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Diet of the Antillean manatee (*Trichechus manatus manatus*) in Belize, Central America

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*Belize contains important habitat for Antillean manatees (*Trichechus manatus manatus*) and provides refuge for the highest known population density of this subspecies. As these animals face impending threats, knowledge of their dietary habits can be used to interpret resource utilization. The contents of 13 mouth, six digestive tract (stomach, duodenum and colon) and 124 faecal samples were microscopically examined using a modified point technique detection protocol to identify key plant species consumed by manatees at two important aggregation sites in Belize: Southern Lagoon and the Drowned Cayes. Overall, 15 different items were identified in samples from manatees in Belize. Five species of seagrasses (*Halodule wrightii, Thalassia testudinum, Ruppia maritima, Syringodium filiforme *and* Halophila *sp.) made up the highest percentage of items. The red mangrove (*Rhizophora mangle*) was also identified as an important food item. Algae (*Ulva *sp.,* Chara *sp.,* Lyngbya *sp.) and invertebrates (sponges and diatoms) were also consumed. Variation in the percentage of seagrasses, other vascular plants and algae consumption was analysed as a 4-factor analysis of variance (ANOVA) with main effects and interactions for locality, sex, size classification and season. While sex and season did not influence diet composition, differences for locality and size classification were observed. These results suggest that analysis of diet composition of Antillean manatees may help to determine critical habitat and use of associated food resources which, in turn, can be used to aid conservation efforts in Belize.*

Keywords: feeding ecology, dietary habits, microhistological analysis, herbivory, seagrass

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INTRODUCTION

Sirenians are known to consume large quantities of vegetation (Bengtson, 1981, 1983; Best, 1981; Marsh *et al.*, 1982; Hurst & Beck, 1988). The large-scale grazing habit of these marine mammals is thought to have a positive impact on species biodiversity in seagrass beds (Packard, 1984) and a positive effect on the structure and dynamics of these communities (Aragones & Marsh, 2000). Knowledge of the diet requirements of sirenians is important for protecting the habitats in which these endangered species reside.

The Antillean manatee (*Trichechus manatus manatus*), a subspecies of the West Indian manatee (*Trichechus manatus*), occupies shallow coastal waters surrounding many islands throughout the central Caribbean and also shallow waters adjacent to mainland areas from the Yucatan Peninsula of Mexico south to Alagoas State, Brazil. Manatee numbers within this range are relatively low despite their widespread distribution and suitable habitat to support a larger population (Rathbun *et al.*, 1983; Reynolds *et al.*, 1995; Perez, 2005). There is, however, an estimated population of 1000 manatees within Belize (Auil Gomez, 2011), and the coastal waters adjacent to Belize are recognized as a critical habitat for the subspecies' continued survival (Quintana-Rizzo & Reynolds, 2007). A Manatee Recovery Plan has been enacted by the Belizean government to protect the manatee population (Auil, 1998), but the most recent population trends suggest a decline in what was previously thought to be a stable population (Auil, 2004). Because of declining numbers and low genetic variation in Antillean manatee populations (Hunter *et al.*, 2012), conservation of these manatees is a priority.

Belize contains favourable manatee habitat: 386 km of coastline along with several rivers, tidal lagoons, barrier islands (cayes) to the east, and mangrove lagoons bordering the Mesoamerican Barrier Reef. Recent surveys indicated that manatees were most numerous in the region from Chetumal Bay in the north to Placencia Lagoon in the south and east to the cayes off Belize City (Morales-Vela *et al.*, 2000; Auil, 2004; Edwards *et al.*, 2014). These areas are lined with seagrass beds extending from the shoreline to the outerlying cayes and islands, a coastal system of lagoons and bays that connect with the Caribbean (CZMAI, 2014), as well as networks of freshwater rivers that provide manatees with access to drinking water sites.

Numerous studies have focused on the types of food that sirenians consume in the wild (Best, 1981; Marsh *et al.*, 1982; Gallivan & Best, 1986; Mignucci-Giannoni & Beck,

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1998; Lanyon & Sanson, 2006; Castelblanco-Martinez *et al.*, 2009). Several plant species have been documented as occurring within the digestive tract of Florida manatees (*T. manatus latirostris*) (Best, 1981; Ledder, 1986; Hurst & Beck, 1988), Antillean manatees (Mignucci-Giannoni & Beck, 1998; Castelblanco-Martinez *et al.*, 2009; Navarro-Martinez *et al.*, 2014), Amazonian manatees (*T. inunguis*) (Colares & Colares, 2002; Guterres-Pazin *et al.*, 2014) and the dugong (*Dugong dugon*) (Heinsohn & Birch, 1972; Lipkin, 1976; Marsh *et al.*, 1982). Best (1981) conducted the first comprehensive review on the feeding behaviour, digestive physiology, consumption and diet of sirenians in wild and captive settings. A study focused on the diet of the Amazonian manatee identified a total of 24 different macrophytes from digestive tract and faecal samples with higher diversity in types of vegetation consumed during the dry season; manatees appeared to be more selective on what they consumed during the wet season (Colares & Colares, 2002; Guterres-Pazin *et al.*, 2014). Some of the most comprehensive diet data for manatees are specific to the Florida manatees (Bengtson, 1983; Hurst & Beck, 1988; Ames *et al.*, 1996; Alves-Stanley *et al.*, 2010). In Florida, manatees are known to consume over 60 different species of plants (Hartman, 1979; Bengtson, 1981, 1983; Best, 1981; Hurst & Beck, 1988) of varying nutritional value (Siegal-Willott *et al.*, 2010). Antillean manatees in Puerto Rico were reported to consume 10 different species of vegetation (Mignucci-Giannoni & Beck, 1998). A wide range of estimates exists with regard to the amount of food manatees consume in a given day, from 9 to 80 kg (Severin, 1955; Crandall, 1964; Pinto de Silveira, 1975; Hartman, 1979; Best, 1981; Lomolino & Ewel, 1984), and between 4–9% (Bengtson, 1983) to 10–15% of their body weight per day (Reep & Bonde, 2006). The quantity of vegetation eaten is dependent on the animals' size, activity level, nutritional value of the food source, metabolic requirements and perhaps reproductive condition. Consumption is also influenced by the availability of plants, which is dependent on a broad suite of environmental conditions.

Manatees select habitat based on the availability of food and proximity to freshwater resources (Hartman, 1979; Packard & Wetterqvist, 1986; O'Shea & Kochman, 1990; Gannon *et al.*, 2007). In order to meet their metabolic requirements, manatees must consume large quantities of vegetation on a daily basis (Smith, 1993). Seagrasses are an important food source for West Indian manatees and unfortunately, there have been documented declines in seagrass productivity (biomass) and biodiversity in many areas (Short & Wyllie-Echeverria, 1996; Duarte, 2002; Orth *et al.*, 2006; Waycott *et al.*, 2009), including Belize (Short *et al.*, 2006; Parham-Garbutt, 2015). Manatees also face habitat loss within many parts of their range which limits the resources necessary for their survival (Smith, 1993).

Several methods have been used to study the diet of herbivores, including direct observation and examination of ingesta and faecal samples using microhistological analysis employing a microscope point technique (Hurst & Beck, 1988). Microhistological analysis is a favoured method for the identification of ingesta and faecal samples collected from terrestrial herbivores (Holechek & Vavra, 1981) and has been employed also to study the diets of aquatic herbivores (Owen, 1975; Black *et al.*, 1994; Carriere *et al.*, 1999; Castelblanco-Martinez *et al.*, 2009; Flores-Cascante *et al.*, 2013) including sirenians (Channels & Morrissey, 1981; Hurst & Beck, 1988; Mignucci-Giannoni & Beck, 1998). This modified microscope point technique has proved to be an effective, yet inexpensive, method to gather information on diets of herbivores, and the methodology outlined by Hurst & Beck (1988) was followed for this study.

Here we provide the first in-depth information on manatee diet in Belize. Two high-use areas of Belize were compared to determine locational differences in manatee diet and to determine which habitats are likely to provide important resources for manatees. A better understanding of how Antillean manatees utilize these different areas will be necessary to develop and implement effect management plans for this endangered species.

MATERIALS AND METHODS

Subjects and sampling areas

Samples were obtained from manatees temporarily retained for telemetry studies at two locations in Belize (Figure 1): Southern Lagoon (17°12′40″N 88°20′17″W) near Gales Point, Belize District from 1997–2008, 2010 and 2012, and the Drowned Cayes (17°29′25″N 88°08′10″W) off Belize City, Belize District from 2004–2007, 2012 and 2013. Ingesta also were obtained at necropsy from manatee carcasses collected near Belize City in 1999, 2002, 2003, 2008 and 2013.

Collection methods

From 1997–2013, health assessments were conducted in Belize as part of a tagging study involving the capture and release of wild manatees. Individual manatees were net captured by an experienced crew from Florida and Belize, and pulled onto land or onto the deck of a specialized boat for a detailed physical examination (Bonde *et al.*, 2012; Wong *et al.*, 2012). Routine measurements and biological samples were collected from 137 manatees, including 13 mouth and

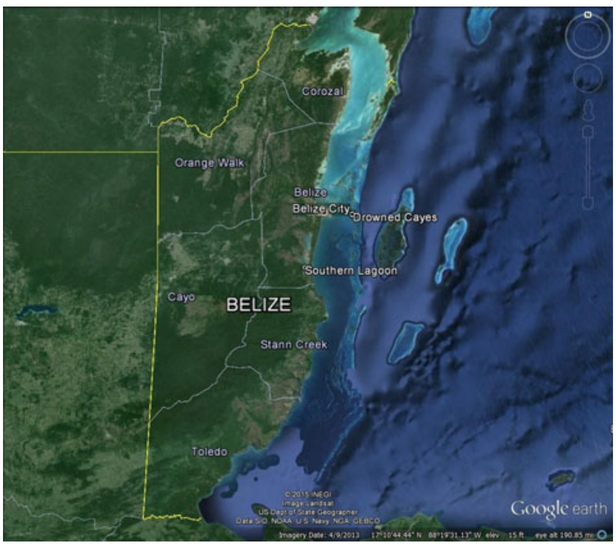

Fig. 1. District map of Belize showing areas of sample collection in the Drowned Cayes and Southern Lagoon, and carcasses collected near Belize City.

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124 faecal content. Additional ingesta samples from the stomach (4), duodenum (1) and colon (1) were obtained from six manatee carcasses (collected by the Belize Marine Mammal Stranding Network), yielding a total of 143 samples for analysis. In total, 111 samples were taken from animals captured in Southern Lagoon and 32 from animals captured in the Drowned Cayes. All samples were preserved in 70% EtOH upon collection and stored until ready for examination.

Microhistological analysis

Samples were not processed to achieve a uniform size as has been done in other diet studies, since a large fragment size was preferred to enable easier identification. Prior to examination, each sample was rinsed with tap water over a 30-mesh (0.52 mm) screen to remove sand, dirt and other fine particulate matter that might obscure microscopic observation of plant cellular structures. After rinsing, a subsample of the digesta was placed on a 2 × 3 inch glass slide to which several drops of Hertwig's solution was added. The slide was then held over an alcohol flame to facilitate the clearing of pigments from the plant cells, allowing for easier viewing of cellular structures. After clearing, the subsample was divided onto five additional 2 × 3 inch glass slides for microhistological examination.

During microscopic observation, each slide was first observed at 40× for the purpose of scanning the contents. Samples were then observed at 100× and analysed for content. Each slide was analysed through the microscope by identifying five points visible in an eyepiece micrometer grid along a prescribed transect sequence at 20 different coordinates on the stage; observations were recorded at each coordinate. This allowed for 100 different points of identification on each slide and was repeated five times for each sample. Using this modified microscope point technique developed by Owen (1975) and Holechek *et al.* (1982a, b), and detailed in Hurst & Beck (1988) and Beck & Clementz (2012), 500 points in each sample were identified using microhistological characters of visible plant fragments. The frequency of items was identified for the overall diet of manatees in Belize by recording the number of times each item was found in a sample, divided by the total number of samples studied.

To assist with identification, plant fragments were compared with reference voucher slides and photomicrographs available at the USGS Sirenia Project laboratory, along with illustrations from Hurst & Beck (1988) that describe leaf, stem, flower, root and rhizome fragments of over 100 plant species catalogued for the study of manatee diet through microhistological examination. Some species of algae were identified using field guides (Littler *et al.*, 1989; Littler & Littler, 2008) and outside expert analysis. Photomicrographs of some algal fragments and intact samples were sent to Dr Donald W. Ott at the University of Akron for identification by election microscopy. Photographs were obtained of some ingested items for subsequent confirmation of identification.

Data analysis

Samples from manatees in Belize were divided into groups and evaluated based on location, sex, size classification and season. Size classifications for manatees were based on records maintained for 280 manatee health assessments conducted in Belize, and defined as follows: calves (<200 cm), juveniles (>200–<245 cm) and adults (>245 cm). Per cent frequency of species observed was determined by adding the total count of each species type detected in the samples, divided by the total number of samples analysed for each group, and then divided by 500 (see Microhistological analysis), i.e. $P_F = \frac{n_{sp}}{500}$. Diet composition was also described through per cent occurrence of samples analysed across four categories: seagrasses, other vascular plant material, algae and invertebrates. Variation in per cent occurrence of seagrasses, other vascular plant material, and algae was further analysed statistically as a factorial analysis of variance (ANOVA) with main effects and interactions for locality, sex, size classification and season. Prior to analysis, the data were transformed to ranks to adjust for the non-normal distribution of percentages. All statistical analyses were carried out using the SAS PROC GLM utility (SAS Institute Inc., 2013).

RESULTS

Microhistological analysis revealed the contents of each sample by identifying plant fragments through microscopic investigation. The fragment sizes in mouth and stomach samples were larger than those found in faecal samples. Mouth samples contained almost complete, intact pieces of plant material, thus facilitating identification. As samples progressed further along the digestive tract, advancing from the stomach to distal colon, sample integrity and the ease of identifying fragments decreased due to digestive processes. When possible, ingesta were identified to genus as well as fragment component (e.g. leaf, stem, rhizome), then categories of species were summarized based on their occurrence within the samples.

Components of the manatee diet in Belize

The number of unique species identified in each sample ranged from 1 to 6. Mouth samples consisted of 1–2 species of seagrass, whereas 1–4 species were identified in GI-tract samples, and 1–6 different species were identified in faecal samples. Most samples, however, contained fragments from more than one diet category. Of the 143 samples, mixed seagrass rhizome was found in 129 (90.21%) samples. The seagrass *Halodule wrightii* was the second most frequently detected dietary item and occurred in 114 (79.72%) samples. In samples with mixed seagrass rhizome, the exact species of seagrass was not always discernible. Overall, 15 different items were observed in samples in addition to the highest ranked component of seagrass rhizome (Table 1). The relative occurrence of the dietary items in all samples (N = 143) by category is summarized in Table 2.

All 143 samples were examined to identify per cent occurrence relative to 500 identification points in each sample (Table 2) and to classify the average composite dietary make-up of each specimen. Identities were type categorized as 'seagrasses' (*Halodule wrightii, Thalassia testudinum, Ruppia maritima, Syringodium filiforme, Halophila* sp. and seagrass rhizome), 'vascular plant(s) – other' (e.g. *Rhizophora mangle* and unidentified vascular plant), 'algae' (e.g. *Ulva* sp., unidentified filamentous algae), or 'invertebrates' (e.g. unknown poriferan, unknown invertebrate). Seagrass leaf and/or rhizome had the highest average per

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Table 1. Per cent frequency of items identified in manatee ingesta.

Plant type	*n*	Per cent (%)
Seagrasses		
Mixed rhizome	129	90.21
Halodule wrightii	114	79.72
Thalassia testudinum	54	37.76
Ruppia maritima	52	36.36
Syringodium filiforme	4	2.80
Halophila sp.	2	1.40
Vascular plants – other		
Rhizophora mangle	76	53.15
Unknown vascular plant(s)	2	1.40
Algae		
Unknown filamentous algae	53	37.06
Ulva sp.	9	6.29
Chara sp.	4	2.80
Lyngbia sp.	2	1.40
Unknown calcified algae	1	0.70
Invertebrates		
Sponge	19	13.29
Diatoms	5	3.50
Unknown invertebrates	4	2.80

Table 2. Per cent occurrence of diet items in 143 Belize manatee samples, summarized by plant category.

Plant type	Mean	Min.	Max.	SD	Var	SE	CV
Seagrasses	81.06	0	100	21.34	455.31	1.78	26.32
Vascular plants – other	6.72	0	84	11.99	143.84	1	178.54
Algae	2.48	0	33.80	5.32	28.31	0.45	214.22
Invertebrates	1.60	0	33.20	5.13	26.32	0.43	319.79

cent occurrence in the diet (Table 2). In several samples, there were some fragments that were unidentifiable at the time of observation. Since it was not possible to classify these fragments, they were disregarded for analytical purposes.

Manatee diet by location

Diet contents were analysed from samples collected in two locations (Appendix A). Seagrass rhizome was the predominant ingested dietary item at both Southern Lagoon and the Drowned Cayes (N = 111, 90.09% frequency in Southern Lagoon; N = 32, 90.63% in the Drowned Cayes). *Halodule wrightii* was the most frequently identified component from both Southern Lagoon (N = 85, 76.58%) and the Drowned Cayes (N = 29, 90.63%). *Rhizophora mangle* and *Ruppia maritima* also were common in samples from Southern Lagoon, as were *Thalassia testudinum* and *Rhizophora mangle* in samples from the Drowned Cayes. Per cent frequency of other dietary components by location is provided in Appendix A.

The average per cent occurrence from samples obtained in Southern Lagoon and the Drowned Cayes indicated that seagrass was a primary component in specimens from Southern Lagoon: 83.14% (SD = 20.87) and the Drowned Cayes: 73.18% (SD = 21.89). Per cent occurrence to classify the composite dietary sample by location is provided in Appendix B. In a reduced three-factor ANOVA (to account for no significant difference by sex), locality had a significant effect on seagrass consumption ($P = 0.03$) due to a higher estimated mean in Southern Lagoon (83.5 ± 2.12) compared with the Drowned Cayes (70.5 ± 4.58). However, per cent consumption of both mangrove and algae were significantly higher ($P = 0.03$) in the Drowned Cayes (mangrove: 14.7 ± 2.35, algae 4.6 ± 1.00) when compared with Southern Lagoon (mangrove: 5.4 ± 1.08, algae 1.5 ± 0.46).

Manatee diet by sex

Samples were collected from 65 males and 76 females. Samples from both male and female manatees contained primarily seagrass rhizome and leaf material, with an average of 83.41% (SD = 19.05) seagrass in males and an average of 78.97% (SD = 23.15) seagrass in females. There was no significant difference in diet composition by sex ($P > 0.09$). Per cent frequency of other dietary components by sex is provided in Appendix C; per cent occurrence to classify the composite dietary sample by location is provided in Appendix D.

Manatee diet by size classification

For all size classifications, diets were very similar with mixed seagrass rhizome, *Halodule wrightii*, and *Rhizophora mangle* (red mangrove) occurring most frequently in both locations. Per cent frequency of other dietary components compared between size classifications is provided in Appendix E.

Size classifications also were analysed to examine per cent occurrence between each plant type. Seagrasses were again the type seen most frequently. Samples from manatee calves contained a mean 85.02% seagrass (SD = 17.86), juvenile manatee samples averaged 79.26% seagrass (SD = 25.24), and adult samples consisted of a mean of 82.23% seagrass (SD = 20.20). Per cent occurrence to classify the composite dietary sample by location is provided in Appendix F. Per cent algae consumption was also significantly affected by size classification ($P = 0.04$) due to a higher estimated mean for manatees >245 cm (3.8 ± 0.65) compared with manatees ≤245 cm (2.3 ± 0.89).

Manatee diet by season

Belize experiences a wet season from June to November, with peak rainfall in July and August, and a dry season from December to May. Samples from the wet (N = 89) and dry season (N = 52) contained rhizome in the majority of samples (wet = 82, 92.13%, dry = 47, 90.38%), followed by *Halodule wrightii* (wet = 75, 84.27%, dry = 39, 75.00%). Wet and dry seasons were compared by per cent occurrence of each type. Seagrass occurred most frequently in samples from both seasons. Wet season samples contained 79.86% seagrass, while samples from the dry season contained 83.00% seagrass (SD = 20.31). There was no significant difference in diet composition by season ($P > 0.30$). Per cent frequency of other dietary components by sex is provided in Appendix G; per cent occurrence to classify the composite dietary sample by location is provided in Appendix H.

DISCUSSION

The items present in diet samples from this study in Belize have been previously reported for manatees in other locations

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throughout the Atlantic and broader Caribbean regions (Best, 1981; Ledder, 1986; Hurst & Beck, 1988; Mignucci-Giannoni & Beck, 1998; Borges *et al*., 2008; Castelblanco-Martinez *et al*., 2009). The findings reported here are similar to those from studies in nearby areas, i.e. Mexico and Belize (Castelblanco-Martinez *et al*., 2009; Flores-Cascante *et al*., 2013), and are comparable to studies conducted in similar habitats around Puerto Rico (Mignucci-Giannoni & Beck, 1998). Manatees feed predominantly on seagrasses, as determined in previous studies, and the seagrasses consumed by manatees in this study are in similar order of importance as reported by Mignucci-Giannoni & Beck (1998), Castelblanco-Martinez *et al*. (2009) and Flores-Cascante *et al*. (2013). The findings are also congruent with results from stable isotope analysis of manatee tissues from Belize (Alves-Stanley *et al*., 2010). Other vascular plant material (mangrove specifically) made up a considerable portion of the identified diet items. Similar findings have been reported for manatees in Puerto Rico, Mexico and Belize (Mignucci-Giannoni & Beck, 1998; Castelblanco-Martinez *et al*., 2009; Flores-Cascante *et al*., 2013). Fragments of *Ulva* sp., *Chara* sp., and *Lyngbya* sp. were identified, but unidentified algal remains were a frequent occurrence. Of the three discernible algal species, two have been reported from Antillean manatees in other locations: *Ulva* sp. in Puerto Rico (Mignucci-Giannoni & Beck, 1998) and *Chara* sp. in Mexico (Castelblanco-Martinez *et al*., 2009). All three algal species have been observed in content samples from Florida (Hurst & Beck, 1988). Manatee diet samples in Belize also contained small amounts of invertebrates, primarily identified as an unknown poriferan.

Invertebrates often occur in close association with seagrasses and incidental ingestion is likely (Hartman, 1979; Best, 1981; Ledder, 1986; Hurst & Beck, 1988; Courbis & Worthy, 2003), although manatees and dugongs are known to be omnivorous when resources are limited (Lipkin, 1976; Powell, 1978; Preen, 1995a). Sand grains, detrital material and microalgae were observed in the samples we examined and were probably ingested incidentally. Mouth and stomach samples were the least digested and contained the most identifiable fragments. Manatees have a very long digestive tract and a 4–7 day passage time (Larkin *et al*., 2007). Faecal samples, which are more fully digested, were the greatest challenge for identification. Faecal samples therefore may not precisely reflect individual feeding habits, since some components of the diet may no longer be identifiable. As expected, faecal samples contained a higher amount of unknown or unidentifiable points during examination and contained a higher percentage of rhizomes which is not as easily degraded through digestion. Because some portions of the samples contained unidentified fragments, the complete composition of each sample could not be attained. For example, not all algae were identifiable, but filamentous algae were more often observed in our Belize samples.

Diet differences between locations

Seagrass was found in more samples and in higher percentages in samples collected in Southern Lagoon ($P = 0.03$); algae and mangrove made up a larger proportion of those samples from the Drowned Cayes ($P = 0.03$). Likewise, Alves-Stanley *et al*. (2010) observed a difference in $\delta^{13}C$ and $\delta^{15}N$ values between manatees sampled in the Drowned Cayes and Southern Lagoon. Observed variation in ingested food items between manatees in Southern Lagoon and Drowned Cayes may be attributed to environmental differences between the two sites.

As manatees are able to move between fresh, salt and brackish waters, they have been documented to make use of dominant plant types in each type of environment. Differences in diet between the two locations in Belize illustrated only slight dietary differences. By comparison, manatee diets in Florida are highly variable by region (Alves-Stanley *et al*., 2010). Florida manatee diets often contain the same seagrass types as manatees in the Caribbean (Best, 1981; Ledder, 1986; Hurst & Beck, 1988; Mignucci-Giannoni & Beck, 1998; Castelblanco-Martinez *et al*., 2009; Flores-Cascante *et al*., 2013), but also contain several additional genera of algae and freshwater plants not identified in these Belize samples (e.g. *Chara, Gracilaria, Hydrilla, Myriophyllum, Najas, Vallisneria*). Antillean manatee diet samples in Brazil were comprised of 21 different types of algae, seagrasses and invertebrates, but predominantly contained rhodophytes (Borges *et al*., 2008), while Amazonian manatees consumed at least 24 different plant species within the central Amazon (Borges *et al*., 2008).

The presence of mangrove fragments detected in the samples obtained from manatees in the Drowned Cayes (59%) was higher than those for individuals sampled from Southern Lagoon (51%). In the Drowned Cayes, manatees were usually associated with, and captured near, mangrove forest islands located offshore of the mainland. Mangrove islands provide shelter for manatees in these open-water marine environments, and additionally, mangrove leaves store fresh water (Odum & McIvor, 1990). The higher detection of mangrove ingesta in the manatees from the Drowned Cayes may indicate, by association, the use of mangrove forage to supplement their need for fresh water. The fresh water available in this vascular plant may enable manatees to spend longer periods of time in marine environments.

Diet differences between sexes and sizes

There were no significant differences observed in diet preferences between male and female manatees in Belize. This finding is consistent with a previous study carried out in Mexico (Castelblanco-Martinez *et al*., 2009). No other known published account has demonstrated a significant difference in diet between the sexes. Of the 76 females in our study, four were sampled when lactating. Pregnant or lactating females may have additional nutritional needs, but no obvious difference in diet composition of these females was discernible.

No difference in manatee diet between size classifications was detected for seagrass or [other] vascular plant consumption, but adult manatees (>245 cm) consumed a statistically greater proportion of algae: adult mean 3.8 ± 0.65, juveniles 2.3 ± 0.89 ($P = 0.04$). No previous studies have analysed the relationship between manatees' size (length) and diet. Influencing factors may be a result of larger manatees consuming a greater amount of food and/or the duration of time spent feeding.

Diet differences between seasons

Manatees in Belize have been observed to utilize different habitat types in the wet and dry seasons (Morales-Vela *et al*., 2000; Self-Sullivan *et al*., 2003; Auil, 2004; Auil *et al*., 2007), however, no statistical differences in the diet samples were observed in this study. Similar to Belize, no seasonal differences in diet were observed nearby in Chetumal Bay, Mexico (Castelblanco-Martinez *et al.*, 2009), and no seasonal differences in diet have been observed in the dugong as well (Preen, 1995b). In the Amazon, manatees have been observed to be more selective during the rainy season, but fed on a more diverse number of plants during the dry season (Colares & Colares, 2002; Guterres-Pazin *et al.*, 2014). Although seasonal habitat use may change within Belize, the uniform similarity of food plants available for consumption year-round may account for the lack of seasonal diet differences reported in this study.

Alves-Stanley *et al.* (2010) used stable-isotopes to infer seasonal changes in manatee diet and observed a difference in $\delta^{13}C$ and $\delta^{15}N$ values between manatees sampled in the Drowned Cayes and Southern Lagoon. Rather than attribute this simply to environmental differences between the two sites, this could be a result of changes in manatee resource selection (food or habitat use), and/or seasonal variability in the stable isotope ratios of vegetation. Manatees in Belize have been known to make seasonal changes in habitat use (Morales-Vela *et al.*, 2000; Auil *et al.*, 2007) and have been documented moving between the two sampling sites within the same day (RKB, JAP, personal observation). As most of the specimens examined in this study were faecal samples, a precise snapshot of manatee diet differences cannot be assumed due to a manatees' long gut transit time.

Conclusions and future recommendations

Belize is a central location for the Antillean manatee population (O'Shea & Salisbury, 1991) and provides important habitat for the long-term survival of the subspecies (Quintana-Rizzo & Reynolds, 2007; Auil Gomez, 2011). Manatee populations can be used to assess the health of marine ecosystems as they are a sentinel species for habitat quality (Bonde *et al.*, 2004). In Belize, manatees face an increasing threat from anthropogenic and natural causes of mortality including boat strikes and habitat alteration from construction and contaminated effluents (Auil Gomez, 2011). An understanding of the types, species, areas and feeding preferences of manatees is helpful for developing conservation and habitat protection plans for manatees.

This study found that the seagrasses *Halodule wrightii, Thalassia testudinum* and *Ruppia maritima* are the predominant food items consumed by manatees in Belize. Red mangrove (*Rhizophora mangle*) also made up a significant portion of the observed manatee diet. Algae and invertebrates were detected in small quantities. The high frequency of seagrass rhizome and mangrove leaves observed in the faecal samples may be attributed to the indigestibility and toughness of these fragments, and, therefore, the overall proportions may be overrepresented. Further, the amount of rhizome consumed is dependent on the species and substrate. Our findings emphasize the importance for protection and preservation of seagrass and mangrove habitats in Belize to promote a positive outcome for this important regional population of manatees.

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Appendix A. Per cent frequency: location.

Location	*n*	Per cent (%)
Southern Lagoon		
Seagrasses		
Mixed rhizome	100	90.09
Halodule wrightii	85	76.58
Ruppia maritima	49	44.14
Thalassia testudinum	33	29.73
Syringodium filiforme	4	3.60
Halophila sp.	1	0.90
Vascular plants – other		
Rhizophora mangle	57	51.35
Unknown vascular plants	2	1.80
Algae		
Unknown filamentous algae	38	34.23
Ulva sp.	6	5.41
Chara sp.	1	0.90
Lyngbia sp.	1	0.90
Invertebrates		
Sponge	6	5.41
Unknown invertebrates	2	1.80
Drowned Cayes		
Seagrasses		
Mixed rhizome	29	90.63
Halodule wrightii	29	90.63
Thalassia testudinum	21	65.63
Ruppia maritima	3	9.38
Halophila sp.	1	3.13
Vascular plants – other		
Rhizophora mangle	19	59.38

Continued

Appendix A. Continued

Location	*n*	Per cent (%)
Algae		
Unknown filamentous algae	15	46.88
Ulva sp.	3	9.38
Chara sp.	3	9.38
Lyngbia sp.	1	3.13
Unknown calcified algae	1	3.13
Invertebrates		
Sponge	13	40.63
Diatoms	5	15.63
Unknown invertebrates	2	6.25

Appendix B. Belize manatee diet sample composite: location.

Location	Mean	Min.	Max.	SD	Var	SE	CV
Southern Lagoon							
Seagrasses	83.14	14.20	100	20.87	435.42	1.98	25.10
Vascular plants – other	5.65	0	53.80	9.63	92.81	0.91	170.49
Algae	1.55	0	33.80	3.94	15.51	0.37	253.53
Invertebrates	0.43	0	13	1.99	3.96	0.19	460.16
Drowned Cayes							
Seagrasses	73.18	0	100	21.89	478.99	4	29.91
Vascular plants – other	11.11	0	84	18.02	324.84	3.29	162.18
Algae	5.03	0	20.80	6.32	39.94	1.15	125.55
Invertebrates	6.05	0	33.20	9.38	87.99	1.71	155.13

Appendix C. Per cent frequency: sex.

Sex	*n*	Per cent (%)
Male		
Seagrasses		
Mixed rhizome	58	89.23
Halodule wrightii	52	80
Ruppia maritima	26	40
Thalassia testudinum	26	40
Halophila sp.	2	3.08
Syringodium filiforme	1	1.54
Vascular plants – other		
Rhizophora mangle	29	44.62
Unknown vascular plants	2	3.08
Alga		
Unknown filamentous algae	24	36.92
Ulva sp.	4	6.15
Chara sp.	2	3.08
Invertebrates		
Sponge	6	9.23
Diatoms	3	4.62
Female		
Seagrasses		
Mixed rhizome	69	90.79
Halodule wrightii	60	78.95
Thalassia testudinum	27	35.53
Ruppia maritima	26	34.21
Syringodium filiforme	3	3.95

Continued

Appendix C. Continued

Sex	*n*	Per cent (%)
Vascular plants – other		
Rhizophora mangle	47	61.84
Algae		
Unknown filamentous algae	28	36.84
Ulva sp.	5	6.58
Chara sp.	2	2.63
Lyngbia sp.	2	2.63
Unknown calcified algae	1	1.32
Invertebrates		
Sponge	13	17.11
Unknown invertebrates	4	5.26
Diatoms	2	2.63

Appendix D. Belize manatee diet sample composite: sex.

Sex	Mean	Min.	Max.	SD	Var	SE	CV
Male							
Seagrasses	83.41	27.40	100	19.05	363.09	2.36	22.84
Vascular plants – other	5.02	0	39.60	8.22	67.64	1.02	163.98
Algae	2.06	0	20.80	3.93	15.47	0.49	191.08
Invertebrates	1.30	0	33.20	5.27	27.81	0.65	404.22
Female							
Seagrasses	78.97	0	100	23.15	536.02	2.66	29.32
Vascular plants – other	8.35	0	84	14.43	208.21	1.66	172.81
Algae	2.49	0	33.80	5.36	28.71	0.61	214.77
Invertebrates	1.90	0	29.20	5.09	25.86	0.58	267.27

Appendix E. Per cent frequency: size classification.

Size class	*n*	Per cent (%)
Calf		
Seagrasses		
Halodule wrightii	11	91.67
Mixed rhizome	10	83.33
Thalassia testudinum	4	33.33
Ruppia maritima	4	33.33
Vascular plants – other		
Rhizophora mangle	5	41.67
Algae		
Unknown filamentous algae	3	25
Lyngbia sp.	1	8.33
Unknown calcified algae	1	8.33
Invertebrates		
Sponge	2	16.67
Unknown invertebrates	1	8.33
Subadult		
Seagrasses		
Mixed rhizome	34	89.47
Halodule wrightii	28	73.68
Thalassia testudinum	8	21.05
Syringodium filiforme	3	7.89
Halophila sp.	1	2.63

Continued

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Appendix E. Continued

Size class	*n*	Per cent (%)
Vascular plants – other		
Rhizophora mangle	24	63.16
Unknown vascular plants	1	2.63
Algae		
Unknown filamentous algae	8	21.05
Ulva sp.	4	10.53
Chara sp.	2	5.26
Invertebrates		
Unknown invertebrates	2	5.26
Adult		
Seagrasses		
Mixed rhizome	84	92.31
Halodule wrightii	74	81.32
Thalassia testudinum	41	45.05
Ruppia maritima	29	31.87
Halophila sp.	1	1.10
Syringodium filiforme	1	1.10
Vascular plants – other		
Rhizophora mangle	47	51.65
Unknown vascular plants	1	1.10
Algae		
Unknown filamentous algae	41	45.05
Ulva sp.	5	5.49
Chara sp.	2	2.20
Lyngbia sp.	1	1.10
Invertebrates		
Sponge	14	15.38
Diatoms	5	5.49
Unknown invertebrates	1	1.10

Appendix F. Belize manatee diet sample composite: size classification.

Size class	Mean	Min.	Max.	SD	Var	SE	CV
Calf							
Seagrasses	85.02	47.40	100	17.86	318.85	5.15	21
Vascular plants – other	3.25	0	15.20	5.45	29.65	1.57	167.55
Algae	2.20	0	18.40	5.32	28.31	1.54	241.86
Invertebrates	1.10	0	5.60	2.10	4.42	0.61	191.09
Subadult							
Seagrasses	79.26	0	100	25.24	637.20	4.09	31.85
Vascular plants – other	10.91	0	84	18.45	340.31	2.99	169.08
Algae	1.07	0	12.60	2.59	6.70	0.42	241.14
Invertebrates	1.10	0	16.20	3.73	13.94	0.61	339.38
Adult							
Seagrasses	81.23	23.40	100	20.20	408.14	2.12	24.87
Vascular plants – other	5.57	0	53.80	8.49	72.06	0.89	152.37
Algae	2.82	0	33.80	5.28	27.88	0.55	187.54
Invertebrates	1.92	0	33.20	5.91	34.96	0.62	308.50

Appendix G. Per cent frequency: season.

Season	*n*	Per cent (%)
Wet		
Seagrasses		
Mixed rhizome	82	92.13
Halodule wrightii	75	84.27
Thalassia testudinum	39	43.82
Ruppia maritima	33	37.08
Syringodium filiforme	1	1.12
Vascular plants – other		
Rhizophora mangle	55	61.80
Unknown vascular plants	2	2.25
Algae		
Unknown filamentous algae	29	32.58
Ulva sp.	7	7.87
Chara sp.	3	3.37
Invertebrates		
Sponge	12	13.48
Diatoms	3	3.37
Unknown invertebrates	2	2.25
Dry		
Seagrasses		
Mixed rhizome	47	90.38
Halodule wrightii	39	75
Ruppia maritima	19	36.54
Thalassia testudinum	15	28.85
Syringodium filiforme	3	5.77
Halophila sp.	2	3.85
Vascular plants – other		
Rhizophora mangle	21	40.38
Algae		
Unknown filamentous algae	24	46.15
Lyngbia sp.	2	3.85
Ulva sp.	2	3.85
Chara sp.	1	1.92
Unknown calcified algae	1	1.92
Invertebrates		
Sponge	7	13.46
Diatoms	2	3.85
Unknown invertebrates	2	3.85

Appendix H. Belize manatee diet sample composite: season.

Season	Mean	Min.	Max.	SD	Var	SE	CV
Wet							
Seagrasses	79.86	0	100	22.04	485.93	2.34	27.60
Vascular plants – other	8.53	0	84	14.22	202.30	1.51	166.74
Algae	2.11	0	20.80	3.99	15.93	0.42	188.73
Invertebrates	1.71	0	33.20	5.55	30.83	0.59	323.86
Dry							
Seagrasses	83	27.40	100	20.31	412.64	2.82	24.47
Vascular plants – other	3.87	0	18.20	5.97	35.67	0.83	154.21
Algae	2.60	0	33.80	5.84	34.13	0.81	224.69
Invertebrates	1.48	0	21.60	4.46	19.93	0.62	302.28

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