Trophic linkages of Intracoastal Waterway seagrass beds in Broward County, Florida

Christina Gabriel[(1)], David W. Kerstetter[(1)], and Amy C. Hirons[(2)]

[(1)]Nova Southeastern University Oceanographic Center, 8000 North Ocean Drive, Dania Beach, FL 33004
[(2)]Nova Southeastern University, Farquhar College of Arts and Sciences, 3301 College Avenue, Davie, FL 33314

Abstract Seagrass habitats support marine food webs and provide essential habitat for a variety of species. Seagrasses and associated algae at three locations along the Intracoastal Waterway in Broward County, FL were assessed for their trophic contribution to the marine organisms in the area. Two seagrass species, along with associated algae, invertebrates, and vertebrates, were analyzed for stable carbon and nitrogen isotope ratios to determine trophic relationships. Significant differences were found in $\delta^{13}C$ and $\delta^{15}N$ between both seagrass species and among the three sites. The $\delta^{13}C$ of Johnson's seagrass *Halophila johnsonii* ranged from −16.28 to −11.27‰ while shoal grass *Halodule wrightii* ranged from −15.78 to −13.36‰. The $\delta^{15}N$ for shoal grass ranged from 4.69 to 7.08‰ versus 0.80 to 7.86‰ for Johnson's seagrass. Neither seagrass species was a dominant food source and epiphytes appeared to be the greater trophic contributor. However, the $\delta^{13}C$ (−16.28 to −11.27‰) and $\delta^{15}N$ (0.80 to 7.86‰) of both seagrass species did fall in the fractionation range of potential consumers suggesting that seagrass material could be ingested incidentally while grazing on epiphytes and other primary producers. Our results indicate that seagrass in Broward County are valuable both as a direct food source and as substrate for epiphytes.

Keywords $\delta^{13}C$, $\delta^{15}N$, food resource, seagrass, stable isotope ratios

Introduction

Seagrasses are highly productive angiosperm plants that are ecologically important to coastal marine environments through sediment stabilization, organic carbon production and export, oxygen provision, and trophic contributions both locally and to nearby habitats (Dawes 1987, Hemminga and Duarte 2000). Seagrasses have been acknowledged as important habitat for sirenians, sea turtles, and commercially and recreationally important fishes (Jackson et al. 2001). They also play a major role in preventing coastal erosion and siltation of coral reefs through the stabilization of inshore sediments (Fonseca and Fisher 1986, Fonseca 1989).

Seagrass beds support surrounding ecosystems (i.e., coral reefs, mangroves, and oyster beds) by providing a complex nursery habitat for smaller organisms and serving as substrate for algae and epiphytic organisms, such as

Corresponding author: Amy C. Hirons, hirons@nova.edu

sponges, bryozoans, and foraminifera. Seagrass habitats are utilized by organisms including bacteria, fungi and algae to invertebrates, fish, reptiles, birds and mammals (Green and Short 2003). Some reef-associated fishes will also migrate to seagrass beds at night for food or shelter (Hemminga and Duarte 2000, Hammerschlag et al. 2010).

Seagrasses can serve as food directly to some marine organisms, like turtles and manatees, and indirectly as nutrients through bacterial breakdown of seagrass tissues. However, seagrasses are not utilized in every location as a food source. In many places, their main ecosystem functions are habitat, protection, and shelter. When considering seagrasses as a food source, the question is whether the organisms are consuming the seagrass itself or the epiphytic algae that can be found on the seagrass leaves. Both seagrass and epiphytes have proven to be of nutritional value to a variety of organisms (Fry et al. 1982, Fry 1984, Kitting et al. 1984, Fry et al. 1987). Some organisms may focus solely on consumption of the epiphytes, but because the epiphytes are found directly on the seagrass leaves, both epiphytes and seagrass are frequently consumed together (Cebrián et al. 1996).

Epiphytes are an important component of highly productive seagrass ecosystems (Tomasko and Lapointe 1991, Frankovich and Fourqurean 1997), and the large surface area of seagrass leaves often results in high epiphyte densities. Prior research determined that epiphytic algae are the primary food source in coastal seagrass ecosystems (Fry 1984, Moncreiff and Sullivan 2001), and they contributed the greatest amount of carbon to consumers in a seagrass ecosystem (Kitting et al. 1984, Frankovich and Fourqurean 1997).

Stable isotope ratios have been used increasingly in ecosystem studies as tracers to study trophic dynamics, migration, and geologic formation within ecosystems. Some elements have more than one isotope, defined as atoms of the same element having more than one atomic mass. Slight increases in atomic mass are due to the addition of at least one extra neutron in the atom. The composition, or ratio, of the heavier stable isotope to the lighter, more abundant form of an element is expressed as per mil (‰). For example, a $\delta^{13}C$ of 3.4‰ represents 3.4 ^{13}C atoms per one thousand ^{12}C atoms. Common elements with isotopes used for ecosystem studies include carbon (C), nitrogen (N), sulfur (S), hydrogen (H), and oxygen (O) (Peterson and Fry 1987).

When analyzing carbon isotope composition, the ratio is a reflection of a consumer and its diet with the consumer being slightly enriched in ^{13}C compared to its diet (DeNiro and Epstein 1978, Fry and Sherr 1989). Any organism feeding on seagrass would have a similar or slightly enriched $\delta^{13}C$. Nitrogen isotope composition helps determine trophic level. DeNiro and Esptein (1981) documented approximately 3‰ enrichment in $\delta^{15}N$ of consumers compared to their diet which is indicative of one trophic level; therefore carnivores' $\delta^{15}N$ will be enriched compared to herbivores. The objective of this study was to use stable isotope analysis to evaluate the trophic contributions of seagrasses and nearby primary producers to surrounding organisms at three sites in the vicinity of Port Everglades seaport.

Figure 1. Map of the three study sites along the Intracoastal Waterway in proximity to Port Everglades, Broward County (Florida). Seagrass beds from a 2005 survey of the area are shown in dark grey (all species combined; location data from DC&A 2006). Site 1 was north of the Dania Beach Boulevard Bridge, Site 2 was directly east of the Dania Cutoff Canal (DCC), and Site 3 was southeast of the Port Everglades turning basin.

Materials and Methods

Study area. Samples of seagrasses and associated biota were collected at three sites located within a segment of the Intracoastal Waterway (ICW) in Broward County, FL from June 2009 through October 2010. Site 1 was located immediately north of the Dania Beach Boulevard Bridge, Site 2 was located directly east of the Dania Cutoff Canal (DCC), and Site 3 was located southeast of the Port Everglades turning basin (Figure 1). The three sites were chosen based on National Oceanic

and Atmospheric Administration (NOAA) visual surveys which determined the presence or absence of seagrass beds in 1999-2001, 2006 (DCA 2006), and 2008 (ISVS 2008).

Several methods were used to collect biological samples. Segments of seagrass leaves, rhizomes, and roots were collected by hand via snorkeling gear, along with macroalgae and detritus. Sediment and infauna were collected with a 5 centimeter (cm) diameter polyvinyl chloride (PVC) corer to a depth of 5 cm no greater than 10 cm. Fishes and crustaceans were caught with a beach seine (<5 millimeter (mm) mesh) and baited, minnow traps with a 0.64 cm-opening wire mesh. Specimens and samples were frozen at -10° C until processed.

Stable isotope analysis. Organisms were thawed and rinsed with tap water and then soaked in deionized water. Epiphytes were scraped from seagrass leaves with a clean razor blade being extremely careful not to rip the blade of the plant and contaminate the tissues. Roots and rhizomes of seagrasses were separated from the leaves and analyzed separately. Some rhizomes were found along the sediment surface and could be used as a possible carbon source for prey.

Tissue samples were fumed with concentrated HCl for 12–24 hours to remove trace calcium carbonates. All samples were oven dried at 60° C in aluminum tins up to 72 hours. Tissue samples were homogenized with a Wig-L-Bug homogenizer and stored in clean glass shell vials. Between 5–8 milligrams (mg) of plant material and 0.5–0.8 mg of proteinaceous tissues were weighed to the nearest 0.001 mg and placed in tins for mass spectroscopy analysis.

Stable isotope composition was determined with a Costech 4010 elemental analyzer coupled to a Delta V Advantage stable isotope mass spectrometer via a Conflo IV interface in continuous flow mode. Duplicate sub-samples of the tissues were analyzed. Stable isotope ratios were reported in the standard delta notation (‰):

$$\delta \mathrm{X}(‰) = \left[\left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1\right] * 1000$$

where X is ^{13}C and ^{15}N and R is the $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively. The standard for carbon was Pee Dee belemnite and atmospheric air for nitrogen. All sample preparation was performed at the NSU Oceanographic Center and the mass spectroscopy was performed at the Museum Support Center, Smithsonian Institution (Suitland, MD).

Statistical analysis. Data were separated into sites, seagrass tissues (leaves, roots, and rhizomes), and species. Descriptive statistics were generated for all data and a Shapiro-Wilks test was used to test for normality. The separate and combined effect of the carbon and nitrogen isotope ratios were assessed to look for changes in carbon source and trophic status relative to potential prey items, as well as location and temporal effects, using one-way and multiple analysis of variance (ANOVA and MANOVA, respectively). The ANOVA determined if there was a significant difference between $\delta^{13}C$ and $\delta^{15}N$ separately and seagrass species, sites, and seagrass tissues. MANOVA determined if there was a significant difference in seagrass species, tissues, and sites and both $\delta^{13}C$ and $\delta^{15}N$ combined. Standard linear regression techniques were also used to compare the relationships of the stable isotope ratios. Statistical analyses were performed with SPSS (version 20).

Results

Seagrasses. Two seagrass species were found at all three study sites: Johnson's seagrass (*Halophila johnsonii*) and shoal grass (*Halodule wrightii*). *H. wrightii* $\delta^{15}N$ ranged from 4.69 to 7.08‰ while *H. johnsonii* ranged from 0.80 to 7.86‰. The overall mean $\delta^{15}N$ for *H. wrightii* was 5.88 ± 0.20‰ and 5.31 ± 0.18‰ for *H. johnsonii* (Figure 2) (Table 1). *H. johnsonii* $\delta^{15}N$ were not normally distributed ($F = 0.929$, $df = 75$, $p < 0.001$), while H. *wrightii* were normally distributed ($F = 0.991$, $df = 12$, $p = 1.000$). No significant difference

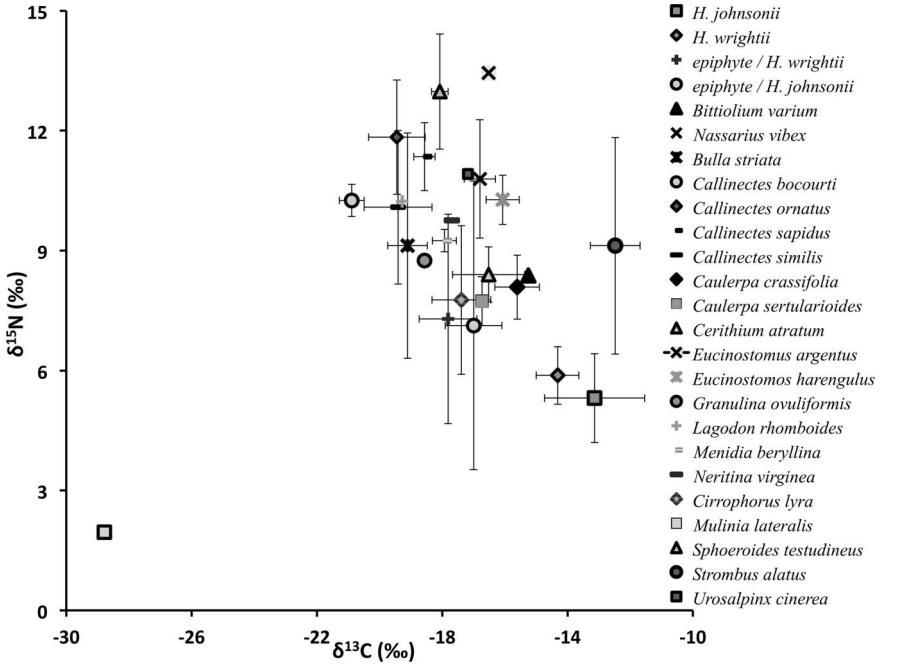

Figure 2. Mean (center value) and standard deviation (SD; vertical and horizontal bars) of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) for all collected plant and animal species at all three study sites in the Intracoastal Waterway, Broward County (Florida) from August 2009 to October 2010. Species without SD bars represent n=1 specimens.

was found in $\delta^{15}N$ between seagrass species (ANOVA: $F = 1.102$, $df = 1$, $p = 0.297$). *H. wrightii* $\delta^{13}C$ ranged from −15.76 to −13.36‰ while *H. johnsonii* ranged from −16.28 to −11.27‰. The overall mean $\delta^{13}C$ for *H. wrightii* was −14.32 ± 0.21‰ and −13.14 ± 0.13‰ for *H. johnsonii* (Figure 2) (Table 1). *H. johnsonii* $\delta^{13}C$ values were not normally distributed ($F = 0.954$, $df = 75$, $p = 0.008$), but they were normally distributed for *H. wrightii* ($F = 0.953$, $df = 12$, $p = 0.675$). An ANOVA indicated a significant difference in $\delta^{13}C$ between the two species ($F = 13.249$, $df = 1$, $p<0.001$).

Seagrass $\delta^{15}N$ was not significantly different between the three sites ($p = 0.212$). Seagrass $\delta^{13}C$ was significantly different among all three sites: Site 1 and 2, $p < 0.001$; Site 1 and Site 3, $p = 0.002$; Site 2 and Site 3, $p = 0.031$ (Figure 2).

A significant difference existed between the rhizomes and leaves of *H. wrightii* and *H. johnsonii*, with *H. johnsonii* slightly depleted in both stable isotopes (MANOVA; $F = 3.116$, $df = 3$, $p = 0.050$). The mean $\delta^{15}N$ of *H. wrightii* leaves was slightly enriched (6.63 ± 0.17‰) compared to that of the rhizomes (5.48 ± 0.18‰). The mean $\delta^{13}C$ for *H. wrightii* leaves was −14.24 ± 0.35‰ and −14.28 ± 0.30‰ for rhizomes. The mean $\delta^{15}N$ of *H. johnsonii* leaves was slightly more enriched (5.73 ± 0.22‰) than the rhizomes (4.95 ± 0.27‰).

Table 1. Flora and fauna samples from the three study locations along the Intracoastal Waterway, Broward County (Florida) during the period from June 2009 to October 2010. Rhizomes and leave were significantly different from each other in both species. Epiphytes were not significantly different between seagrass species.

Phylum	Scientific Name	Common Name	n	$\overset{n}{x}\,\delta^{15}N \pm SE$	$\overset{n}{x}\,\delta^{13}C \pm SE$	Tissue Sample	Diet
Mollusca	*Bittiolium varium*	grass cerith	1	8.38	−15.25	Whole	Herbivore
	Cerithium atratum	dark cerith	3	8.40 ± 0.67	−16.52 ± 0.40	Whole	Herbivore
	Nassarius vibex	bruised nassa	14	10.79 ± 0.13	−16.80 ± 0.39	Whole	Carnivore
	Bulla striata	common Atlantic bubble	10	9.13 ± 0.20	−19.11 ± 0.89	Whole	Carnivore
	Granulina ovuliformis	teardrop marginella	1	9.47	−19.33	Whole	Herbivore
	Neritina virginea	virgin nerite	1	9.76	−17.70	Whole	Herbivore
	Mulinia lateralis	dwarf surf clam	1	1.96	−28.78	Whole	Omnivore
	Strombus alatus	Florida fighting conch	2	9.12 ± 0.56	−12.47 ± 0.05	Muscle	Herbivore
	Urosalpinx cinerea	Atlantic oyster drill	1	10.91	−17.17	Whole	Carnivore
Crustacea	*Callinectes bocourti*	Bocourt swimming crab	4	10.25 ± 0.20	−20.89 ± 0.20	Muscle	Omnivore
	Callinectes ornatus	ornate blue crab	7	11.84 ± 0.34	−19.44 ± 0.54	Muscle	Omnivore
	Callinectes sapidus	Atlantic blue crab	10	11.35 ± 0.11	−18.57 ± 0.27	Muscle	Omnivore
	Callinectes similis	lesser blue crab	12	10.08 ± 0.31	−19.41 ± 0.55	Muscle	Omnivore
Chordata	*Eucinostomus argenteus*	spotfin mojarra	1	13.44	−16.51	Muscle	Carnivore
	Eucinostomos harengulus	tidewater mojarra	18	10.27 ± 0.12	−16.10 ± 0.15	Muscle	Carnivore
	Lagodon rhomboides	pinfish	1	10.23	−19.28	Muscle	Omnivore
	Menidia menidia	Atlantic silverside	8	9.25 ± 0.13	−17.93 ± 0.10	Muscle	Omnivore
	Sphoeroides testudineus	checkered pufferfish	7	12.98 ± 0.10	−18.08 ± 0.55	Muscle	Carnivore
Annelida	*Cirrophorus lyra*	polychaete	5	7.77 ± 0.42	−17.39 ± 0.83	Whole	Detritivore
Tracheophyta	*Halodule wrightii*	shoal grass	38	5.48 ± 0.18	−14.28 ± 0.30	Rhizomes	-
		shoal grass	48	6.63 ± 0.17	−14.24 ± 0.35	Leaves	-
	Halophila johnsonii	Johnson's seagrass	31	4.95 ± 0.27	−13.02 ± 0.20	Rhizomes	-
		Johnson's seagrass	44	5.73 ± 0.22	−13.17 ± 0.17	Leaves	-
Rhodophyta	*Acanthophora spicifera*	spiny seaweed	2	8.00 ± 0.09	−20.35 ± 1.06	Whole	-
Chlorophyta	*Caulerpa crassifolia*	green algae	2	8.09 ± 0.50	−15.61 ± 0.56	Whole	-
	Caulerpa sertularioides	feather algae	3	7.74 ± 0.04	−16.73 ± 0.35	Whole	-
	-	Epiphytic algae from *H. wrightii*	3	7.29 ± 0.28	−17.81 ± 0.15	Whole	-
	-	Epiphytic algae from *H. johnsonii*	23	7.13 ± 0.17	−17.00 ± 0.68	Whole	-

The mean $\delta^{13}C$ for the leaves of *H. johnsonii* was $-13.17 \pm 0.17‰$ and $-13.02 \pm 0.20‰$ for the rhizomes.

Epiphytes. Epiphytic algae present on seagrass leaves were removed and analyzed separately. While some seagrass cellular material may have been mixed with the epiphytes during removal, the mass of epiphyte tissue would have overshadowed any isotopic contribution from the seagrass. The mean $\delta^{15}N$ for epiphytes was $7.19 \pm 0.17‰$ while the mean $\delta^{13}C$ was $-17.23 \pm 0.68‰$. Analysis of variance showed no significant difference between the epiphyte $\delta^{15}N$ of *H. wrightii* and *H. johnsonii* ($F = 0.047$, $df = 1$, $p = 0.831$). Nor was there a significant difference between the epiphyte $\delta^{13}C$ from both seagrass species ($F = 0.093$, $df = 1$, $p = 0.763$).

Fauna. A variety of invertebrate and vertebrate organisms were caught and grouped according to their diet (Table 1) (Marcus and Marcus 1964, Fantle et al. 1999). Most organisms ($n = 51$) were considered carnivores, followed by omnivores ($n = 43$), herbivores ($n = 8$), and detritivores ($n = 5$). Pair-wise comparison tests indicated no significant difference in $\delta^{15}N$ between any of the dietary groups (MANOVA: $F = 2.319$, $df = 3$, $p = 0.080$) (Figure 2).

Kruskal-Wallis and pair-wise comparisons found significant differences in $\delta^{13}C$ for three dietary pairings (omnivores and herbivores: $p = 0.001$, omnivores and carnivores: $p < 0.001$, omnivores and detritivores: $p < 0.001$), but not between herbivores and carnivores ($p = 0.36$) or herbivores and detritivores ($p = 0.67$).

Discussion

Primary producers. Stable nitrogen isotopes ratios can help determine trophic relationship to consumers in relation to their food source. The mean $\delta^{15}N$ of the primary producers in this study were trophically similar ($< 2‰ \Delta$) to each other (*H. wrightii*: 5.88‰, *H. johnsonii*: 5.31‰, *H. johnsonii* and epiphytes: 6.24‰, epiphytes: 7.19‰, green algae: 7.61‰, and red algae: 7.85‰). Based on a 3‰ increase per trophic level (DeNiro and Epstein 1981, Peterson and Fry 1987), all the primary producers in this study were within one trophic level of each other. McClelland et al. (1997) were able to use $\delta^{15}N$ values to show incorporation of nitrogen from anthropogenically derived sources (e.g., sewage outfalls and fertilizers) into estuarine plants and animals. Given the similar $\delta^{15}N$ among the flora at all three sites and the sites' proximity to each other (Figure 1), this would indicate that all these plants were likely exposed to the same nitrogen sources. Moncreiff and Sullivan (2001) found a mean $\delta^{15}N$ of 6.0‰ for *H. wrightii* in Mississippi Sound which was similar to the $\delta^{15}N$ found for *H. wrightii* in this study as well as very close to the value found for *H. johnsonii.* Epiphytes in this study had a mean $\delta^{15}N$ of 7.19‰ which was more enriched than both *H. wrightii* and *H. johnsonii*, but not the red and green macroalgae. Because the values were more enriched (1.1 to

2.6‰) than the seagrasses, this suggested that the epiphytes may have acquired additional nitrogen from the water column (Corredor et al. 1999).

The $\delta^{13}C$ of the primary producers in this study were all isotopically distinguishable from each other (*H. wrightii*: −14.32‰, *H. johnsonii*: −13.14‰, epiphytes: −17.23‰, green algae: −18.66‰, red algae: −20.14‰). Seagrasses were significantly more enriched in $\delta^{13}C$ than the epiphytes and the macroalgae, with the red algae having the most depleted $\delta^{13}C$ values. The variability of carbon isotope ratios for seagrasses and other submerged aquatic vegetation can have multiple causes, such as differences in the carbon pathways (C_3 versus C_4) (Cooper and DeNiro 1989). Increased water flow can enhance diffusion of inorganic carbon to the plant (Osmond et al. 1981, Raven et al. 1982, Cooper and DeNiro 1989). Seasonal variability due to biological processes, such as photosynthetic fixation of carbon (Simenstad and Wissmar 1985, Cooper and DeNiro 1989) and lower water temperatures (Degens et al. 1968, Wong and Sackett 1978, Cooper and DeNiro 1989) can create more depleted $\delta^{13}C$ values. Differential use of bicarbonate and dissolved carbon dioxide during photosynthesis can also alter $\delta^{13}C$ (Andrews and Abel 1977, Benedict et al. 1980, Faganeli et al. 1986, Cooper and DeNiro 1989), and light intensity has been reported to affect carbon isotope ratios due to alteration of the photosynthetic rate (Wefer and Killingley 1986, Cooper and DeNiro 1989).

Consumers. Carnivores had the most enriched mean $\delta^{15}N$ (10.58‰) while the herbivores had the most depleted mean value of 8.95‰. This is expected in any ecosystem; the carnivores are found at higher trophic levels than herbivores because they have foraged on prey that may or may not have foraged directly on primary producers (Post 2002). The omnivores and detritivores had $\delta^{15}N$ intermediate between carnivores and herbivores, indicating ingestion of both plant and animal material.

A broad range of $\delta^{13}C$ values was found for consumers at all three sample sites. The Florida fighting conch (*Strombus alatus*), a herbivore, had the most enriched $\delta^{13}C$, −12.47‰, while the dwarf surf clam (*Mulinia lateralis*), a filter feeder, had the most depleted $\delta^{13}C$ at −28.78‰. This was similar to other studies that found depleted bivalve $\delta^{13}C$ values; −24.8‰ for *Corbicula japonica* in Kushida Estuary, Japan and −17.4‰ for *Mytilus edulis* in Aiguillon Bay, France (Riera et al. 1999, Kasai and Nakata 2005). Because there is such a large range in stable carbon isotope ratios and consumers are usually enriched slightly in $\delta^{13}C$ compared to their diet, this supports the idea that fauna found in this study were herbivores, carnivores, omnivores, or detritivores feeding on various carbon sources; this idea of trophic contribution with a variety of carbon sources is also upheld by the $\delta^{15}N$ data which displays organisms in different trophic levels (Figure 2). In many seagrass ecosystems, there are a variety of primary carbon sources, such as seagrass, mangroves, macroalgae, epiphytes, and detritus (Loneragan et al. 1997, Winning et al. 1999, Mendoza-Carranza et al. 2010). The only consumer that had a $\delta^{13}C$ similar to the seagrasses was the Florida fighting conch which was found only

at Site 3, and had a mean $\delta^{13}C$ of −12.47‰. This was approximately 1‰ enriched compared to the mean $\delta^{13}C$ of *H. johnsonii* (−13.28‰), indicating that the conch could have been foraging on *H. johnsonii*.

The majority of the consumers had $\delta^{13}C$ values in the range of −20 to −16‰. None of the consumers within this range were grouped into the category of herbivores, but rather carnivores or omnivores. It was possible that the omnivores had been feeding on herbivores as well as epiphytic algae found on the seagrass blades; some of the consumers' $\delta^{13}C$ mirrored those of epiphytic algae after accounting for trophic enrichment. For example, the gastropod *Cerithium atratum* (dark cerith) is an herbivore known to feed on algae (Marcus and Marcus 1964). Three dark ceriths found at Site 1 had a mean $\delta^{13}C$ of −16.52‰, which was within the standard error for epiphytes found at Site 1 and could account for the dietary fractionation (Figure 2).

It is difficult to determine the primary carbon source in a complex, highly modified and impacted ecosystem such as the ICW in South Florida. Few organisms appeared to directly graze on the seagrasses, but the contribution of epiphytic algae in consumer diets appeared to dominate the suite of consumers captured. The consumers in this study had a $\delta^{13}C$ range from −28.78 to −12.47‰, values which overlapped with the $\delta^{13}C$ for *H. wrightii*, *H. johnsonii*, and epiphytic algae, and, thus, making it impossible to determine which primary producers were the dominant carbon sources to the food web. Additional analyses, including total organic carbon (TOC) and trace element analysis, may help future research delineate the specific organic carbon contributions within this local food web.

This study focused on the role of seagrasses in Port Everglades area as a carbon source and trophic contributor to the seagrass ecosystem. Through analysis of $\delta^{13}C$ and $\delta^{15}N$, the organisms found near the seagrass outcrops of *H. johnsonii* and *H. wrightii* did not appear to utilize the seagrass as a direct energy source, but rather consumed the epiphytes off the seagrass. These results further support the need to protect seagrass ecosystems because of their additional role as habitat for both epiphytic flora and fauna.

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