Florida manatees *Trichechus manatus latirostris* actively consume the sponge *Chondrilla caribensis*

William Fitt
Odum School of Ecology, University of Georgia, Athens, GA, USA

**ABSTRACT**

The Florida manatee (*Trichechus manatus latirostris* Linnaeus 1758) actively selects and consumes the “chicken-liver” sponge *Chondrilla caribensis*. Manatees ate over 10% of *C. caribensis* on a sample dock, mostly from pylons that received no direct sunlight. Since manatees reportedly eat mostly seagrasses and algae, it was thought that the chlorophyll-a content of the symbiotic cyanobacteria in *C. caribensis* might be correlated to the amount eaten; however the correlation was not significant (*P > 0.05*). *C. caribensis* has variable chemical defenses and round spherasters (spicules), but these do not appear to be effective deterrents to predation by manatees. This is the first direct evidence that manatees actively seek out and consume a sponge.

**Subjects** Conservation Biology, Ecology, Marine Biology, Biological Oceanography

**Keywords** Manatee, Predation, Sponges

**INTRODUCTION**

Florida manatees (*Trichechus manatus latirostris*) are generally considered to be strictly herbivorous mammals (e.g., seagrasses, algae, seeds, acorns; O’Shea, 1986; Guterres-Pazin, Rosas & Marmontel, 2012), only incidentally consuming invertebrates or fish (Powell, 1978). However, in spite of the fact that stomach and fecal analyses find mostly seagrasses and algae, there have been a few instances where manatees have been observed to eat invertebrates (e.g., Courbis & Worthy, 2003). Barnacles, tunicates, bivalves, gastropods, crustaceans, polychaetes, other small invertebrates and fish have been ingested by manatees and dugongs (Powell, 1978; Reeves, Tuboku-Metzger & Kapindi, 1988; Anderson, 1989; O’Shea et al., 1991; Preen, 1995; Courbis & Worthy, 2003; Guterres-Pazin, Rosas & Marmontel, 2012; Vélez-Juarbe, 2014). Spicules of sponges seen in necropsy samples obtained from manatee carcasses are generally considered incidentally ingested with seagrasses and algae (e.g., Allen et al., 2017). In addition, Florida manatees ingest undigestible debris while feeding, often killing the animal (Beck & Barros, 1991).

*Chondrilla caribensis* (= *C. nucula* “chicken liver sponge”), an encrusting sponge, has photosynthetic cyanobacteria and non-photosynthetic bacterial symbionts (Wilkinson & Vacelet, 1979; Hill et al., 2006), releases nitrate onto reef ecosystems (Corredor et al., 1988), and is an important competitor for space in tropical mangrove ecosystems in Florida, Bahamas, and the Caribbean (Hill, 1998). Presumably, symbiotic cyanobacteria conduct photosynthesis, fix nitrogen, and metabolize ammonia (oxidizing it to nitrate).
that is excreted by the sponge (Wilkinson & Fay, 1979; Corredor et al., 1988). Sponges have variable concentrations of anti-predation compounds and structural defenses in their tissues (Jones, Blum & Pawlik, 2005). C. caribensis inhibits growth in chickens (Yacowitz & Zaccone, 1982) and is reported to be toxic to fish (Green, 1977), but tends to be eaten by reef fish more than other sponges (Chanas & Pawlik, 1995). In fact, C. caribensis is the most frequently found sponge in the digestive tracts of fish (Randall & Hartman, 1968) and when transplanted from mangroves with few fish predators to the reef with lots of fish predators, it is completely consumed by fish (Swearingen & Pawlik, 1998). C. caribensis is also the main sponge eaten by hawksbill (Meylan, 1988; Pawlik, Loh & McMurray, 2018) and green (Bjorndal, 1990) turtles.

Chondrilla caribensis has a low spicule content to organic matter ratio, which is thought to be less of a deterrent to certain predators (Randall & Hartman, 1968; Wulff, 2006). The siliceous spicules are round spherasters (ca. 28.8 um) with about 25 spines on each, plus minute secondary spines that are identified with scanning electron microscopy (Rützler, Duran & Piantoni, 2007). All of the sponges in the genera are rich in amino acids, protein (Yacowitz & Zaccone, 1982), and collagen (Rützler, Duran & Piantoni, 2007), possibly reasons why manatees and fish eat the sponge. Chlorophyll-a and phycobilin concentrations in bacterial symbionts living in C. caribensis determine the color variations of the sponge, which range from whitish or cream color (sponge) to dark grey-brown (sponge + symbionts) (Fig. 1). It is not known whether any of these factors are important in the nutrition of manatees.

Researchers, students and lay-people have observed manatees eating C. caribensis off docks, pylons and hard surfaces in the Florida Keys for at least twenty-five years (1992–2017). This paper describes intentional feeding on the sponge C. caribensis by the Florida manatee T. manatus latirostris. The following hypotheses were addressed: (H1) Manatees “select” the sponge C. caribensis from others, (H2): Manatees eat varying amounts (>10%) of C. caribensis, (H3): Manatees prefer eating C. caribensis in the shadiest area of the sample dock, (H4): Manatees eat C. caribensis containing more chlorophyll.

MATERIAL AND METHODS

Observations of Florida manatees eating C. caribensis were made in all months of the year, for multiple years between 1992 and 2017. Manatees are commonly found in Buttonwood Sound, Florida Keys during the cooler months (November –May), but are less numerous in the warmer months (June –October). Sponges involved in other experiments (e.g., predation by starfish, competition, growth studies) were returned to Florida Bay by tie-wrapping the sponges to one or two cement bricks so that they would not die rolling around in the seagrasses. The species of sponge tied to bricks included those listed in Table 1. The bricks were placed a 1–2 m from the dock in about less than a meter of water, easily observed from the dock. They were monitored at least daily for approximately 1 week after placement.

A sample dock was selected in Buttonwood Sound in the Upper Keys (longitude 25.101908, latitude −80.438824) after observing manatees eating C. caribensis from the
Figure 1  Manatees eating *C. caribensis* off pylons of a dock in Key Largo, Florida. Manatees eating *C. caribensis* off pylons of a dock in Key Largo, Florida. (A) Three manatees, (B) one manatee, (C) a manatee eating *C. caribensis* (*m* = manatee, *white* is the sponge tissue, grey-brown is the symbiotic cyanobacteria in the outer layers of the sponge), (D) pieces of *C. caribensis*, showing its grey-brown external color that is due to the symbiotic cyanobacteria in the sponge.

pylons in the winter months. Evidence of *C. caribensis* predation by manatees included that the sponge (1) was shredded, (2) had missing layers, and (3) appeared white rather than the greyish brown color due to eating the outer sponge layer containing the symbiotic cyanobacteria.
bacteria. Some of the *C. caribensis* were scraped completely off the pylons by manatees, while remnants of others were hanging from the pylons by thin strands of tissue. Such injuries of *C. caribensis* were monitored over a week-long period from December 4–8, 1995. We do not know the full recovery time in which the symbiotic cyanobacteria grows back and the color of the sponge returns to a greyish brown color, though it is longer than one week. Percent of eaten *C. caribensis* was estimated by point-intercept methods from all four sides of each of the 11 dock pylons holding up the dock. Clear plexiglass (ca. 0.33 × 0.33 m) was marked with dots 2.5 cm apart for a total of 121 dots. Each side of each pylon was scored from the surface of the water to the bottom as “eaten” or “uneaten” *C. caribensis* or “something else”. There were rarely other species of sponge found on the pylons. The sides of pylons were divided into two groups: those that were exposed to direct sunlight coming from the east, west or south (11 sides), and those that had no direct sunlight (33 sides).

Since manatees eat mostly seagrasses and algae, preference for *C. caribensis* that have more chlorophyll-*a* (from symbiotic cyanobacteria) in them was tested. A small piece of *C. caribensis* (1.75 cm² wide circle by about 0.5 cm thick) was collected from each side of each pylon on December 8–9, 1995 and placed in a small vial. Chlorophyll-*a* per gram of wet weight and dry weight were determined from 8 pieces of *C. caribensis* on August 7, 1997. Four ml of acetone were added to each of these samples to extract the chlorophyll and the vial was placed in a freezer at −10 °C. After 24 hr the absorbance of the chlorophyll extract was read on a spectrophotometer, and the amount of chlorophyll-*a* (µg/cm²) was calculated (11.43*663 nm –0.64*630 nm) × (volume of the acetone).

The Florida Wildlife Commission sent stomach contents of a dead manatee (MNW17086) which was found in August 2017 near the Crystal River, Citrus County, Florida (longitude 28.922051, latitude −82.690457). It presumably died from exposure to red tide. While some areas have known resident populations, this manatee was not a known animal, so the Florida Wildlife Commission does not know its foraging range. The Florida manatee can range from Texas, to the Bahamas, and north to Massachusetts. The
stomach sample was sent by mail from the Florida Wildlife Commission, and analyzed microscopically for the shape and size of spicules.

**RESULTS**

The Florida manatee was commonly observed over a twenty-five year period (1992–2017) removing and swallowing the sponge *C. caribensis* off pylons and hard surfaces both during the daytime and when it is dark in Buttonwood Sound, Florida Bay in the Florida Keys (Fig. 1). Most of the time the manatees were just swimming by, but when they stopped by a dock or seawall they appeared to be eating *C. caribensis*. The dark outside of the *C. caribensis* was shredded, exposing the white interior of the sponge, making the predation events very visible (Fig. 1). Unexpectedly it was found that at least 20 manatees (not identified except by size) over a 20 year period (1995–2014) made a choice of eating *C. caribensis* and no other sponges from the bricks during the week after they were put out (Supplementary data). There was no evidence of other predators on *C. caribensis*, and no such signs of manatee feeding on other species of sponge on the bricks, the bottom and sides of a dock. A small starfish *Echinaster spinulosus* is uncommonly found on *C. caribensis* in the mangroves of Florida Bay, but shows no evidence of removal of sponge tissue (probably a micro-predator), and moves off of *C. caribensis* in less than a day.

Manatees fed mostly on the interior and north sides of pylons of the sample dock (Fig. 2). Manatees ate an average of 10.8 ± 6.8% (s.d., *n* = 44) of the *C. caribensis* off the sides of pylons (Figs. 1, 3A), where the percent cover varied from approximately 5 to about 50%. There were 15/33 (45.5%) sides of pylons with no direct sunlight that had >10% *C. caribensis* eaten and only 3/11 (27.3%) sides of pylons that were facing either east, west or south with direct sunlight that had at least 10% eaten (Figs. 2, 3A). The value of >10% was picked because the average that the manatees ate was close to this (10.8 ± 6.8%). The two pylons that showed no signs of grazing by manatees had anemones (*Aiptasia pallida*) occurring on the *C. caribensis*, whereas the other sides of pylons had no visible anemones on the sponge.

The µg chlorophyll-a/cm² of *C. caribensis* tissue is relatively constant on all sides of the pylons, with an average value of 46.6 ± 22.6 (s.d., *n* = 44) (Fig. 3B). Mean values of 19.3 ± 12.1 µg chlorophyll-a/g wet weight or 107.9 ± 64.7 chlorophyll-a/g dry weight were recorded (95% CI, *n* = 8). The percent of *C. caribensis* eaten as related to µg chlorophyll-a/cm² is not significant (linear regression *r*² = 0.04, *p* > 0.05, *n* = 44).

Spicules from a dead manatee (FSW17086) were analyzed, and found to contain more than one species of sponge (e.g., several sharp monaxon and tetraxon vs. round spheraster spicules). There were many *Chondrilla*-type spheraster microscleres seen in the sample (Fig. 4), but it was difficult to tell if any of the species of sponge was directly or incidentally eaten.

**DISCUSSION**

H1: Manatees “select” the sponge *C. caribensis* from others.
Manatees in Florida are known to eat barnacles, bivalves, gastropods, crabs, and tunicates (O’Shea et al., 1991; Courbis & Worthy, 2003). Powell (1978) reported carnivory by Antillean manatees of fish from gill nets in Jamaica. While it is unusual for any marine animal to eat chemically defended prey, such as certain sponge species (Green, 1977; Swearingen & Pawlik, 1998), the Florida manatees select and consume the sponge *C. caribensis*, removing *C. caribensis* off of docks, pylons, seawalls, or any hard surface. There was no evidence that any other species of sponge was directly consumed by manatees, though this may be possible with some sponges containing variable or no chemical defenses and/or round vs sharp spicules. Sponges from other experiments that were not eaten by manatees were typically chemically defended or had sharp monaxon spicules (e.g., Table 1, Jones, Blum & Pawlik, 2005).

**H2:** Manatees eat varying amounts (>10%) of *C. caribensis*

Manatees ate over half of the average cover eaten of *C. caribensis* (over 10%) from sides of pylons of the sample dock in Florida Bay (Figs. 1–3). Six docks near the sample dock, many pylons, seawalls, and hard surfaces show signs of manatees feeding on *C. caribensis*.

**H3:** Manatees prefer eating *C. caribensis* in the shadiest area of the sample dock

Manatees in this study are about twice as likely to forage in the shady area vs. a sunny portion of the dock. The shadier areas were usually sides of pylon surfaces that were completely covered by the dock, compared to the sides of pylons that were exposed for some time to direct sun (the eastern, southern, and western sides that were not fully shaded by the dock). This could be due to desire of manatees to minimize exposure to ultra-violet light, maximize cooler conditions, avoid boats and/or humans, or it could be some unknown aspect of consumption of *C. caribensis* by manatees.

**H4:** Manatees eat *C. caribensis* containing more chlorophyll
It was thought that because manatees forage seagrasses and algae, they would also prefer eating a sponge containing high amounts of chlorophyll, possibly for nutritional purposes. However, manatees apparently do not distinguish *C. caribensis* based on the amount of chlorophyll-*a* (*p* > 0.05). There is no evidence that any aquatic mammal can detect the relative amount of chlorophyll in food.

Why do manatees consume *C. caribensis*? Manatees and dugongs incidentally consume invertebrates that occur on the blades of seagrasses (e.g., O'Shea et al., 1991; Allen et al., 2017), which would include sponges, however this is not considered active feeding on
Figure 4  Spicules found in dead manatee MNW17086. (A, B) Microscleres of Chondrilla (caribensis?) from the stomach of manatee MNW 17086 (light background); (C) Microscleres from type specimens of C. caribensis (dark background, Rützler, Duran & Piantoni, 2007). Dark bar is 10 µm long.

While manatees may be eating C. caribensis because local food resources might be diminished, possibly due to global warming (e.g., O’Shea, 1986), some scientists propose that manatees eat invertebrates for the nitrogen within. Manatees living in marine habitats...
eat mostly seagrasses, which take-up nitrogen mostly through their leaves and are thought to be nitrogen limited (Duarte, 1990; Nayer et al., 2018). Up to 50% of nitrogen requirements of seagrasses are supplied by epiphytes living on the leaves, and seagrasses provide 8–22% protein per dry weight equivalent to corn and wheat (Walsh & Grow, 1972). It certainly seems possible that manatees could supplement their nitrogen (protein) consumption by eating sponges.

While protective compounds are normally found in sponges, those are evidently not as potent in C. caribensis as in other sponges (Table 1), enabling predation by fish and turtles (Randall & Hartman, 1968; Chanas & Pawlik, 1995; Swearingen & Pawlik, 1998; Pawlik, Loh & McMurray, 2018). The “mechanical defenses” include siliceous spherasters (round) in C. caribensis, rather than pointed spicules as in other species. C. caribensis has minute secondary spines on round spicules (Rützler, Duran & Piantoni, 2007) that apparently interfere minimally with consumption by turtles (Meylan, 1988; Bjorndal, 1990; Pawlik, Loh & McMurray, 2018), fish and manatees. It appears that C. caribensis has a combination of variable chemical defenses coupled with round rather than pointed spicules (Table 1), that enables manatees to eat it.

CONCLUSION

The manatee T. manatus latirostris has been observed to directly feed on the sponge C. caribensis. This sponge has a symbiotic relationship with cyanobacteria, but the correlation of chlorophyll-a with percent consumed is insignificant. Manatees eat more of C. caribensis from the shaded areas under a dock compared to non-shaded areas, which could be a defense of manatees to boats, humans, or both. C. caribensis has variable chemical defenses along with round (rather than pointed) spicules, which could explain its palatability to manatees.

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ADDITIONAL INFORMATION AND DECLARATIONS

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The author declares there are no competing interests.
Author Contributions

- William Fitt conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

Raw data are available as a Supplemental File.

Supplemental Information

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REFERENCES

Allen AC, Beck CA, Bonde RK, Powell JA, Gomez NA. 2017. Diet of the Antillean manatee (Trichechus manatus manatus) in Belize, Central America. Journal of the Marine Biological Association of the United Kingdom 98(7):1831–1840 DOI 10.1017/S0025315417000182.

Anderson PK. 1989. Deliberate foraging on macro-invertebrates by dugongs. National Geophysical Research 5:4–6.

Beck CA, Barros NB. 1991. The impact of debris on the Florida manatee. Marine Pollution Bulletin 22(10):508–510 DOI 10.1016/0025-326X(91)90406-I.

Bjorndal KA. 1990. Digestibility of the sponge Chondrilla nucula in the green turtle, Chelonia mydas. Bulletin of Marine Science 47:567–570.

Chanas B, Pawlik JR. 1995. Defenses of Caribbean sponges against predatory reef fish II. Spicules, tissue toughness, and nutritional quality. Marine Ecology Progress Series 127:195–211 DOI 10.3354/meps127195.

Corredor JE, Wilkinson CR, Vicente VP, Morell JM, Otero E. 1988. Nitrate release by Caribbean reef sponges. Limnology and Oceanography 33:114–120 DOI 10.4319/lo.1988.33.1.0114.

Courbis SS, Worthy GAJ. 2003. Opportunistic carnivory by Florida manatees (Trichechus manatus latirostris). Aquatic Mammals 29:104–107 DOI 10.1578/016754203101023942.

Duarte CM. 1990. Seagrass nutrient content. Marine Ecology Progress Series 67:201–207 DOI 10.3354/meps067201.

Green G. 1977. Ecology of toxicity in marine sponges. Marine Biology 40:207–215 DOI 10.1007/BF00390876.

Guterres-Pazin MG, Rosas FCW, Marmontel M. 2012. Ingestion of invertebrates, seed, and plastic by the Amazonian manatee (Trichechus inunguis)(Mammalia, Sirenia). Aquatic Mammals 38:322–324 DOI 10.1578/AM.38.3.2012.322.

Hill M. 1998. Spongivory on Caribbean reefs releases corals from competition with sponges. Oecologia 117:143–150 DOI 10.1007/s004420050642.
Hill M, Hill A. 2002. Morphological plasticity in the tropical sponge anthosigmella varians: responses to predators and wave energy. *Biological Bulletin* 202:86–95 DOI 10.2307/1543225.

Hill M, Hill A, Lopez N, Harriott O. 2006. Sponge-specific bacterial symbionts in the Caribbean sponge, *Chondrilla nucula* (Demospongiae, Chordrosida). *Marine Biology* 148:1221–1230 DOI 10.1007/s00227-005-0164-5.

Jones AC, Blum JE, Pawlik JR. 2005. Testing for defensive synergy in Caribbean sponges: bad taste or glass spicules? *Journal of Experimental Marine Biology and Ecology* 322(1):67–81 DOI 10.1016/j.jembe.2005.02.009.

Loh TL, Pawlik JR. 2014. Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* 111:4151–4156 DOI 10.1073/pnas.1321626111.

Meylan A. 1988. Spongivory in hawksbill turtles: a diet of glass. *Science* 239:292–295.

Nayer S, Loo MGK, Tanner JE, Longmore AR, Jenkins GP. 2018. Nitrogen acquisition and resource allocation stategies in the temperate seagrass *Zostera nigricaulis*: uptake, assimilation and translocation processes. *Scientific Reports* 8:17151 DOI 10.1038/s41598-018-35549-3.

O’Shea TJ. 1986. Mast foraging by West Indian manatees (*Trichechus manatus*). *Journal of Mammalogy* 67(1):183–185 DOI 10.2307/1381020.

O’Shea TJ, Rathbun GB, Bonde RK, Biergelt CD, Odell DK. 1991. An epizootic of Florida manatees associated with a dinoflagellate bloom. *Marine Mammal Science* 7:165–179 DOI 10.1111/j.1748-7692.1991.tb00563.x.

Pawlik JR, Loh TL, McMurray SE. 2018. A bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what’s old, what’s new and future directions. *PeerJ* 6:e4343 DOI 10.7717/peerj.4343.

Powell JA. 1978. Evidence of carnivory in manatees (*Trichechus manatus*). *Journal of Mammalogy* 59(2):442 DOI 10.2307/1379938.

Preen A. 1995. Diet of dugongs: are they omnivores? *Journal of Mammalogy* 76(1):163–171 DOI 10.2307/1382325.

Randall JE, Hartman WD. 1968. Sponge-feeding fishes of the West Indies. *Marine Biology* 1:216–225 DOI 10.1007/BF00347115.

Reeves RR, Tuboku-Metzger D, Kapindi RA. 1988. Distribution and exploitation of manatees in Sierra Leone. *Oryx* 22:75–84 DOI 10.1017/S0030605300027538.

Rützler K, Duran S, Piantoni C. 2007. Adaption of reef and mangrove sponges to stress: evidence for ecological speciation exemplified by *Chondrilla cariben-sis* new species (Demospongiae, Chondrosidia). *Marine Ecology* 28:95–111 DOI 10.1111/j.1439-0485.2007.00183.x.

Swearingen DC, Pawlik JR. 1998. Variability in the chemical defense of the sponge *Chondrilla nucula* against predatory reef fishes. *Marine Biology* 131:619–627 DOI 10.1007/s002270050354.

Vélez-Juarbe J. 2014. Ghost of seagrasses past: using sirenians as a proxy for historical distribution of seagrasses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 400:41–49 DOI 10.1016/j.palaeo.2013.05.012.
Walsh GE, Grow TE. 1972. Composition of *Thalassia testudium* and *Ruppia maritima*. *Quarterly Journal of the Florida Academy of Sciences* 35(2/3):97–108.

Wilkinson CR, Fay P. 1979. Nitrogen fixation in coral reef sponges with symbiotic cyanobacteria. *Nature* 279:527–520 DOI 10.1038/279527a0.

Wilkinson CR, Vacelet J. 1979. Transplantation of marine sponges to different conditions of light and current. *Journal of Experimental Marine Biology and Ecology* 37(1):91–104 DOI 10.1016/0022-0981(79)90028-5.

Wulff JL. 2006. Ecological interactions of marine sponges. *Canadian Journal of Zoology* 84:146–166 DOI 10.1139/z06-019.

Yacowitz H, Zaccone TG. 1982. Study of the nutritional value of the marine sponge, *Chondrilla nucula* [Abstract 1570]. *Poultry Science Association* 61.