



# Evidence of a dietary shift by the Florida manatee (*Trichechus manatus latirostris*) in the Indian River Lagoon inferred from stomach content analyses

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## ABSTRACT

Investigating the long-term fluctuations of the feeding ecology of megaherbivores such as sirenians is important, as any changes could be indicative of shifts in resource availability. The Indian River Lagoon (IRL), eastern Florida, USA, is a critical habitat for the Florida manatee (*Trichechus manatus latirostris*). However, the IRL has experienced a substantial decline in seagrass due to the persistence of several harmful algal blooms. Using microhistological analysis, we examined the diet of manatees over a discontinuous sampling period spanning over 38 years using stomach contents collected from carcasses recovered in the IRL. Samples collected between 2013–2015 (post-seagrass die-off,  $n = 90$ ) were compared to archived stomach samples collected between 1977–1989 (pre-seagrass die-off,  $n = 103$ ). Samples analyzed from 1977–1989 contained primarily seagrasses (61.7%), followed by algae (28.4%) and vascular plants (1.7%). In contrast, stomach samples from the post-seagrass die-off primarily contained algae (49.5%), followed by seagrasses (34%) and vascular plants (2.7%). Between 1977–1989 and 2013–2015, manatees in the IRL experienced a 44.9% decline in seagrass consumption, and a 74.3% increase in algal consumption. This dietary shift was not influenced by body length, a proxy of age, or sex. Our results indicate that the dietary shift experienced by manatees is due to the decline of available seagrass forage in the IRL, and highlight the dietary plasticity of manatees in the face of changes in resource availability. However, the individual health and population-level consequences of this dietary shift are unknown. An increase in mortality due to undetermined causes in this region since 2012 can be associated with deteriorating body conditions of manatees in the IRL, possibly resulting from a lack of seagrass diet. Future research should further investigate behavioral changes affecting manatees in relation to seagrass decline in the IRL, including the energetic costs of this dietary change.

## 1. Introduction

Aquatic megaherbivores such as sirenians (manatees, *Trichechus* spp. and the dugong, *Dugong dugon*) rely on abundant sources of macrophytes in freshwater and coastal marine ecosystems (Marsh et al., 2011). These animals can have profound impacts on macrophyte communities and food web dynamics across a range of freshwater and coastal (i.e., seagrass) ecosystems (Thayer et al., 1984; Aragonés et al., 2006). However, little is known about how these large organisms respond to changes in

the abundance and composition of macrophytes, which is critical for assessing their ecological plasticity in the face of environmental changes due to habitat degradation and climate change (Marsh et al., 2011).

Florida manatees (*Trichechus manatus latirostris*) inhabit the shallow coastal bays and estuaries throughout the southeastern United States. They occur in salt, fresh, or brackish waters along the Atlantic Ocean and Gulf of Mexico (Irvine and Campbell, 1978). Although manatees were downlisted from Endangered to Threatened status in 2017 under the U.S. Endangered Species Act (United States Fish and Wildlife

**Abbreviations:** IRL, Indian River Lagoon; HAB, harmful algal bloom; UME, unusual mortality event; USGS, United States Geological Survey; FWC, Florida Fish and Wildlife Conservation Commission; NSU, Nova Southeastern University.

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Service, 2017), they continue to face increasing anthropogenic pressures from a growing human population in Florida and a range of effects on coastal marine ecosystems, including habitat alterations, collisions with watercraft, pollution, and various sources of disturbance (Bonde et al., 2004; Allen et al., 2014; Reep and Bonde, 2021).

Manatees consume from 4–9% (Bengtson, 1983; Etheridge et al., 1985) to 10–15% (Reep and Bonde, 2021) of their body weight per day, spending approximately four to 8 h a day feeding (Hartman, 1979; Etheridge et al., 1985). Their diet includes a wide variety of aquatic plants, seagrasses, and algae (Hartman, 1979; Best, 1981; Bengtson, 1983; Etheridge et al., 1985; Ledder and Thesis, 1986; Hurst and Beck, 1988; Reep and Bonde, 2021). In Florida, manatees have been documented to consume over 60 different species of plants (Hartman, 1979; Best, 1981; Bengtson, 1983; Etheridge et al., 1985; Ledder and Thesis, 1986; Hurst and Beck, 1988). The Indian River Lagoon (IRL) in eastern Florida, USA, shelters over 4300 species of flora and fauna, making it one of the most biodiverse estuarine ecosystems in the world (St. Johns River Water Management District, 2007). These waters are a critical habitat for manatees, with a majority of the population on Florida's east coast migrating through the estuary during the winter months, although manatees use the IRL on a year-round basis (Provancha and Provancha, 1988; Lefebvre et al., 1989; Lefebvre and Powell, 1990; Deutsch et al., 1998, 2003; Deutsch and Barlas, 2016). Aerial surveys are conducted nearly every winter to document the distribution and relative abundance of Florida manatees; in 2018, a minimal abundance of 3,731 manatees was counted on the east coast of Florida (Florida Fish and Wildlife Conservation Commission, 2019). The highest population numbers are seen during cooler winter months, but the IRL maintains an abundant manatee population year-round.

The feeding ecology of manatees in the IRL is poorly known. However, Provancha and Hall (1991) observed that during spring, hundreds of manatees leave the warm water refuges and move to the Banana River to feed on large seagrass beds, primarily consisting of *Syringodium filiforme* and *Halodule wrightii*. Preliminary stable isotope analyses of manatee tissue samples from the IRL have revealed that manatees feed primarily on marine (e.g., *S. filiforme*, *H. wrightii*) (67%) and estuarine (e.g., *Ruppia maritima*) vegetation (33%) (Reich and Worthy, 2006), and is supported by studies directly observing manatees feeding in this area (Packard, 1984; Lefebvre and Powell, 1990; Lefebvre et al., 2017). Seagrass coverage in the IRL was documented as increasing or stable through 2006 (Virnstein et al., 2007; Morris et al., 2016, 2018, 2021; Indian River Lagoon National Estuary Program, 2020). However, in early 2011, a harmful algal bloom (HAB) was detected in the IRL that extended from early spring through late fall, causing a widespread seagrass die-off (Barlie, 2018; Lapointe et al., 2015, 2020; Morris et al., 2016, 2018, 2021). This HAB proliferated in the lagoon as a result of anthropogenic nutrient inputs, which caused depleted oxygen levels (Kamerosky et al., 2015; Lapointe et al., 2015, 2020; Sneed et al., 2017; Barlie, 2018). An increase in turbidity and low light conditions further contributed to a decline in the abundance and extent of seagrass beds in the lagoon (Phlips et al., 2015; Morris et al., 2016, 2018, 2021). During this time, an increase in salinity and extended periods of decreased water temperatures for two consecutive years prior to the bloom affected the photosynthetic capacity of seagrasses and subsequently contributed to their decline in the area (Kamerosky et al., 2015; Morris et al., 2016, 2018, 2021). Consecutive years of HAB events likely caused the IRL to undergo a regime shift from seagrass to a phytoplankton-driven primary production environment (Phlips et al., 2015, 2021). There was over a 50% decline in seagrass observed across the IRL (Morris et al., 2018, 2021, 2022). Total loss of seagrass was between 45% (~32,000 acres) (Morris et al., 2016) and 56–58% (~40,000 acres) lost since prior to these HAB events (Morris et al., 2018, 2021, 2022), with loss estimates as high as approximately 95% between Ft. Pierce and Ponce Inlet in the northern IRL (Lapointe et al., 2020). While there have been previous declines and recoveries in seagrass coverage in the IRL (Morris and Virnstein, 2004), this ongoing, widespread decline

that commenced in 2011 is the most severe on record to date (Morris et al., 2018, 2021, 2022).

Monitoring the dietary habits of manatees over time is important to assess how changes in the environment can affect resource selection and ultimately individual fitness and population dynamics. Here, we investigated long-term changes in the diet of manatees in the IRL by analyzing the stomach contents from carcasses recovered in the lagoon. Our specific objective was to evaluate how manatee feeding habits changed over time in the IRL. We utilized archived stomach content samples from manatee carcasses collected in the IRL between 1977–1989 to compare to stomach content samples collected between 2013–2015 during a manatee unusual mortality event (UME) declared by the National Oceanic and Atmospheric Administration (2021). We predicted that a disturbance like the decline in seagrass availability would create a measurable change in the diet of manatees in the IRL. Additionally, we provide preliminary insight into a possible relationship between manatee mortality and diet during the time of the seagrass die-off.

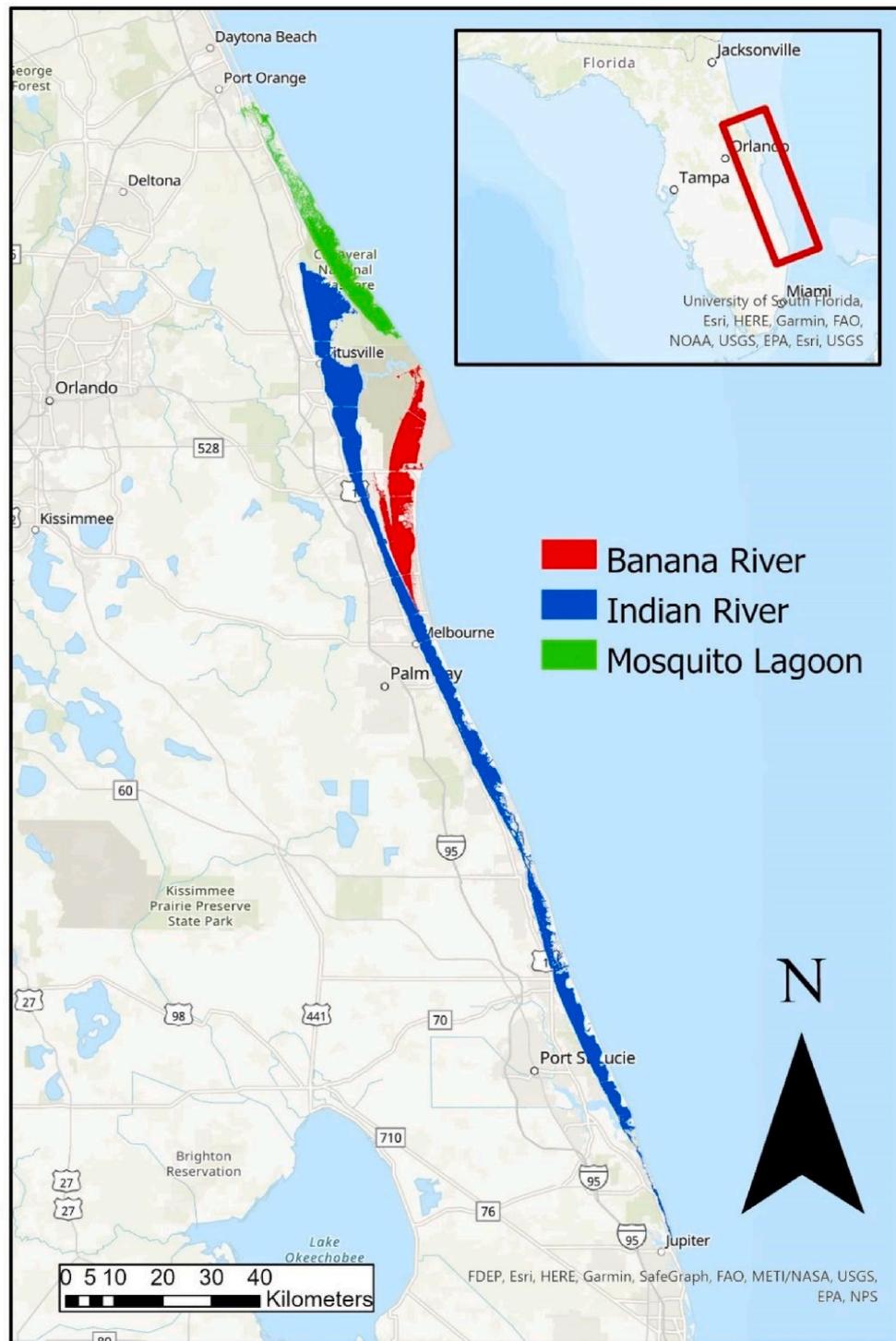
## 2. Methods

### 2.1. Study area

The Indian River Lagoon (26°N to 29°N) is situated on the central-east coast of Florida and includes the Mosquito Lagoon, Banana River, and Indian River. The estuary extends 251 km from Ponce Inlet (29°04'25" N, 80°55'15" W) south-southeast to Jupiter Inlet (26°56'38" N, 80°04'46" W), covering a watershed of 5700 km<sup>2</sup> and is comprised of several fingers of sheltered waterways (Fig. 1). Seven seagrass species have been identified in the IRL – *Halodule wrightii*, *Halophila decipiens*, *Halophila englemanni*, *Halophila johnsonii*, *Ruppia maritima*, *Syringodium filiforme* and *Thalassia testudinum*. The most common species within the lagoon are *H. wrightii* and *S. filiforme*, with *R. maritima* the least common species (Thompson, 1978; Dawes et al., 1995; Morris et al., 1999, 2021; Provancha and Scheidt, 1999; Littler et al., 2008). The three relatively diminutive *Halophila* species are moderately abundant to common, while *T. testudinum* is limited to the southern portion of the IRL (Virnstein, 1995; Morris et al., 1999, 2021; Provancha and Scheidt, 1999; Littler et al., 2008). Much of the benthic macrophytic cover has been comprised historically of *S. filiforme* and *H. wrightii* interspersed, with large distributions of drift algae that consist primarily of *Gracilaria* spp. and hold a key role in nutrient dynamics and primary production in the IRL (Thompson, 1978; Virnstein and Carbonara, 1985).

### 2.2. Sampling

All samples were collected from the stomach of manatee carcasses during necropsy. Sampled individuals had various causes of death, including boat strike, cold stress syndrome, and other human-related, natural or unknown causes determined at necropsy. Necropsies were performed by the United States Geological Survey (USGS) or the Florida Fish and Wildlife Conservation Commission (FWC) Marine Mammal Pathobiology Laboratory and other FWC field stations. Stomach content samples were preserved in 70–95% EtOH upon collection and stored until further examination could be performed. Archived samples collected between 1977–1989 were analyzed between April 1985 and March 1991 at the USGS-Wetland and Aquatic Research Center in Gainesville, FL. Samples collected between 2013–2015 were analyzed at the Nova Southeastern University (NSU) Halmos College of Arts and Sciences-Oceanographic Center in Dania Beach, FL and the FWC-Tequesta Field Laboratory in Tequesta, FL between January and December 2015. No stomach samples were collected or archived in the interim years, 1990–2012. All activities were conducted under Federal Fish and Wildlife Permits MA791721 issued to the USGS-Sirenia Project and MA773494 issued to the FWC.



**Fig. 1.** Map of the state of Florida zoomed in to show the extent of the Indian River Lagoon: Mosquito Lagoon (red), Banana River (blue), and Indian River (green) in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 2.3. Microhistological analysis

Microhistology is a useful tool to directly determine dietary composition, particularly to assess the relative contribution of macrophytes in the diet (Hurst and Beck, 1988; Mignucci-Giannoni and Beck, 1998; Castelblanco-Martinez et al., 2009; Beck and Clementz, 2012; Allen et al., 2017). Gastrointestinal tract samples from manatee carcasses were examined for microhistological characteristics of visible plant, algal, or animal fragments consumed using techniques developed

by Owen (1975), Holechek et al. (1982a, 1982b), and Hurst and Beck (1988). This technique has previously been used to investigate the diet of manatees in Florida and in the Caribbean (Hurst and Beck, 1988; Mignucci-Giannoni and Beck, 1998; Beck and Clementz, 2012; Castelblanco-Martinez et al., 2009; Allen et al., 2017). For analysis, a modified microscope point technique was used to analyze stomach contents quantitatively. Samples were not processed to achieve a homogenous size since larger fragment sizes were preferential for easier identification of individual items consumed. Following Hurst and Beck (1988), each

sample was rinsed with tap water over a 30-mesh (0.52 mm) screen to remove sand, dirt, and fine particulate that might obscure identification of magnified structures. Prior to examination, a subsample of the digesta was placed on a 2 x 3-inch glass slide with acidified chloral hydrate-glycerol (Hertwig's solution) and held over a flame to clear the pigments from plant tissues and allow for easier observation of cellular structures. After clearing the pigments, the subsample was divided into five additional 2 x 3-inch glass slides for microscopic analysis.

Microscopic observations were initially made at 40X for the purpose of scanning contents and then scrutinized for identification at 100X. Each slide was analyzed through the microscope by identifying five points visible on an eyepiece with a micrometer grid along a pre-determined transect sequence at 20 separate coordinates on the stage. Observations were recorded at each coordinate, resulting in 100 different points of identification on each slide. This was repeated 5 times for each sample allowing for a total of 500 points of identification in each digesta sample. To aid in identification, plant fragments were compared with photographs on file and illustrations from Hurst and Beck (1988) that describe leaf, stem, flower, root, and rhizome parts of over 100 plant species catalogued for the study of manatee diet through microhistology. Some algal specimens were analyzed through electron-light microscopy and identified using field guides and outside experts. The identified fragments observed under the microscope were then compared for each period of time (1977–1989 and 2013–2015). Photographs of the most common digesta items were obtained for confirmation of identification. Data were then analyzed to determine temporal differences.

#### 2.4. Data analysis

Digesta samples from manatees in the IRL were divided into groups based on the years collected (1977–1989 and 2013–2015). The percent frequency of each individual dietary element observed was determined by adding the total count of each type seen in digested samples, dividing by 500 for each individual point identified (see above), and dividing by the total number of samples analyzed for each group. Diet composition was also described through the percent occurrence of dietary elements classified across four broad taxa categories: seagrasses, algae, vascular plants, and invertebrates. Similar methods to describe manatee diet have been used previously (Allen et al., 2017), and results were further

analyzed statistically.

Kruskal-Wallis tests were used to examine differences in the diet of manatees between the two sampling periods, 1977–1989 and 2013–2015. The influence of size class (calf < 235 cm, subadult 235–264 cm, and adult > 264 cm) – a proxy of age, and sex (male and female) of the manatees within each temporal subset was also investigated using the same method. The nonparametric Kruskal-Wallis test was utilized to assess the equality of medians from every group. Medians were compared since the data was not normally distributed. All statistical analyses were carried out using Minitab Statistical Software (Minitab, LLC) version 19.1.1. Statistical significance was determined using an alpha less than or equal to 0.05.

### 3. Results

A total of 193 manatees were sampled for this study, with 103 specimens sampled between 1977–1989, and 90 specimens between 2013–2015. Manatee stomach samples collected between 1977–1989 were comprised of 61.74% seagrasses, 28.39% algae, 1.68% vascular plants, 1.39% invertebrates, and 6.80% unknowns. Samples collected between 2013–2015 contained 49.46% algae, 34.04% seagrasses, 2.74% vascular plants, 2.22% invertebrates, and 11.53% unknowns (Fig. 2).

Among all samples collected between 1977–1989, 26 different types of dietary items were recorded, while samples collected between 2013–2015 contained 14 unique items (Table 1). Among individual samples, all (except one sample from 2013–2015) contained more than one species; samples collected between 1977–1989 contained a maximum of 11 different items (mean = 5.69, SD = 1.93, min = 2, max = 11) and samples collected between 2013–2015 contained a maximum of 8 different items (mean = 4.03, SD = 1.49, min = 1, max = 8). Of samples collected between 1977–1989, mixed seagrass rhizome was observed most frequently (26.9%), followed by seagrass leaf fragments from: *Halodule wrightii* (18.3%) and *Syringodium filiforme* (13.9%); *Gracilaria* spp. (13.1%) was the most frequently occurring item that was not classified as seagrass. Within samples collected between 2013–2015, the algae *Gracilaria* spp. (24.7%) and *Chaetomorpha* spp. (22.1%) occurred most frequently followed by seagrasses *H. wrightii* (14.2%) and mixed seagrass rhizome (13.4%). The relative frequency of each prominent dietary source in all samples between temporal subsets is summarized in Table 1.

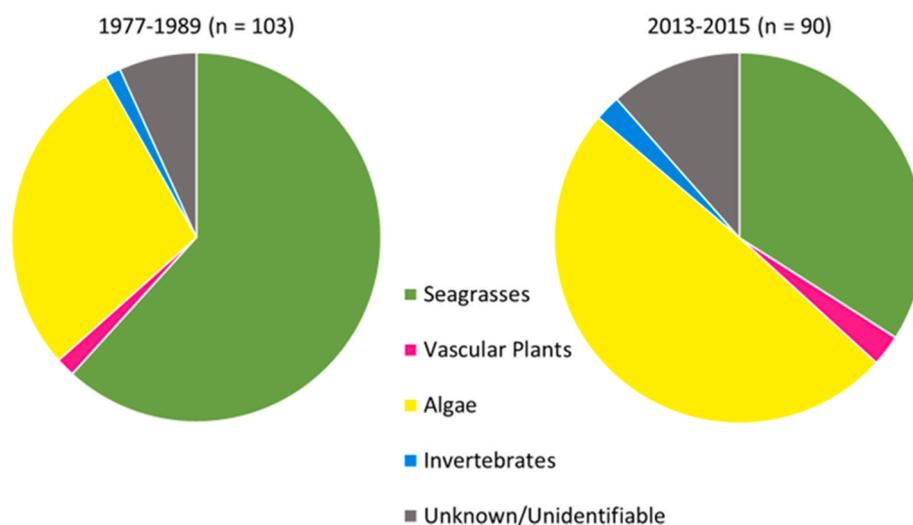


Fig. 2. Frequency of broad taxa consumed by Florida manatees in the Indian River Lagoon from 1977–1989 (left) and 2013–2015 (right).

**Table 1**  
Stomach contents identified at the lowest taxonomic level in samples collected between 1977–1989 and 2013–2015.

1977–1989		2013–2015	
<b>SEAGRASSES</b>	<b>61.74%</b>	<b>SEAGRASSES</b>	<b>34.04%</b>
Mixed Seagrass Rhizome	26.91%	Mixed Seagrass Rhizome	13.36%
<i>Halodule wrightii</i>	18.25%	<i>Halodule wrightii</i>	14.20%
<i>Syringodium filiforme</i>	13.94%	<i>Syringodium filiforme</i>	0.66%
<i>Halophila</i> spp.	0.59%	<i>Halophila</i> spp.	2.47%
<i>Thalassia testudinum</i>	0.86%	<i>Thalassia testudinum</i>	3.34%
<i>Ruppia maritima</i>	1.20%		
<b>ALGAE</b>	<b>28.39%</b>	<b>ALGAE</b>	<b>49.46%</b>
<i>Gracilaria</i> spp.	13.14%	<i>Gracilaria</i> spp.	24.69%
<i>Chaetomorpha</i> spp.	5.35%	<i>Chaetomorpha</i> spp.	22.07%
<i>Caulerpa</i> spp.	3.70%	<i>Caulerpa</i> spp.	0.61%
<i>Ulva</i> spp.	2.54%	<i>Ulva</i> spp.	2.10%
Other Algae Species	0.09%		
Unknown Algae Species	3.56%		
<b>VASCULAR PLANTS</b>	<b>1.68%</b>	<b>VASCULAR PLANTS</b>	<b>2.74%</b>
<i>Rhizophora mangle</i>	0.19%	<i>Rhizophora mangle</i>	1.49%
Various Vascular Plants	1.49%	Various Vascular Plants	1.26%
<b>INVERTEBRATES</b>	<b>1.39%</b>	<b>INVERTEBRATES</b>	<b>2.22%</b>
Phyla: Porifera	0.71%	Phyla: Porifera	0.78%
Various Invertebrates	0.68%	Various Invertebrates	1.44%
<b>UNKNOWN/ UNIDENTIFIABLE</b>	<b>6.80%</b>	<b>UNKNOWN/ UNIDENTIFIABLE</b>	<b>11.53%</b>
<b>TOTAL</b>	<b>100.00%</b>	<b>TOTAL</b>	<b>100.00%</b>

There was a 44.9% decline in the consumption of seagrasses by manatees between 1977–1989 and 2013–2015 ( $\chi^2 = 33.3901$ ,  $P < 0.0001$ ). There was also a 74.3% increase in consumption of algae between these two time periods ( $\chi^2 = 20.3821$ ,  $P < 0.0001$ ). No differences were observed in the occurrence of vascular plants ( $\chi^2 = 0.0012$ ,  $P > 0.05$ ) and invertebrates ( $\chi^2 = 0.7214$ ,  $P > 0.05$ ) in the diet of manatees between the two time periods. There were no dietary differences among size classes (seagrasses:  $\chi^2 = 4.9360$ ,  $P > 0.05$ ; algae:  $\chi^2 = 1.7141$ ,  $P > 0.05$ ; vascular plants:  $\chi^2 = 0.9432$ ,  $P > 0.05$ ; invertebrates:  $\chi^2 = 3.3587$ ,  $P > 0.05$ ) or sexes (seagrasses:  $\chi^2 = 0.3209$ ,  $P > 0.05$ ; algae:  $\chi^2 = 0.1312$ ,  $P > 0.05$ ; vascular plants:  $\chi^2 = 2.0027$ ,  $P > 0.05$ ; invertebrates:  $\chi^2 = 0.1294$ ,  $P > 0.05$ ).

#### 4. Discussion

The results of our study confirm that IRL manatees experienced a dietary shift from primarily consuming seagrasses to mainly feeding on algae over the two sampling periods, from 1977–1989 to 2013–2015. Despite a discontinuous sampling (1990–2013), we are confident that this pattern reflects a change in the diet of manatees that is independent of factors such as age (inferred from body length) and sex. The Florida manatee has a relatively broad diet (at least 60 species recorded) compared to other extant sirenians (Hartman, 1979; Best, 1981; Bengtson, 1983; Etheridge et al., 1985; Ledder and Thesis, 1986). However, in the IRL, prior stable isotope analysis has revealed that the majority of their diet consists of marine (67%) and estuarine (33%) vegetation (Reich and Worthy, 2006). As a herbivorous marine mammal, Florida manatees are dependent on submerged vegetation for nutrition and have displayed a preference for *H. wrightii* in the Indian River Lagoon (Lefebvre et al., 2000). Algae consumption by Florida manatees has been documented previously using observational and stomach content data, though presumably as a dietary supplement during winter months (Hartman, 1979; Lewis et al., 1984; Hurst and Beck, 1988). Shane (1984) also observed manatees consuming *Gracilaria* spp. (red algae) at warm-water sources (power plants) in the IRL but did not provide information on the importance of this species in their diet. Algae are commonly found in the diet of Antillean manatees (*T. manatus manatus*) in the Caribbean (Mignucci-Giannoni and Beck, 1998; Borges et al. 2008; Castelblanco-Martinez et al., 2009; Allen et al., 2017), but the relative importance of algae in their diet is minimal in comparison to seagrasses, making up < 2.5% of the Antillean manatee diet in Belize

(Allen et al., 2017). Overall, as described from published literature, algae do not seem to constitute a substantial food source for Florida manatees (Shane, 1984; Snipes, 1984; Reich and Worthy, 2006). The results from our study indicate that algae were an important source of food during our first sampling period (1977–1989, 28.4%), and more prominently during the period post-seagrass die-off that started in 2011 (2013–2015, 49.5%).

Long-term changes in the diet of sirenians have not been previously described. However, manatees and the dugong are known to exhibit short-term dietary changes when their main resources are scarce, consuming alternative plant species in regions experiencing shifts in resource abundance and availability (Best, 1981; Baugh et al., 1989; Whiting, 2002). Baugh et al. (1989) observed manatees feeding on emergent vegetation, primarily saltmarsh cordgrass (*Spartina alterniflora*), in coastal Georgia and northwest Florida, areas devoid of seagrasses. Short-term changes (e.g., seasonal) of the diet of Florida manatees have not been reported. This differs from other species such as Amazonian manatees (*Trichechus inunguis*), which have been observed to feed on a wider range of plants during the dry season when varieties of plants may not be as readily available and exhibit a more specialized diet during the wet season (Colares and Colares, 2002). West African manatees (*Trichechus senegalensis*) consume floating and emergent vegetation opposed to submerged vegetation like seagrasses, but have also been documented consuming bivalves, crustaceans, and fishes during the dry season when little or no vegetation is present (Powell, 1996; Keith Diagne, 2014; Mayaka et al., 2019). Dugongs (*Dugong dugon*) have been observed consuming algae when no seagrass is present (Whiting, 2002) and after cyclone disturbances (Spain and Heinsohn, 1973). These examples demonstrate the dietary plasticity of sirenians in response to changes in season and food availability. Our study is the first to report a long-term change in the diet of manatees in a relatively small geographic region and imply that manatees exhibit greater dietary plasticity than previously known.

Although the drivers of the dietary change suggested by our results are not well understood, the decline of seagrass in the IRL, particularly following the die-off recorded in 2011 (Morris et al., 2016, 2018; Indian River Lagoon National Estuary Program, 2020; National Oceanographic and Atmospheric Administration, 2021), probably played a major role in this dietary shift. Prior to 2011, seagrass beds in the IRL were stable or even expanding in some areas (Phlips et al., 2015, 2021). However, phytoplankton blooms were observed in 2011 (and then subsequently in 2016 and 2017–2018) and were followed by an extensive reduction in seagrass coverage, > 50% (Morris et al., 2018, 2021, 2022). With long residence times, blooms persisted for up to 13 months at a time and have not allowed for the recovery of seagrass (Morris et al., 2018, 2021). As a result, manatees continue to face a resource limitation in the IRL.

In 2021, 1101 manatee mortalities were recorded, eclipsing the previous record of 830 set in 2013 (Florida Fish and Wildlife Conservation Commission, 2021a; Florida Fish and Wildlife Conservation Commission, 2021b). Yet initial reports from the majority of carcasses recovered from the IRL from 2011, when the seagrass decline was first noted, through 2015, showed no obvious cause of death. The combination of the results of this study and the diminishing seagrass in the IRL signify that manatees are facing a critical decline in their main food source (Lapointe et al., 2015, 2020; Morris et al., 2016, 2018, 2021). The dietary shift detected using stomach content analyses might suggest that algae may not be a suitable source of food for manatees (“junk food hypothesis”). Future studies are needed to assess the status of seagrasses and macroalgae communities in the IRL and to determine the carrying capacity of this system to predict how changes in macrophyte communities can affect the health and distribution of manatees along the east coast of Florida.

In conclusion, this is the first study documenting a long-term dietary shift in any sirenian and the first study to document algae as the primary food source for manatees. The data provide conclusive evidence of a change in the diet of manatees within the IRL, an important habitat for

this species in Florida. This study can be used as a baseline to examine manatee response to changes in resource availability. Continued investigation can build upon the efforts being made to make management decisions in relation to resource availability and further investigate the extent of the impact this limitation has on the manatee population in Florida.

Future research is valuable to determine how changes in the diet of manatees might impact individual health and population-level fitness of this threatened species. An examination of how nutrient content, digestibility, and the occurrence of any toxins might vary across species consumed by manatees in the IRL could clarify the effects of this dietary shift and whether manatees may persist in this region. Further information on the effects of resource loss can show how resilient or susceptible manatees are, as well as how manatees adjust to changing conditions. Such studies would be useful to discover how manatees respond to the impacts of global climate change. Additional follow-up studies may also compare changes in manatee diet once seagrass resources return to the IRL.

#### CRediT authorship contribution statement

**Aarin Conrad Allen:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Cathy A. Beck:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft, Writing – review & editing. **Danielle C. Sattelberger:** Data curation, Formal analysis, Investigation, Resources, Visualization, Writing – review & editing. **Jeremy J. Kiszka:** Resources, Supervision, Validation, Writing – review & editing.

#### Declaration of competing interest

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

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2022.107788>.

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