wrack was collected from the water off of the Keys Marine Lab dock in Greater Florida Bay (24.825875° N, -80.814375° W). The bulk of the collected wrack was primarily *S. filiforme*, with *T. testudinum* and *Sargassum sp.* also present. To establish the composition of the treatments, collected wrack was separated by species to isolate the two seagrass species of interest: *T. testudinum* and *S. filiforme*. The second treatment of wrack consisted of the collected wrack, without any separation of species or removal of algae. The experiment contained 97% *S. filiforme* and 3% *T. testudinum*, by wet weight and was considered *S. filiforme*.

Three flow-through tanks with 36 psu raw seawater pumped from Greater Florida Bay were established, each representing a single treatment type: *T. testudinum* wrack, *S. filiforme* wrack, and a mixed species wrack, which was approximately 97% *S. filiforme*. Each treatment tank contained three replicate flow-through bins with mesh sides. Flow-through tanks were located outside, thus maintaining ambient air temperature and light. Water temperature was maintained at ambient Greater Florida Bay temperature via the flow-through system. For each treatment, a

similar amount of biomass was added to the replicate flow-through bins. Wet weight for each replicate was determined after removing excess water from each sample by blotting with paper towels and spinning in a salad spinner.

Material settling to the bottom of each bin was collected daily. Wet weight was determined as described for initial weights of wrack. Dry weight was determined by rinsing samples with fresh water to remove salt, then drying samples at 50°C until completely dry, at least 18 hours. All remaining floating macrophyte material was collected at the end of the experiment and wet and dry weight were measured to determine total loss of mass over the study period.

Syringodium filiforme and *T. testudinum* biomass samples from day 1 (initial) and day 12 (final) were analyzed for carbon and nitrogen content on a Costech Elemental Analyzer peripheral of a Thermo Delta V Advantage continuous flow Isotope Ratio Mass Spectrometer (EA IRMS) in the Tobias Lab, Department of Marine Sciences, University of Connecticut. For comparison, samples harvested from beds of each type of seagrass, and from naturally occurring *S. filiforme* wrack were also analyzed for carbon and nitrogen content.

2.5 Regeneration of Nutrients from Wracks to the Water Column

Floating wrack regenerates nutrients and CDOM to the water column as the wrack biomass decomposes with time and exposure to sun and weather. To estimate the regeneration of nutrients and production of CDOM, naturally collected wrack from seagrass and the macroalgae *Sargassum* sp. wrack, as well as a control treatment with no wrack, were incubated in an enclosed container in the dark, for 11 days. *Sargassum* sp. is a floating macroalgae commonly

found in the region and was used to compare nutrient dynamics from seagrass detritus versus living macroalgae.

Naturally occurring fresh seagrass and *Sargassum sp.* wrack was collected from the surface water off of the Keys Marine Laboratory dock. Seagrass was composed of *S. filiforme* (97%, wet weight), *T. testudinum* (<3%, wet weight), and a small amount of *Sargassum sp* (<0.05%, wet weight).

Three treatment buckets containing 12 L of raw Greater Florida Bay seawater (36 psu) were established in a covered outdoor flow-through tank to maintain ambient Greater Florida Bay water temperatures. The buckets were contained in thick black plastic bags, to keep the treatments in the dark and aerated. Two of the three treatment buckets held a different composition of wrack, the third was a raw seawater control. The wrack placed into the two buckets were of similar volume. The seagrass wrack initial wet weight was 310 g, the *Sargassum sp.* initial wet weight was 256 g. Amount of wrack included in each treatment was determined by choosing similar sizes of each type of wrack, which were aggregated at time of collection. Wet weight was determined as described for the previous experiment. Due to the difference in initial biomass weights, a factor of 1.2 was applied to all *Sargassum sp.* nutrient results (μM) to normalize the concentrations to a similar starting wet weight.

Water samples were collected to determine nutrients and colored dissolved organic material. Samples were collected daily for the first 8 days, then every-other day. The total length of the incubation was 14 days. Three days are not included in the analysis (days 5, 8, and 12) because

the ammonium values were impossibly high in the seawater treatment (four times the total nitrogen values). While ammonium values were more reasonable in the seagrass and seawater treatments on these days ($\text{NH}_4^+ = 0.04$ TDN and $\text{NH}_4^+ = 0.01$ TDN, respectively), ammonium was typically 0.2 to 0.3 of the total dissolved nitrogen during the rest of the incubation, thus these values are also suspect. All inorganic data from these days are not included in the analysis.

Dissolved inorganic nutrients (ammonia, nitrate, nitrite) were determined from samples filtered through Whatman glass fiber filters (GF/F, pore size of $0.45\ \mu\text{m}$) and delivered into acid washed plastic 18 mL, HDPE, scintillation vials. Samples were held at -20°C until analysis. Water samples were analyzed for dissolved inorganic nitrogen on a WestCo SmartChem Autosampler in the Department of Marine Sciences' SMALER Lab, University of Connecticut.

Dissolved organic nutrients (organic carbon, total nitrogen) were determined from samples filtered through Whatman GF/F filters and delivered into acid washed, combusted glass vials and acidified with HCl to a pH of 2. Separate water samples were filtered through a $0.22\ \mu\text{m}$ Millipore polycarbonate filter to estimate the contribution of bacteria to dissolved organic carbon and total nitrogen in the incubation water. Dissolved organic carbon and total dissolved nitrogen were analyzed using a Shimadzu TOC/TN V analyzer in the Department of Marine Sciences' SMALER Lab, University of Connecticut.

Particulate nitrogen and carbon were determined from filtering known volumes of water through Whatman glass fiber filters (GF/F, pore size of $0.45\ \mu\text{m}$). Filters were held dry in a dessicator

until analysis on a Fisons Instruments Elemental Analyzer in the Department of Marine Sciences' SMALER Lab, University of Connecticut.

Colored dissolved organic material was determined from samples filtered through a 0.22 μm Millipore polycarbonate filter and collected for immediate measurement by cuvette on an Analytical Spectral Devices (ASD) FieldSpec4 spectroradiometer. The ASD was field calibrated with Milli-Q Synthesis A10 ASTM Type I reagent grade water from the Department of Marine Sciences' SMALER Lab, University of Connecticut.

2.6 Statistical Analyses

All statistical tests were conducted in *SigmaPlot* 11.0. When data did not meet the assumptions of normality and equal variance, nonparametric alternatives were used.

3.0 Results

3.1 Export of Wrack from Seagrass Beds

Seagrass wrack was observed in large quantities within Greater Florida Bay as well as on the Atlantic Ocean side of the Keys during January. Wrack on the sea surface was observed to be 97% *S. filiforme* and <3% *T. testudinum* (Dierssen et al., 2015). The experimental seagrass bed located within Greater Florida Bay (Figure 1) was primarily *S. filiforme*, with patches of *T. testudinum* located within the bed. Export from this actively growing seagrass beds was estimated in terms of leaf litter amount and distance the detritus traveled on the sea surface.

Production of seagrass detritus was estimated both with and without flow. The average daily shedding rate normalized to area ($\text{g d}^{-1} \text{m}^{-2}$) for the observed seagrass bed with flow was approximately $70 \pm 50 \text{ g d}^{-1} \text{m}^{-2}$ for *S. filiforme* and approximately $1 \pm 0 \text{ g d}^{-1} \text{m}^{-2}$ for *T. testudinum*. Without flow, the seagrass bed exhibited a daily shedding rate per m^2 of meadow of $20 \pm 5 \text{ g d}^{-1} \text{m}^{-2}$ for *S. filiforme*, and shed no *T. testudinum* over the observation period.

3.2 Transport of Wrack

Drifter buoys deployed over the dense seagrass beds north of Long Key during low to high wind conditions provided an estimate of the distance that leaf detritus formed in Greater Florida Bay traveled on the sea surface due to winds and currents. The first buoy deployment coincided with a strong wind event ($>13 \text{ m s}^{-1}$) coming from the north ($0/360^\circ$) and all three drifters travelled through tidal channels between the islands and out into the Atlantic Ocean (Figure 2, Figure 3). The drifters stayed in close proximity to each other and were collected floating in the middle of a large aggregation of wrack approximately 90 km southwest of the initial deployment area ($24.722425 -80.878236$) (Figure 3). Leaf litter became aggregated due to circulation patterns driven by wind and tides, as well as Gulf Stream fronts (Dierssen et al. 2015). Wracks found in the Atlantic Ocean were in dense “whorls”, weighing about 300 g wet weight and measuring about 20 cm in diameter and 10 cm in depth (Figure 4).

During the second drifter deployment, wind speed remained low to moderate ($< 8 \text{ m s}^{-1}$) and the drifters remained within Greater Florida Bay circulating with the tidal cycle until southerly winds develop over 10 m s^{-1} on 16 January and the buoys traveled south and washed ashore on Long Key (Figure 2, Figure 3). The buoys were collected with large amounts of beached *S.*

filiforme wrack. We note that had the buoys been located further to the west they may have traveled through the channel and been advected to the Atlantic Ocean similar to the other deployments.

The third drifter deployment from 17-19 January began with southerly winds ($> 12 \text{ m s}^{-1}$) and the buoys were advected to the Atlantic Ocean through the tidal channels (Figure 2, Figure 3). Communication with the third buoy was lost. However, this was the first deployment where the buoy paths diverged and one of the buoys headed west and the other east along the continental shelf.

3.3 Temporal Loss of Biomass from Wracks

Experimental measurements of the loss of biomass from floating seagrass detritus provided an indication of the sinking rates and length of time that wracks may remain afloat. In all treatments, a large fraction of the seagrass detritus remained floating for the duration of the experiment (>14 days) (Figure 5). The high variability during the first 5 days of the experiment is notably different than days 6-14, as is the average value. For this reason the average of the initial period (days 1-5) are compared to the average of the latter period (days 6-14) to assess differences between time and among treatment. The shedding rates of the single species *S. filiforme* wrack and the 97% *S. filiforme* wrack were significantly different during the first 5 days of the experiment compared with the last 9 days (Table 1, Figure 5). While the shedding rates of the single species *T. testudinum* wrack and the whorl of *S. filiforme* did not exhibit this same temporal difference (Table 1, Figure 5), they were also analyzed as day 1-5 and day 6-14 to allow for comparison with the other two treatments.

Sinking rates of the loose non-aggregated *S. filiforme* leaves were statistically higher in the initial portion of the experiment (Days 1-5) compared to the latter half of the experiment (Days 6-14) (1-way ANOVA, $F(7,79) = 15.522$, $P = <0.001$). The wrack lost 13% per day of the initial wrack initially and the shedding rate decreased to 2% at the end of the experiment.

This was in contrast to the other two treatments where no statistical differences were found in shedding rates for *T. testudinum* and the whorl treatments over the duration of the experiment.

The lowest shedding rates were found in the whorl treatments where only 2% was lost per day. However, the shedding rate over time for all the treatments converged to the lowest rate of 1% per day.

Treatments of *S. filiforme* and the 97% *S. filiforme* seagrass were statistically similar to each other in the initial portion (days 1-5) of the experiment. Those initial days for the *S. filiforme* and the 97% *S. filiforme* seagrass were different than the initial portion (days 1-5) of shedding for *T. testudinum* and the whorl treatments, as well as all treatments in the later portion (days 6-14) of the experiment (Table 2).

Table 1: Results from of the 2-way ANOVA, $F(1,3) = 13.151$, $p = 0.001$, and the Holm-Sidak multiple comparison procedure indicate significant differences (sinking wet mass (g) normalized to initial wet weight (g) of each treatment) between the first and second portions of the

experiment for *S. filiforme* and 97% *S. filiforme* wrack treatments, but not for *T. testudinum* or the whorl treatments. Overall significance level=0.05.

Treatment	<i>S. filiforme</i>	97% <i>S. filiforme</i>	<i>T. testudinum</i>	Whorl
Mean (1-5)	0.12	0.14	0.03	0.02
SEM	0.02	0.02	0.02	0.02
Mean (6-end)	0.04	0.03	0.05	0.01
SEM	0.01	0.01	0.02	0.02
Difference of Means	0.08	0.11	0.02	0.00
Significant?	Yes	Yes	No	No
t	3.722	4.903	0.776	0.144
P value	0.001	<0.001	0.445	0.887

Table 2: Days 6-14 for all treatments are similar in sinking rate (1-way ANOVA $F(7,79) = 15.522$, $p < 0.001$). Green boxes indicate significance between days and amongst treatments, red boxes indicate no significance between days and amongst treatments.

	<i>S. filiforme</i> initial	<i>S. filiforme</i> final	97% <i>S. filiforme</i> initial	97% <i>S. filiforme</i> Final	<i>T. testudinum</i> initial	<i>T. testudinum</i> final	Whorl initial	Whorl Final
<i>S. filiforme</i> initial								
<i>S. filiforme</i> final								
97% <i>S. filiforme</i> initial								
97% <i>S. filiforme</i> Final								
<i>T. testudinum</i> initial								
<i>T. testudinum</i> final								
Whorl initial								
Whorl Final								

The sum of the wet weight collected and the final wet weight of the floating material left at the end of the experiment was greater than the original wet weight at the start of the incubation. The final wet weight of the material still floating and the mass collected over the course of the experiment was approximately 1.2 times the initial wet weight for the 97% *S. filiforme* wrack and the single species *T. testudinum* wrack; and approximately 1.1 times the initial weight for the single species *S. filiforme* wrack and the whorl. This increase in biomass is likely due to the growth of epiphytes, accounting for a 10 to 20% increase in biomass over the 14 days.

3.4 Dissolved nitrogen wrack exudate

Besides shedding particulate matter, seagrass wrack exudes nutrients as it ages. This wrack incubation experiment was performed in the dark in order to quantify a high-end estimate of wrack exudate, purposefully excluding processes such as water exchange and photosynthesis.

Total dissolved nitrogen (TDN) in all treatments was primarily composed of dissolved organic nitrogen (DON) with a lower fraction of dissolved inorganic nitrogen (DIN). There is very little pattern with time based on the measured values of DON as a fraction of TDN (Figure 6).

DON as a fraction of TDN was variable on the incubation, and a one-way repeated analyses of variance of effective day on the fraction of DON showed some significant differences, $F(2,7) = 8.908$, $p = <0.001$. DON as a fraction of TDN was approximately 80% for seagrass, 75% for *Sargassum sp.* and 70% for seawater (Table 3, Figure 7). The remaining fraction in all cases was DIN, which was comprised mostly of ammonium.

Table 3: Fraction of dissolved organic nitrogen in total dissolved nitrogen Shapiro-Wilk normality test for Seagrass, *Sargassum sp.*, and seawater treatments, including descriptive statistics for each treatment.

Treatment	Seagrass	<i>Sargassum sp.</i>	Seawater
W-Statistic	0.834	0.914	0.830
p-value	0.065	0.380	0.060
Normal?	Yes	Yes	Yes
Mean	0.800	0.763	0.698
Standard Deviation	0.204	0.151	0.139

To look at the TDN data differently, the variation of the mean for DON as a fraction of TDN with time was considered. Days 6-7 for all treatments appear different from the rest of the days (Figure 8).

The fraction of DON in TDN differing from the mean for the days 6-7 showed statistically significant differences among the groups (one-way repeated measures ANOVA $F(5,18) = 9.062$, $p < 0.001$). In the days 6-7 all treatments showed an lower concentration of DON (μM) as a fraction of TDN (μM). During days 6-7 DON as a fraction of TDN for seagrass and seawater treatments measured approximately 50% for and 60% for *Sargassum sp.*, while during the rest of the sampling period DON was approximately 80% of TDN for all treatments (Table 4, Figure 6).

Table 4: Seagrass, *Sargassum sp.*, and seawater treatments showed differences in the DON as a fraction of TDN between their respective days 6-7, and rest of the days sampled (1-way ANOVA, $F(5,18) = 9.062$, $P < 0.001$).

Treatment	Seagrass	<i>Sargassum sp.</i>	Seawater
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Mean (days 6-7)	0.49	0.59	0.49
Standard deviation of mean (days 6-7)	0.06	0.06	0.03
Mean (rest of days)	0.85	0.82	0.77
Standard deviation of mean (rest of days)	0.11	0.12	0.06

DIN comprised the remainder of the TDN. DIN consisted primarily of ammonium (NH_4^+), with nitrate (NO_3^-) and nitrite (NO_2^-) often below the detection limit of the instrument.

TDN was chosen to represent nitrogen patterns based on the analyses of fraction of DON in TDN (Figure 8). Values of daily rate of change of TDN for all treatments were not variable through time ($p=0.930$). The rate of change of TDN within each treatment were not statistically different from each other (1-way ANOVA $F(6,2) = 0.0123$, $p = 0.351$), because the rates of change for each treatment were variable with time. The mean daily rate of change for TDN was $0.436 \pm 3.665 \mu\text{M d}^{-1}$ for the seagrass, $0.259 \pm 1.081 \mu\text{M d}^{-1}$ for *T. testudinum*, and $0.312 \pm 0.548 \mu\text{M d}^{-1}$ for seawater (Figure 8).

In order to assess the net change over two weeks in nutrient concentration in the treatments, the difference between last and first day concentrations were calculated. These net changes were compared among treatments to determine if the rate of regeneration of nutrients varied by wrack type. The first and last sample day of all treatments found to be statistically different from each other (Table 5). Treatments were variable and ultimately ended the experiment on a different value of TDN (μM) than it began, which for all treatments was a larger value. These experiments were conducted in the dark in a contained environment, in order to find the maximum exudate a

wrack could produce in a simulated decay only environment. However, not all processes were accounted for, such as bacterial activity.

Table 5: TDN increased for all sample treatments between the initial and final sample days. PN values were variable for the initial and final sample days. All values were normalized to a starting wet weight mass of 310 g of wrack, the wet weight of the seagrass wrack. These values are for a two-week time period, coinciding with the experiment length and the record of wrack movement tracked by drifters. Total nitrogen is the sum of TDN and PN.

	Seagrass	Sargassum	Seawater
initial TDN (μM , avg \pm std dev)	14.3 \pm 0.18	15.3 \pm 0.23	13.5 \pm 0.28
final TDN (μM , avg \pm std dev)	20.3 \pm 0.38	22.3 \pm 0.32	16.6 \pm 0.79
2 week difference in TDN (μM , avg \pm std dev)	6.08 \pm 0.42	6.99 \pm 0.40	3.08 \pm 0.84
initial vs. final: 1-way ANOVA F(1,2) statistic	428.982	620.383	27.008
initial vs. final: 1-way ANOVA p-value	0.002	0.002	0.035
initial PN (μM)	19.6	8.14	6.01
final PN (μM)	16.8	14.0	7.08
2 week difference in PN (μM)	-2.81	5.86	1.07
2 week difference in TN (μM , avg \pm std dev)	3.27 \pm 0.42	12.9 \pm 0.40	4.15 \pm 0.84
volume (L)	15	15	15
wrack wet mass (g)	310	310	0
N mass regenerated over 14 days (mmoles N / kg wrack, avg \pm std dev)	0.158 \pm 0.020	0.624 \pm 0.019	0.200 \pm 0.041
N mass regenerated over 14 days (mg N / kg wrack, avg \pm std dev)	4.42 \pm 0.56	17.5 \pm 0.52	5.6 \pm 1.1
1-way ANOVA, comparing treatments	F(2,3) = 175.077; p-value<0.001		
Holm-Sidak multiple comparisons (letters indicate similarity)	a	a	b

Increases in PN indicate uptake of nutrients, thus the TDN observed values underestimate the actual TDN exuded from the wrack. In treatments with wrack, particulate nitrogen (PN) may infer bacterial activity. Values for the seawater treatment were subtracted from the values of the treatments with wrack in order to calculate the change due to wrack exudate (Figure 9). Day 3 is missing due to a missing sample for the seawater treatment.

Particulate nitrogen normalized to water (μM) was variable throughout the study period and were not statistically significant from each other, $F(9,1) = 0.796$, $p = 0.630$. The seagrass and *Sargassum sp.* treatments were not statistically different from each other, $F(1,9) = 0.696$, $p = 0.426$.

3.5 Dissolved carbon wrack exudate

Seagrass wrack in the incubation experiment produced large amounts of dissolved organic carbon (DOC) in the water compared to the control treatment. The daily rate of change in concentration of DOC was variable over the observation period (Figure 10).

Table 6: Daily rate of change of dissolved organic carbon Shapiro-Wilk normality test for Seagrass, *Sargassum sp.*, and seawater treatments, including descriptive statistics for each treatment.

Treatment	Seagrass	<i>Sargassum sp.</i>	Seawater
W-Statistic	0.962	0.981	0.961
p-value	0.798	0.972	0.780
Normal?	Yes	Yes	Yes
Mean	18.9	37.4	2.87
Standard Deviation	28.3	10.1	15.9

To look at the DOC data differently, the variation from the mean for DOC with time was considered. None of the treatments had statistical differences between the values of DOC differing from the mean ($p = 0.905$) (Figure 11). This is due to the rate of change of DOC in all of the treatments being variable.

In order to see the true difference between the beginning and end, the difference between last and first day differences of actual DOC sample value for each treatment were compared to see the total change. All treatments first and last days were found to be statistically different from each other (1-way ANOVA Seagrass: $F(1,2) = 6058.319$, $p < 0.001$; *Sargassum sp.*: $F(1,2) = 8877.911$, $p < 0.001$; Seawater: $F(1,2) = 28.924$, $p = 0.033$). Treatments were variable and ultimately ended the experiment on a different value of DOC (μM) than it began, which for all treatments was a larger value. These experiments were conducted in the dark in a contained environment, in order to find the maximum exudate a wrack could produce in a simulated decay only environment. However, not all processes were accounted for, such as bacterial activity.

Increases in particulate carbon (PC) indicate uptake of nutrients, thus the DOC observed values underestimate the actual DOC exuded from the wrack. In treatments with wrack, PC may infer bacterial activity. Values for the seawater treatment were subtracted from the values of the treatments with wrack in order to calculate the change due to wrack exudate (Figure 12). Day 3 is missing due to a missing sample for the seawater treatment.

Particulate carbon normalized to water (μM) was variable throughout the study period and were not statistically significant from each other, $F(10,1) = 0.652$, $p = 0.744$. The seagrass and *Sargassum sp.* treatments were also not statistically different from each other, $F(1,10) = 0.0591$, $p = 0.813$.

3.6 Wrack as Colored Dissolved Organic Matter (CDOM) Source

A portion of the dissolved organic carbon (DOC) produced by the wrack was colored dissolved organic matter (CDOM). CDOM, also referred to as gilvin, gelbstoff, or yellow substance, is largely humic substances produced from degradation processes that absorb visible light and color the water yellow (Kirk 1994). During our sample period, seagrass and *Sargassum* sp. both produced large amounts of CDOM daily. Units of CDOM are given in optical units as the absorption coefficient (m^{-1}) of blue light at 440 nm (a_{440}). Similar amounts of CDOM were produced daily by the different incubation treatments. The autochthonous CDOM (a_{440}) produced by *S. filiforme* was approximately 0.5 day^{-1} and by *Sargassum* 0.8 day^{-1} (Figure 13). Over the sample period, the CDOM was highly correlated to DOC and increased linearly with increasing DOC (Figure 14). The equation describing the relationship is:

$$\text{Seagrass CDOM} = -3.233 + (0.0285 * \text{Seagrass DOC}), r^2 = 0.970, p = 0.080$$

$$\text{Sargassum sp. CDOM} = -3.086 + (0.0301 * \text{Sargassum sp. DOC}), r^2 = 0.990, p = 0.732$$

4.0. Discussion

Floating seagrass wrack can provide ecological connectivity from the shallow benthos to the oligotrophic ocean and serves as an ecological “hot spot” contributing to the survival of many species in the form of habitat and food source. This study contributes knowledge of this floating ecosystem by evaluating the export of floating wrack from the beds using in situ cage experiments, persistence of wrack through shedding experiments, transport of the wrack to the oligotrophic ocean with surface drifters, and evaluation of the nutrients provided by decomposition of the wrack in the surrounding waters through mesocosm experiments. Together these data show that the large amounts of floating wrack produced in Greater Florida Bay can

remain buoyant for weeks releasing dissolved and particulate carbon and nitrogen into surrounding waters as they are advected to distant oligotrophic habitats.

4.1 Amount and fate of exported seagrass as wrack

Wracks of seagrass can be found throughout Greater Florida Bay, as well as in the Atlantic heading towards the Gulf Stream (Figure 3). Seagrass wrack begins with the export of buoyant, shed leaves from seagrass beds. However, few studies have documented how much wrack is produced by different species of seagrass. While not comprehensive over time and space, our results suggest that considerable amounts of wrack can be produced, especially under high wind conditions. As expected, when unaffected by flow, seagrass leaves shed at a fairly consistent rate. However, when the study beds were affected by natural flow, the rate of leaf shedding was higher and variable depending on environmental conditions. This is an indication that shedding in and around Greater Florida Bay is flow-dependent, yet variable. Under protected conditions, the older leaves are maintained by the plant for a much longer period of time, but will be shed as the plant ages and older leaves are released from the plant. During summer months, wind speed averages are lower (summer average of about 4 m s^{-1} , winter average of about 5.5 m s^{-1}) (NOAA NDBC). However, growth rate is typically higher in summer, so more leaves are aging and being shed by the plant. Thus seagrass beds may shed leaf litter at any point during the year. While the data collected in on leaf shedding in January cannot be extrapolated to the rate during summer, the expectation is that shedding will be relatively similar in magnitude.

The shed leaves from the Greater Florida Bay seagrass bed that were buoyant floated to the surface and were advected away from the beds. While those leaves observed Greater Florida Bay

were floating individually, in the Atlantic Ocean the wrack observed was aggregated into large continuous patches. Aggregation of seagrass vegetation is common in shallow waters due to slow counter-rotating vortices at the ocean's surface known as Langmuir circulation (Faller, 1971). Langmuir circulation occurs with steady wind over a body of water, and is best observed as windrows of floating macrophytes, debris, and marine foam. In the case of floating wrack, convergence zones associated with the Langmuir circulation aid to create the seagrass "whorls" (Figure 4). This arrangement of tangled leaves results in older, less-buoyant leaves being supported by more buoyant leaves. Thus, leaves that would have otherwise sunk to the bottom are maintained by their neighbors in the floating wrack. A linearly arrayed wrack, however, may allow the older plants to sink without support from their neighbors. The floating seagrass wrack observed in January 2014 ranged in length and width. Depths of observed wrack were typically between 5 and 10 cm deep. A more rafted, dense wrack would likely allow for a longer period of floating time.

For both the linear array of wrack and the whorled array, older leaves are advected or lost from the wrack as it travels. The question is where the wrack sinks to the bottom: Greater Florida Bay or the Atlantic Ocean? In the case of the first drifter deployment, the drifters washed ashore in only 5 days. In the second drifter deployment, it took a mere 2 days to travel approximately 90 km toward the Gulf Stream. The study monitoring temporal loss of biomass from wracks found that the largest rate of loss occurred within the first 6 days (Figure 5). Thus during the study period in January 2014, most of the shed material from the wracks may have been lost from the wrack within Greater Florida Bay. This is important because it infers a limited export of wrack to

the more oligotrophic waters over coral reefs, as well as possibly providing seagrass beds in Greater Florida Bay more chance to recycle the nutrients in leaf material.

4.2 Effect of carbon and nitrogen remineralized from wrack

Wrack often washes ashore as the Keys act as a natural barrier to water moving from Greater Florida Bay into the Atlantic Ocean. The wrack that was found washed ashore varied in age, from very dark, almost indiscernible as seagrass; to fresh, green, just accumulated seagrass. Seagrass that has washed ashore is important in providing a marine subsidy to terrestrial nutrient sources. Decomposing wrack on the shore is a vital resource in replenishing intertidal sediment organic nutrients (Orr et al., 2005). Beached wrack could be important to the remineralization process by increasing intertidal DIN and DON concentrations (Dugan, et al., 2011). This important remineralization step makes nutrients once sequestered in biomass available to nearshore waters and primary producers,. This recycling effect fuels observed increases in CO₂ fluxes (Rowe et al., 1975; Rauch and Denis, 2008).

The wrack that does not wash ashore close to the source seagrass bed can be advected out to sea or onto more distant beaches surrounding Greater Florida Bay. In one drifter deployment, all three drifters were retrieved from the midst of large wracks travelling on a course towards the Gulf Stream, while in the other deployment, drifters were all found washed ashore amid new and old decomposing wrack (Figure 3, Figure 15). While these results are intriguing in their variability, horizontal advection of wrack material has not been well characterized. The distance and fate of advected wrack is an area of potential future research which could inform our understanding of these wracks as refuges for organisms and their role in nutrient cycling.

While biomass is lost from the wrack as it travels, the wrack itself is also remineralizing dissolved nutrients and CDOM as biomass is degraded. As the travelling floating wrack is continually exposed to the sun, it degrades, and contributes to nutrient pools, especially total dissolved nitrogen, dissolved organic carbon, and colored dissolved organic material pools. Seagrass wrack often covers a large area, ranging from just a few square centimeters to kilometers long. The wrack can be large, up to 300 meters long and 15 meters wide (570 m³). Nearly 50% of the DOC a wrack will release in its lifetime is within the first two weeks of floating (Lavery, et al., 2013). In this study, both DOC and TDN exhibited variable rates of concentration change over the study period, though a measurable increase in nutrients was observed from the initial to the final days of the study (Figure 8, Figure 10). A lower concentration of DON as a fraction of TDN for seagrass and seawater treatments was exuded, measuring approximately 50% for and 60% for *Sargassum sp.*. However, during the rest of the sampling period DON was approximately 80% of TDN for all treatments (Table 4, Figure 6). While understanding nutrient delivery from seagrass wrack could play an important role in understanding the nitrogen and carbon budgets, the concentration of nutrients exuded from the wrack is fairly low. A conservative, high-end estimate of the potential dissolved and particulate nitrogen maximum to the system over wrack movement timescale is approximately 0.16 mmoles N Kg⁻¹ of seagrass wrack (Table 5).

Instead it is more useful to consider the wrack as a nutrient hot-spot. The Atlantic Ocean side of the Florida Keys is historically oligotrophic. Historical values for total nitrogen (including

dissolved and particulate) are an order of magnitude smaller than the high-end estimate of TN delivery from seagrass wrack (approximately 160 $\mu\text{moles N Kg}^{-1}$) (Table 5, Table 7).

Table 7: The annual and seasonal total nitrogen (TN) values (μM) in Long Key Channel from April 2003 to November 2004 (Gibson, Boyer, and Smith, 2007).

Long Key Channel	Spring	Summer	Fall	Winter	Annual
TN (μM)	13.30	14.67	23.60	13.73	18.15

Due to the concentration of nutrients exuded from the wrack compared to the oligotrophic surrounding waters of the Atlantic Ocean, it is likely TDN and DOC are recycled locally, rather than exported. Macroalgal wrack has long been recognized as an important ecosystem engineer, an organism that directly modifies the availability of resources for other species. As a rudimentary example, in our experiments wrack that was older had accumulated more epiphytes than fresh wrack. Depending on the type of epiphytes and the state of decomposition of the wrack, some of the exuded nutrients may be used in the small water volume of the wrack itself. Algal and phytoplankton epiphytes may be expected to consume more inorganic nutrients that are exuded, while animal epiphytes may benefit from the organic nutrients demineralized from the wrack and increased phytoplankton supported by the inorganic nutrients from the wrack. In large quantities, wrack could possibly sustain a high amount of life with the release of nutrients, especially carbon and nitrogen. This community supported by floating wrack also serves as a feeding source for larger pelagic fish, which feed on the smaller organisms living on and near the wrack.

Seagrass wrack provides important ecosystem service, one of which is exporting nitrogen and carbon out of seagrass beds to both the coastal shore and the seafloor (Heck et al., 2008; Mateo et al., 2006). For some types of seagrasses, including *T. testudinum*, a large fraction of carbon is likely recycled within the seagrass bed and surrounding areas, providing a means for nutrient and carbon sequestration which benefits the overall issue of too much carbon in the atmosphere, a process termed blue carbon sequestration (Burdige, Hu, & Zimmerman, 2008; Mcleod et al., 2011).

5.0 Conclusion

This study indicates a large fraction of seagrass leaves remained buoyant for over 14 days in the mesocosms with daily shedding rates of individual leaves statistically decreasing over time from 10-15% initially to less than 5% after 6 days. As the drifters were beached by day 6 in the first deployment, and in the Atlantic Ocean by day 2 for the second deployment, most of the shed leaf material from the wrack is likely deposited within Greater Florida Bay. For wrack which remains buoyant, the contribution to the local nutrient pool is variable but ultimately increased concentration from initial to final days of incubation.

This study suggests seagrass wrack can be a locally important source of nutrients, acting as a nutrient hot-spot and micro-ecosystem, but due to the large dilution moving away from the wrack, the effect on organisms outside of the wrack will likely be negligible. While the advection and decay of wrack may contribute small amounts to the larger area over which wrack travels, we predict the greatest influence of nutrient remineralization and CDOM production to be on the organisms in the immediate areas of the wrack.

6.0 References

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7.0 Appendix: Figures



Figure 1: A. Map indicating Long Key, where the experimental study site was located. The site of the experimental seagrass bed within Greater Florida Bay where the flow and no-flow leaf shedding observations were conducted is indicated.

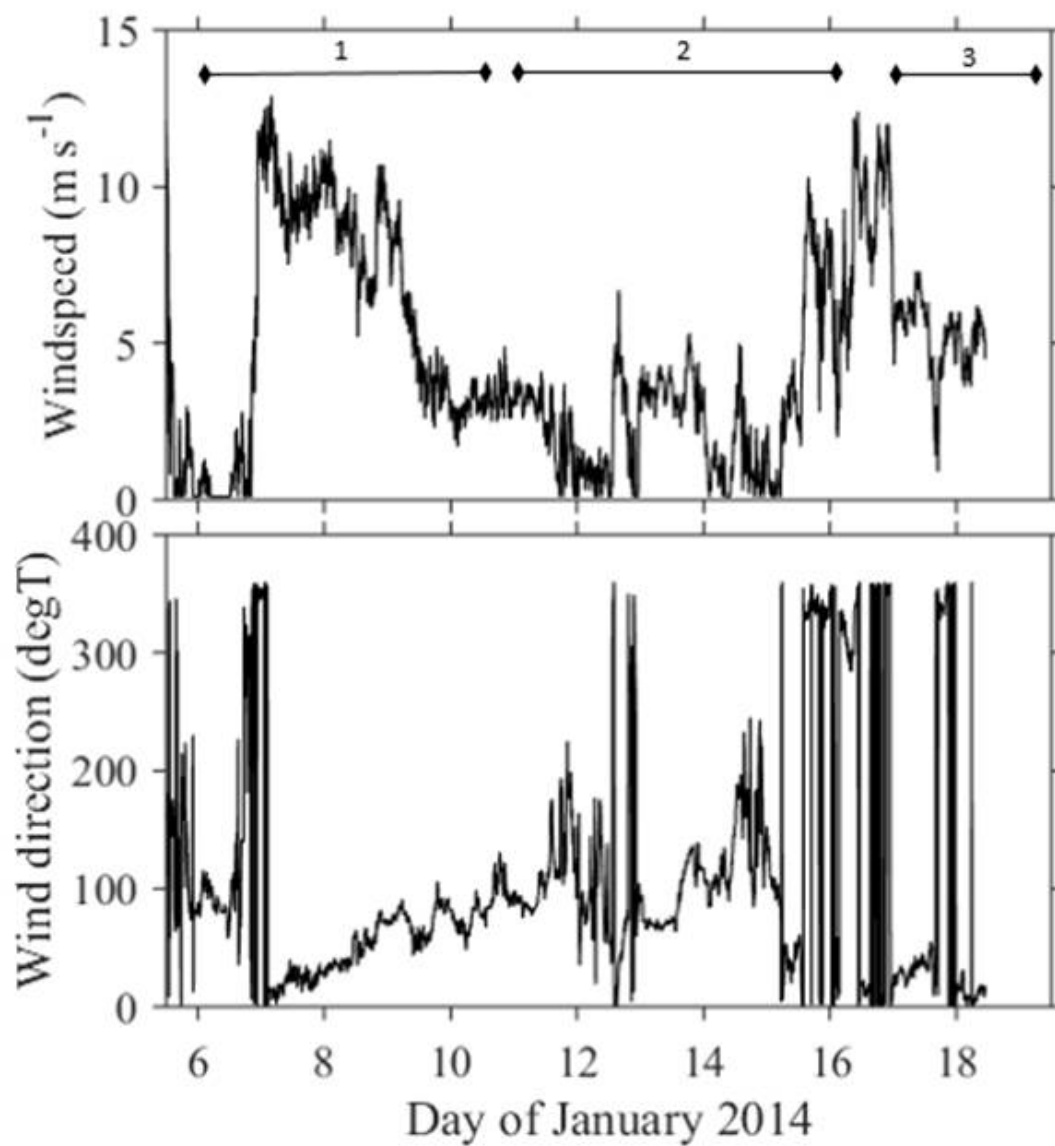


Figure 2: Windspeeds (top) in relation to the wind direction (bottom) during the three drifter deployments (indicated by lines at the top of the graphic, 1,2,3). Windspeeds ranged from 0 ms^{-1} to 13 ms^{-1} .

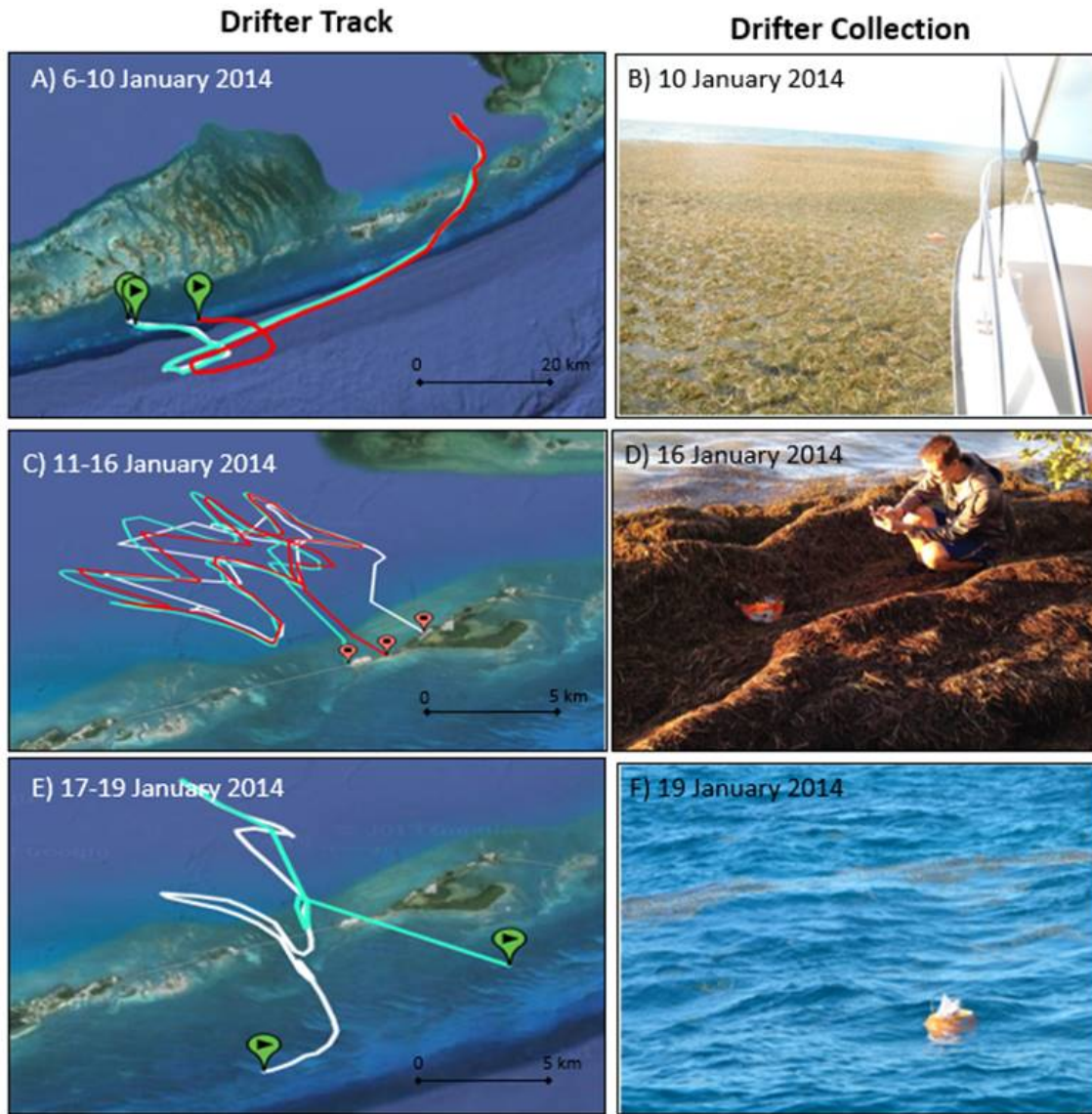


Figure 3: Image of drifter buoys movement patterns (left) and the location of the buoys, always found with seagrass (right). The three colors on the map (blue, red, white) represent the three drifters released together.



Figure 4: Seagrass wrack as seen looking up from below the surface of the water. This wrack, composed primarily of *Syringodium filiforme*, also containing *Thalassia testudinum* and *Sargassum sp.*, is aggregated in the “whorl” arrangement (photo credit Adam Chlus).

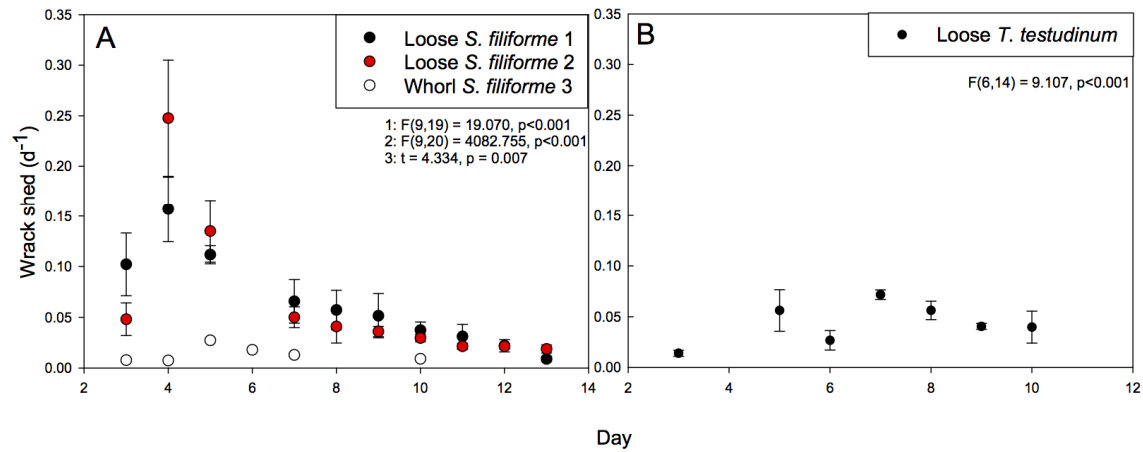


Figure 5: The daily shedding rate for wet mass normalized to the initial starting wet mass of the wrack for the four treatments; in (A) non-aggregated *S. filiforme* (Loose *S. filiforme* 1), non-aggregated 97% *S. filiforme* (Loose *S. filiforme* 2), and whorled *S. filiforme* (Whorl *S. filiforme* 3); in (B) Loose *T. testudinum* only.

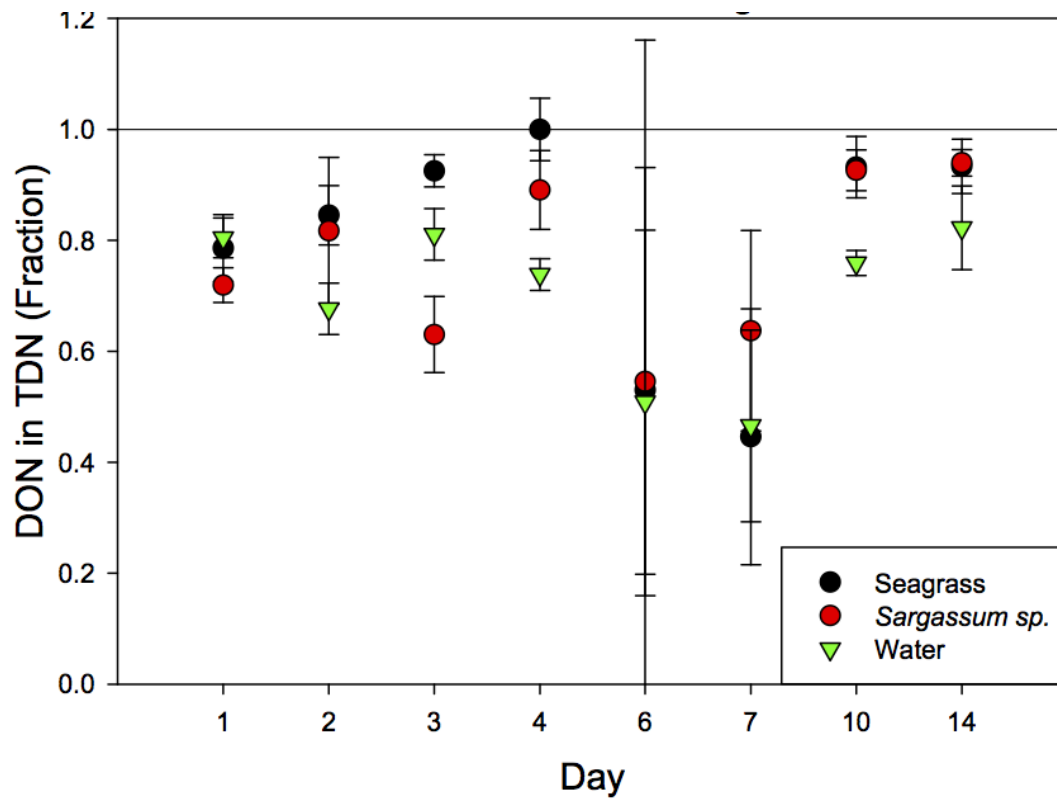


Figure 6: Differences in the fraction of dissolved organic nitrogen in total dissolved nitrogen from the mean for each treatment. The line indicates 1, the whole fraction.

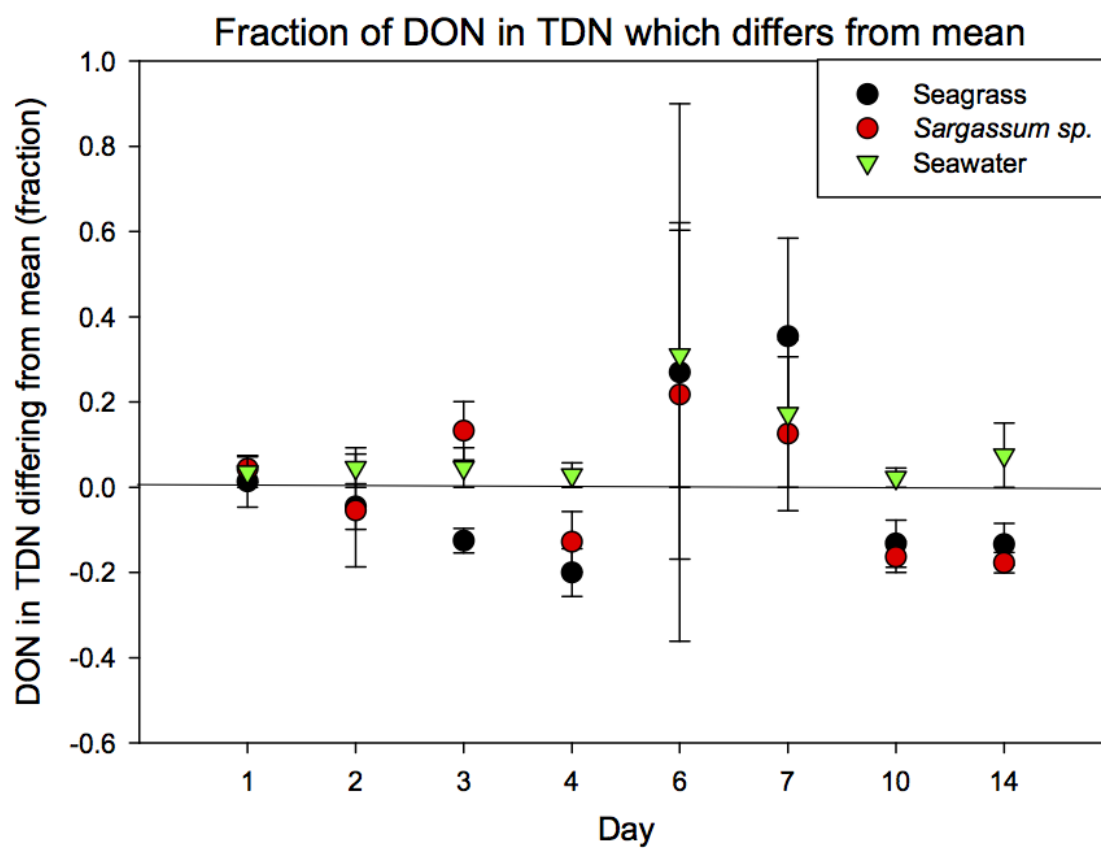


Figure 7: The fraction of dissolved organic nitrogen in total dissolved nitrogen which differs from the mean. Values were variable about the mean for all treatments, but values for days 6 and 7 look especially different for all treatments.

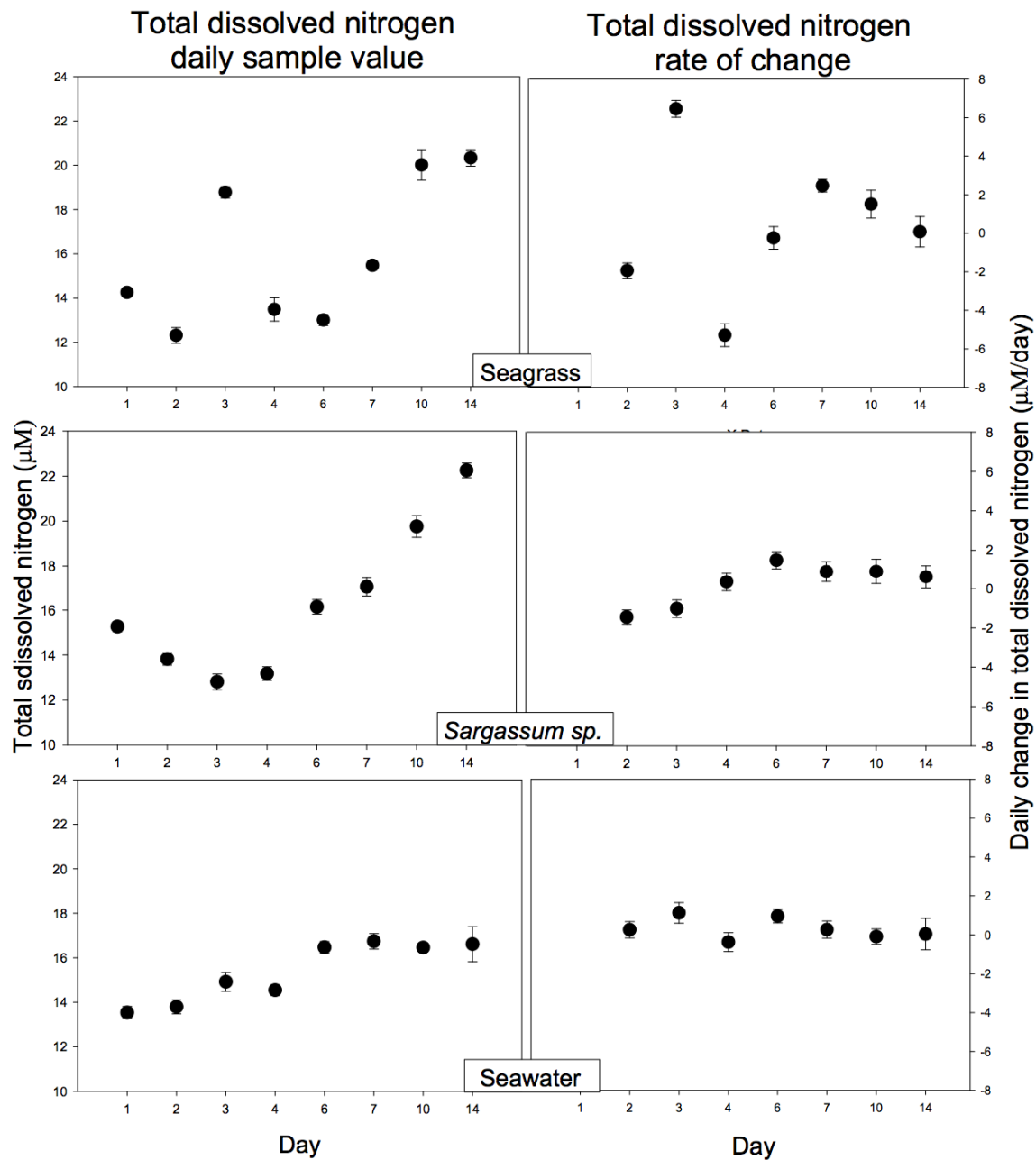


Figure 8: The left column shows the actual sampled values of total dissolved nitrogen (μM) per day for each treatment (top to bottom, seagrass, *Sargassum sp.*, and seawater). The y-axis for all treatments is between 10 and 24. The right column shows values for the daily rate of change of total dissolved nitrogen ($\mu\text{M d}^{-1}$) per day for each treatment (top to bottom, seagrass, *Sargassum sp.*, and seawater). The y-axis for all treatments is between -8 and 8.

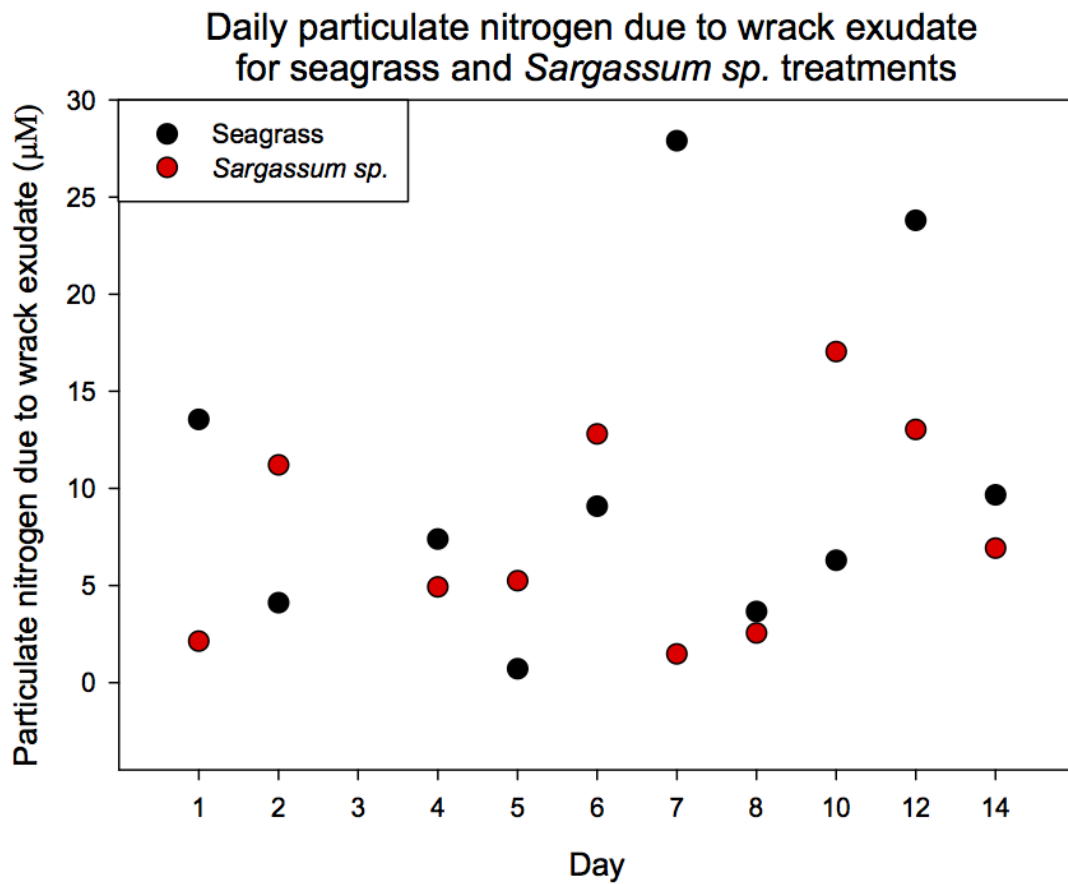


Figure 9: Daily particulate nitrogen values for seagrass and *Sargassum sp.* treatments normalized to seawater. Daily values for the seawater treatment were subtracted from daily values of the wrack treatments in order to find particulate nitrogen due to wrack exudate.

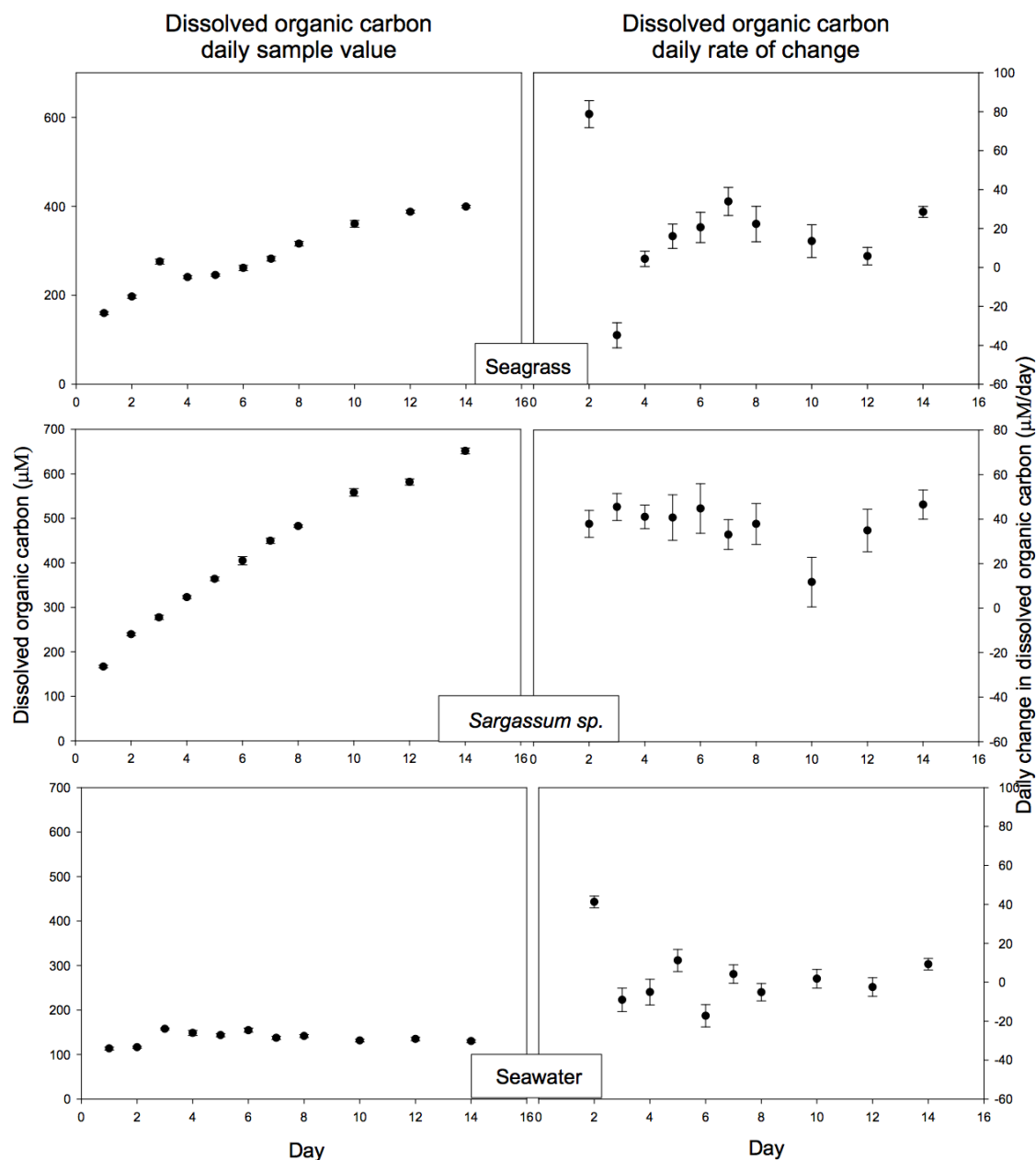


Figure 10: The left column shows the actual sampled values of dissolved organic carbon (μM) per day for each treatment (top to bottom, seagrass, *Sargassum sp.*, and seawater). The y-axis for all treatments is between 0 and 700. The right column shows values for the daily rate of change of dissolved organic carbon ($\mu\text{M d}^{-1}$) per day for each treatment (top to bottom, seagrass, *Sargassum sp.*, and seawater). The y-axis for all treatments is between -60 and 100.

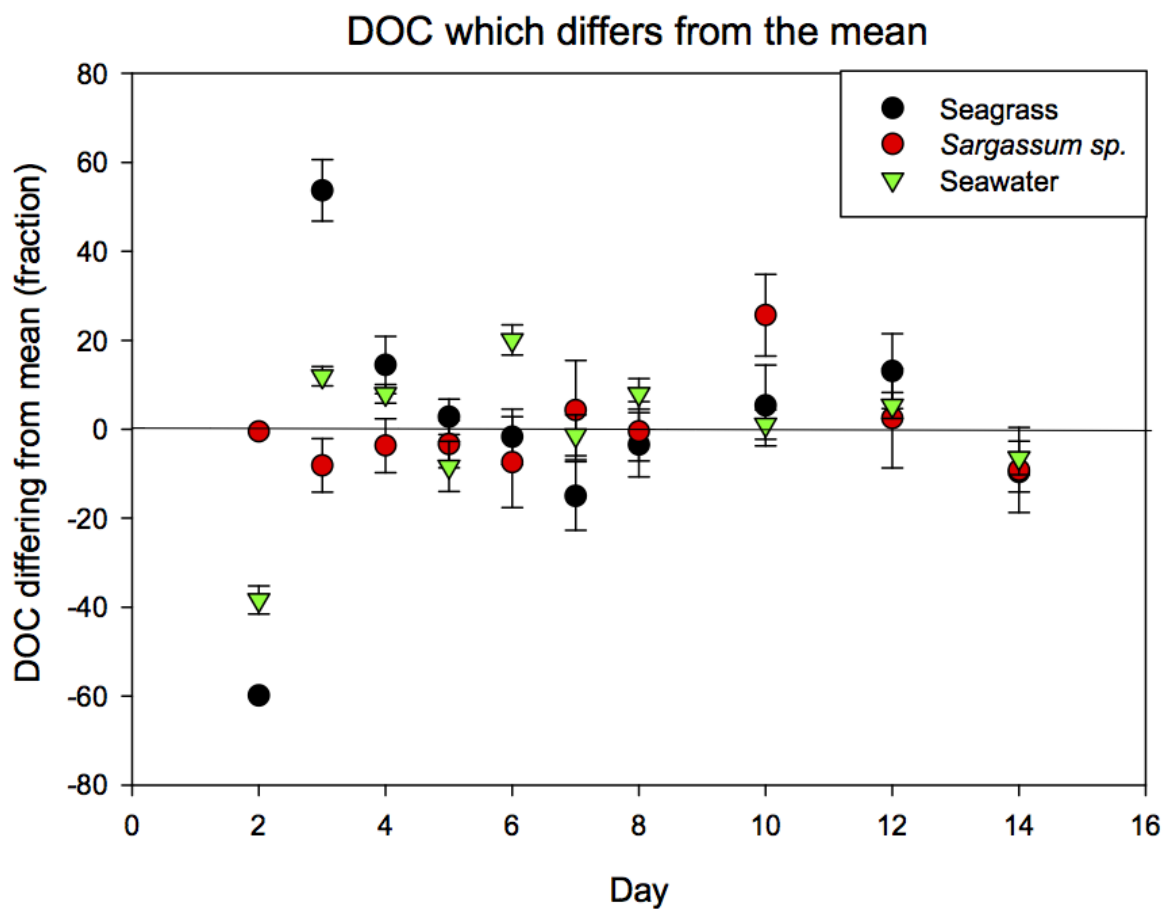


Figure 11: Dissolved organic carbon which differs from the mean. Values were variable about the mean for all treatments.

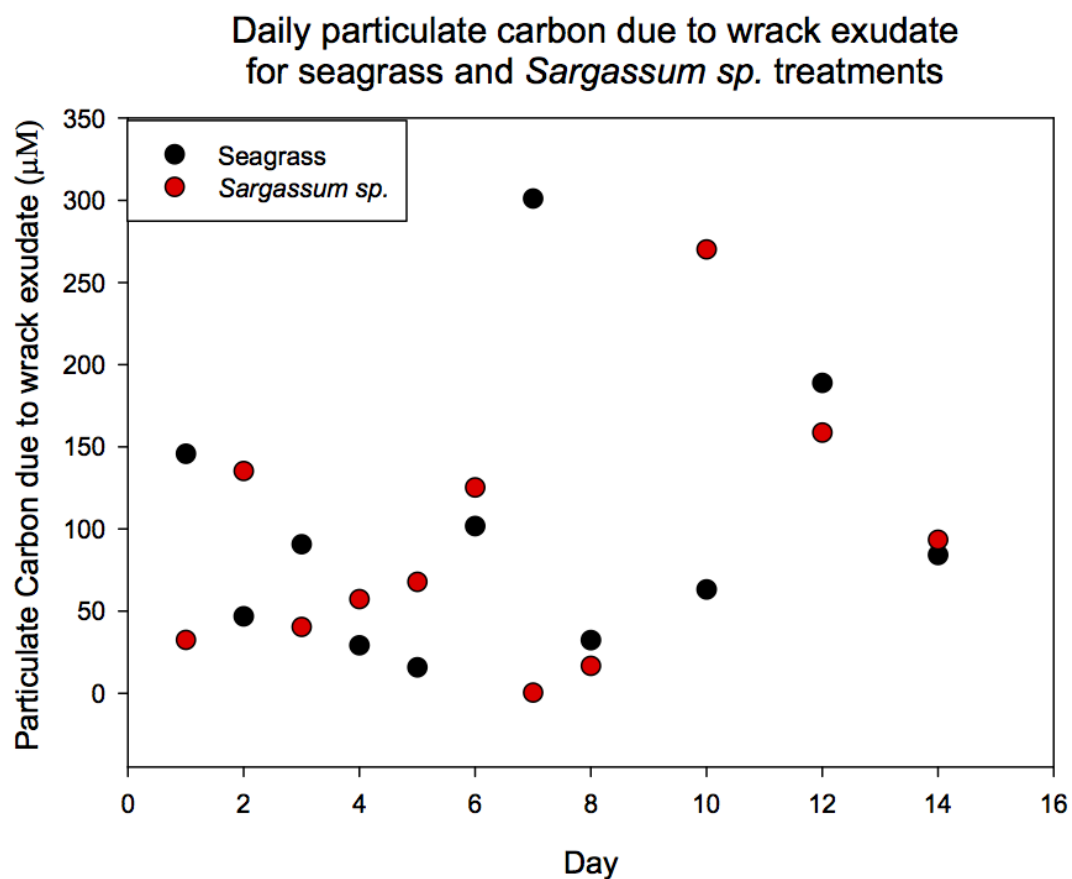


Figure 12: Daily particulate carbon values for seagrass and *Sargassum sp.* treatments normalized to seawater. Daily values for the seawater treatment were subtracted from daily values of the wrack treatments in order to find particulate nitrogen due to wrack exudate.

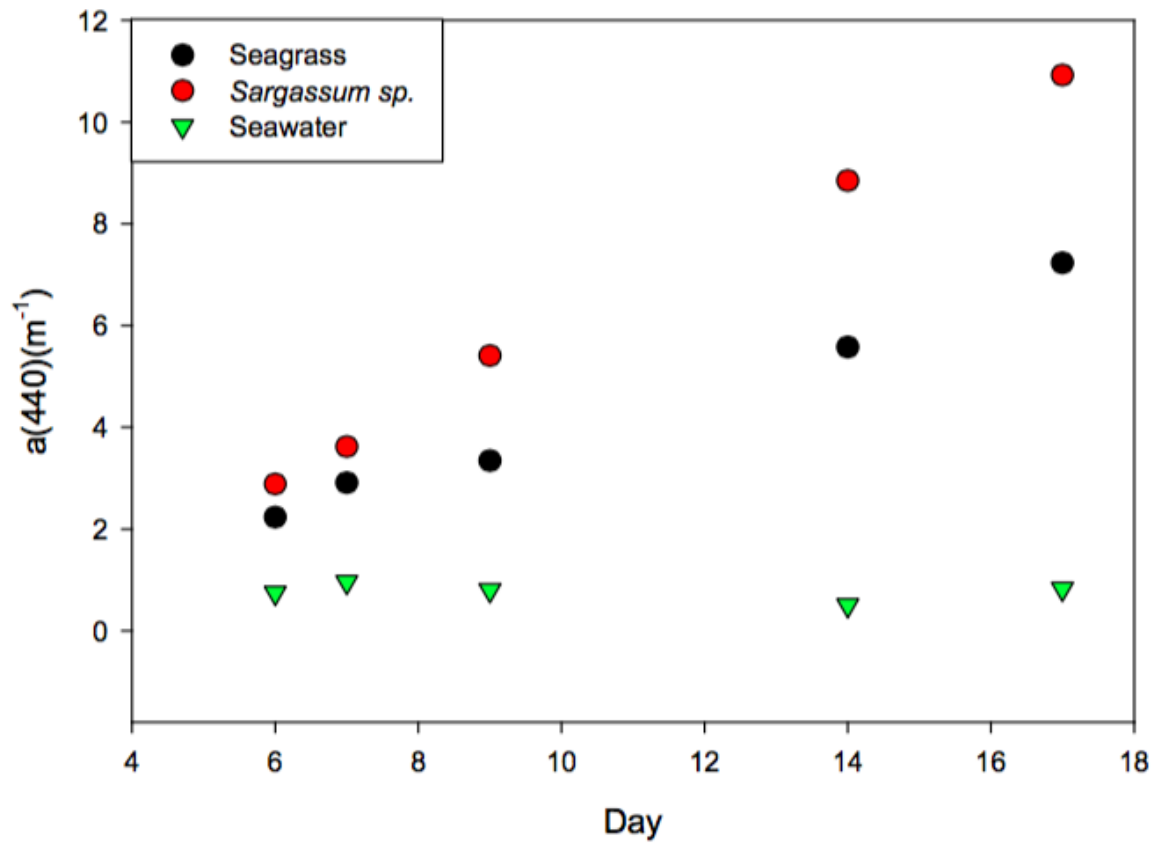


Figure 13: Daily measurements of colored dissolved organic material (CDOM) for three treatments, seagrass (black), *Sargassum sp.* (red), and seawater (green). As the days increased, so did the CDOM concentrations.

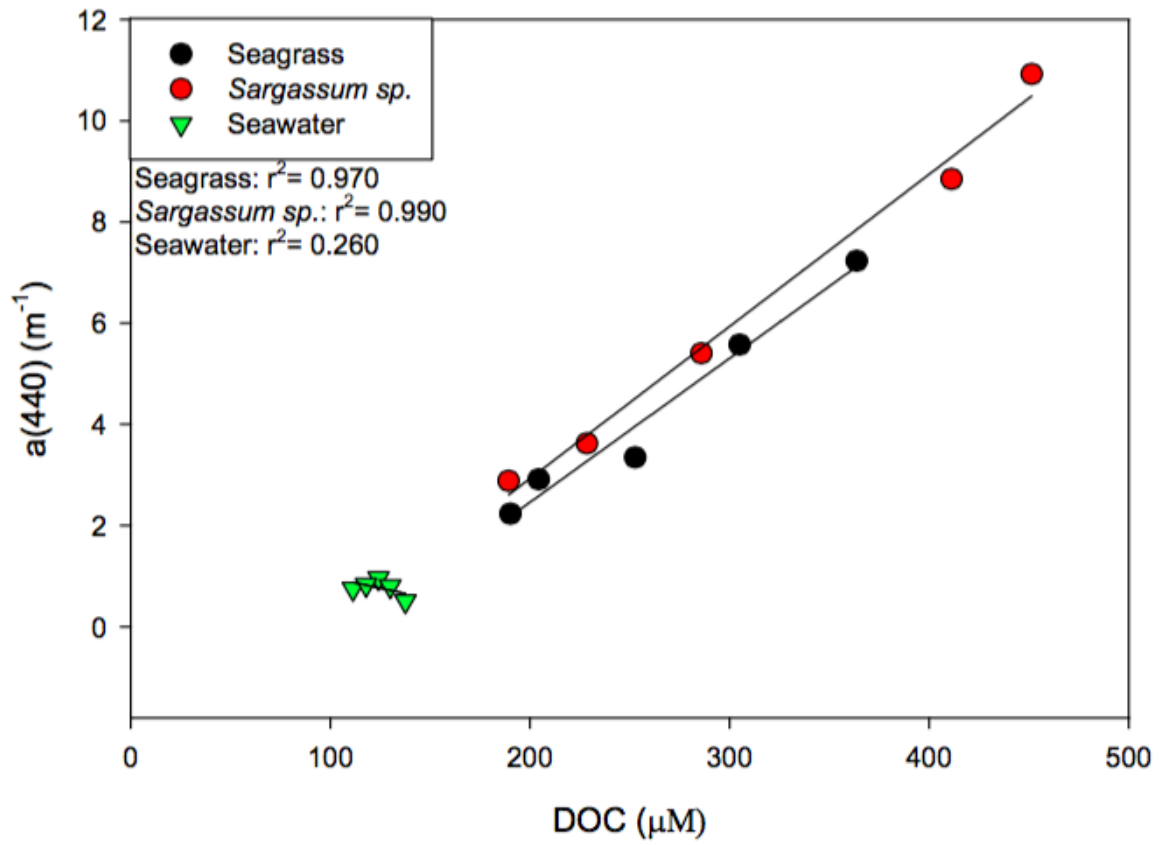


Figure 14: Relationship between dissolved organic carbon (μM) and colored dissolved organic material (a_{440} , m^{-1}) for all treatments.



Figure 15: Researcher Adam Chlus recovering a drifter from within a large amount of beached, decaying wrack.