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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

FACTORS AFFECTING GREEN TURTLE FORAGING ECOLOGY ACROSS

MULTIPLE SPATIAL SCALES

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Elizabeth R. Whitman

2018

To: Dean Michael R. Heithaus
       College of Arts, Sciences and Education

This dissertation, written by Elizabeth R. Whitman, and entitled Factors Affecting Green Turtle Foraging Ecology Across Multiple Spatial Scales, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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Date of Defense: October 15, 2018

The dissertation of Elizabeth R. Whitman is approved.

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Dean Michael R. Heithaus
College of Arts, Sciences and Education

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Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2018

DEDICATION

To my mother Linda Gardner and late grandfather Thomas Gardner whose small lessons in the mechanics and value of the natural world and whose support made my pursuit of a higher education possible.

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inspiring me from an early age to be curious about the world around me and for always being just a phone call away, and my partner in life, Mauricio Bolivar, who, despite not always understanding the process, sees my passion for pursuing my goals and continually strives to find ways to support me.

ABSTRACT OF THE DISSERTATION

FACTORS AFFECTING GREEN TURTLE FORAGING ECOLOGY ACROSS

MULTIPLE SPATIAL SCALES

by

Elizabeth R. Whitman

Florida International University, 2018

Miami, Florida

Professor Michael R. Heithaus, Major Professor

The hierarchical levels at which resource selection occurs can have important

consequences for individual and population energy budgets and structure the impacts of a

forager on its ecosystem. Assessing factors affecting resource selection of large marine

herbivores across scales is important because of their potentially large impacts on

seagrass community dynamics and historical and current changes in their population sizes

and those of their potential predators. I explored the factors (predation risk, resource

abundance, quality and identity) affecting resource use of large marine herbivores (green

turtles, *Chelonia mydas*) from the scale of habitat patches to forage species within

patches. I used a combination of in-water surveys, aerial drone video transects, baited

camera surveys, and seagrass community and nutrient content analyses to provide

insights into resource use by turtles in multiple ecological contexts.

In Abaco, The Bahamas I found relatively intact shark populations, including

apex predators, relative to other parts of the Caribbean. In the context of healthy predator

populations in Abaco, I tested *a priori* predictions rooted in Ideal Free Distribution (IFD)

theory. Green turtles off Abaco deviated from predictions of an IFD determined by the

standing stocks of seagrass. Instead, distributions are consistent with predictions of the foraging arena hypothesis with turtles largely restricted to safe habitat patches and selecting locations within these where seagrass N content is relatively high.

Marine invasive species can have detrimental effects on coastal ecosystems and economies. Therefore, understanding the effects of, and factors influencing the rate of spread of the invasive seagrass *Halophila stipulacea* in the Caribbean is important. In the French West Indies (Guadeloupe, Martinique and St. Martin), I investigated foraging preferences for native versus invasive seagrass species and whether green turtles might facilitate or attenuate the invasion through their choice of habitats and feeding patterns. Green turtle distributions were correlated with native seagrass distributions. Also, despite similar nutrient contents, turtles preferred feeding on native seagrasses irrespective of their relative abundance within a patch. These results suggest that, as predicted by the Enemy Release Hypothesis, green turtles likely facilitate the invasion and spread of the invasive seagrass that may reduce energy flow into turtle populations.

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CHAPTER I

GENERAL INTRODUCTION

Large grazers occupy important positions in ecosystems across diverse settings. Many of them can have tremendous impacts on the structure and function of ecosystems (Johnson and Cushman, 2007; Waldram, Bond and Stock, 2008), but these impacts are influenced by decisions they make in the face of spatiotemporal variation in both top-down (*i.e.,* risk from large-bodied predators; Heithaus *et al.* 2014; Wirsing, Heithaus, and Dill 2007) and bottom-up (*e.g.,* forage quantity and quality, species invasions; (Power, 1992; Burkholder, Heithaus and Fourqurean, 2012) factors. Assessing the role of large herbivores in marine systems, therefore, is particularly important because of dramatic and virtually world-wide declines in populations of their predators (large sharks; Ferretti *et al.* 2010), ongoing conservation programs focused on large grazers (Aryal *et al.,* 2017; Makecha and Ghosal, 2017; Mazaris *et al.,* 2017), and major changes to the base of food webs through eutrophication, habitat destruction, and species invasions (Binzer *et al.,* 2016; Mougi and Kondoh, 2016; David *et al.,* 2017).

Green turtles (*Chelonia mydas*), whose primary food source in most populations is seagrass (Bjorndal, 1985), are endangered on a global scale (Jackson, 2001; Seminoff *et al.,* 2007), but as a result of focused conservation and management efforts, some regional populations are increasing (Mazaris *et al.,* 2017). As grazers, green turtles have the potential to affect seagrass communities (Fourqurean *et al.,* 2010; Kelkar *et al.,* 2013; Christianen *et al.,* 2014). In Bermuda, where conservation efforts have been particularly successful and shark populations are reduced, unchecked grazing by green turtles has led to the collapse of some local seagrass meadows (Fourqurean *et al.,* 2010), and despite the decline in seagrass availability, green turtles are not shifting away from seagrass as their major food source (Burgett *et al.,* 2018). Therefore, my dissertation research focused on

identifying the factors affecting green turtle foraging ecology, including food availability and predation risk, in multiple ecological contexts. I investigated the factors influencing turtle habitat use and foraging across three levels of Johnson (1980)'s hierarchy. In Abaco, The Bahamas I investigated how predation risk, food availability, and food quality (nutrient content) affect turtle habitat use at the scale of population home ranges and areas within the home ranges. In the French West Indies (FWI), I elucidated how habitat use within home ranges and food selection varied across gradients of native and invasive seagrass abundance and food quality.

In Chapter II, I investigated potential predation risk faced by turtles by conducting the first survey of abundance and species composition of sharks, the top non-human predator of sea turtles (Heithaus *et al.,* 2008), in Abaco, The Bahamas. The Bahamas was established as a shark sanctuary in 2011 (S.I. No. 64 of 2011) and has relatively high species richness relative to other areas of the Caribbean (Ward-Paige *et al.,* 2010; Brooks *et al.,* 2011). I used baited remote underwater videos (BRUVs) to survey shark populations on four fringing reefs (>50 km combined length) and in two seagrass lagoons (9 km^2 each). Most studies of green turtle foraging behavior have been conducted in areas with already depleted predator populations (*e.g.*, Fourqurean *et al.,* 2010; Kelkar *et al.,* 2013; Christianen *et al.,* 2014), with one notable exception in Shark Bay, Western Australia where green turtles in relatively good body condition avoided areas where they were likely to encounter tiger sharks despite the availability of high quality forage (Heithaus *et al.,* 2007). In Chapter III, I used data from the shark surveys in Chapter II to help explore the importance of predation risk, food abundance and food quality on green turtle habitat using *a priori* predictions derived from Ideal Free Distribution (IFD) theory.

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While changes in predator abundance might have profound effects on the spatiotemporal pattern of turtle grazing, invasive species also have the potential to shape sea turtle habitat use and foraging and, in turn, turtles may either facilitate or attenuate the rate of invasion by marine plants. *Halophila stipulacea*, a seagrass native to the western Indian Ocean, has successfully spread to the Caribbean (Ruiz & Ballantine, 2004; Willette *et al.,* 2014). The invasive *H. stipulacea* is fast-growing, produces many seeds, and can tolerate a wide range of salinities, temperatures, light levels, and disturbance regimes (Short *et al.,* 2010). Yet, little is known about the ecological consequences of the invasion of the Caribbean (Willette and Ambrose, 2012). In Chapter IV, I investigated space use of turtles within foraging areas across three sites in the French West Indies (Guadeloupe, Martinique and Saint Martin) that represent a gradient of invasive species presence. I conducted snorkel transect surveys of green turtle density, point surveys of the macrophyte community, and macrophyte nutrient content analysis to determine whether turtles avoided areas with high cover of invasive species, preferred such areas, or selected habitats irrespective to the overall composition of seagrass communities. In Chapter V, I tested the Enemy Release Hypothesis (Keane and Crawley, 2002) and the potential factors influence turtle foraging preferences of green turtles at the individual and population level using turtle focal follows and macrophyte nutrient content analysis off the west coast of Guadeloupe (French West Indies).

In my concluding chapter, I synthesize the results of the four studies to identify common patterns in green turtle, and more generally large herbivore, resource selection and suggest further avenues for research that will help us better understand the

consequences of turtle behavioral decisions and more effectively manage marine

ecosystems.

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CHAPTER II

SPATIAL VARIATION IN THE RELATIVE ABUNDANCE AND SPECIES
COMPOSITION OF SHARK COMMUNITIES IN NEARSHORE WATERS OF
ABACO, THE BAHAMAS

Abstract

As upper trophic level predators, sharks may play important roles in shaping reef and seagrass ecosystems through both direct predation and risk effects. The over-exploitation of sharks, therefore, has the potential to induce cascading effects on marine ecosystems. For example, in the absence of intact shark populations, sea turtle foraging behavior may be less constrained and population sizes may increase more rapidly and to larger population levels than in the presence of sharks. Therefore, increasing turtle populations have the potential to overgraze seagrass habitats. Protection of sharks began in The Bahamas in 2011, and the impacts on local shark populations are unknown at this time. Although previous studies suggest that shark populations of The Bahamas are less depleted than other areas of the Caribbean, many areas of The Bahamas have not been surveyed for shark populations. Here, I provide the first assessment of shark relative abundance, species composition and distribution in reef and seagrass habitats of Great Abaco. Between 2015 and 2016, I sampled four fringing reefs (>50 km combined reef length) and two seagrass-dominated bays (9 km^2 each) adjacent to these reefs using baited remote underwater video (BRUV) systems. A total of 331 videos comprising 815 hours of recording were collected across all six sites. I identified nine shark species (*Carcharhinus acronotus*, *Carcharhinus limbatus*, *Carcharhinus perezi*, *Galeocerdo cuvier*, *Ginglymostoma cirratum*, *Negaprion brevirostris*, *Rhizoprionodon spp.*, *Sphyrna mokarran*, *and Sphyrna tiburo*), with most species observed in both reef and seagrass habitats. Caribbean reef sharks (*C. perezi*) had the highest occurrence and relative abundance overall and dominated the reef habitats. Nurse sharks (*G. cirratum*) were also common on reefs and were the most abundant shark in seagrass habitats followed by the

small-bodied blacknose shark (*C. acronotus*) and apex predatory tiger shark (*G. cuvier*). Only Carribean reef, blacknose, and nurse sharks ever exhibited maxN counts over 1. These results suggest that, similar to other areas of The Bahamas, shark populations of Great Abaco remain healthy compared to most areas of the Caribbean and still feature true apex predators that could play important roles in ecosystem dynamics.

Introduction

Apex predators can initiate cascading effects on ecosystem processes through their control of large herbivores and lower trophic level predators (Estes *et al.,* 2011). As upper trophic level predators, sharks can impact marine ecosystems through consumptive effects, risk effects, and their interaction (Heithaus *et al.,* 2008, 2010). For example, green turtles and dugongs in Shark Bay, Australia preferentially forage on seagrasses, and forego forage with greater nutritional value, when and where they are less likely to encounter tiger sharks (Heithaus *et al.,* 2007; Wirsing, Heithaus and Dill, 2007; Burkholder *et al.,* 2013). In the absence of intact shark populations, foraging behavior of prey species may go unchecked such as in the case where green turtles (*Chelonia mydas*) forage free of risk and may overgraze seagrass meadows (Fourqurean *et al.,* 2010; Heithaus *et al.,* 2014). Although the strength and context dependence of top-down impacts of sharks still requires considerable attention, the virtually worldwide over-exploitation of sharks is likely affecting the current state of many marine systems (Ferretti *et al.,* 2010; Worm *et al.,* 2013; Estes *et al.,* 2016). To slow and reverse these impacts, conservation strategies that include the creation of marine protected areas and

improved fisheries management are being implemented in many regions (Ward-Paige, 2017).

Central to adaptive management are population baselines from which to monitor changes relative to varying human activities and interventions. Despite at least one quarter of elasmobranchs being threatened with extinction (Dulvy *et al.,* 2014), there are few studies that provide baseline information for shark populations, especially those unaffected by humans (e.g., Shipley *et al.* 2017) Assessments of reef shark populations and communities are particularly important to evaluate the effectiveness of large-scale, shark specific no-take zones, referred to as "shark sanctuaries" that have been designated in numerous countries (Ward-Paige, 2017).

In The Bahamas, legal protection of sharks began in 2011 (S.I. No. 64 of 2011) following gillnet and longline prohibitions in the early 1990s. The legal protection established The Bahamas as a national shark sanctuary extending throughout the 628,026 km^2 exclusive economic zone (EEZ). Fines are imposed for the take, trade, sale or possession of any shark species or their parts with exceptions made for permitted research (summarized by Ward-Paige, 2017). No standardized shark monitoring program exists, and with no commercial fishery and associated catch data, permanent research stations located on Bimini, and Eleuthera, provide the only time-series data for assessment (Shipley *et al.,* 2017; Hansell *et al.,* 2018). Surveys of sharks, particularly tiger sharks (see Heithaus *et al.,* 2014), are particularly important in light of recent protections (2009) of sea turtles in The Bahamas EEZ.

Here, I used baited remote underwater video (BRUV) surveys to 1) provide a snapshot of shark relative abundance and species composition, and 2) test for differences in the community composition and relative abundance of sharks from reef and adjacent seagrass habitats of Great Abaco, The Bahamas. The BRUVs also yield comparable or better results than visual surveys for non-cryptic species (Lowry *et al.,* 2012) and longline catch per unit effort data (Brooks *et al.,* 2011). The use of BRUVs is an appropriate method for my study because they remove behavioral effects of humans in the water and observer bias during visual surveys. The limited field of view of mono-BRUVs (*i.e.*, single camera BRUVS) can reduce the ability to detect differences in relative abundance among sites with high shark abundance, however, for sites that do not exceed a threshold of six to seven focal sharks, the limited field of view is unlikely to affect differences in detection (Kilfoil *et al.,* 2017). Furthermore, BRUVs provide a more appropriate tool than unbaited cameras for assessing the presence and relative abundance of species at relatively low population densities which is often the case for apex predators.

Methods

Study site

The Abacos are located in the northern Bahamas and include Little Abaco, Great Abaco, and many smaller cays. The study occurred offshore of Great Abaco, the third largest island in The Bahamas, and its Atlantic-facing cays (Fig 1). Although human

population is currently low on Abaco at 17,224 according to the All Bahamas Census

2010 Report (2012), the most recently published census, it is rapidly increasing (up

30.78% from 2000 to 2010).
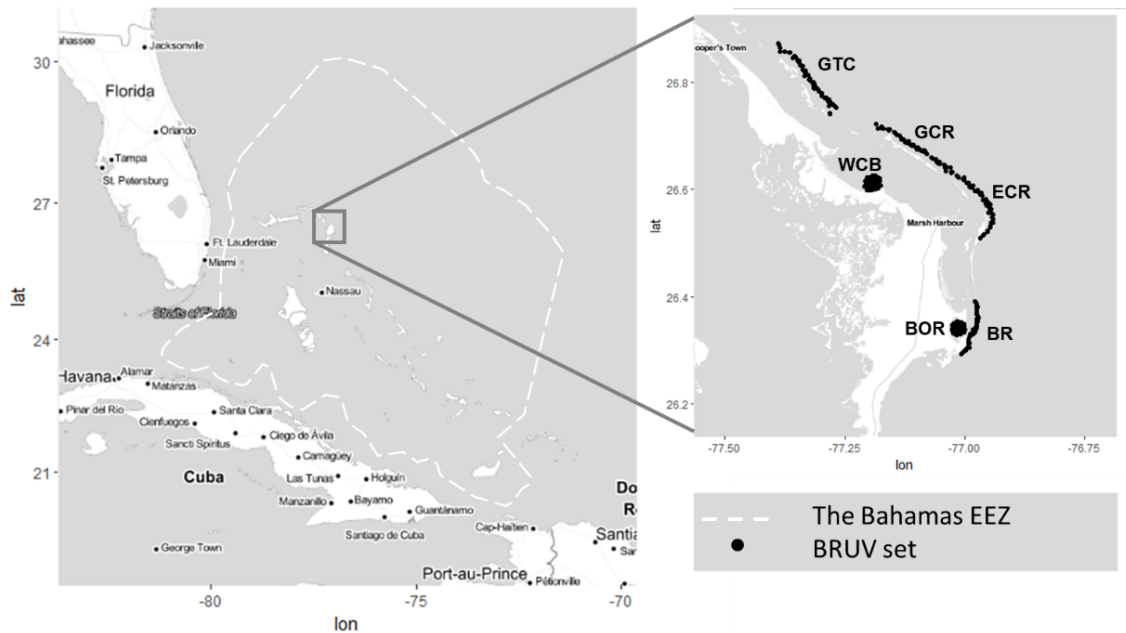
Figure 1. Map of The Bahamas shark sanctuary (left) and the study area offshore of Great Abaco (right). The white dash delineates the EEZ of The Bahamas that serves as a shark sanctuary. Individual BRUV locations are displayed with black dots in the right panel.

The coastline of Great Abaco is characterized by shallow tidal creek systems that

give way to semi-enclosed, shallow (<1 to 10 m) bays comprising diverse habitats

including patch reefs, hard-bottom and sandy-bottom interspersed within the dominant

seagrass habitat (Yeager, Layman and Allgeier, 2011). The tidal creeks are lined by red

dwarf mangroves (*Rhizophora mangle*) with some black and white mangroves

(*Avincennia germinans* and *Laguncularia racemosa,* respectively) also present

(Valentine-Rose *et al.,* 2007). The most abundant seagrass in the bay and creek systems

is *Thalassia testudinum* with other seagrasses (*Syringodium filiforme* and *Halodule wrightii*) and macroalgae occurring in mixed meadows and at lower densities (Chapter III). The eastern shoreline is further protected by a chain of smaller barrier islands and fringing coral reef systems.

I sampled four fringing reefs along the Atlantic-facing reef tract outside of Abaco's many Cays (Fig 1) including two northeast facing reefs [Green Turtle Cay Reef (GTC) and Guana Cay Reef (GCR)] and two east facing reefs [Elbow Cay Reef (ECR) and the Bight Reef (BR)]. I also sampled two seagrass-dominated bays: The Bight of Old Robinson (BOR) and Water Cay Lagoon (WCB). One bay site, BOR, is accessible primarily from Little Harbour, a small, isolated settlement that is currently slated for development including a 44-slip marina (Roberts, 2016, 2018). The second bay site, WCB, is the southern end of a northeast facing bight in the Sea of Abaco, and construction on a new marina and housing development on the shoreline of WCB began shortly after the sampling for this study was completed.

Field methods

The BRUV units consisted of a concrete base (*ca.* 12 kg) poured into a 37-cm diameter piling cap. Threaded rods were fitted with a series of nuts and washers that were set into the concrete. A GoPro HERO® high definition video camera was attached to a PVC coupling on a 0.91 m vertical rod. A buoy line was attached to an eye bolt at the top of the vertical rod. The bait cage, made from 2.54 cm mesh poultry fencing, was attached

to the end of the 1.82 m rod that was set at an angle to position the cage in front of the camera. To keep the bait off the bottom, a PVC bipod was added to support the bait arm (Figure 2A).

All simultaneously deployed BRUVs were deployed at points haphazardly selected at least 1 km apart. When set for reef habitat sampling (Figure 2B), 5-10 BRUVs were recorded simultaneously along the forereef at depths of 4-17 meters. No more than 18 total BRUVs were collected in a single day. In seagrass habitats (Figure 2C), BRUV units were set at depths of 1.25-5.5 meters with a maximum of six BRUVs deployed simultaneously and no more than 12 deployed in one day.

Systems were baited with 1 kg of pilchard (*Sardinops* spp.) and positioned so the bait was downstream of the camera. All BRUVs were deployed during daylight hours (7:00 – 18:00) and retrieved after a minimum soak time of 90 minutes, with batteries providing up to *ca.* 4 hours of continuous recording. Many BRUV surveys use shorter soak times (Bond *et al.,* 2012; Kilfoil *et al.,* 2017). I chose to soak BRUVs for longer than standard periods, however, to increase detection probability of large-bodied species that are likely to be ecologically important (*e.g.,* tiger sharks) and typically occur at lower abundances (Ward-Paige *et al.,* 2010).
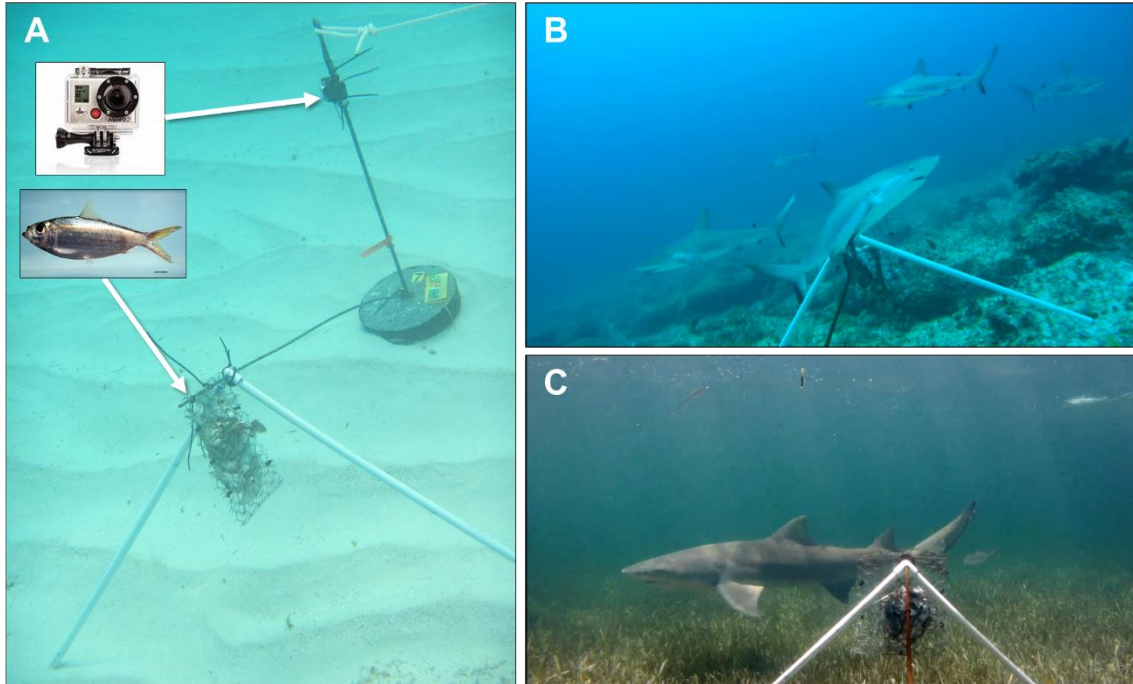
Figure 2. BRUVs (A) were set in both reef (B) and seagrass (C) habitats. We calculated maxN separately for each species. In B), five Caribbean reef sharks are observable while, a single lemon shark is shown in C)

Video analysis

Each reef BRUV was watched at normal (1x) speed and annotated independently by at least two observers, using the Global FinPrint Annotator software (www.globalfinprint.org). Because shark occurrences and relative abundances were lower in the bays than on the reefs, bay BRUVs were watched at normal (1x) speed by only one observer. Data recorded by observers included species identification and the maximum number of individuals from each species within a single frame (maxN) (Bond *et al.,* 2012; Lowry *et al.,* 2012). The Annotator software captures a still image of all observations, so species identifications and count data could be verified.

Data analysis

I used R version 3.4.1 (R Core Team, 2016) for all statistical and spatial analysis

to compare data collected across the across six sites from two habitat types: reefs (n = 4)

and two bays (n = 2). Four metrics were used to describe relative shark abundance from

individual BRUVS: maxN, sum of maxN, presence/absence, and species richness. The

maxN of each shark species was recorded by video observers, and the sum of maxN was

calculated as:

$$maxN_{sum} = \sum_{i}^{n} maxN_i \qquad \text{(Eqn. 1)}$$

where *n* is the total number of species observed on a BRUV, and *i* is the maxN of a

species. BRUVs were assigned were assigned a score of "1" if present and "0" if absent

for each species. Species richness is the total number of species observed and was

calculated using the present/absent scores of all species for each BRUV:

$$Spp_r = \sum_{i}^{n} p_i \qquad \text{(Eqn. 2)}$$

where Spp_r is species richness, *p* is the presence of a shark species on a BRUV, and *n* is

the total number of shark species.

To further define differences among sites and between habitat types, I used the

percent of BRUVs with at least one shark observation (per species and any species):

$$Obs\ \% = \frac{\Sigma p}{n} * 100 \qquad \text{(Eqn. 3)}$$

where *Obs %* is the percent of BRUVS with shark observations, *p* is the presence of a shark or species on a BRUV, and *n* is the total number of BRUVs for a site or habitat type. I used a generalized linear model (GLM) to test the effects of habitat type (reef or bay) on occurrence (*i.e.,* presence/absence) and maxN for each species with a maxN > 1, and the sum of maxN. Presence/absence data were analyzed using a generalized linear mixed model (GLMM) fit by maximum likelihood (Adaptive Gauss-Hermite) with link logit:

$$Species \sim habitat\_type + (1 \,|\, site)$$

where *Species* is the species of shark being modeled, *habitat_type* is as a fixed effect, and *site* is the random effect. I used Chi-square to test for differences among reef sites. Because of low counts in bay habitat, I used Fisher's Exact Test to compare bay sites.

Mean BRUV diversities were also compared among sites and between habitats using Wilcoxon Rank Sum tests. Diversity indices are described as the variance measures of species abundance distribution (Oksanen, 2018). To calculate species diversity, I used the Shannon Weiner diversity from the 'vegan' package:

$$H = -\sum_{i=1}^{S} p_i \, log_e p_i \qquad \qquad (Eqn. 4)$$

where p_i is the proportion of species *I*, *S* is the number of species, and log_e is the natural log (Oksanen, 2018).

Rhizoprionodon spp. were not identified to the species level because of the difficulty of distinguishing between *Rhizoprionodon porosus* (Caribbean sharpnose

shark) and *Rhizoprionodon terraenovae* (Atlantic sharpnose shark) without a physical inspection. Nine other shark observations out of a total of 629 shark observations were identifiable only to the genus level (*Carcharhinus*). Three of these were the only observations in their respective BRUVs, and the other six appeared at least 30 min from any other shark observation. These observations were included in calculations of overall shark occurrence and pooled maxN, however, only individuals identified to the species level (with the exception of *Rhizoprionodon* spp.) were included in species richness.

Results

In total, 331 BRUVs provided 815 hours of video across all sites (Table 1). Overall, there were 419 maxN observations from 9 shark species: blacknose shark (*Carcharhinus acronotus*), blacktip shark (*Carcharhinus limbatus*), Caribbean reef shark (*Carcharhinus perezi*), tiger shark (*Galeocerdo cuvier*), nurse shark (*Ginglymostoma cirratum*), lemon shark (*Negaprion brevirostris*), sharpnose shark (*Rhizoprionodon* spp), great hammerhead shark (*Sphyrna mokarran*), and bonnethead shark (*Sphyrna tiburo*). Sharks were present on 68.9% (228 of 331) of all BRUVs. Sharks were observed at all sites with species-level maxN values ranging from one to six (Table 1, Figure 3). *Rhizoprionodon* spp. and *S. mokarran* were only observed in reef habitat and *S. tiburo* was observed only in bay habitat. There was variation between habitat types in the occurrence of sharks (all species pooled: ($Z = 5.787$, $P < 0.0001$) with at least one shark appearing on 85.2% (179 of 210) of reef BRUVs compared to 40.5% (49 of 121) of bay BRUVs. Not all species were observed equally between habitat types (Figure 4). Habitat

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type (reef or bay) had a significant effect on the occurrence of *C. perezi* ($Z = 5.928$, $P <$ 0.0001), *G. cuvier* ($Z = -2.686$, $P = 0.007$), and *G. cirratum* ($Z = 2.130$, $P = 0.03$) (Table 2). Two species, *C. perezi* and *G. cirratum*, were found more often at reef habitats and *G. cuvier* were observed more often in bay habitats (Figure 4, Table 2, Appendix I). Habitat type had a significant effect on maxN (reef > bay) of all species pooled ($Z = 5.677$, $P <$ 0.0001) and *C. perezi* ($Z = 5.138$, $P < 0.0001$) that had the highest total sum of maxN at BR (Table 2).

Table 1. Summary of BRUVs. Total BRUVs only include usable BRUVs; total hours are the sum of video time analyzed; mean hours (SD) are the average length of video time analyzed per BRUV

Site	Total Sets	Total hours	Mean hours
Bay Total	121	357.73	2.96 ± 0.36
Bight of Old Robinson Bay	61	182.31	2.99 ± 0.30
Water Cay Bay	60	175.43	2.92 ± 0.42
Reef Total	210	457.23	2.18 ± 0.70
Bight Reef	52	105.76	2.03 ± 0.54
Elbow Cay Reef	53	115.80	2.18 ± 0.55
Green Turtle Cay Reef	54	142.19	2.63 ± 0.92
Guana Cay Reef	51	93.49	1.83 ± 0.43
Grand Total	331	814.96	2.46 ± 0.71
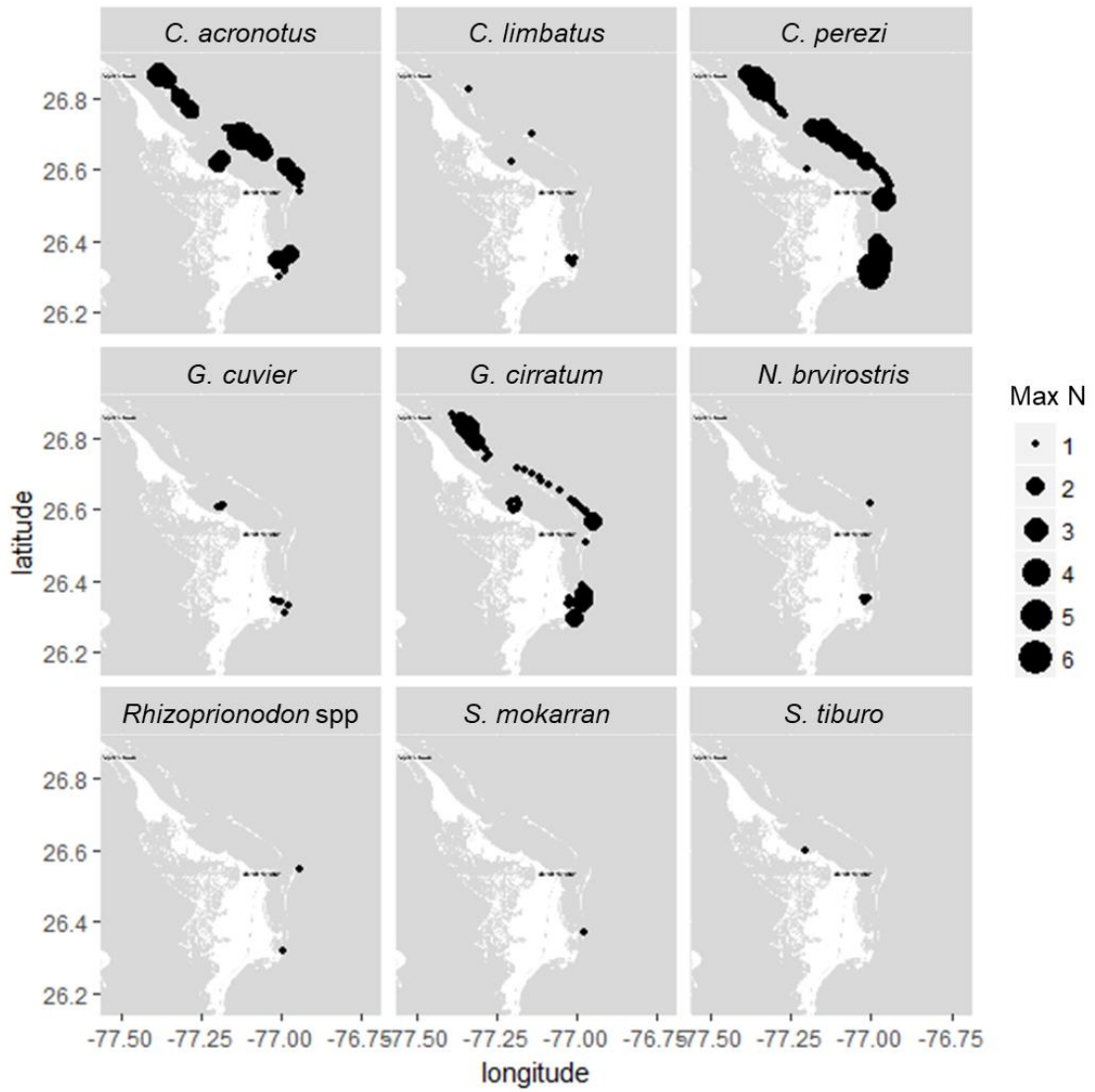
Figure 3. Location of occurrences of all shark species observed on BRUVs. The size of dots reflects maxN per BRUV
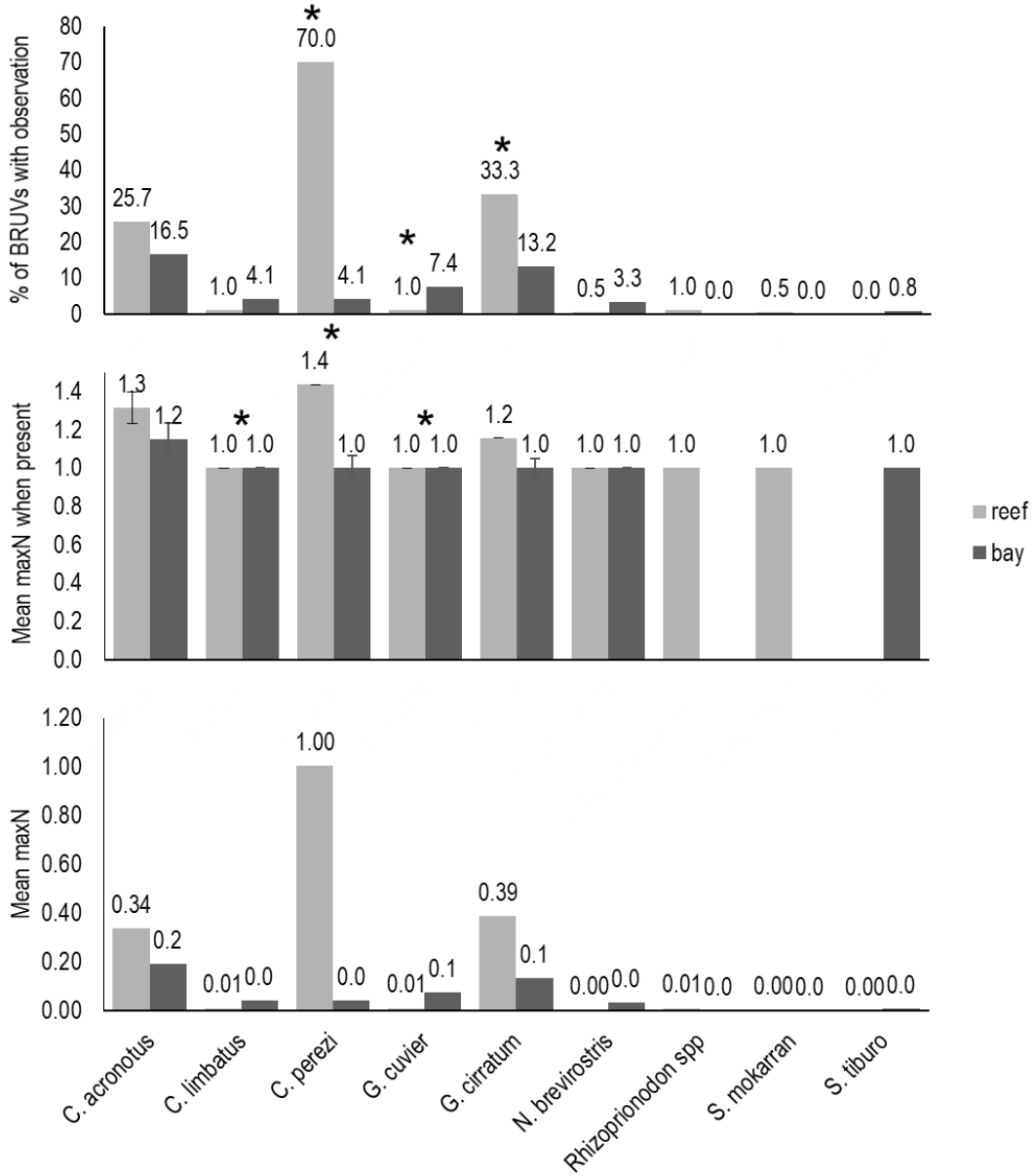
Figure 4. Species-specific occurrence and maxN across habitat types. Observations per species in reef habitat (light bars) and bay habitat (dark bars); top: percent of BRUVs with species observation; middle: mean of maxN when species is present (maxN > 0) ±SE; bottom: mean maxN including videos with species absent; asterisks denote significant differences in presence and absence or maxN values between habitat types (Table 2)

Table 2. Results of GLMM testing for differences in presence/absence and maxN between reef and bay habitats; shaded *P*s denote significant differences between habitat types; NA signifies not enough observations for analysis

Sample	Presence/Absence		Max N	
	Z-value	*P-value*	*Z-value*	*P-value*
All species	5.787	<0.0001	5.677	<0.0001
C. acronotus	1.032	0.30	-0.423	0.67
C. limbatus	-1.776	0.08	-2.573	0.01
C. perezi	5.928	<0.0001	5.138	<0.0001
G. cuvier	-2.686	0.01	-3.505	0.0005
G. cirratum	2.13	0.03	0.748	0.45
N. brevirostris	-1.419	0.16	-1.858	0.06
Rhizoprionodon spp	NA	NA	NA	NA
S. mokarran	NA	NA	NA	NA
S. tiburo	NA	NA	NA	NA

Despite similar species richness (reef n = 8 species, bay n = 7 species) (Figure 5), Shannon Weiner diversity of sharks was higher in reefs (0.36) than in bays (0.10) ($W = 3300$, $P = 0.003$). Within sites, WCB and BOR did not differ in species diversity ($W = 349.5$, $P = 0.16$). Of all sites, GTC had the highest Shannon-Weiner diversity (0.45) but the lowest species richness (4), suggesting more even relative abundance across species compared to other sites. In contrast, WCB had the lowest diversity (0.10) and the highest species richness (6). This site was dominated by *C. acronotus* (sum maxN = 12) and *G. cirratum* (sum maxN = 9) with other species represented by one to five individuals each (Figure 6).
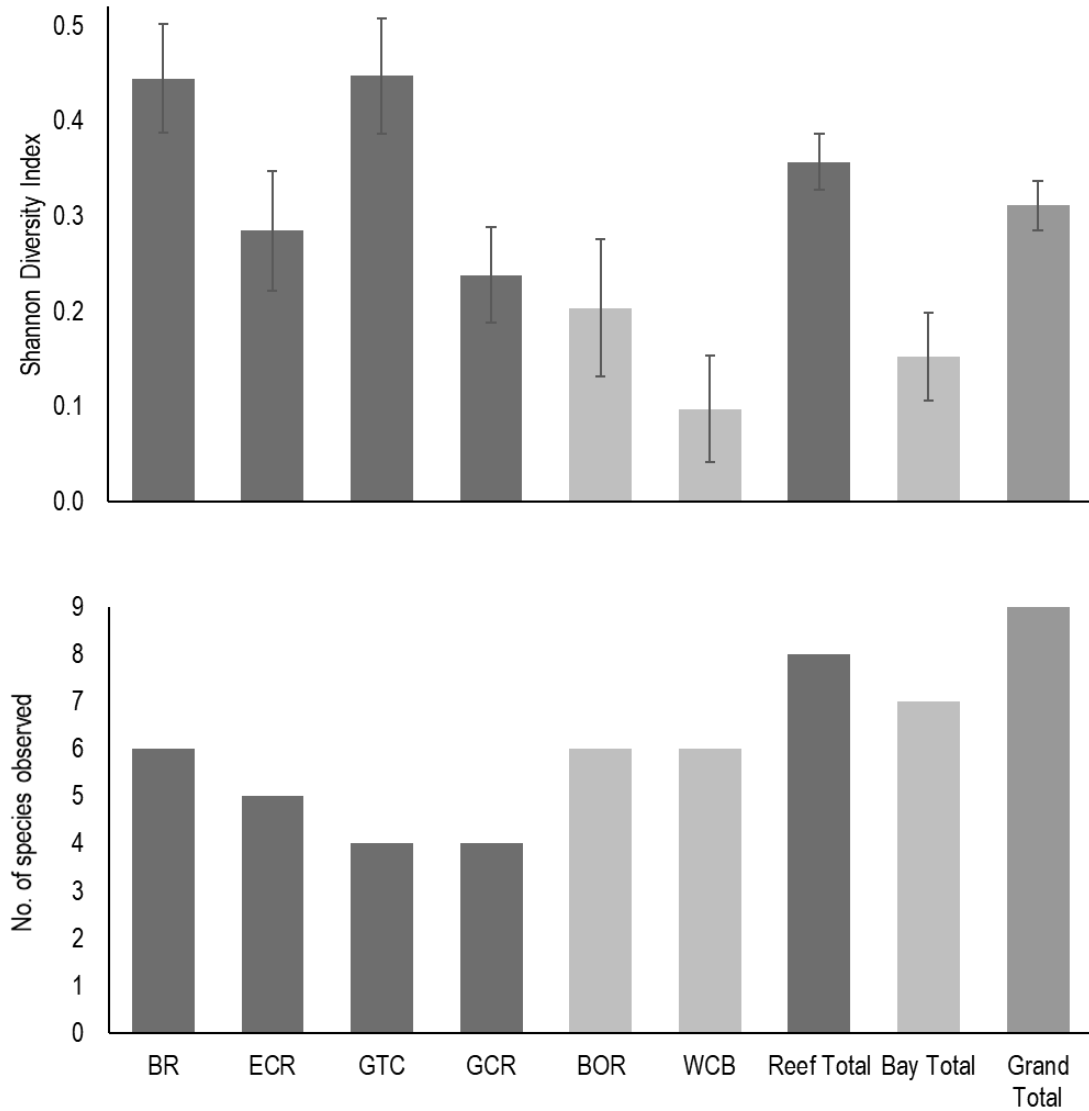
Figure 5. Mean BRUV diversity (excluding BRUVs with zero observations) and total richness of each site, habitat type and total; top: mean BRUV diversity (±SE) per category; bottom: number of species observed per category (richness)
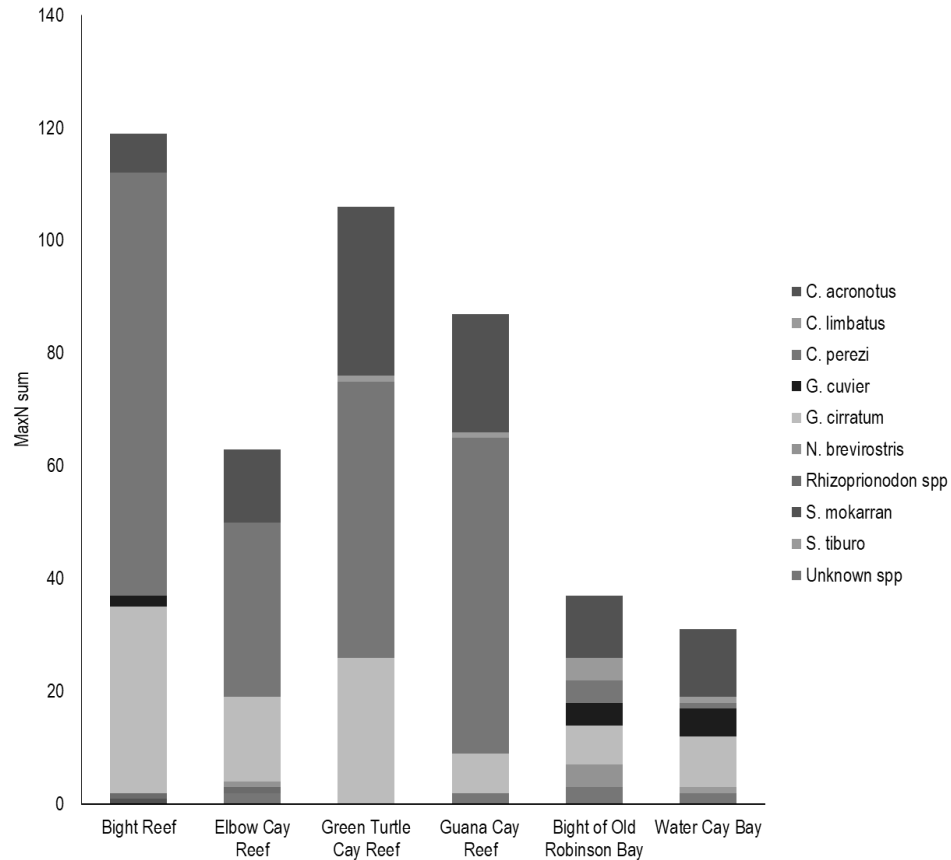
Figure 6. Total site-level sum of maxN broken down by species

I found no significant difference between the two bay sites in presence/absence ($P = 0.21$), nor the sum of maxNs ($P = 0.30$) using Fisher's Exact Test. There were significant differences among reef sites in both presence/absence ($X^2 = 39.3$, df = 21, $P = 0.009$), and sum of maxNs ($X^2 = 53.57$, df = 24, $P = 0.0005$). Of the reefs, BR had the greatest and ECR the lowest sum of maxNs (total sum of maxNs = 119 and 63, respectively; Figure 6), and GTC had the greatest and ECR the lowest observations (total observations = 83 and 53, respectively) (see Appendix II for contingency tables).

Discussion

The prohibition of gillnet and longline fishing has been credited for the relatively high reef-associated shark abundances in the central Bahamas (Ward-Paige *et al.,* 2010). Still, in 2011, The Bahamas went beyond gear regulations to create a 628,026 km^2, multi-island, national shark sanctuary. Even low levels of fishing mortality, however, can cause sharp declines in shark populations (Ward-Paige *et al.,* 2010), and despite current protections, culling of large "nuisance" sharks and shark fishing still occur in the Abaco waters (*pers. obs.*). Despite this level of fishing, I found that shark populations off Great Abaco appear to be similar to those in other parts of The Bahamas (Brooks *et al.,* 2011).

Shark species richness was high in both reef and seagrass-dominated bay habitats, although shark diversity and species-level occurrence differed between habitat types and even among reef sites. As highly mobile species, sharks have the ability to move among sites and habitat types, and all species observed by more than two BRUVs were observed in both reef and bay habitats (Figure 4, Appendix I). However, not all species were represented at all sites, and all species occurred at different relative abundances using the maxN values. Both of these factors contributed to the observed differences in diversity among sites and habitats. Shark relative abundances are similar in the bays, but reef sites differed in the overall occurrence and concentration of sharks.

The relative abundances observed in Abaco are, in many ways, consistent with the current literature on species distributions and habitat use in other locations. Distributions of *S. tiburo* and *C. limbatus* are affected by factors such as water temperature, depth and distance to tidal creek inlet in Texas estuaries (Froeschke, Stunz and Wildhaber, 2010;

Cortés *et al.,* 2016). In Abaco, the sole observation of *S. tiburo* was in shallow seagrass habitat near to the coastline and tidal creeks in WCB. I observed *G. cuvier* significantly more often in the relatively shallow, seagrass-dominated bays than on the fringing reef. In other systems, such as Shark Bay, Australia tiger sharks also preferred shallow habitat where their prey (*e.g.,* dugongs, sea turtles and sea snakes) are most abundant (Heithaus *et al.,* 2002).

The species observed in this study represent diverse trophic levels including apex predators (*G. cuvier* and *S. mokarran*) and more generalist, mesopredators (*e.g., C. perezi*) (Bond *et al.,* 2018). The presence of apex predators is particularly notable since they have the potential to structure populations and behaviors of prey and, ultimately, the dynamics of ecosystems. For example, the fear response elicited by encounters with an apex predator (*G. cuvier*, Heithaus *et al.,* 2007) on sea turtles decreases grazing pressure on seagrasses in risky habitats. Some shark species such as *S. mokarran* also prey on large taxa and elasmobranch mesopredators (including rays) and may therefore play a similarly large role in structuring ecosystems (Heithaus *et al.,* 2008). The singular observation of *S. mokarran* in Abaco was in reef habitat, but this species can occupy a large range of habitats from close inshore habitats to continental shelves offshore (Compagno, 2001). Because of the relatively low abundance of *S. mokarran* observed in Abaco and their susceptibility to perishing when hooked (Gallagher, Hammerschlag, Shiffman, & Giery, 2014), further studies to determine population status and trajectories are warranted.

Both *C. perezi* and *G. cirratum* were observed significantly more often in reef

habitats than in bays, not surprisingly since they are both well known as coral-reef

associated species. Their presence in bay habitats is also not surprising considering the

broad ecological niche of *G. cirratum* (Tilley, López-Angarita and Turner, 2013) and

studies suggesting *C. perezi* exerts pressure on prey from multiple trophic levels (Bond *et

al.,* 2018). Observations of *N. brevirostris* were made across habitats, but they were

observed most often in BOR, the site with the most extensive tidal creek system along its

coastline. Research on *N. brevirostris* in Bimini, The Bahamas suggests that juveniles

select shallow (<50 cm) and warm (>30ºC) habitats with rocky or sandy substrate

(Morrissey and Gruber, 1993; Morrissey *et al.,* 1993), all of which can be found in the

tidal creeks of BOR that may provide critical nursery habitat for juvenile *N. brevirostris*.

Rhizoprionodon spp. are also known to use enclosed bays as nursery areas, but in Abaco,

all observations were in reef habitat.

The significant differences observed among reef sites suggests that shark

occurrence and relative abundance are affected by more than broad habitat types. On a

greater-Caribbean scale, human pressures have been identified as factors leading to the

broad-scale absence of reef sharks (Ward-Paige *et al.,* 2010), but the central Bahamas

was identified as one of the few locations with a high shark sighting frequency and a

relatively large human population. All sites surveyed for my study in the northern

Bahamas are easily accessed by small boat. The townships on Green Turtle Cay, Guana

Cay, and Elbow Cay offer direct human access to GTC, GCR, and ECR. One reef site,

BR, however, is not adjacent to a human-populated cay and is nearly 20 km away from

the Marsh Harbour, the largest township on Great Abaco. BR had the second highest

diversity score (0.44), the highest species richness (6), and the highest sum of maxN (119) of all sites.

Reef sharks are known to have some level of site fidelity in the Caribbean (Bond *et al.,* 2012), but they have also been observed traveling among sites up to 30 km apart and across deep open-water (Chapman *et al.,* 2005). The reef tract we sampled extended more than 80 km, but the maximum distance between adjacent reef sampling sites was 13 km and the maximum distance between a bay site and the nearest reef site was 9 km. Therefore, the differences in occurrence and maxN between habitat types and among reef sites are unlikely the result of movement limitations or site fidelity alone. Additional studies of interactions among shark species are needed to elucidate patterns in species richness and diversity within habitats.

The Abaco study, combined with other studies in The Bahamas, provide a baseline for future studies to measure the effectiveness of The Bahamian shark sanctuary and national management efforts. Continued monitoring will be key, and additional research is needed on the role of inter-species dynamics in distributions and abundances at multiple spatial scales.

Acknowledgments

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Table A. Shark species presence/absence observed per species: number of videos with presence (count), percent of videos with presence (%)

	C. acronotus		C. limbatus		C. perezi		G. cuvier		G. cirratum		N. brvirostris		Rhizoprionodon spp		S. mokarran		S. tiburo	
	count	%	count	%	count	%	count	%	count	%	count	%	count	%	count	%	count	%
BR	6	11.54	0	0.00	42	80.77	2	3.85	28	53.85	0	0.00	1	1.92	1	1.92	0	0.00
ECR	11	20.75	0	0.00	26	49.06	0	0.00	14	26.42	1	1.89	1	1.89	0	0.00	0	0.00
GTC	25	46.30	1	1.85	36	66.67	0	0.00	21	38.89	0	0.00	0	0.00	0	0.00	0	0.00
GCR	12	23.53	1	1.96	43	84.31	0	0.00	7	13.73	0	0.00	0	0.00	0	0.00	0	0.00
BOR	10	16.39	4	6.56	4	6.56	4	6.56	7	11.48	4	6.56	0	0.00	0	0.00	0	0.00
WCB	10	16.67	1	1.67	1	1.67	5	8.33	9	15.00	0	0.00	0	0.00	0	0.00	1	1.67
Reef Total	54	25.71	2	0.95	147	70.00	2	0.95	70	33.33	1	0.48	2	0.95	1	0.48	0	0.00
Bay Total	20	16.53	5	4.13	5	4.13	9	7.44	16	13.22	4	3.31	0	0.00	0	0.00	1	0.83
Grand Total	74	22.36	7	2.11	152	45.92	11	3.32	86	25.98	5	1.51	2	0.60	1	0.30	1	0.30

CHAPTER III

MULTI-LEVEL HABITAT SELECTION BY A LARGE MARINE HERBIVORE
(*CHELONIA MYDAS*) IN A SHALLOW COASTAL ECOSYSTEM: THE INFLUENCE
OF PREDATION RISK, FOOD ABUNDANCE, AND FORAGE NUTRIENT
CONTENT

Abstract:

Despite their potential to structure ecosystems, the factors that define habitat quality and shape habitat use of large marine herbivores remain poorly understood. In the absence of predators, foragers are predicted to be distributed across habitats proportional to the availability of food or relative to other indices of forage quality (*e.g.,* nutrient content). However, the presence of predators can modify habitat use patterns. For example, the foraging arena hypothesis suggests that foragers may restrict their habitat use to safe arenas but select areas within these safer arenas on the basis of foraging considerations. Green turtle populations in the Caribbean have been greatly reduced by overexploitation, but many populations are now rebounding. Because they can greatly impact benthic community structure, it is important to understand the factors that shape their habitat use patterns. I used ideal free distribution (IFD) theory to develop and test *a priori* predictions of green turtle habitat use across gradients of seagrass availability, nutrient composition, and predation risk. Within a *ca.* 9 km^2, seagrass-dominated bay and adjacent *ca.* 3 km^2 tidal creek area of Abaco, The Bahamas, I estimated relative predation risk and quantified food availability and quality. At the site level, green turtles did not conform to a basic IFD founded on food abundance. Green turtle densities were much lower than predicted for open habitats that had abundant seagrass, but lower N content in seagrass and the highest risk of encounter with predatory sharks. Turtle abundances were highest in creek habitats, where potential predators were absent. Within tidal creek habitats, green turtle distributions were positively associated with forage quality (N content) and not food abundance. Allochthonous nutrient inputs from nearby blue holes may allow seagrasses in tidal creeks to maintain high nutrient content in the face of heavy

herbivory. Consistent with the foraging arena hypothesis, this study highlights the importance of multi-level analyses of grazer habitat use that incorporate measures of predation risk and food abundance and quality.

Introduction

Historically, habitat selection and population densities of large-bodied marine grazers (sea turtles and sea cows) have been thought to be driven exclusively by bottom-up forces (Jackson, 2001). It remains unclear, however, the degree to which individuals select habitats relative to the abundance, productivity, or quality of primary producers or other factors like predation risk (*e.g.,* Power, 1992; Massé and Côté, 2009; Shepperd *et al.* 2010; Wirsing, Heithaus and Dill, 2007; Heithaus *et al.,* 2008). In terrestrial systems, forage distributions (*e.g.,* Svalbard reindeer, *Rangifer tarandus platyrhynchus*, Van der Wal *et al.,* 2000) and quality (*e.g.,* bison, *Bison bison*, Seagle and Mcnaughton, 1992; ungulates, Raynor, Joern and Briggs, 2015) have significant effects on grazer habitat use and foraging behaviors. In the Serengeti, the patchy spatial distributions of grazing ungulates are attributed to heterogeneity in the nitrogen content of forage across the landscape (Seagle and Mcnaughton, 1992). In marine systems, green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*) also preferentially forage on seagrasses with high nitrogen and soluble carbohydrate content and low levels of indigestible fiber (Bjorndal, 1985; Preen, 1993; Sheppard *et al.,* 2010). Green turtles will select for forage of relatively high nutritional value (Gilbert, 2005), possibly because nutrition of forage is positively correlated to individual growth (Bjorndal, 1982; Hadjichristophoroua and

Grove, 1983). Other studies also consistently found dugongs over seagrass patches with high nitrogen, but when habitat choices were limited by low tides, individuals selected patches of high seagrass biomass (Sheppard *et al.,* 2010). The foraging habitat use of some green turtle populations, including juveniles in Eleuthera, The Bahamas (Gary, 2017) and nesting females in Cyprus (Hays *et al.,* 2002), also appears to be driven by forage availability, however, the diet composition of sea turtles is not always proportionate to the abundance of available forage species (Brand-Gardner, Lanyon and Limpus, 1999; Chapters IV and V).

Making studies of marine megagrazer habitat use especially complex is the relatively recent realization that predators (primarily large sharks) can shape the habitat use and behavior of both sea turtles (inluding adults and large juveniles; Heithaus, 2013) and sea cows (Wirsing, Heithaus and Dill, 2007). In a relatively pristine ecosystem in Shark Bay, Australia, predation risk helps shape large grazer distributions and foraging habitat use. Dugongs (Wirsing, Heithaus and Dill, 2007) and healthy green turtles (Heithaus *et al.* 2007) underuse high-risk habitat relative to expectations determined by habitat quality when tiger sharks (*Galeocerdo cuvier*) are present. Habitat use decisions, in turn, affect the structure of seagrass communities, resulting in lower seagrass biomass and altered species composition in low-risk habitats compared to high-risk ones (Burkholder *et al.,* 2013). Indeed, it is possible that the primarily bottom-up view of megagrazer habitat use in marine ecosystems is the result of the degraded nature of large shark populations found almost worldwide (*e.g.,* Ferretti *et al.,* 2010).

Understanding the role of predators and bottom-up factors in shaping habitat use decisions of large herbivores is particularly important with increasing efforts to conserve both predator and grazer populations in terrestrial and marine ecosystems. Grazers left unchecked by predation have the potential to overgraze to the point where forage species are not able to maintain themselves over time (Mysterud, 2006). The losses or reintroductions of large predators and grazers, for example, has been credited with large-scale ecosystem changes (Estes *et al.,* 2011, 2016). The reintroduction of wolves to Yellowstone National Park in 1995 and 1996, for example, has caused a shift in the behavior of their prey including elk who forego foraging in grass lands of high-quality food to forested areas that provide refuge from wolf predation (Creel *et al.,* 2005).

Green turtles (*Chelonia mydas*), whose primary food source in the Caribbean is seagrass (Bjorndal, 1985), have been exploited for centuries, and their populations are probably millions of adults lower than was present historically (Jackson 1997; Jackson 2001). Such declines likely have triggered ecosystem changes and many conservation efforts have been put in place to recover sea turtle populations. In some areas, these efforts have been highly successful (*e.g.,* Weber *et al.,* 2014). However, in multiple ocean basins, seagrass communities have begun to collapse under heavy turtle grazing pressure where predator populations have been greatly reduced (Fourqurean *et al.,* 2010; Christianen *et al.,* 2014; Heithaus *et al.,* 2014). Importantly, such declines in seagrass are not apparent in areas with large turtle populations and intact predator populations (Heithaus *et al.* 2014). Further studies of habitat use of sea turtles are needed from areas with relatively intact shark populations to reveal the relative importance of predation risk and foraging considerations in driving habitat use decisions.

Theory derived from the Ideal Free Distribution (IFD; Fretwell and Lucas 1970) provides an excellent framework for investigating habitat use under spatial variation in resources and predation risk (Heithaus, Wirsing and Dill, 2012). The most basic IFD model suggests that a population's distribution among resource patches will be proportional to the available resources in each patch. In the basic IFD model, grazers would be expected to occupy all habitats if individual intake rates in high quality habitats decline with increasing occupancy to a point where it is energetically beneficial for some individuals to occupy other habitats. Deviations from a basic IFD can occur for several reasons. For herbivores, the quality of food (*e.g.,* nutrient content) may be even more important than the rate at which energy can be harvested (Simpson *et al.,* 2004) which could cause deviations from IFD predications determined solely by the availability of forage. Also, most species face a trade-off between foraging opportunities and risk of being killed by a predator because the most profitable habitats are often the most dangerous. In the face of an energy-risk trade-off, most individuals are willing to give up foraging opportunities or accept lower intake rates to remain in low-risk habitats (*e.g.,* Heithaus *et al.,* 2012). Some individuals may still use high-risk habitats, especially those in lower body condition (*e.g.,* Serengeti wildebeest, *Connochaetes taurin*, Sinclair and Arcese, 1995; green turtles, Heithaus *et al.*, 2007), because the fitness benefits of foraging in high-risk areas outweigh the potential of being killed. In some situations where risk is too high in habitats that might be profitable energetically, food-risk tradeoffs and factors influencing habitat selection may occur across a spatial hierarchy. For example, the "foraging arena hypothesis" posits that individuals will avoid high risk

areas entirely and constrain their habitat use to safer foraging arenas where bottom-up considerations are paramount (Walters and Juanes 1993).

Here, I used IFD theory and a hierarchical framework to develop *a priori* predictions about how green turtles in the nearshore waters of Great Abaco, The Bahamas might distribute themselves according to spatial variation in food abundance and quality and predation risk. I used in-water surveys of seagrass abundance, seagrass nutrient content analysis, aerial video surveys of green turtles, and baited remote underwater video (BRUV) data on shark relative abundance to conduct the first explicit test of whether turtle foraging distributions in the Caribbean reflect a tradeoff between risk and energy intake or if foraging considerations alone likely determine spatial variation in turtle densities.

Methods

Study site

In The Bahamas, legal protection of sea turtles began in 2009 (S.I. 85/2009, s. 2.), and legal protection of sharks began in 2011 (S.I. No. 64 of 2011). In general, shark populations in The Bahamas are more intact than other locations in the Caribbean (Chapter II, Ward-Paige *et al.* 2010) making it a regionally important location to investigate green turtle habitat use under potential predation threat.

The study took place offshore of Great Abaco, The Bahamas. Abaco is located in the northern Bahamas and comprises Great Abaco, Little Abaco, and many smaller Cays.

Great Abaco, the largest of the Abacos (Figure 1), is characterized by shallow tidal creek systems and sheltered bays supporting multiple tropical marine ecosystems including coral reef, hardbottom, rocky shoreline, mangrove, and seagrass ecosystems. Its eastern shoreline is further protected by a chain of smaller barrier islands and fringing reef systems. The seagrass-dominated system, with a maximum tidal range of 1.3 m, hosts the three most common Caribbean seagrass species: *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*. The most common species found in the waters of Abaco is *T. testudinum*, turtle grass. Abaco is within the geographic range of five sea turtle species including the three most common species in the Caribbean: green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and hawksbill (*Eretmochelys imbricata*) turtles. Large-bodied sharks that may pose a risk to sea turtles are also found in coral reef and bay habitats around Abaco including tiger sharks (*Galeocerdo cuvier*) (Chapter II).

The study took place in the Bight of Old Robinson (BOR), a *ca.* 9 km^2, seagrass-dominated bay on the eastern coastline of Great Abaco (see Chapter II for a detailed description), (Figure 1), and the *ca*. 3 km^2 adjacent tidal creeks. The tidal creeks are uninhabited watersheds with relatively little human impact (Stoner *et al.,* 2011). Tidal creeks and bays in The Bahamas are typically oligotrophic (Allgeier, 2010), but the 18 marine blue holes (underwater caves) found in the tidal creeks adjacent to the Bight of Old Robinson may be a source of nutrients to the system (Lapointe *et al.,* 2004). The maximum depth of the sampling area, near the mouth of BOR, was *ca*. 6 m and the minimum sampled was *ca*. 0. 3 m.
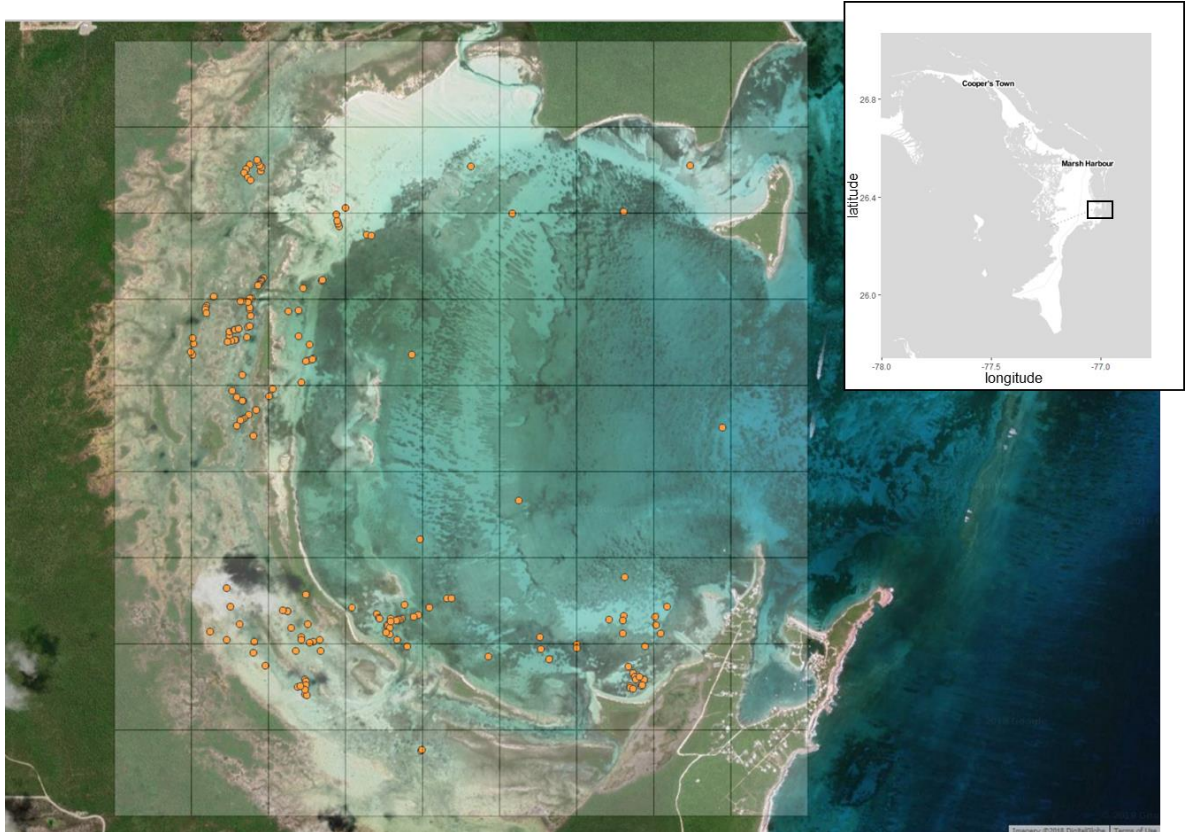
Figure 1. Bight of Old Robinson, along the east coast of Great Abaco (inset). The grid divides the bay into 500 m x 500 m cells. Orange dots are turtle sightings.

Green turtles are the most abundant species along the eastern coastline of Great Abaco. Out of 99 individuals captured opportunistically during the summers of 2013-2017, 89 were green turtles ranging in size from 26 to 71 cm minimum curved carapace length. Of these, 17.9% (16 of the 89) had recent injuries or scars (Figure 2) or missing limbs (*pers. obs.*).

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Figure 2. Green turtle captured in a tidal creek north of the Bight of Old Robinson. The scratches and puncture marks on the carapace, plastron, and soft tissue are potential evidence of shark inflicted injuries.

Habitat categorization

I divided the study area into 500 m x 500 m cells that featured waters deep enough for turtles to occupy (Figure 1) using a vector grid layer in QGIS version 2.18.11 (QGIS Development Team, 2018). The 0.25 km^2 resolution results in cells that are relatively homogenous with respect to habitat type (*e.g.,* tidal creek, nearshore, open water). All grid cells were assigned to one of three habitat types (Figure 3). Creeks (n = 14 cells) contained tidal creeks and inlets, nearshore habitat (n = 23 cells) were adjacent to shore had water depths less than 2m, and open habitats (n = 19 cells) were farther from shore and > 2 m average depth with the exception of the cells at the mouth of the bay. These cells were close to land but featured water depths and benthic habitats more similar to other open habitats than nearshore ones. Using the "join attributes" function in QGIS, I extracted all survey data (*i.e.,* drone, seagrass and BRUV surveys) per cell.

Figure 3. Habitat assignments of cells within the study area. C = creek (pink), N = nearshore (green), and O = open (blue). Cells not included in study are uncolored.

Forage availability

I assessed macrophyte abundance and community composition from randomly selected points from each drone flight path for a total of 131 survey points across habitat types. The random survey points fell within 9 creek habitat cells, 23 nearshore habitat cells, and 18 open water habitat cells. At each point, I estimated the abundance of each macrophyte species within four, 0.25 m^2 quadrats using an adaptation of the Braun-Blanquet scale for rapid vegetation assessments (Braun-Blanquet, 1932, 1964). The Braun-Blanquet method, commonly used to assess the abundance of seagrass and

macroalgae, is efficient, highly repeatable, and minimizes observer differences

(Fourqurean *et al.,* 2001). Within each plot, two observers independently assigned scores

(Table 1) for each seagrass species within each of two quadrats each, and the mean of the

four scores was used for analysis (Fourqurean *et al.,* 2001).

Table 1. Braun-Blanquet density scores (Fourqurean *et al.,* 2001)

Score	Cover
0	Taxa absent from quadrat
0.1	Taxa represented by a solitary shoot, <5% cover
0.5	Taxa represented by a few (<5) shoots, <5% cover
1	Taxa represented by many (>5) shoots, <5% cover
2	Taxa represented by many (>5) shoots, 5 - 25% cover
3	Taxa represented by many (>5) shoots, 25 - 50% cover
4	Taxa represented by many (>5) shoots, 50 - 75% cover
5	Taxa represented by many (>5) shoots, 75 - 100% cover

Forage nutrient content

Five *T. testudinum* short shoots (*i.e.*, bundles of leaves growing vertically

upwards from the rhizome composing the above ground biomass) were collected from

within or nearby the quadrat sampling points (where seagrass occurred) for nutrient

content analysis. Seagrass was not found at all random survey points, so seagrass was

collected from 7 creek habitat cells, 22 nearshore habitat cells, and 17 open water habitat

cells. *T. testudinum* was selected because it is the primary component of green turtle diets

in the Greater Caribbean (Bjorndal, 1997) and it was the only seagrass found at the

majority (85.5%) of our sampling plots. Furthermore, comparisons of nutrient content

within a species is most useful for assessing spatial variation in nutrient content overall (Duarte, 1990) and *T. testudinum* is commonly used to assess nutrient content at this study site (Allgeier, Rosemond and Layman, 2011; Yeager, Acevedo and Layman, 2012) and other Abaco seagrass habitats (Stoner *et al.,* 2014). The seagrass samples were scraped free of epiphytes, dried in a food-grade dehydrator, ground to a fine powder with a mortar and pestle, and transported to Florida International University for nutrient content analysis. Total C and N content of seagrass biomass from each sampling point were quantified using a CE Flash 1112 elemental analyzer using standard procedures. Total P was analyzed colorimetrically following modified methods from Solorzano and Sharp (1980) on a Shimadzu UV-2101PC spectrophotometer.

Predator relative abundance

To estimate spatial variation in predation risk, I deployed 61 baited remote underwater video (BRUV) cameras between July and August of 2016. Each BRUV camera deployment included one kg of oily fish in bait cages positioned downstream of a high definition video camera on threaded rods attached to a 37 cm diameter concrete base (*c.a.* 12 kg). All simultaneously deployed BRUVs were deployed at least 1 km apart and set at depths of 1.25-5.5 meters. No more than six BRUVs were deployed simultaneously and no more than 12 were deployed in one day. Each deployment lasted 3 – 4 hrs. Extremely shallow water depths precluded deployments of standard BRUV equipment in the creeks, but these waters are inaccessible to potential sea turtle predators (none were observed during drone flights in these habitats). To test this assumption, I deployed

modified BRUVs (camera and *ca*. 1 kg of bait on adjacent cinder blocks) nine times during the summer of 2018.

Each video was watched at normal (1x) speed by at least one observer and annotated using the Global FinPrint Annotator software (http://globalfinprint.org/). Data recorded by observers included species identification and the maximum number (maxN) of individuals from each species within a single frame (Bond *et al.,* 2012; Lowry *et al.,* 2012). The annotation software captures a still image and an eight second video clip whenever a shark is recorded in frame, allowing verification of species identity and counts data.

Turtle abundance and distributions

To determine turtle densities, I used a DJI Phantom 3 Advanced quadcopter drone, equipped with a high definition video camera and controlled through an iPad Mini 4 and remote control. Drones are increasingly being used in marine system studies (*e.g*., Kiszka *et al.,* 2016; Rees *et al.,* 2017) because they can reduce field time and costs and provide access to otherwise inaccessible or dangerous habitats. Critical for this study was 1) the ability to survey turtles that may be especially sensitive to human disturbance because of the less than a decade old ban on turtle harvesting and 2) to be able to survey turtles at all depths of the water column due to the clarity of the water and shallow depths throughout the study area.

For my study, the drone was recalibrated daily at sea level to ensure precise flight data and launched under manual control from a 5 m long outboard motor boat. After launching, flight mode was switched to autonomous flight through the Hangar Autopilot© application. Flights were pre-programmed to occur at an altitude of 10 m above the water's surface along predetermined paths connecting points determined by a random point generator (http://www.geomidpoint.com/random/). In the rare cases when Australian pine (*Casuarina* spp) growing on rocky cays posed potential obstacles to the flight path, transects were flown at 15 m and the transect area adjusted using the increased field of view for analysis. The land area in the creek and nearshore habitats reduced the survey area. The length of each transect (distance flown) varied by the distance between random points and was restricted by battery life (*ca.* 18 min flight time). Transects were selected using random number assignments each day, with no more than eight transects flown per day, and no consecutive flights were flown within any one cell. Given that the survey area is relatively sheltered from wind, turbidity is minimal, and a polarized filter for the camera minimized glare, the probability of missing individuals is extremely low (Figure 4). Furthermore, perception bias was minimized by only flying when Beaufort Sea state and wind scales were ≤ 2, when glare could be minimized to $< 20\%$ of the field of view, and when water clarity allowed easy viewing of the bottom at the greatest study area depths.
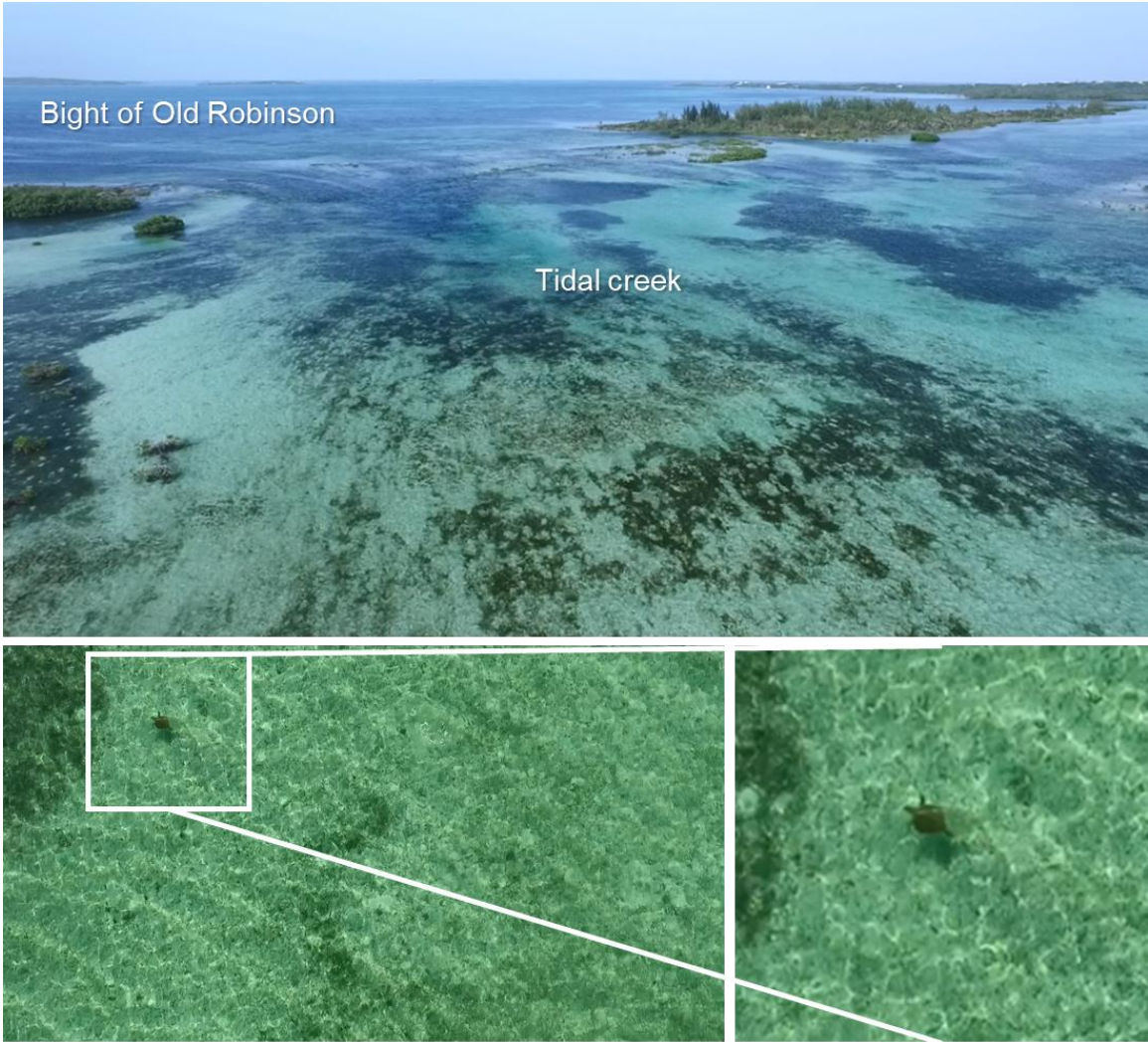
Figure 4. Still frames from drone video taken by DJI Phantom 3 Advanced; Top: view from the tidal creeks looking into the Bight of Old Robinson; Bottom: turtle sighting during drone transect in tidal creek with full field of view (left) and magnified (right)

One observer viewed each video for turtle sightings, number of individuals present at each sighting, and the video timestamp. Sightings were verified by a second observer. Flight data extracted through AirData UAV, Inc. were matched to the video timestamp to determine sighting location and to calculate transect area:

$$T_{area} = \tan\theta * a * 2 * l,$$

where T_{area} is the transect area in m², $\theta = 81.7°$ is the camera's horizontal field of view

calculated using the reported 94° diagonal field of view (DJI, 2015), a is the altitude or

distance from the water to the camera in meters, and l is the total transect length in

meters. Results of field of view calculations were compared to calculations based on

visual measurements from five videos where the boat was clearly visible and within

frame. Using the known width of the boat stern I found the horizontal field of view to use

in the T_{area} calculation. The empirically tested width of the field of view was 0.19 m ±

0.58 SD smaller than the calculated values with a range of -0.87 to 0.65 m. Turtles

observed during manual flight when altitudes exceeded 15 m were not included in the

analysis. Turtle sighting density was calculated by dividing the number of turtles sighted

transect $^{-1}$ cell^{-1} by the transect area transect $^{-1}$ cell^{-1}, and the mean sighting density per

cell was used in analyses.

Data analysis

I used R software (R Core Team, 2016) to run all statistical tests. Logistic

regression was used to test for differences in tiger shark observations among habitats. I

used a Wilcoxon rank sum test to explore differences in the distributions between habitat

types of turtle sighting density, nutrient content and macrophyte abundances. Mean turtle

density per cell was calculated by taking the mean turtle density (number of animals

sighted by the transect area surveyed) of all transect segments within a cell. A

generalized linear mixed effects model from R Package 'lme4' was used to test for

relationships between turtle sightings counts, with a Poisson distribution, and habitat

variables with habitat type set as the random intercept and effort (log(area surveyed)) as the model offset (a comparison to linear mixed effects models using turtle sighting density [sightings/survey area] as the response variable and with Satterthwaite's degrees of freedom in the R Package 'lmerTest' can be found in Appendix I). Survey area was converted to hectares prior to model selection. I used a model selection table created using the R Package 'AICcmodavg' (function = aictab, Mazerolle, 2017) for stepwise model selection using Akaike information criterion (AIC) and Akaike weights. Models that did not converge were not included in the selection, and the model with the lowest AIC score was selected to describe the data.

Results

Forage availability

Seagrass abundance (Braun-blanquet scores) and composition varied across habitats (Table 2). The abundance of *T. testudinum,* the most abundant species overall (Figure 5), was significantly greater in open habitat ($W = 20.5$, $P = 0.02$) than creek habitat but was not significantly different between creek and nearshore ($W = 72$, $P = 0.19$) nor between nearshore and open habitats ($W = 269$, $P = 0.11$). The seagrass *S. filiforme* was significantly greater in open habitat than creek habitat ($W = 16$, $P = 0.0006$) and nearshore habitat ($W = 325$, $P = 0.002$) and greater in nearshore than creek ($W = 62$, $P = 0.048$). Another seagrass, *H. wrightii* abundance was significantly greater in the creek habitat than nearshore ($W = 168$, $P = 0.004$) and open ($W = 134$, $P = 0.005$), but not significantly different between nearshore and open habitats ($W = 208$, $P = 1.00$).

Total seagrass abundance significantly was significantly greater in open habitat than

nearshore ($W = 291$, $P = 0.03$) but did not differ between creek and nearshore ($W = 106.5$, $P = 0.92$) nor creek and open ($W = 46$, $P = 0.08$). Total algae did not significantly

differ across habitats (Figure 6).

Table 2. Wilcoxon rank sum test results of turtle sighting density and habitat variables between habitats; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Variable	Habitat 1	Habitat 2	W	P-value	
Turtles/ha	creek	near	204	0.0223	**
Turtles/ha	creek	open	206	0.0000	***
Turtles/ha	open	near	75	0.0001	***
Depth	creek	near	29	0.0189	*
Depth	creek	open	0	0.0002	***
Depth	open	near	370	0.0000	***
Tt	creek	near	72	0.1936	
Tt	creek	open	20.5	0.0020	**
Tt	open	near	269	0.1059	
Hw	creek	near	168	0.0044	**
Hw	creek	open	134	0.0045	**
Hw	open	near	208	1.0000	
Sf	creek	near	62	0.0480	*
Sf	creek	open	16	0.0006	***
Sf	open	near	325	0.0016	**
Algae	creek	near	142	0.1159	
Algae	creek	open	101	0.3158	
Algae	open	near	276	0.0740	.
N	creek	near	145	0.0001	***
N	creek	open	119	0.0000	***
N	open	near	48	0.0000	***
P	creek	near	129	0.0064	**
P	creek	open	88	0.0749	.
P	open	near	226	0.2791	
C	creek	near	116	0.0481	*
C	creek	open	87	0.0866	.
C	open	near	214	0.4574	
CN	creek	near	9	0.0001	***
CN	creek	open	0	0.0000	***
CN	open	near	338	0.0000	***
NP	creek	near	80	0.9010	
NP	creek	open	86	0.0995	.
NP	open	near	97	0.0101	*
CP	creek	near	31	0.0178	*
CP	creek	open	33	0.0995	.
CP	open	near	146	0.2546	
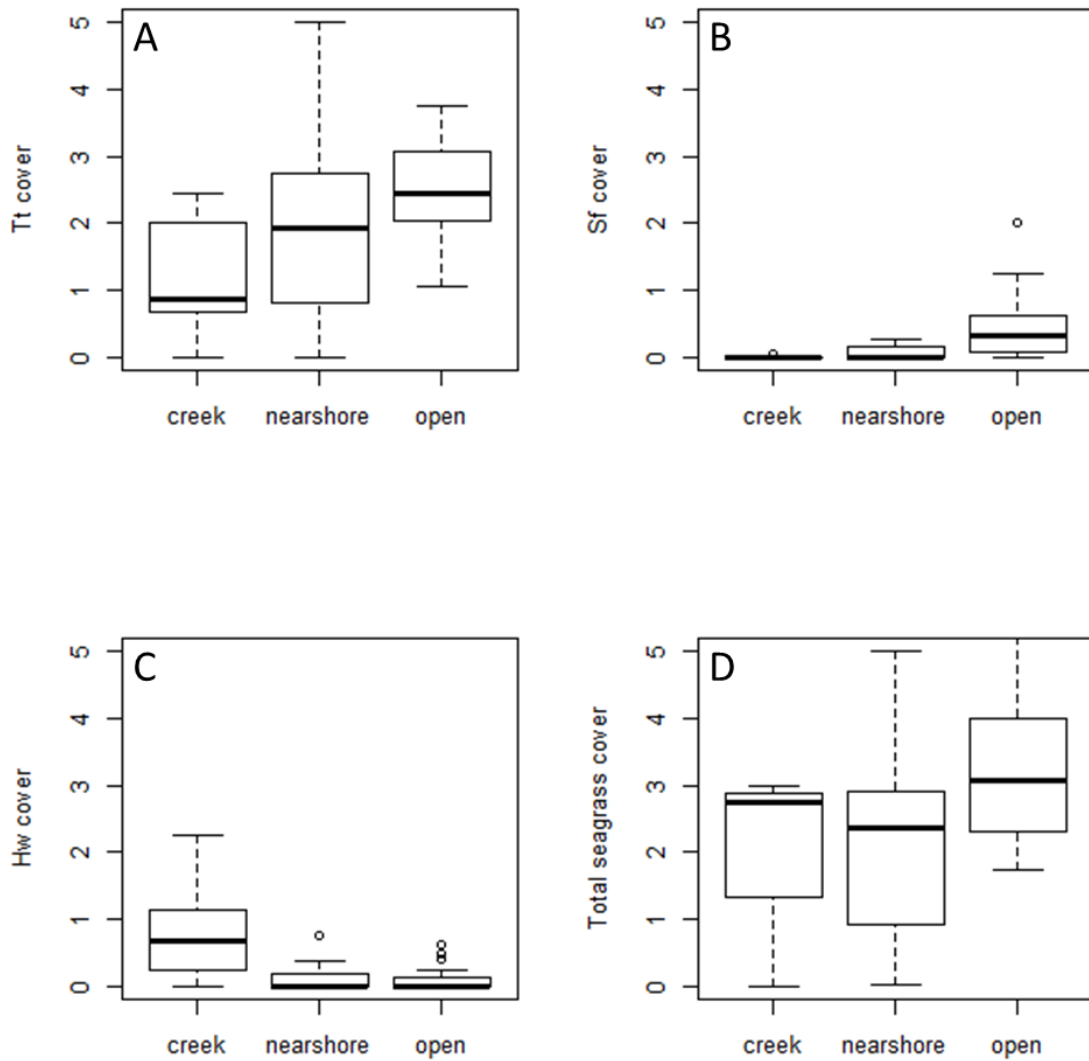
Figure 5. Box and whisker plots where the midline is the median, upper and lower limits of the box represent the 75th and 25th percentile, whiskers extend to minimum and maximum values except for data exceeding 1.5 times the interquartile range and are displayed as dots (possibly outliers). Spatial variation in mean Braun-Blanquet scores of seagrass for A) *T. testudinum* (Tt), B) *S. filiforme* (Sf), C) *H. wrightii* (Hw), and D) total seagrass cover (sum of scores of all seagrasses can exceed the max score of 5 because of the broad scoring categories (Fourqurean *et al.,* 2001)
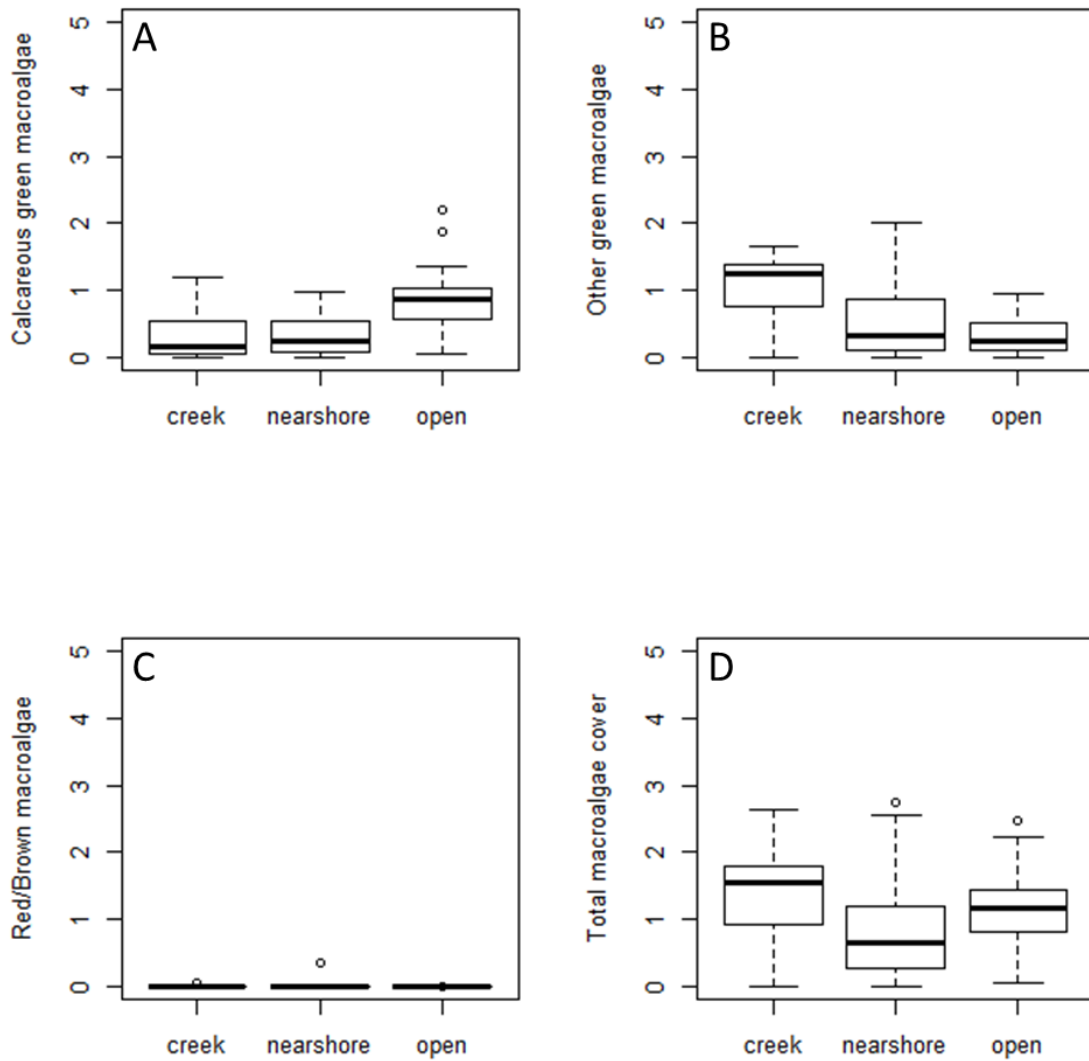
Figure 6. Mean Braun-Blanquet scores of macroalgae for A) calcareous green algae, B) other non-calcareous green algae, C) red and brown algae, and D) total macroalgae cover (sum of scores of all macroalgae can exceed the max score of 5 because of the broad scoring categories (Fourqurean *et al.,* 2001)

Forage nutrient content

      T. testudinum leaf elemental values and ratios differed among habitats (Table 2, Figure 7). Nitrogen content was significantly greater in creek habitat than nearshore ($W = 145$, $P = 0.0001$) and open ($W = 119$, $P < 0.0001$) and greater in nearshore than open ($W = 48$, $P < 0.0001$). Carbon content did not differ across habitats creek and nearshore ($W = 116$, $P = 0.048$), creek and open ($W = 87$, $P = 0.09$), and open and nearshore ($W = 214$, $P = 0.46$). Phosphorus content was significantly greater in creek than nearshore ($W = 129$, $P = 0.006$), but did not differ between open and creek ($W = 88$, $P = 0.075$) or nearshore ($W = 226$, $P = 0.28$). The C:N ratios were significantly greater in open than nearshore ($W = 338$, $P < 0.0001$) and creek ($W = 0$, $P = 0.0001$) and greater in nearshore than creek ($W = 9$, $P = <0.0001$). The C:P ratios were significantly greater in nearshore than creek ($W = 31$, $P = 0.02$) but did not differ between open and creek ($W = 33$, $P = 0.1$) or nearshore ($W = 146$, $P = 0.25$). The N:P ratios were significantly greater in nearshore than open ($W = 97$, $P = 0.01$) but did not differ between creek and nearshore ($W = 80$, $P = 0.90$) or open ($W = 86$, $P = 0.1$). The C:N and C:P ratios in the nearshore and open habitats were both greater than Redfield ratios, suggesting that those habitats are nutrient limited, and the low N:P ratio suggests that the open habitat is limited by N. Conversely, the high N:P ratios in the creek and nearshore habitats suggest that those habitats are likely P limited.
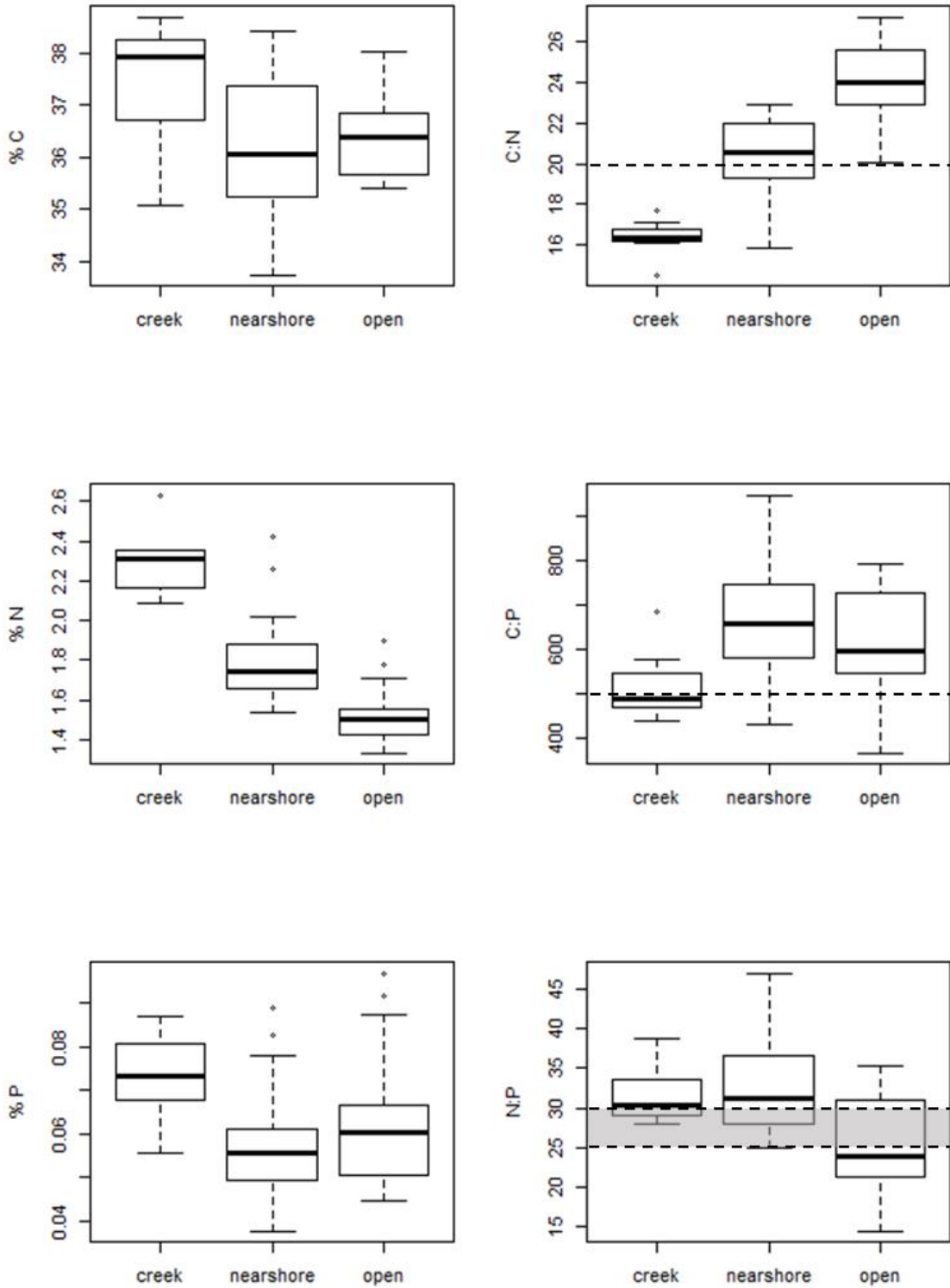
Figure 7. Spatial variation in nutrient content of seagrasses. Left (top-bottom): C, N, and P content *T. testudinum* per habitat; Right: Ratios of C:N, C:P, and N:P for *T. testudinum* per habitat; the dashed lines represent the seagrass Redfield ratio.

Predator relative abundance

Sharks were observed on 27 of 61 (44%) BRUVs deployed in BOR. Six species including *Carcharhinus acronotus* (blacknose shark), *Carcharhinus limbatus* (blacktip shark), *Carcharhinus perezi* (Caribbean reef shark), *Galeocerdo cuvier* (tiger shark), *Ginglymostoma cirratum* (nurse shark), and *Negaprion brevirostris* (lemon shark) were observed. Tiger sharks, which regularly include sea turtles in their diets (*e.g.,* Heithaus *et al.* 2008), were sighted on four of the 61 (6.6%) BRUVs. Three of the four tiger sharks were captured on BRUVs in the open habitat and one in nearshore habitat, however, logistic regression revealed no significant difference in tiger shark observations between open and nearshore habitats ($Z = 1.09$, $df = 43$, $P = 0.28$).

Sharks were observed on 8 of nine (89%) BRUVs deployed in the creek habitat in 2018. However, only juvenile lemon sharks, that represent no risk to turtles, were observed.

Turtle abundance and distributions

Turtles were sighted 285 times on aerial video transects. Most sightings were of individual turtles, but up to 11 turtles were observed within a single video frame. The mean number of turtles per video frame during a sighting was 1.71 ± 1.44 (SD). Creeks had the highest total sightings (180) and mean sighting density (3.11 ± 7.19 turtles/ha) compared to nearshore (102 sightings; 1.14 ± 5.77 turtles/ha) and open (3 sightings; 0.03 ± 0.18 turtles/ha) habitats (Figure 8). Wilcoxon rank sum tests revealed significant

differences in sighting densities between open and nearshore habitats (W = 77.5, *P* <

0.0001) and open and creek habitats (W = 234, *P* = 0.0002), but sighting densities were

not significantly different between creek and nearshore habitats (W = 209, *P* = 0.13)

(Figure 9). Mean sighting densities and high standard deviations occurred because turtles

were concentrated in a few areas and absent in others (Figure 1).
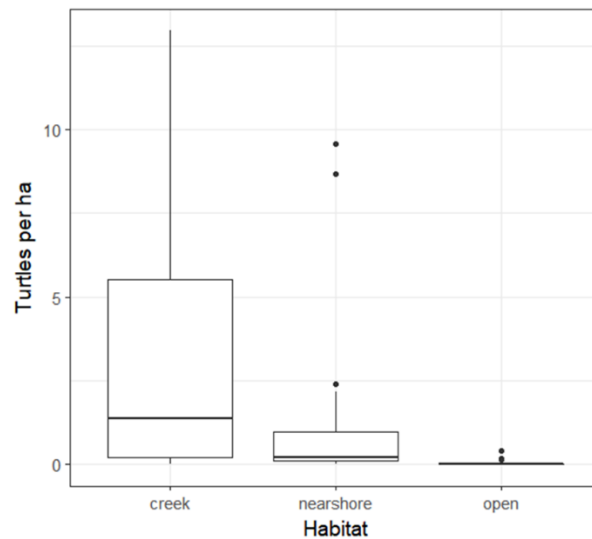
Figure 8. Turtle sighting density per habitat.

Model selection

Stepwise model selection of the generalized linear mixed effects model identified

the best fit model to be:

$$Turtles \sim Tt * N + Hw + (1 \mid Habitat) + offset(\log(Area))$$

where *Turtles* is the sightings count, *Tt* and *Hw* represent the mean abundance of *T.*

testudinum and *H. wrightii*, respectively, *N* is the percent concentration of nitrogen in *T.*

testudinum leaves, *Habitat* is set as the random effect and *log(Area)* is effort as the model

offset. The interaction *T. testudinum* and N is represented by *Tt*N*. Predictor variables

and interactions considered in the model selection are listed in Table 3.

Table 3. Model selection table with models ranked by AIC score from best fitting model to worst, where K is the number of parameters in the model, AICc is the information criterion for each model, δAICc is the difference between the AIC of respective model and the best fitting model, ModelLik is the relative likelihood of the model given the data, AICcWt are the Akaike weights and indicate the level of support for the model being the most parsimonious, LL is the log-likelihood, and Cum.Wt is the cumulative model weight (Mazerolle, 2017).

Model	K	AICc	δAICc	ModelLik	AICcWt	LL	Cum.Wt
Tt*N+Hw	6	226.21	0.00	1.00	0.99	-106.03	0.98784
Tt+Hw+Sf+Algae+N+C+P+Depth+Tt*N	11	235.01	8.80	0.01	0.01	-102.50	0.99997
Tt*N+P	6	249.04	22.83	0.00	0.00	-117.44	0.99998
Tt*N+P+Depth	7	249.18	22.97	0.00	0.00	-116.08	0.99999
Tt*N	5	251.31	25.10	0.00	0.00	-119.90	1.00
Tt*N+P+Depth+C	8	251.51	25.30	0.00	0.00	-115.75	1.00
Tt+Hw+Sf+Algae+N+C+P+Depth	10	271.74	45.53	0.00	0.00	-122.64	1.00
Tt+Hw+Sf+Algae+N+C+P	9	275.22	49.01	0.00	0.00	-126.11	1.00
Tt+Hw+Sf+Algae+N	7	278.84	52.63	0.00	0.00	-130.95	1.00
Tt+Hw+Sf+Algae+N+C	8	281.48	55.27	0.00	0.00	-130.79	1.00
P	3	340.72	114.51	0.00	0.00	-167.07	1.00
Depth	3	354.73	128.53	0.00	0.00	-174.08	1.00
N	3	359.93	133.73	0.00	0.00	-176.68	1.00
C	3	361.94	135.73	0.00	0.00	-177.68	1.00
Tt+Hw+Sf+Algae	6	378.42	152.21	0.00	0.00	-182.23	1.00
Tt+Hw+Sf	5	380.09	153.89	0.00	0.00	-184.37	1.00
Tt+Hw	4	382.33	156.12	0.00	0.00	-186.72	1.00
Tt	3	388.85	162.65	0.00	0.00	-191.17	1.00
Sf	3	406.53	180.33	0.00	0.00	-200.01	1.00
Hw	3	408.46	182.25	0.00	0.00	-200.97	1.00
Algae	3	410.50	184.29	0.00	0.00	-201.99	1.00

Accounting for differences among habitats by setting habitat as the random effect,

turtle abundance is negatively correlated with *T. testudinum* and positively correlated

with *H. wrightii* abundance (Table 4). The significant interaction between *T. testudinum* abundance and N content shows that, especially in the tidal creeks, although turtles were observed in areas with high *T. testudinum* abundance and low N, the highest turtle densities were observed in areas with low *T. testudinum* abundance and high N (Figure 10).

Table 4. Results of generalized linear mixed effects best fit model; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Fixed effects:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-3.14	1.19	-2.64	0.01	**
Tt	-3.71	0.54	-6.94	0.00	***
N	-0.62	0.56	-1.11	0.27	
Hw	0.94	0.19	5.01	0.00	***
Tt:N	2.36	0.29	8.07	0.00	***
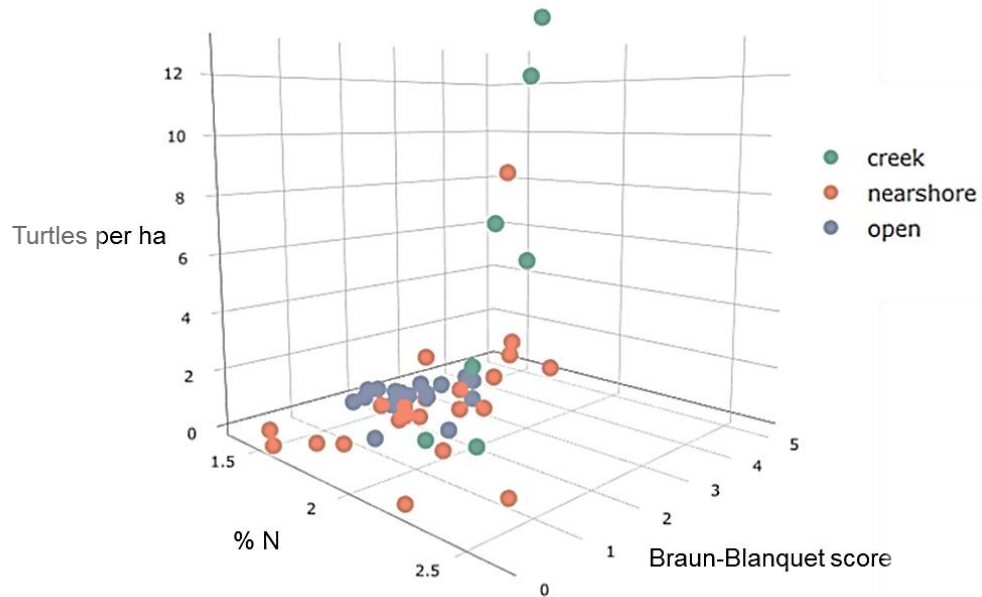
Figure 10. Turtle sightings per ha by % N content and Braun-Blanquet scores *T. testudinum.*

Discussion

      Herbivore habitat use decisions can be affected by both bottom-up and top-down forces. The basic Ideal Free Distribution (IFD; Fretwell and Lucas 1970) predicts that grazers should be distributed across habitats proportional to the availability of food. If this were the case, we would have expected higher turtle abundances in open habitats than in creek habitats. If turtles were avoiding predators, however, we predicted that turtles would largely avoid open and nearshore waters and instead select for creek habitat. Green turtle distributions were not consistent with an IFD using only seagrass cover. At broad spatial scales it appears that turtles are not using open foraging habitats despite these habitats having the greatest seagrass abundance. Indeed, only three turtles were observed in this habitat during the study suggesting that it is largely avoided.

      While it is likely that avoiding predators plays some role in the space use decisions of turtles off Abaco at a broader spatial scale (*i.e.,* avoiding open habitats almost entirely and low densities in most nearshore cells), food resources appear to shape turtle densities at small spatial scales and within particular habitats. Indeed, while the relationships between measures of food abundance and quality and turtle density were weak or even negative within open and nearshore habitats, within creek habitats, turtle densities were positively correlated with both N content of seagrasses and the presence of *Haladule wrightii*. The seagrass *H. wrightii* was most abundant in tidal creeks overall, but it was patchily distributed. In general, turtles were more abundant in areas with relatively high cover of *H. wrightii*, but their abundances were still high relative to nearshore and open habitats even in areas of creeks where *H. wrightii* was absent. Although it has been documented as a diet component of green turtles (see review by Forbes, 1996), it has not

been documented as a major component of their diets. Relative to other seagrass species, *H. wrightii* in other parts of the Caribbean has high N content (Chapter IV). If turtles off Abaco are using *H. wrightii* as a N rich food source, carrying capacity (K) in areas like the tidal creeks could be higher than estimates based solely on *T. testudinum*.

Herbivores often forage selectively to meet nutritional requirements (Simpson *et al.,* 2004). The non-gregarious, non-territorial, high-arctic Avalbard reindeer (*Rangifer tarandus platyrhinchus*) in habitats with low forage availability and productivity selected home ranges and resource patches on the basis of productivity, however, reindeer in habitats with high forage availability and productivity selected habitats based on conditions supportive of high forage quality over forage biomass (Hansen *et al.,* 2009). Dugong (*Dugong dugong*) habitat selection is context dependent in that they will selected seagrass patches for high nitrogen concentrations during high tides, however, when habitat space was limited by low tides, their habitat use shifted to patches with high seagrass biomass (Sheppard *et al.,* 2010). Green turtles in other parts of the Caribbean select forage according to nutrient content (N, P, and soluble sugars) relative to other available forage options (Bjorndal, 1997; Christianen *et al.,* 2018).

Although turtles off Abaco face a food abundance-safety tradeoff, they do not appear to need to trade off food quality for safety. Indeed, turtle densities in creeks showed a positive correlation with N content, and all samples of *T. testudinum* from creeks had higher N content than all samples from open habitats and most from nearshore habitats. Therefore, it is possible that turtles may be able to obtain adequate energy and nutrient intake rates in creek habitats that are safe and support continued growth of

seagrasses that have high nutrient content. The ability of the tidal creeks to support the current local turtle population, however, would require that turtles on the Abaco foraging ground are not bottom-up limited and not near the carrying capacity of the Bight of Old Robinson overall. Indeed, if the resident turtle population was near carrying capacity, we would expect lower-condition turtles to begin using suboptimal habitats or those that feature higher predation risk (*e.g.,* Heithaus *et al.* 2007).

Off Great Abaco, turtles may benefit from the geological setting of their foraging habitats. Indeed, seagrasses within what would normally be oligotrophic tidal creeks appear to be benefiting from allochthonous nutrient inputs from nearby blue holes (Lapointe *et al.,* 2004), which could combine with the enhanced nutrient cycling facilitated by the turtles themselves (Thayer, Engel and A. Bjorndal, 1982; Bjorndal, 1997; Kelkar *et al.,* 2013) to allow seagrasses to maintain high nutrient content in the face of heavy herbivory. Because other tidal creeks without blue holes support grazing turtle populations off Abaco (*pers. obs.*), further studies of the links between nutrient inputs and turtle contributions to turtle nutrient recycling are needed to test the hypothesis that nutrient outputs from blue holes provide adequate nutrients to support seagrasses under concentrated grazing pressure. Such studies should help in identifying likely high-quality habitats for turtles that should be targeted for conservation in the face of increasing human pressures on coastal systems.

Green turtles in Abaco appear to conform to the Foraging Arena hypothesis with the population divided into vulnerable and invulnerable population components (Ahrens, Walters and Christensen, 2012; Colléter *et al.,* 2015). The vulnerable population

component in open and nearshore waters is at generally very low density and densities do not correlate with measures of food abundance or quality. In contrast, a relatively high density invulnerable population occurs in the foraging arena of tidal creeks. At the current population density, green turtles may be able to maintain the vulnerable component at low densities because of the relatively high nitrogen content in the creek habitat seagrass. This contrasts with studies in Shark Bay, Australia where, although both turtles (Heithaus, Frid and Dill, 2002; Heithaus *et al.,* 2007) and dugongs (Wirsing, Heithaus and Dill, 2007) trade-off food for safety, they are constrained because the vast majority of foraging options are in dangerous areas. Unlike in Abaco, the Shark Bay herbivores are limited in their ability to reduce the vulnerable population component because of the limited forage in less dangerous areas. Also, there are no habitats in Shark Bay where these herbivores can forage free from risk. Even "safe" habitats are risky to some degree, whereas in Abaco turtles have a true refuge from large predators where they can forage. Because trophic interactions are restricted to the vulnerable prey foraging arenas, if population and individual growth rates increase the invulnerable population component could exceed carrying capacity of the tidal creeks in Abaco and push individuals into vulnerable habitats, increasing the turtle densities in nearshore and open water habitats.

Tidal creeks may be particularly critical habitats for rebuilding sea turtle populations. The high variance in nearshore waters because of turtle concentrations in several cells found very close to shore in the SE portion of the study area, suggests that identifying critical habitat for herbivores requires analysis of their habitat use at multiple scales (*i.e.,* landscape and patch). Continued monitoring of green turtle distributions and

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partitioning of the population should be considered in future management and protection plans. The protected shark populations in Abaco may be preventing unchecked grazing by green turtles, and the exchange of individuals from the invulnerable (creek) to the vulnerable (open water) population components could signal that the preferred habitat has reached carrying capacity, thus requiring updates to any current conservation and management plans.

Previous estimates of green turtle carrying capacity (K) in the Caribbean used seagrass (*T. testudinum*) cover and productivity as a proxy for food availability (Bjorndal and Jackson 2002; Jackson 2001), however, Heithaus *et al.* (2008) argued that the available foraging habitat for green turtles is restricted by risk of predation. Green turtle distributions in Abaco support the argument that K estimates derived from seagrass cover are likely overestimates. Updated regional estimates of K would benefit from the consideration of other factors that may constrain foraging habitat use such as predation (this Chapter, Heithaus *et al.* 2008), human impacts (Frid and Dill, 2002), and invasive species (Chapters IV and V).

Acknowledgments

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Appendix I.

  Parametric and non-parametric mixed effects model selection methods yielded comparable results. Linear mixed effects models with Satterthwaite's degrees of freedom in the lmerTest package were used to test for relationships between turtle sighting density, with an assumed Gaussian distribution, and habitat variables with habitat type set as the random intercept for all complete cells (*i.e.,* no missing data). Backward reduced fixed-effect model selection was employed to identify factors that affected turtle sighting densities (Table A. Kuznetsova, Brockhoff and Christensen, 2018). The parametric methods yielded the best fit model:

$$Turtles\_per\_ha \sim Tt \, + \, Hw \, + \, N \, + \, (1 \,|\, Habitat)$$

where *Turtles_per_ha* is the sighting density of turtles, *Tt* and *Hw* represent the mean abundance of *T. testudinum* and *H. wrightii*, respectively, *N* is the percent concentration of nitrogen in *T. testudinum* leaves, and *Habitat* is set as the random effect. Predictor variables and interactions considered in the backward reduced fixed-effect model selection are listed in Table A. This best fit model differs from the non-parametric model only in that it does not include the interaction between *Tt* and *N*.

Table A. Backward reduced fixed-effect table with Satterthwaite's degrees of freedom method used to compute the denominator degrees of freedom (DenDF); The simply additive model yielded the same results, but interactions are included in the table for comparison; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Backward reduced fixed-effect table:

	Eliminated	Df	Sum of Sq	RSS	AIC	F value	Pr(>F)	
Tt:P	1	1	0.001	170.72	84.001	0.0001	0.991155	
Sf	2	1	0.104	170.82	82.028	0.0201	0.888134	
Tt:C	3	1	0.178	171	80.075	0.0353	0.852009	
C	4	1	0.467	171.47	78.198	0.0957	0.758921	
P	5	1	0.485	171.95	76.325	0.1018	0.751554	
Depth	6	1	0.524	172.48	74.462	0.1127	0.739022	
Tt:Algae	7	1	2.39	174.87	73.081	0.5265	0.472545	
Algae	8	1	9.688	184.55	73.508	2.1608	0.149597	
Tt:N	9	1	17.013	201.57	75.476	3.6874	0.061976	.
Tt	0	1	27.795	229.36	79.289	5.6536	0.022164	*
Hw	0	1	48.103	249.67	83.107	9.7845	0.003234	**
N	0	1	59.996	261.56	85.201	12.2035	0.001158	**

The best fit linear mixed effects model suggests that turtle sighting density is positively correlated with Tt and Hw (Table B). This differs from the generalized mixed effects model in the direction of correlation with Tt. Because the sighting data were heavily skewed with a high number of zeros and small values, the non-parametric generalized linear mixed effects model was selected over this parametric model.

Table B. Results from the best fit linear mixed effects model; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	-6.2075	3.3453	14.7062	-1.856	0.0837	.
Tt	0.7724	0.3334	38.0402	2.317	0.026	*
Hw	2.2873	0.9532	40.9977	2.4	0.021	*
N	3.2757	1.6612	25.9234	1.972	0.0594	.

CHAPTER IV

LARGE-BODIED FORAGING HABITAT USE AND RESOURCE SELECTION IS AFFECTED BY THE INVASIVE SEAGRASS, *HALOPHILA STIPULACEA*, IN THE FRENCH WEST INDIES

Abstract

Invasive plant species can alter grazer foraging habitat use and resource selection - and ultimately affect survival and fitness - if the invasive species is of lower quality than native species or herbivores fail to recognize it as potential food. Across three islands of the French West Indies (Guadeloupe, Martinique, and Saint Martin), I explored how Caribbean green turtles (*Chelonia* mydas) selected microhabitats, and resources within those microhabitats, at foraging areas that featured mixes of native *Syringodium filiform*, *T. testudinum*, and *Halodule wrightii*, and the invasive seagrass *Halophila stipulacea*. From 2016-2017, I used belt transects to assess spatial variation in turtle densities and resource selection relative to macrophyte abundance, species composition, and nutrient content (C, N, P). Each study site presented unique relationships of nutrients among seagrasses. There was little detectable difference between native *S. filiforme* and invasive *H. stipulacea* in nutrient content off Guadeloupe, however, off Martinique, native *T. testudinum* contained greater N but less P than *H. stipulacea*, and *S. filiforme* was lower in both nutrients than the invasive. Off St. Martin invasive seagrass was not abundant and *T. testudinum* had the highest nutrient content of native species. At all sites turtles selected areas with abundant native seagrasses (*T. testudinum*, *S. filiforme*) and avoided areas typified by macroalgae and the invasive seagrass. Together, these data suggest that the spread of invasive seagrasses is currently resulting in a decrease in the habitat area that turtles perceive as quality foraging habitat, and interspecific variation in nutrient content alone may not be responsible for this pattern. If turtles are energy or nutrient-limited, restricted use of space and resources should have negative consequences on individual- and population-level energy budgets. In addition, turtle avoidance of the

invader likely is facilitating its spread. The ability of green turtle populations to adapt to decreases in habitat because of the invasion of a non-native seagrass or to expand their diets to take advantage of novel food resources, however, remains unclear and is an important aspect of turtle foraging ecology for further investigation in the face of macrophyte invasions.

Introduction

Invasive plants have modified both terrestrial and aquatic ecosystems and affect both biotic and abiotic components of ecosystems. Invasive terrestrial grasses (*Bromus tectorum* and *Bromus rubens*) have altered fire regimes in western North America (Brooks and Esque, 2002; Brooks *et al.,* 2004), negatively affecting critical habitat for many native fauna including the endangered desert tortoise (*Gopherus agassizii*). In the Mediterranean, 19 species of invasive algae were reportedly among the "100 Worst Invasives" in the Mediterranean in 2006 (Streftaris and Zenetos, 2006), causing changes in chemical and physical processes and decreasing macrophyte biodiversity.

Understanding habitat use decisions of herbivores is important in the face of plant species invasions because space-use patterns influence the spatiotemporal pattern of access to resources and top-down impacts on ecosystems. Furthermore, habitat use patterns of herbivores likely are already changing in response to other ecosystem changes including population declines of apex predators and eutrophication and other disruptions to basal resources. Prey species, like the vast majority of herbivores, often have to make foraging decisions on the basis of food-risk tradeoffs (*e.g.,* Power 1983; Verdolin 2006;

Heithaus *et al.* 2007), with the strength of behavioral response likely varying with the

degree of energy stress (*e.g.,* Clark 1994, Lima and Bednekoff 1999, Heithaus *et al.*

2008). In the absence of predation pressure, however, grazers are free to make their

foraging and habitat use decisions using other factors.

The invasion of the seagrass *Halophila stipulacea* is changing the composition of

many seagrass communities in the eastern Caribbean, and there is concern about potential

loss of some ecosystem functions of seagrass meadows because of structural differences

between the invasive and native seagrasses (Figure 1; Willette and Ambrose 2009). The

seagrass, *H. stipulacea*, is native to the Indian Ocean, has successfully spread to the

Mediterranean and Caribbean and is one of only two known invasive seagrass species to

have transoceanic establishment (Ruiz and Ballantine, 2004). Although it is unknown

how *H. stipulacea* will affect ecosystem function, invasive species have the ability to

facilitate native species through direct and indirect interactions (Rodriguez, 2006). An

invasive reed grass (*Spartina alterniflora*) is hybridizing with a native reed grass

(*Spartina foliosa*) in San Francisco Bay creating a more structurally defended grass that

is avoided by grazing western Canada geese (*Branta canadensis moffitti*) (Grosholz,

2010). The only documented trans-oceanic seagrass invader prior to *H. stipulaceae* was

Zostera japonica which positively affected some native species of benthic invertebrates

by providing enhanced refuge because of structural changes in seagrass communities

(Posey, 1988). A review of the impacts of alien marine species in Europe found that of 63

species studied, most were reported to have both positive and negative effects on

ecosystem services and biodiversity, however, the authors suggest that there is often a

preconceived bias against alien species and positive effects may be understudied and

underreported (Katsanevakis *et al.* 2014). Here, I investigate the effects of an invasive seagrass, *H. stipulacea*, on space use of green sea turtles (*Chelonia mydas*) at multiple sites and across multiple sampling events and consider the potential reciprocal effects of turtles on the success of *H. stipulacea*'s invasion.

Figure 1. Juvenile green turtle resting in a mixed seagrass meadow in Malendure Bay, Guadeloupe; *S. filiforme* (native): long cylindrical blades; *H. stipulacea* (invasive): short, densely packed, paddle-shaped blades

Green turtles spend a large part of their life cycle in coastal tropical and subtropical waters, and their selective feeding strategies can structure seagrass community structure (Kelkar *et al.,* 2013). Their diets vary among regions where local populations may be adapted to consume specific forage (*e.g.*, seagrass or algae; Bjorndal, 1980). For example, green turtles off Baja California, Mexico, forage primarily on algae,

whereas green turtles in The Bahamas forage primarily on the seagrass *Thalassia testudinum* (Bjorndal, 1980). In another study at Green Island in Queensland, Australia, a juvenile green turtle population appeared to be generalist, eating seagrass and algae, but individuals specialized on one or the other (Fuentes, Lawler and Gyuris, 2006). Similarly, offshore of Western Australia individual green turtles appear to specialize on seagrass, macroalgae, gelatinous macroplankton or a stable mix of these sources (Burkholder *et al.,* 2011). These studies identify dietary compositions, but few studies have looked at the effects of changes in forage species on space use by green turtles. Because green turtles have the potential to exert top-down control and structure ecosystems through their grazing (Lal *et al.,* 2010; Wabnitz *et al.,* 2010), it is important to understand patterns in their habitat use and resource selection.

Understanding the factors that influence foraging distributions, food selection, and ecological impacts of green turtle populations may be particularly critical in areas where there are bottom-up disruptions to ecosystems like the presence of invasive species. Under the conditions of the Enemy Release Hypothesis, invasive species succeed because they are not controlled by natural enemies (Keane and Crawley, 2002; Cogni, 2010). If local grazer populations preferentially feed on native species, they can facilitate invasions, while preferential herbivory on an invader or indiscriminate feeding may slow or minimize the spread of an invasive species. Hawaiian green turtles have incorporated invasive algae and seagrass into their diets, and the proportion of their diets comprised of invasive species has increased with the prevalence of these taxa within their foraging habitats (Russell *et al.,* 2003; Russell and Balazs, 2009, 2015). However, in Caribbean habitats affected by the *Halophila stipulacea* invasion (Figure 1), green turtles are

selectively foraging on native seagrasses over the invasive seagrass. In Bonaire, green

turtles are facilitating the *H. stipulacea* invasion by selectively feeding on a native

seagrass, *Thalassia testudinum*, which has significantly greater nutrient content than the

invasive species (Christianen *et al.,* 2018). However, turtles may not be avoiding invasive

seagrasses because of variation in nutrient content. Indeed, green turtles off Guadeloupe

positively selected for the native seagrass *Syringodium filiforme* over the invasive

seagrass *H. stipulacea*, despite similar nutritional quality (Chapter IV).

The hierarchical levels at which resource selection occurs can have important

consequences for individual and population energy budgets and structure the impacts of a

forager on its ecosystem as well as determines its potential exposure to threats. First order

selection is at the level of geographical range, second order selection is at the level of

home range, third order is the selection of habitat patches within the home range, and

fourth order is the selection of resources within habitat patches (Johnson, 1980; Massé

and Côté, 2009).

In the context of the *H. stipulacea* invasion, green turtles are selecting native

seagrasses within patches that vary in the proportion of invasive species present (fourth

order selection; Chapter IV, Christianen *et al.* 2018), but whether they select habitats at

broader spatial scales (third order selection) in relation to overall seagrass abundance or

the abundance of preferred species remains untested. Decision making at the patch level

can have consequences beyond those of direct selection and consumption of one species

over another including inter- and intra-patch nutrient transport (Pringle, 2018), inter- and

intraspecific competition among grazers (*e.g.,* Kleynhans *et al.* 2011), and indirect effects

of grazing on other trophic levels (*e.g.,* Waldram, Bond, and Stock 2008; Hays 2005). To

assess the effects of the invasive *H. stipulacea* on patch level green turtle foraging habitat

use, I tested whether green turtles selected foraging sites depending on 1) variation in

nutrient content of seagrasses, 2) spatial variation in the overall abundance of seagrasses,

or 3) relative to the abundance of specific types of macrophytes (*e.g.,* native vs invasive

seagrasses, macroalgae). I also tested fourth order selection of resources to see if green

turtle preference for native seagrasses over the invasive seagrass is consistent across

islands.

Methods

Study sites

The study occurred within three bays along the coasts of Guadeloupe, Martinique,

and St. Martin in the French West Indies (FWI; Figure 2). Malendure (16° 10' N, 61° 46'

W) is a bay on the western coast of Basse-terre, Guadeloupe. The mouth and widest

width of the Bay spans *ca.* 750 m and a beach lines *ca.* 500 m of the inner coast. Grande-

Anse (14° 30' N, 61° 05' W) is a bay within Anses d'Arlet, Martinique. The largest bay

in our study, Grande Anse is nearly two km wide at its mouth and more than 1.3 km of

beach. Baie-Blanche (18° 06' N, 62° 59' W) is a bay on the western coast of Ile

Tintimarre, a small uninhabited island in the Saint Martin Nature Reserve. The smallest

bay in this study, Baie-Blanche is *ca.* 650 m at its mouth, although the survey area

extended beyond this, with a *ca.* 400 m beach. Native seagrasses found in these bays

include *S. filiforme*, *T. testudinum*, and *Halodule wrightii*. Island names will henceforth be used to refer to sites.

The first report of rooted *H. stipulacea* in the Caribbean was in Granada in 2002 (Ruiz and Ballantine, 2004) and has since been documented growing in mixed seagrass patches as far north as Puerto Rico (Ruiz, Ballantine and Sabater, 2017). The seagrass was first documented in Martinique, Guadeloupe, and Saint Martin in 2006, 2010 and 2012, respectively (Willette *et al.* 2014). The natural gradient of invasive species cover, likely resulting from the temporal invasion gradient, provides an excellent opportunity to study the potential effects of the spread of *H. stipulacea* on grazer habitat use.

We conducted surveys of green turtle and seagrass distributions along belt transects during three field trips to Guadeloupe and Martinique in spring 2016, fall 2016, and spring 2017, and to St. Martin in fall 2016, and spring 2017. Because these sites are popular tourist destinations, and the marine life is highly acclimated to the presence of boats, snorkelers, divers and non-motorized marine craft (*e.g.,* kayaks and paddleboards), animals rarely reacted to our presence in the water facilitating observations of natural foraging behaviors.
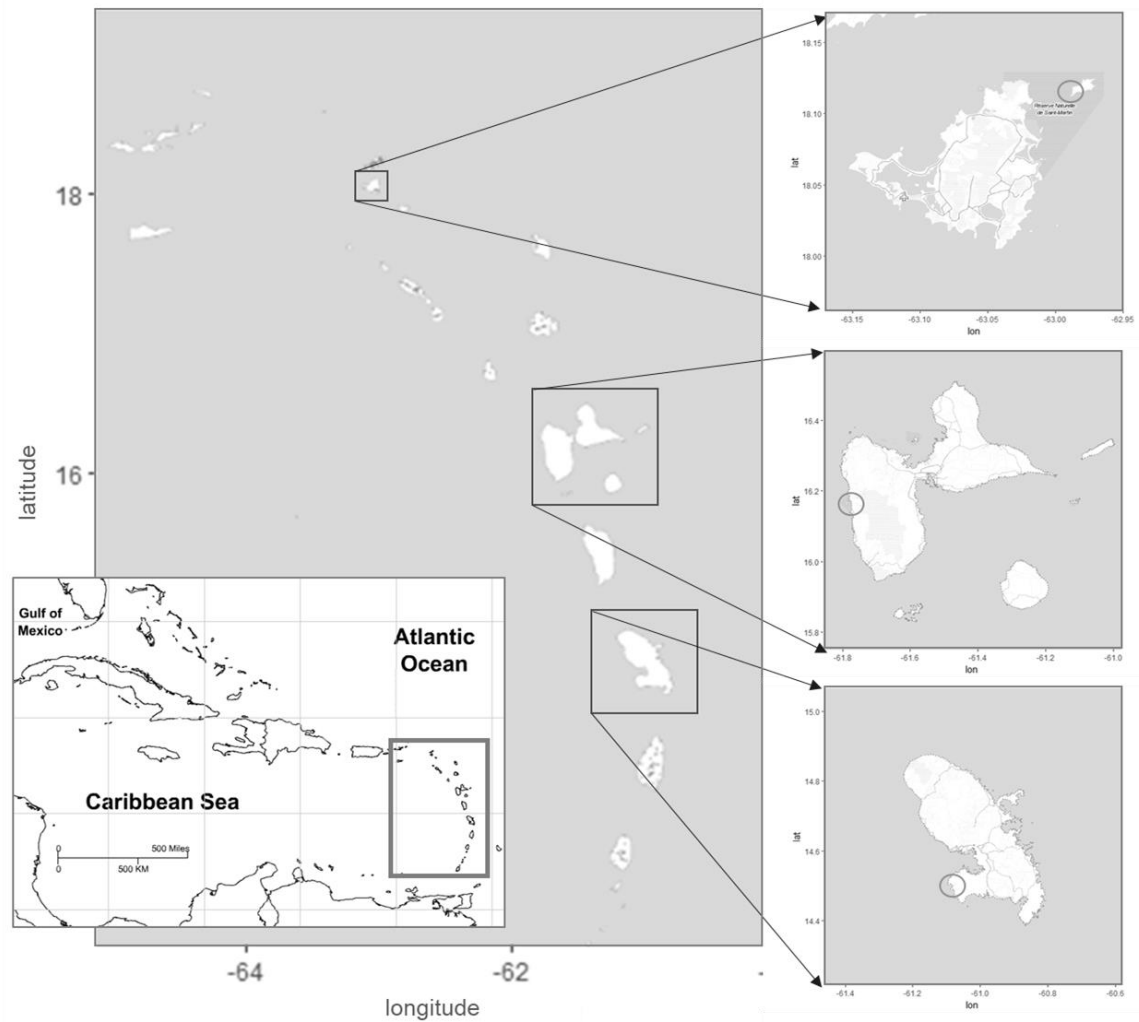
Figure 2. The study was conducted in the Lesser Antilles (left) within the Caribbean Sea (inset). One bay on the islands of St. Martin (top right), Guadeloupe (center right) and Martinique (bottom right) were selected based on the presence of turtles and mixed beds of invasive and native seagrasses.

Habitat classification

I divided each study area into 100 m x 100 m cells using a vector grid layer in QGIS version 2.18.11 (QGIS Development Team, 2018; Figure 3). Data collected within each hectare allowed us to further define the patches by assigning habitat values to each for a quantitative analysis. Using the "join attributes" function in QGIS, I extracted all

survey data [*i.e.,* macrophyte abundance, sampling effort (Figure 3), and turtle sightings] per cell to calculate total and average values per cell. Only cells with data were used in the respective analyses.
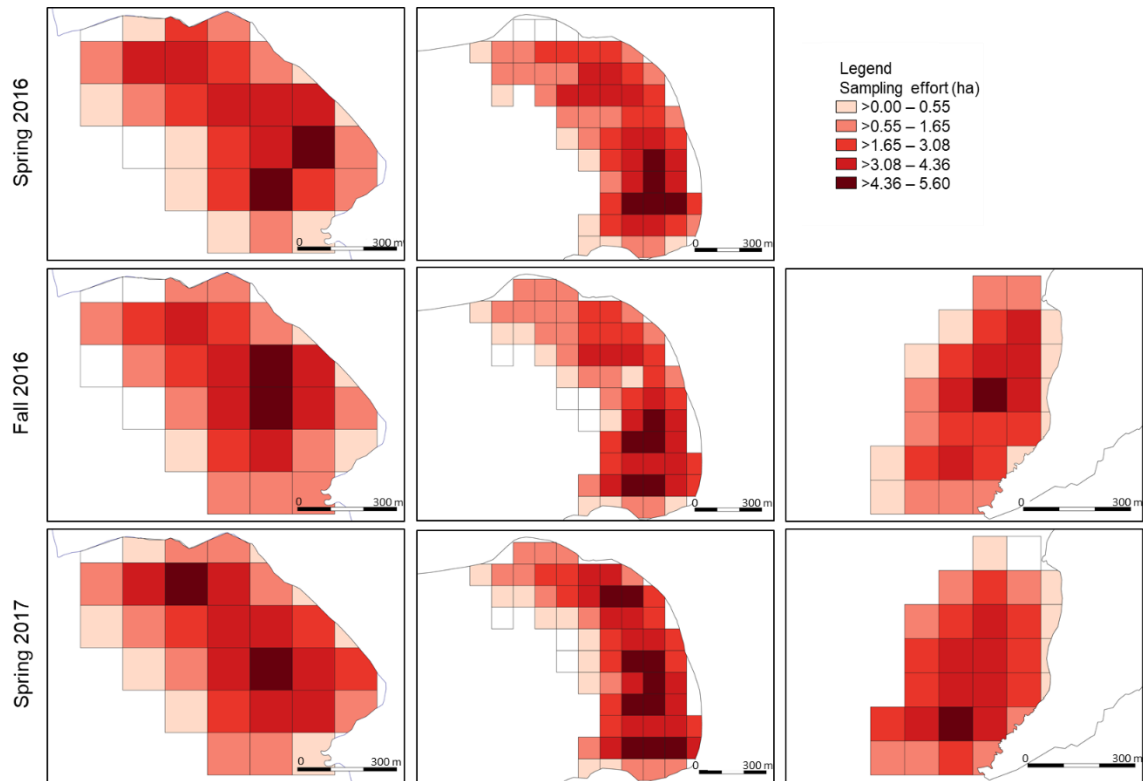
Figure 3. Survey effort in ha surveyed per site per sampling event. Cells on the grid are 100m x 100m. Color breakpoints were autogenerated by QGIS

Forage availability

Detailed surveys of the seagrass community were conducted in each site across multiple field sampling events. Sampling plans evolved as the study progressed (Table 1)

from intense haphazard surveys of Guadeloupe in 2016 (112 points sampled) to pre-

determined 100 m grid points at all sites.

Table 1. Number of sampling plots and methods for macrophyte abundance and nutrient
content collection; dashes indicate no data collection

	Spring 2016		Fall 2016		Spring 2017	
	Abundance	Nutrients	Abundance	Nutrients	Abundance	Nutrients
Guadeloupe	122, haphazard	-	-	12, haphazard	23, 100 m grid	11, haphazard
Martinique	10, haphazard	-	-	19, haphazard	55, 100 m grid	14, grid points
St. Martin	-	-	72, 30 m grid	7, grid points	25, 100 m grid	7, grid points

At each point in each sampling event, two observers, either freediving or on

SCUBA estimated the abundance of each species present within four 50 cm x 50 cm

quadrats. Each macrophyte species was assigned a score according to the Braun-Blanquet

scale for rapid vegetation assessments (Table 2) (Fourqurean *et al.,* 2001). At each

sampling point, each observer estimated abundance of each species with two quadrats for

a total of 4 assessments per point. From the mean of the four assessment scores I

calculate density as the mean score from the four quadrats for each species present at

each sampling point. The Braun-Blanquet method, commonly used to assess the

abundance of seagrass and macroalgae, is efficient, highly repeatable, non-destructive

and minimizes observer differences (Fourqurean *et al.,* 2001).

Table 2. Braun-Blanquet abundance scores of each macrophyte species; the score for each sampling point is the average of scores given to each species based on this scale within four quadrats at each point; reproduced from (Fourqurean *et al.,* 2001)

Score	Cover
0	Taxa absent from quadrat
0.1	Taxa represented by a solitary shoot, <5% cover
0.5	Taxa represented by a few (<5) shoots, <5% cover
1	Taxa represented by many (>5) shoots, <5% cover
2	Taxa represented by many (>5) shoots, 5 - 25% cover
3	Taxa represented by many (>5) shoots, 25 - 50% cover
4	Taxa represented by many (>5) shoots, 50 - 75% cover
5	Taxa represented by many (>5) shoots, 75 - 100% cover

Nutrient content analyses

I collected *ca.* 40 seagrass leaves or equivalent macroalgae biomass of each macrophyte species for nutrient content analysis at haphazardly or grid selected plots (Table 1) in fall 2016 and spring 2017. The samples were collected by hand either while freediving or on SCUBA, placed in labeled plastic sandwich bags, and refrigerated until they could be processed and transported to Florida International University for analysis. Samples were cleaned of epiphytes using a straight-edge razor and dried in a food-grade dehydrator for a minimum of 24 hours within 48 hours of collection. After drying, samples were crushed using a mortar and pestle and stored in airtight vials for transport. C and N were measured using a CE Flash 1112 elemental analyzer using standard procedures, and total P was analyzed colorimetrically following modified methods from Solórzano and Sharp (1980) on a Shimadzu UV-2101PC spectrophotometer.

Turtle abundance and distributions

Each bay was divided into three sections of similar area using identifiable landmarks along the beach as boundary markers. Transects originated from haphazard locations along the beach, within three strata to ensure relatively uniform coverage of the bay. To avoid pseudoreplication, I did not immediately repeat transects. Additionally, sections within each site were surveyed equally in 2-hour time bins from 0700-1700 when there was adequate sunlight to conduct surveys. Two observers on snorkel and tethered to each other with a 15 m rope (see Roos *et al.* 2005) swam transects perpendicular to the beach to survey turtles and seagrasses (Figure 2). Only turtles spotted within the transects (between observers) were counted. When a turtle was spotted, observers signaled each other with two pulls on the line between them. For each sighting the location using a towed handheld GPS (Garmin® GPSmap 78), turtle behavior (foraging, resting, or traveling), forage species consumed (when possible), and an estimate of percent cover of all macrophyte species present were recorded. Transects were terminated when visibility of the benthos mid-distance from each observer was too poor to identify macrophyte species, after which observers swam perpendicular to the beach until the return transect would not overlap with the one just completed.

Using the Vector grid feature in QGIS 2.18, I divided each site into one-hectare grid cells. The join attribute feature allowed me to assign cell identification numbers to all data within each cell (Figure 2). Individual transects crossed multiple cells, so survey effort per cell was calculated as the sum of the area of transect segments occurring within each cell. Macrophyte abundance and nutrients were averaged if more than one survey

point fell within a cell. Turtle sightings per transect segment per cell were summed. I calculated densities (number of animals $* ha^{-1}$) using:

$$D_i = \frac{n^i}{w * L},$$ (Eqn. 1)

where n^i is the number of individuals detected within a transect segment, w is the transect width (15 m) and L is the length of the transect calculated using start and end waypoints recorded with GPS.

Data analysis

All statistical tests were performed using R software (R Core Team, 2016). To test for habitat differences within and among sites and sampling events, I used Kruskal-Wallis and Wilcoxon sign rank tests for differences in seagrass abundance, richness, and nutrient content (CNP). Tests did not include macroalgae, because no turtles were observed foraging on algae during any of the surveys for my study.

I used a mixed-effects model with sampling event as the random effect and forage abundance variables to model predictions depending on forage abundance of each species and depth as the fixed effects to model effects of habitat variables on green turtle distributions at each site. No turtles were observed foraging on macroalgae, so it was excluded from the analyses. Cells with no forage abundance data were not included. Sampling points and sample sizes were not consistent across sampling events, so caution must be used in the interpretation of the temporal comparisons and data were pooled for site comparisons. Because forage nutrient content data were not collected consistently

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during sampling events when forage abundance data were collected, they were not included. I used a model selection table (R Package 'AICcmodavg', function = aictab, Mazerolle, 2017) of models using different combinations and interactions of abundance variables for stepwise model selection using Akaike information criterion (AIC) and Akaike weights. Models that did not converge were not included in the table. Because of the differences among sites in resource availability, model selection for each site was done independently. The fixed effects included in the models also varied because of resource availability. Seagrass species observed within less than five cells across all sampling events were excluded in the analysis for the respective site.

I used the R package adehabitatHS (Calenge, 2006) design III selectivity analysis to test the effects of species composition (resource availability) on foraging (resource use) for each individual turtle. Because of the few observations of foraging on *H. wrightii*, unknown species and of marine debris and animal matter (*i.e.,* ctenophores and bivalve shells), were not included in analyses. No turtles were observed foraging on macroalgae, so it was also excluded from the analysis. Weighted presence (0 = absent, 1 = present, 2 = dominant species present) of each forage species was used as the resource availability input, and the identifiable selection of a forage species was used as the resource use input.

Assuming uniform use of habitats as the null hypothesis, resource use was tested for the population and for individuals using Chi-square goodness-of-fit tests. I calculated Manly's selection ratios (*Wi*, Manly *et al.,* 2002) with Bonferroni confidence intervals with available resources defined for each animal by the categories *H. stipulacea* (Hs), *S.*

filiforme (Sf), and *T. testudinum* (Tt) (Calenge, 2015). Use of a resource was defined by the visual observation of the animal feeding on a seagrass species. Ratios (resource use to resource availability) greater than 1 indicate selection and less than 1 indicate avoidance. Ratios near 1 or confidence intervals for the population overlapping 1 suggest no selectivity.

Results

Forage availability

Guadeloupe

In Spring 2016, native seagrasses *T. testudinum* and *S. filiforme* were found at six (4.9%) and 75 (61.5%) of 122 haphazard sampling points, respectively. One native seagrass, *H. wrightii*, was not found at any site. The invasive *H. stipulacea* was found at 118 (96.7%) sites. Calcareous algae, other green algae, and red and brown algae were found at 70 (57.4%), 12 (9.8%), and 74 (60.7%) sites, respectively, but at very low abundances (Figure 4).

In Spring 2017, two native seagrasses (*T. testudinum* and *H. wrightii*) were not found at any sites while *S. filiforme* occurred at 9 of 23 (39.1%;) 100-m grid sampling points. The invasive *H. stipulacea* was found at 16 (69.6%) sites. Calcareous algae were found at 4 (17.4%) sites at very low abundances (Figure 4) but other green algae, and red and brown algae were not observed at any site.

Mean seagrass richness per site was significantly greater in Spring 2016 than Spring 2017 ($W = 1886.5$, $P = 0.003$). Mean invasive abundance was significantly greater than the sum of all native seagrass abundance scores per plot in both Spring 2016 ($W = 12914$, $P < 0.0001$) and Spring 2017 ($W = 399.5$, $P = 0.002$). Mean *H. stipulacea* abundance did not change significantly between sampling events ($W = 1480.5$, $P = 0.68$), however, mean *S. filiforme* (the only native seagrass observed at survey points during both sampling events decreased significantly from 2016 to 2017 ($W = 399.5$, $P = 0.002$).

Across both sampling events, *S. filiforme* was the most abundant native seagrass and occurred at 57.9% of the 145 total sampling points. The invasive *H. stipulacea* occurred at 92.4% of the points. The mean Braun-Blanquet score for *H. stipulacea* was significantly greater than the score for *S. filiforme* ($W = 3146.5$, $P = <0.0001$). On average, *H. stipulacea* was found at densities 25-50% and as high as 100%. *S. filiforme* was found at densities less than 5% and never more than 50% (Table 3).
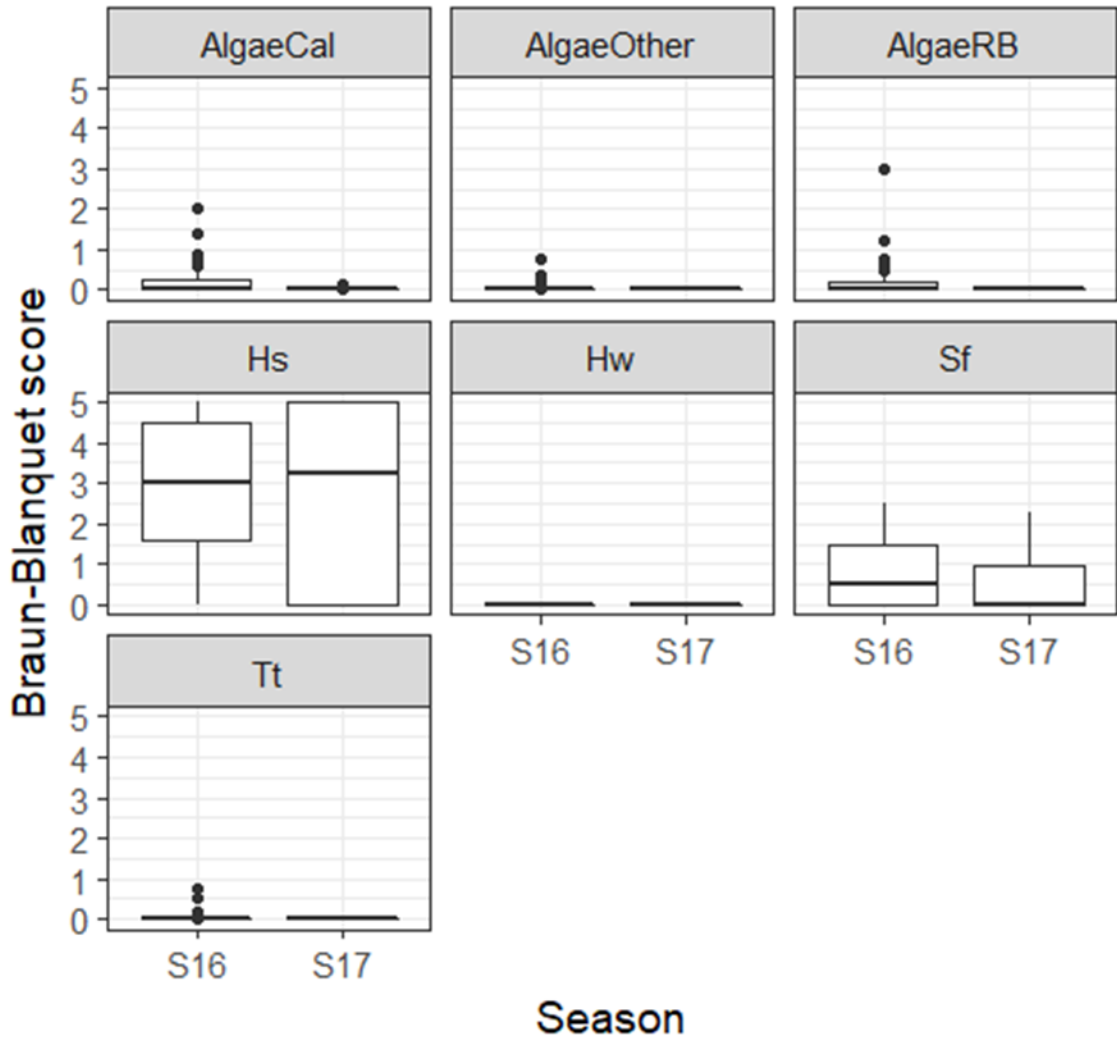
Figure 4. Braun-Blanquet abundance scores for Spring 2016 (S16) and Spring 2017 (S17) from Guadeloupe. The midline of the boxplot is the median, upper and lower limits of the box represent the 75th and 25th percentile, whiskers extend to minimum and maximum values except for data exceeding 1.5 times the interquartile range, which are displayed as dots (possible outliers).

Table 3. Mean and standard deviations of Braun-Blanquet scores for each site and season

Site	Season	Tt	Hw	Sf	Hs	Cal. Algae	Green Algae	R/B Algae
Guadeloupe	Spring 2016	0.01 ± 0.08	0.00 ± 0.00	0.80 ± 0.77	2.89 ± 1.56	0.15 ± 0.28	0.02 ± 0.09	0.15 ± 0.32
Guadeloupe	Spring 2017	0.00 ± 0.00	0.00 ± 0.00	0.51 ± 0.76	2.62 ± 2.20	0.01 ± 0.04	0.00 ± 0.00	0.00 ± 0.00
Martinique	Spring 2016	0.67 ± 0.83	0.00 ± 0.00	0.40 ± 0.84	4.43 ± 0.77	0.24 ± 0.32	0.05 ± 0.08	0.06 ± 0.20
Martinique	Spring 2017	0.42 ± 0.74	0.00 ± 0.00	0.26 ± 0.59	3.02 ± 1.78	0.18 ± 0.32	0.06 ± 0.16	0.35 ± 0.78
StMartin	Fall 2016	0.93 ± 0.99	0.22 ± 0.53	0.73 ± 0.69	0.13 ± 0.57	1.44 ± 1.27	0.02 ± 0.08	0.01 ± 0.05
StMartin	Spring 2017	1.48 ± 1.16	0.17 ± 0.64	1.05 ± 0.90	0.00 ± 0.00	1.64 ± 0.93	0.75 ± 1.06	0.14 ± 0.21

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<u>Martinique</u>

In Spring 2016, native seagrasses *T. testudinum* and *S. filiforme* were found at 7 (70.0%), and 2 (20.0%) of 10 haphazard sampling points, respectively. The native *H. wrightii* was not found at any site. The invasive *H. stipulacea* was found at all 10 points. Calcareous algae, other green algae, and red and brown algae were found at 5 (50.0%), 5 (50.0%), 1 (10.0%) site, respectively, but at very low abundances (Figure 5).

In Spring 2017, native seagrasses *T. testudinum* and *S. filiforme* were found at 24 (43.6%) and 11 (20.0%) of 55 100-m grid sampling points, respectively. One native seagrass, *H. wrightii*, was not found at any site. The invasive *H. stipulacea* was found at 46 sites (83.6%). Calcareous algae, other green algae, and red and brown algae were found at 26 (47.3%), 11 (20.0%), 17 (30.9%), respectively, but at very low abundances at most plots (Figure 5). As a consequence of low sample size in 2016, I did not do a statistical comparison across sampling events.

Across sampling events, *T. testudinum* occurred at 47.7% of the 65 total sampling points, *S. filiforme* at 20.0% of the points, and the invasive *H. stipulacea* at 86.2% of the points. *T. testudinum* had a greater mean Braun-Blanquet score than *S. filiforme* ($W = 1611.5$, $P = 0.006$), and *H. stipulacea* had higher mean abundance scores, usually occurring at densities greater than 50% and up to 100%, than both *T. testudinum* ($W = 521.5$, $P < 0.0001$) and *S. filiforme* ($W = 399.5$, < 0.0001). *T. testudinum* and *S. filiforme* were each found on average at densities less than 5% and never greater than 50% (Table 3).
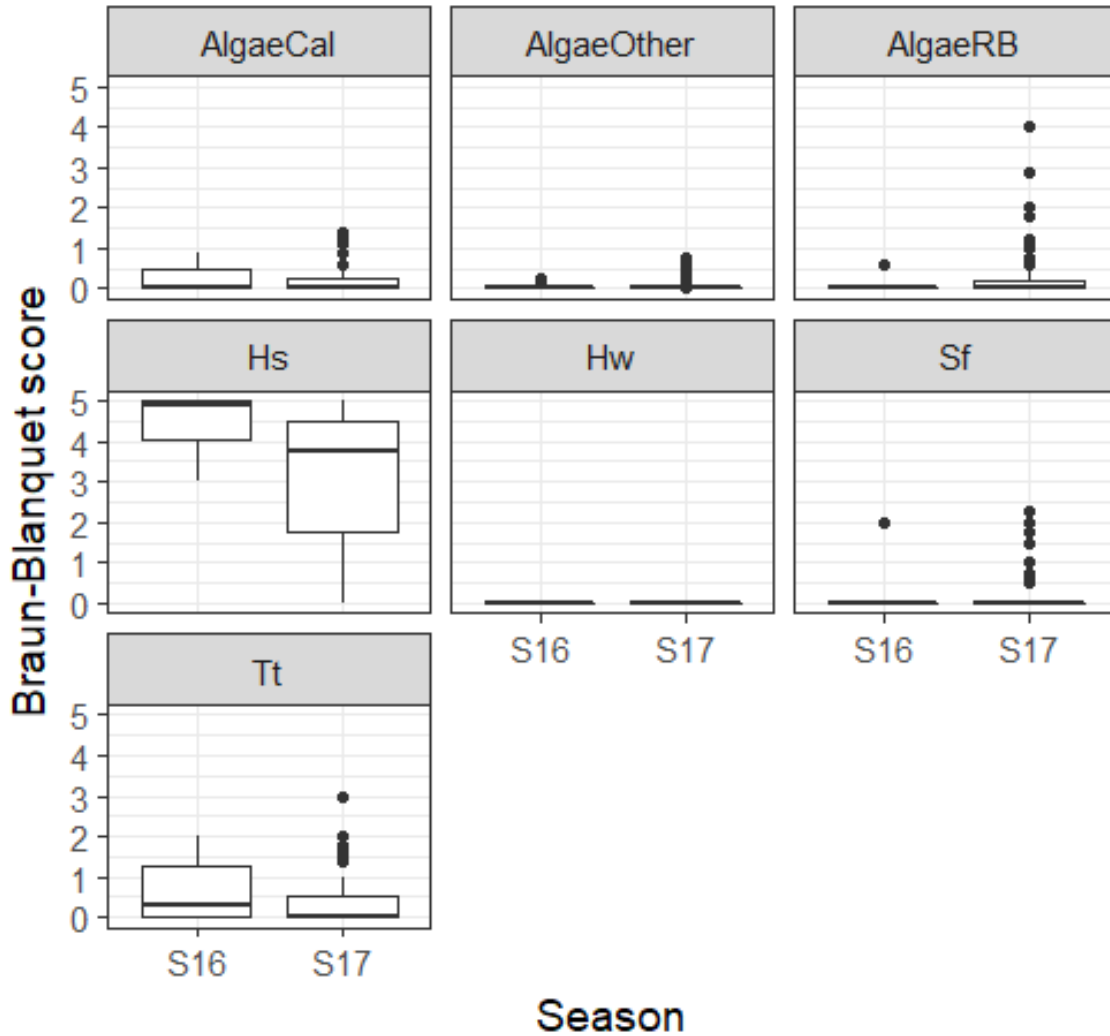
Figure 5. Braun-blanquet abundance scores for macrophytes of Martinique Spring 2016 (S16) and Spring 2017 (S17). The midline of the boxplot is the median, upper and lower limits of the box represent the 75th and 25th percentile, whiskers extend to minimum and maximum values except for data exceeding 1.5 times the interquartile range, which are displayed as dots (possible outliers).

St. Martin

In Fall 2016, native seagrasses *T. testudinum*, *S. filiforme*, and *H. wrightii* were

found at 40 (55.6%), 41 (56.9%), and 15 (20.8%) of 72 30-m grid sampling points,

respectively. The invasive *H. stipulacea* was found at 4 (5.6%). Calcareous algae, other

green algae, and red and brown algae were found at 50 (69.4%), 11 (15.3%), 2 (2.8%), respectively. Calcareous green algae were the most abundant macrophyte within plots (W = 4213, P = < 0.0001) (Figure 6, Table 3).

In Spring 2017, native seagrasses *T. testudinum*, *S. filiforme*, and *H. wrightii* were found at 22 (88.0%), 16 (64.0%), and 2 (8.0%) of 25 100-m grid sampling points, respectively. The invasive *H. stipulacea* was not found at the 2017 sampling points, but it is found in a small (c.a. 100 m^2) monospecific and along the edges of some mixed seagrass beds in the northern section of the bay. Calcareous algae, other green algae, and red and brown algae were found at 23 (0.92%), 12 (48.0%), 10 (40.0%), respectively. Calcareous green algae were also the most abundant macroalgae within plots compared to the sum of all other macroalgae (W = 436.5, P = 0.02) (Figure 6, Table 3).

Mean seagrass richness did not differ between Spring 2016 and Spring 2017 (W = 819, P = 0.46). Mean sum of all algae and mean sum of native seagrass abundances did not differ in either Fall 2016 (W = 280, P = 0.53) nor Spring 2017 (W = 2155.5, P = 0.08). Mean sum of all algae was significantly greater in Spring 2017 than Fall 2016 (W = 657.5, P = 0.04), but did the mean abundances of native seagrasses *S. filiforme* (W = 700.5, P = 0.09) and *T. testudinum* (W = 681.5, P = 0.06) did not differ between the two sampling events.

Across sampling events, *T. testudinum* occurred at 63.9% of the 97 total sampling points, *S. filiforme* at 58.8% of the points, and *H. wrightii* at 17.5% of the points. Mean Braun-Blanquet abundance scores were not significantly different for *T. testudinum* and *S. filiforme* (W = 4055, P = 0.09), however, *H. wrightii* had lower mean abundance

scores than both *T. testudinum* ($W = 7068$, $P < 0.0001$) and *S. filiforme* ($W = 6737$, $<$ 0.0001). On average, *T. testudinum* was found at densities 5-25% and up to 100%, *S. filiforme* and *H. wrightii* were each found at densities less than 5% on average and up to 50% (Table 3). In 2016 *H. stipulacea* was found at densities up to 75%.
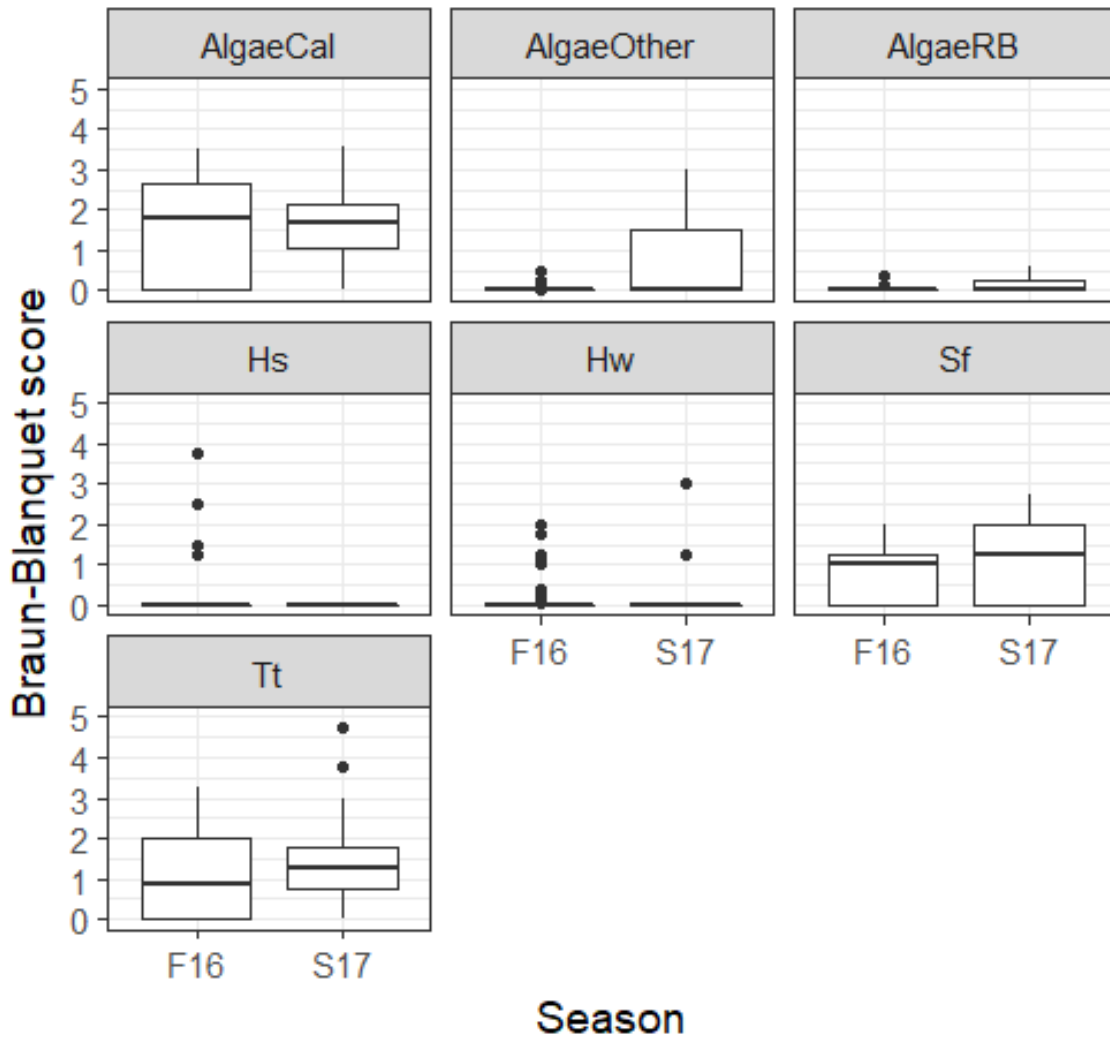
Figure 6. Braun-blanquet abundance scores for macrophytes of St. Martin Fall 2016 (F16) and Spring 2017 (S17). The midline of the boxplot is the median, upper and lower limits of the box represent the 75th and 25th percentile, whiskers extend to minimum and maximum values except for data exceeding 1.5 times the interquartile range, which are displayed as dots (possible outliers).

Forage nutrient content

Guadeloupe

Nitrogen content did not differ between the invasive *H. stipulacea* and most abundant native seagrass *S. filiforme* ($W = 213$, $P = 0.66$). The native seagrasses *H. wrightii* and *T. testudinum* were only found at three and two sampling plots, respectively, across the three sampling events, so they were not included in analyses. No turtles were observed foraging on algae during this study, so macroalgae were also excluded. Mean C content was *ca.* 9% greater in *S. filiforme* than *H. stipulacea* ($W = 121$, $P = 0.01$, Table 4). Total P content did not differ between *H. stipulacea* and *S. filiforme* ($W = 326.5$, $P = 0.08$). The C:N did not differ between *H. stipulacea* and *S. filiforme* ($W = 227$, $P = 0.65$), mean C:P was 27% greater in *S. filiforme* than *H. stipulacea* ($W = 117$, $P = 0.01$), and N:P did not differ between *H. stipulacea* and *S. filiforme* ($W = 151$, $P = 0.06$). The C:N and C:P ratios for all seagrasses were below Redfield ratios suggesting that the site was a nutrient rich site (Table 4, Figure 7).

Table 4. C, N, P content and their ratios ± SD of calcareous green algae (ACG), *H. stipulacea* (Hs), *H. wrightii* (Hw), *S. filiforme* (Sf), *T. testudinum* (Tt) off Guadeloupe

	ACG	Hs	Hw	Sf	Tt
N	1.2 ± 0.4	2.0 ± 0.6	2.5 ± 0.4	2.0 ± 0.3	1.9 ± 0.5
C	21.9 ± 2.1	32.2 ± 1.8	39.4 ± 1.1	35.2 ± 4.2	38.3 ± 2.1
P	0.05 ± 0.01	0.20 ± 0.05	0.29 ± 0.15	0.18 ± 0.03	0.17 ± 0.01
CN	19.0 ± 4.1	16.9 ± 3.2	16.2 ± 2.1	18.2 ± 2.1	20.6 ± 4.1
CP	474.5 ± 127.5	167.3 ± 46.0	156.2 ± 60.9	212.0 ± 52.7	225.8 ± 6.2
NP	25.6 ± 6.4	10.1 ± 3.1	9.9 ± 4.5	11.8 ± 3.3	11.2 ± 1.9
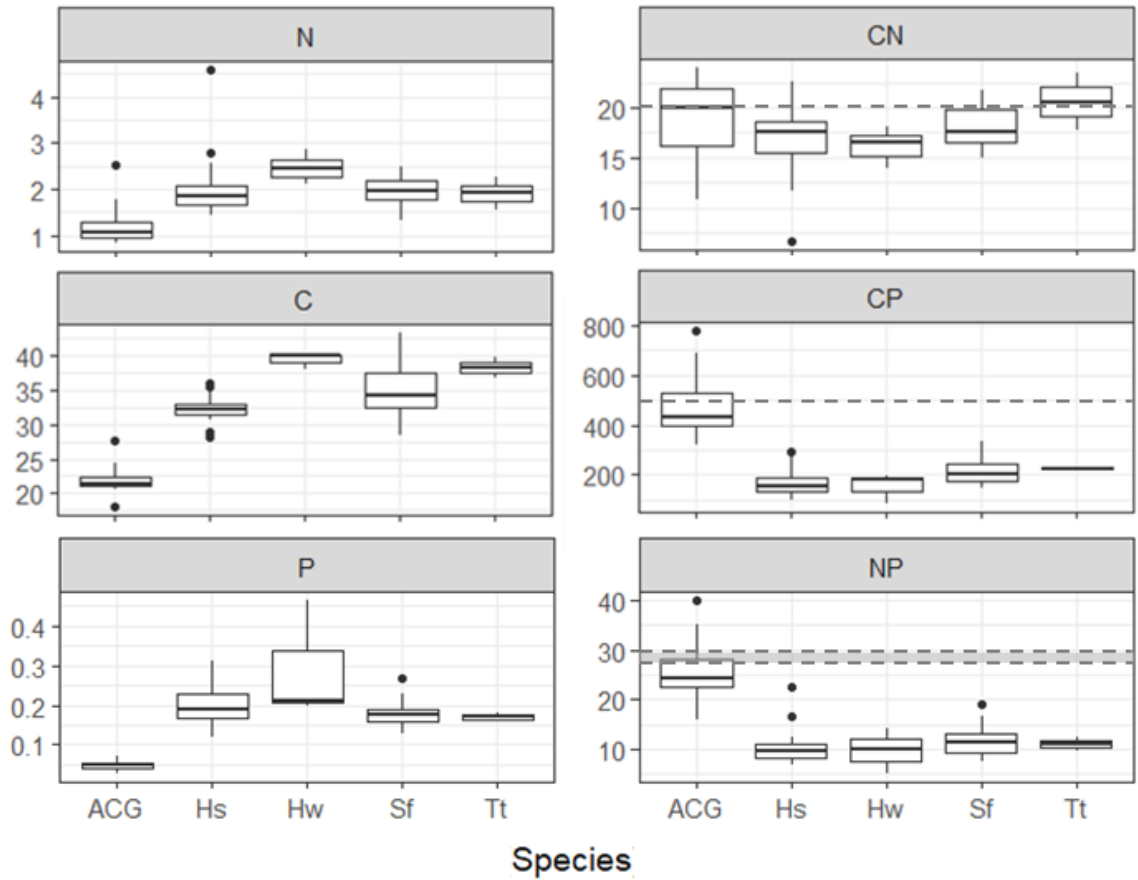
Figure 7. Elemental composition of macrophytes off Guadeloupe; Left (top-bottom): C, N, and P content of calcareous green algae (ACG), *H. stipulacea* (Hs), *H. wrightii* (Hw), *S. filiforme* (Sf), *T. testudinum* (Tt); Right: Ratios of C:N, C:P, and N:P for each species; the dashed lines represent the seagrass Redfield ratio

Martinique

In contrast to patterns observed off Guadeloupe, there was considerable interspecific variation in nutrient content among seagrass species of Martinique (Table 5). Mean N content was 22% greater in the invasive *H. stipulacea* than native *S. filiforme* and 14% greater in *T. testudinum* than *H. stipulacea* (Table 6). Mean N content was 39%

greater in *T. testudinum* than *S. filiforme*. The native seagrass, *H. wrightii*, was only found at one sampling plot, across the three sampling events, so it was not included in analyses. Mean C content was 16% greater in *T. testudinum* than *H. stipulacea* and 17% greater than in *S. filiforme* (Table 6), but not different between *H. stipulacea* and *S. filiforme*. Mean P content was 45% greater in *H. stipulacea* than in *S. filiforme*, and 25% greater than in *T. testudinum*. Mean P content was 16% greater in *T. testudinum* than in *S. filiforme* (Table 6). The C:N of *S. filiforme* was 23% and 21% greater than *H. stipulacea* and *T. testudinum*, respectively. The C:P was 42% greater in both *T. testudinum* and *S. filiforme* than in *H. stipulacea* (Table 6). The N:P in *S. filiforme* was 17% greater than in *H. stipulacea*, and 20% and 40% greater in *T. testudinum* than in *S. filiforme* and *H. stipulacea*, respectively (Table 6). The C:N and C:P ratios for all seagrasses were below Redfield ratios, suggesting that those habitats are nutrient rich, and the low N:P ratio suggests that Martinique site is limited by N (Table 6, Figure 8).

Table 5. Wilcoxon rank sum test results of nutrients among seagrass species off Martinique; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Martinique

Variable	Species 1	Species 2	W	P-value	
N	Hs	Tt	141.5	0.0173	*
N	Hs	Sf	249.0	0.0034	**
N	Tt	Sf	148.0	0.0001	***
C	Hs	Sf	203.0	0.1514	
C	Hs	Tt	0.0	< 0.0001	***
C	Tt	Sf	160.0	< 0.0001	***
P	Hs	Sf	269.0	< 0.0001	***
P	Hs	Tt	390.5	0.0002	***
P	Tt	Sf	133.0	0.0041	**
CN	Hs	Sf	39.0	0.0002	***
CN	Hs	Tt	232.0	0.7300	
CN	Tt	Sf	28.0	0.0050	**
CP	Hs	Sf	21.0	< 0.0001	***
CP	Hs	Tt	28.0	< 0.0001	***
CP	Tt	Sf	80	1.0000	
NP	Hs	Sf	68.0	0.0122	*
NP	Hs	Tt	26.0	< 0.0001	***
NP	Tt	Sf	134.0	0.0034	**

Table 6. C, N, P content and their ratios ± SD of calcareous green algae (ACG), other algae (AO), *H. stipulacea* (Hs), *H. wrightii* (Hw), *S. filiforme* (Sf), *T. testudinum* (Tt) off Martinique

	ACG	AO	Hs	Hw	Sf	Tt
N	1.5 ± 0.7	2.1 ± 0.9	1.9 ± 0.4	3.0 ± NA	1.6 ± 0.3	2.2 ± 0.3
C	21.3 ± 4.4	32.2 ± 9.1	30.7 ± 3.3	39.8 ± NA	30.6 ± 1.6	35.7 ± 1.2
P	0.07 ± 0.04	0.10 ± 0.05	0.21 ± 0.04	0.34 ± NA	0.14 ± 0.02	0.17 ± 0.02
CN	16.8 ± 5.5	17.1 ± 4.8	16.1 ± 2.0	13.2 ± NA	19.8 ± 3.4	16.4 ± 2.3
CP	393.5 ± 134.6	356.1 ± 138.1	150.3 ± 33.3	118.0 ± NA	213.5 ± 22.6	213.4 ± 19.4
NP	25.7 ± 9.4	20.8 ± 5.3	9.4 ± 1.8	8.9 ± NA	10.9 ± 1.5	13.1 ± 1.6
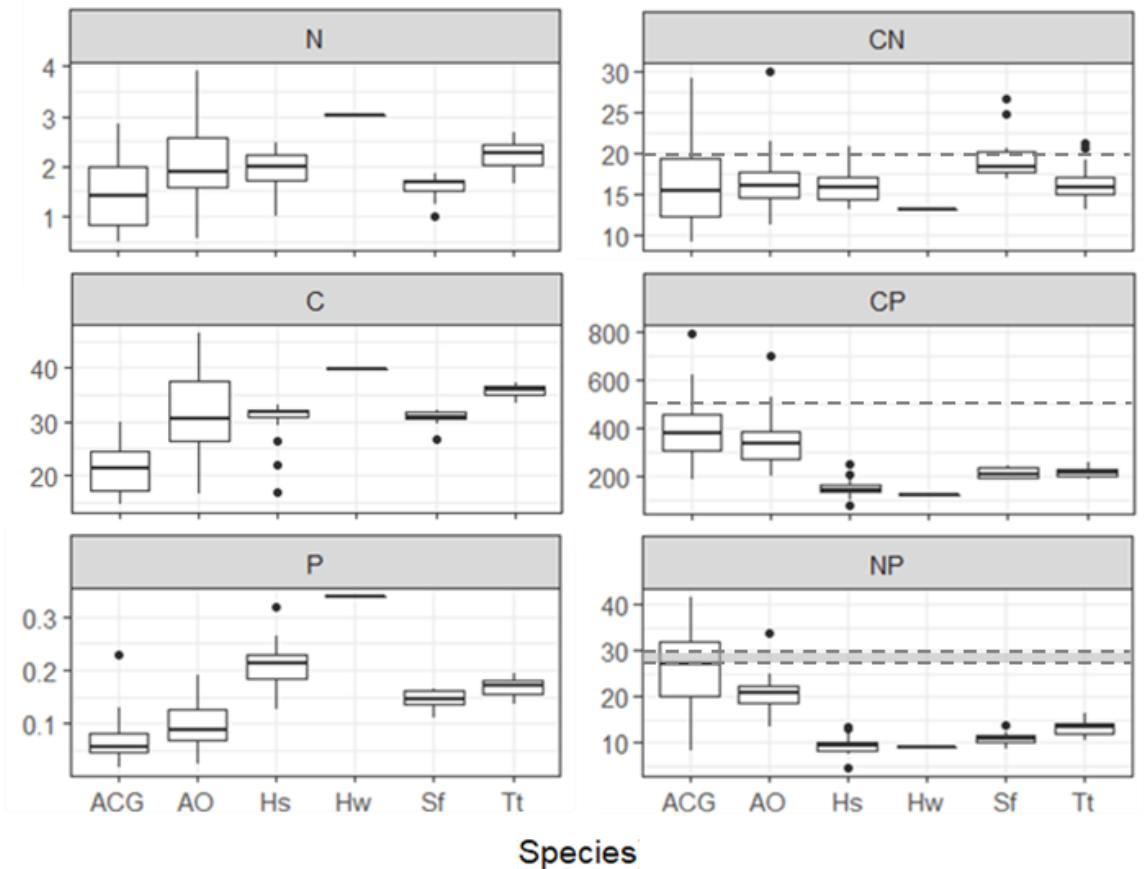
Figure 8. Elemental composition of macrophytes off Martinique; Left (top-bottom): C, N, and P content of calcareous green algae (ACG), other algae (AO), *H. stipulacea* (Hs), *H. wrightii* (Hw), *S. filiforme* (Sf), *T. testudinum* (Tt); Right: Ratios of C:N, C:P, and N:P for each species; the dashed lines represent the seagrass Redfield ratio

St. Martin

Mean N content was 36% greater in *T. testudinum* and 43% greater *H. wrightii* than in *S. filiforme* (Table 7). Mean C content was 9% greater in *T. testudinum* and 12% greater *H. wrightii* than in *S. filiforme*. Mean P content was 35% greater in *T. testudinum* than in *S. filiforme*. *H. stipulacea* was only found at two sampling plots, across the three

sampling events, so it was not included in analyses. C:N was 28% greater in *S. filiforme* than in *H. wrightii*. The C:P in *S. filiforme* was 27% and 23% greater than in *H. wrightii* and *T. testudinum*, respectively. The N:P did not differ among seagrasses. The C:N ratio was not consistent among seagrasses, and C:P ratios for all seagrasses were below Redfield ratios, suggesting that St. Martin site is a nutrient rich habitat. The low N:P ratio in seagrasses suggests that N is the limiting nutrient (Table 8, Figure 9).

Table 7. Wilcoxon rank sum test results of nutrients among seagrass species off St. Martin; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

St. Martin

Variable	Species 1	Species 2	*W*	*P-value*	
N	Hw	Sf	87	0.0099	**
N	Hw	Tt	62	0.7135	
N	Tt	Sf	151	0.0027	**
C	Hw	Sf	80	0.0446	*
C	Hw	Tt	76	0.1876	
C	Tt	Sf	137	0.0255	*
P	Hw	Sf	10	0.1818	
P	Hw	Tt	16	0.1176	
P	Tt	Sf	133	0.0041	*
CN	Hw	Sf	20	0.0199	*
CN	Hw	Tt	52	0.8154	
CN	Tt	Sf	29	0.0019	**
CP	Hw	Sf	20	0.0314	*
CP	Hw	Tt	49	0.6642	
CP	Tt	Sf	23	0.0011	**
NP	Hw	Sf	49	0.9699	
NP	Hw	Tt	49	0.6642	
NP	Tt	Sf	90	0.7810	

Table 8. C, N, P content and their ratios ± SD of calcareous green algae (ACG), other algae (AO), *H. stipulacea* (Hs), *H. wrightii* (Hw), *S. filiforme* (Sf), *T. testudinum* (Tt) off St. Martin

	ACG	AO	Hs	Hw	Sf	Tt
N	1.3 ± 0.8	2.2 ± 1.3	1.9 ± 0.1	1.9 ± 0.4	1.3 ± 0.4	1.8 ± 0.2
C	22.4 ± 5.2	31.7 ± 8.6	32.2 ± 0.2	37.6 ± 1.1	33.4 ± 4.3	36.6 ± 2.0
P	0.05 ± 0.02	0.06 ± 0.03	0.19 ± 0.05	0.16 ± 0.04	0.11 ± 0.02	0.15 ± 0.01
CN	19.1 ± 5.2	24.1 ± 23.3	16.6 ± 0.5	21.0 ± 5.2	27.0 ± 6.0	20.7 ± 2.1
CP	541.3 ± 173.6	715.3 ± 573.5	178.6 ± 50.2	242.1 ± 62.0	307.0 ± 47.1	249.8 ± 19.3
NP	29.8 ± 11.5	33.2 ± 5.9	10.7 ± 2.7	11.7 ± 2.4	11.7 ± 2.7	12.1 ± 1.3
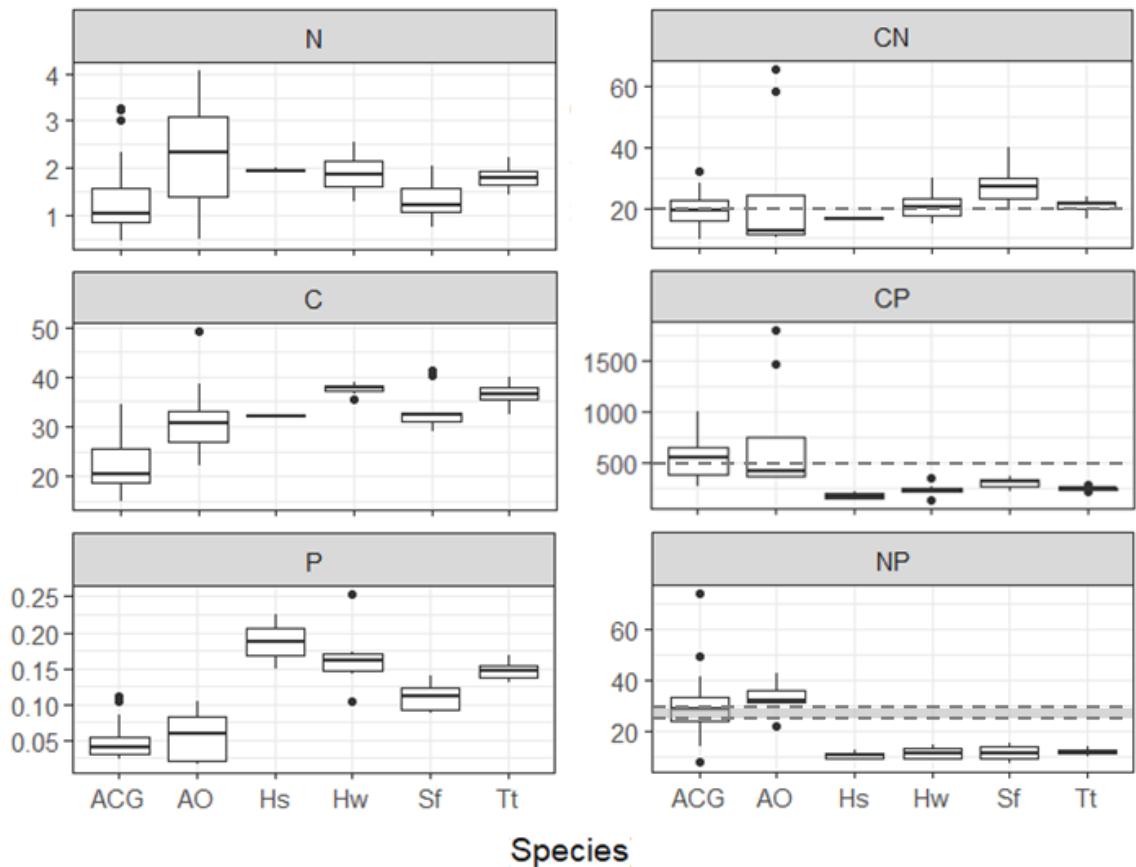
Figure 9. Elemental composition off macrophytes of St. Martin; Left (top-bottom): C, N, and P content of calcareous green algae (ACG), other algae (AO), *H. stipulacea* (Hs), *H. wrightii* (Hw), *S. filiforme* (Sf), *T. testudinum* (Tt); Right: Ratios of C:N, C:P, and N:P for each species; the dashed lines represent the seagrass Redfield ratio

Turtle abundance and distributions

Green turtle sighting density (turtles/ha) did not vary significantly among sampling events within sites (Guadeloupe: $X^2 = 1.70$, df = 2, $P = 0.43$; Martinique: $X^2 = 0.97$, df = 2, $P = 0.462$; St. Martin: $X^2 = 0.001$, df = 2, $P = 0.97$). Overall, the mean density of turtles off Guadeloupe was more than three times that found off Martinique ($W = 11032$, $P < 0.0001$) and St. Martin ($W = 3752.5$, $P < 0.0001$) (Table 9, Figure 10). Turtle sighting density did not significantly differ between Martinique and St. Martin ($W = 5059$, $P = 0.61$).

Table 9. Turtle sighting densities (Turtles/ha), total turtle sightings, transect length sum and total area surveyed for each site and sampling events.

	Turtles/ha	Total turtle sightings	Total transect length (km)	Total area surveyed (ha)
Guadeloupe	7.22 ± 6.98	761	59.93	89.90
F16	6.79 ± 5.31	161	13.51	20.26
S16	9.36 ± 9.11	133	8.21	12.31
S17	5.56 ± 5.43	467	38.22	57.33
Martinique	2.26 ± 3.75	364	97.28	145.91
F16	2.67 ± 4.82	116	32.69	49.04
S16	2.16 ± 3.05	86	23.60	35.40
S17	1.97 ± 3.15	162	40.98	61.47
StMartin	1.76 ± 2.42	171	42.71	64.06
F16	1.75 ± 2.27	69	16.06	24.10
S17	1.77 ± 2.61	102	26.64	39.97
Grand Total		1296	199.92	299.88
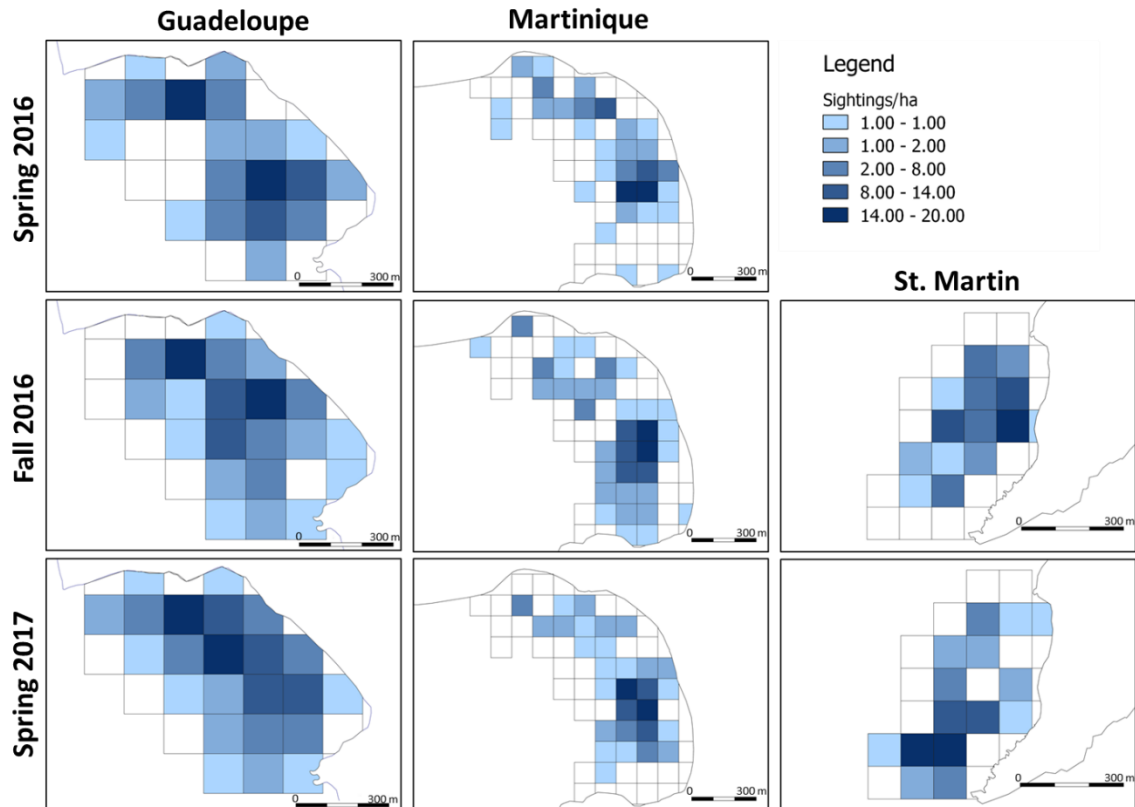
Figure 10. Mean turtle sightings per hectare for each sampling event and site

Model selection

<u>Guadeloupe</u>

Stepwise model selection of the generalized linear mixed effects model identified the best fit model to be:

$$Turtles \sim Sf + (1|season) + offset(log(Area))$$

where *Turtles* is the sightings count, *Sf* and represents the mean abundance of *S. filiforme*, *season* (sampling event) is set as the random effect and *log(Area)* is effort as the model offset. Predictor variables and interactions considered in the model selection

are listed in Table 10, and models with interactions (*) also test each independent

variable. Accounting for differences between sampling events by setting sampling event

as a random effect, turtle sighting abundance was positively correlated with *S. filiforme*

abundance (Table 11, Figure 11).

Table10. Model selection table of turtle sightings in Guadeloupe with models ranked by AIC score from best fitting model to worst, where K is the number of parameters in the model, AICc is the information criterion for each model, δAICc is the difference between the AIC of respective model and the best fitting model, ModelLik is the relative likelihood of the model given the data, AICcWt are the Akaike weights and indicate the level of support for the model being the most parsimonious, LL is the log-likelihood, and Cum.Wt is the cumulative model weight (Mazerolle, 2017). * represents a test of the interaction and individual variables.

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
Sf	3	380.42	0.00	1.00	0.51	-186.92	0.51
Sf * Hs	5	381.41	0.99	0.61	0.31	-184.96	0.82
Tt + Sf + Hs	5	383.96	3.54	0.17	0.09	-186.23	0.91
Tt * Sf	5	384.72	4.30	0.12	0.06	-186.61	0.97
Tt + Sf + Hs + Depth	6	385.81	5.39	0.07	0.03	-185.83	1.00
~	2	433.93	53.51	0.00	0.00	-214.83	1.00
Depth	3	433.93	53.51	0.00	0.00	-213.68	1.00
Hs	3	434.58	54.16	0.00	0.00	-214.00	1.00
Hs * Tt	5	435.75	55.33	0.00	0.00	-212.13	1.00
Tt	3	436.03	55.61	0.00	0.00	-214.73	1.00

Table 11. Results of generalized linear mixed effects best fit model for Guadeloupe; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Fixed effects:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0.37	0.11	-3.40	0.0007	***
Sf	0.39	0.05	7.56	<0.0001	***

Figure 11. Relationship between turtle sighting densities (to account for effort) and Braun-Blanquet scores of *S. filiforme* off Guadeloupe. The shaded area represents the 95% confidence interval; Left: including Braun-Blanquet scores equal to zero; Right: excluding Braun-Blanquet scores equal to zero

Martinique

Stepwise model selection of the generalized linear mixed effects model identified the best fit model to be:

$$Turtles \sim Tt * Sf \; + \; (1|season) \; + \; offset(log(Area))$$

where *Turtles* is the sightings count *Tt* and *Sf* represent the mean abundance of native seagrasses *T. testudinum* and *S. filiforme*, respectively, * represents the interaction of variables, *site* and *season* (sampling event) are set as the random effects and *log(Area)* is effort as the model offset. Models considered in the model selection are listed in Table 12, and models with interactions (*) also test each independent variable. Accounting for differences between sampling events by setting sampling event as a random effect, turtle abundance is affected by an interaction of *T. testudinum* and *S. filiforme* abundance

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(Table 13, Figure 12). Although there are increases in turtle sightings with increasing

abundance of both species, some of the highest turtle densities occurred where *T.*

testudinum was abundant but *S. filiforme* was not (Figure 12).

Table 12. Model selection table of turtle sightings in Martinique with models ranked by AIC score from best fitting model to worst, where K is the number of parameters in the model, AICc is the information criterion for each model, δAICc is the difference between the AIC of respective model and the best fitting model, ModelLik is the relative likelihood of the model given the data, AICcWt are the Akaike weights and indicate the level of support for the model being the most parsimonious, LL is the log-likelihood, and Cum.Wt is the cumulative model weight (Mazerolle, 2017). * represents a test of the interaction and individual variables.

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
Tt * Sf	5	310.68	0.00	1.00	1.00	-149.82	1.00
Tt + Sf + Hs + Depth	6	331.98	21.30	0.00	0.00	-159.24	1.00
Tt	3	333.35	22.67	0.00	0.00	-163.47	1.00
Hs * Tt	5	334.13	23.45	0.00	0.00	-161.54	1.00
Tt + Sf + Hs	5	337.60	26.91	0.00	0.00	-163.27	1.00
Depth	3	351.30	40.62	0.00	0.00	-172.45	1.00
Sf	3	352.45	41.76	0.00	0.00	-173.02	1.00
Sf * Hs	5	356.35	45.67	0.00	0.00	-172.65	1.00
~	2	358.87	48.19	0.00	0.00	-177.34	1.00
Hs	3	359.05	48.37	0.00	0.00	-176.32	1.00

Table 13. Results of generalized linear mixed effects best fit model for Martinique; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Fixed effects:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.79	0.11	-16.22	< 0.0001	***
Tt	0.81	0.10	7.74	< 0.0001	***
Sf	0.76	0.17	4.37	< 0.0001	***
Tt:Sf	-0.63	0.12	-5.12	< 0.0001	***
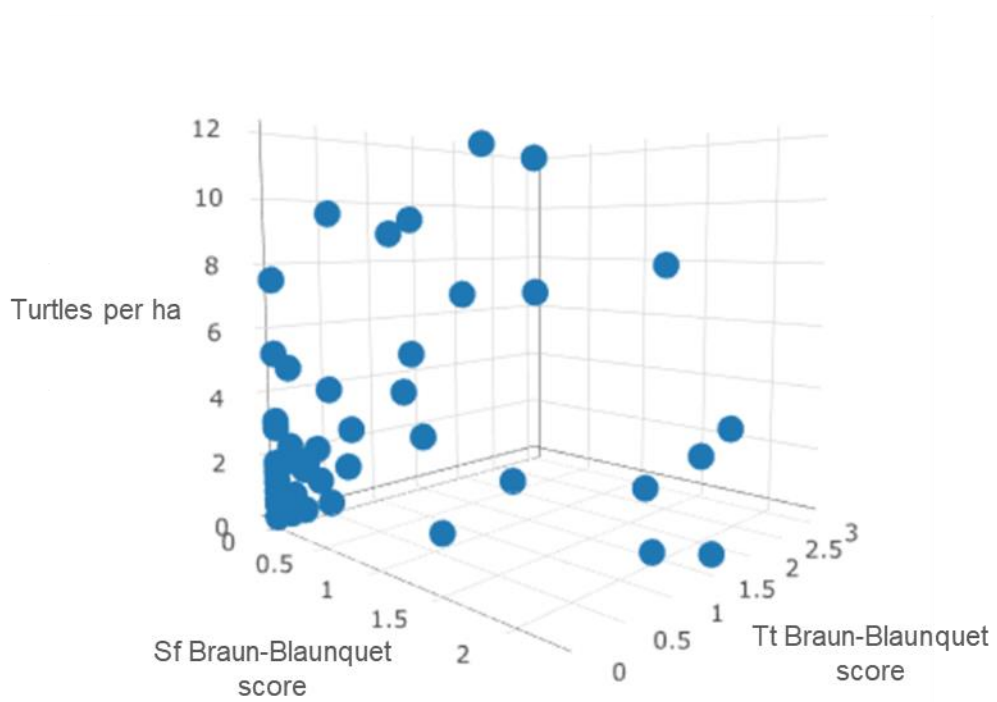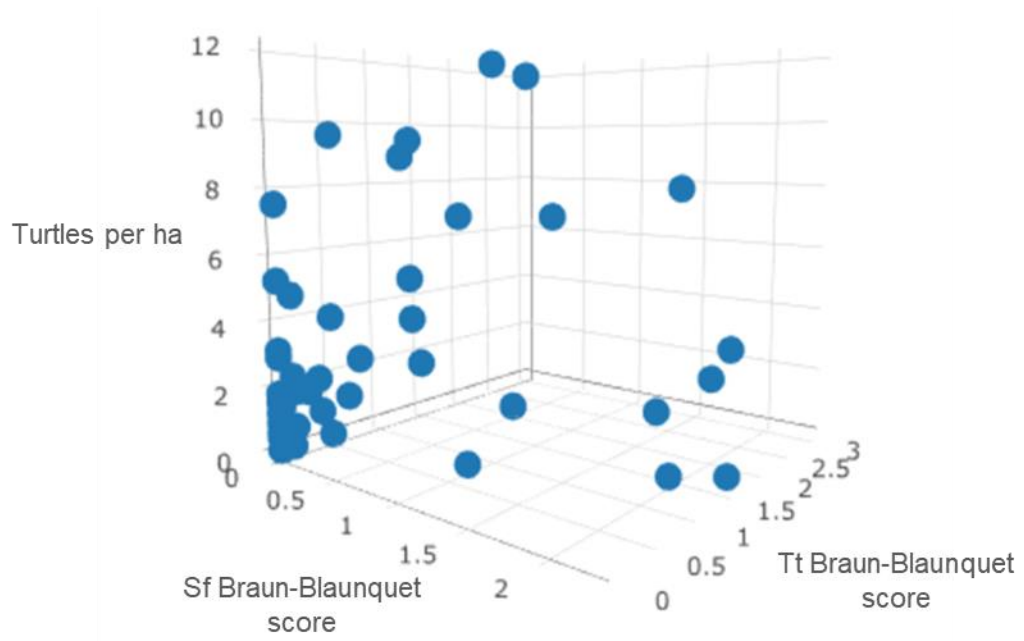
Figure 12. Relationships between turtle sighting densities (to account for effort) and the interaction of *T. testudinum* and *S. filiforme* Braun-Blanquet scores off Martinique of; Top panel includes sum of Braun-Blanquet scores equal to zero. Bottom panel excludes sum of Braun-Blanquet scores equal to zero
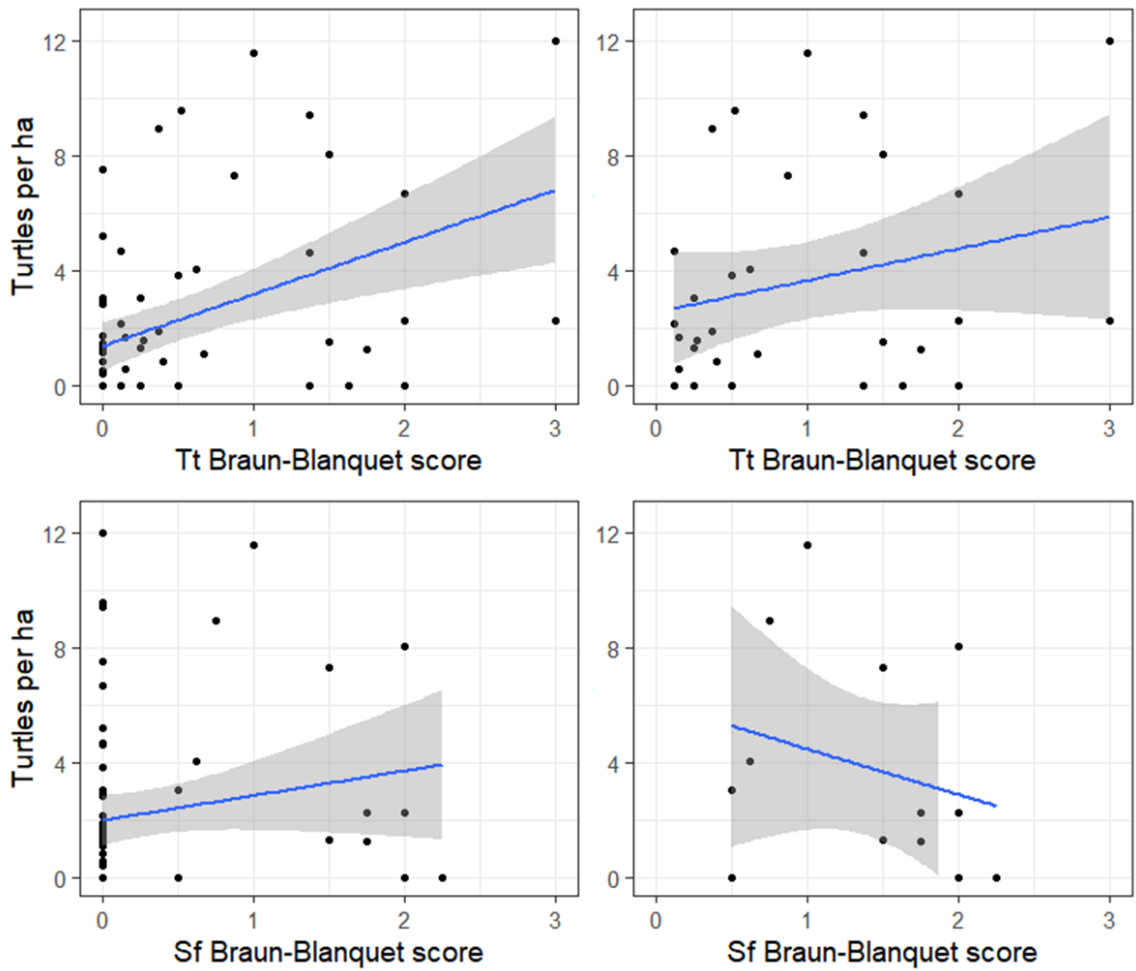
Figure 13. Relationships between turtle sighting densities (to account for effort) and Braun-Blanquet scores off Martinique of; Top: *T. testudinum* and Bottom: *S. filiforme* abundances and turtle sightings. The shaded area represents the 95% confidence interval. Left panels include sum of Braun-Blanquet scores equal to zero. Right panels exclude sum of Braun-Blanquet scores equal to zero.

Stepwise model selection of the generalized linear mixed effects model identified the best fit model to be:

$$Turtles \sim Tt * Sf + Sf * Hw + (1|season) + offset(log(Area))$$

where *Turtles* is the sightings count, *Tt, Sf,* and *Hw* represent the mean abundance of *T. testudinum*, *S. filiforme*, *H. wrightii*, respectively, *season* (sampling event) is set as the random effect and *log(Area)* is effort as the model offset. Predictor variables and interactions considered in the model selection are listed in Table 14, and models with interactions (*) also test each independent variable.

Table 14. Model selection table of turtle sightings in St. Martin with models ranked by AIC score from best fitting model to worst, where K is the number of parameters in the model, AICc is the information criterion for each model, δAICc is the difference between the AIC of respective model and the best fitting model, ModelLik is the relative likelihood of the model given the data, AICcWt are the Akaike weights and indicate the level of support for the model being the most parsimonious, LL is the log-likelihood, and Cum.Wt is the cumulative model weight (Mazerolle, 2017). * represents a test of the interaction and individual variables.

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
Tt * Sf + Sf * Hw	7	243.16	0.00	1.00	0.97	-112.71	0.97
Tt * Sf	5	250.84	7.68	0.02	0.02	-119.48	0.99
Sf * Hw	5	255.29	12.13	0.00	0.00	-121.71	1.00
Sf	3	255.90	12.74	0.00	0.00	-124.60	1.00
Tt	3	257.54	14.38	0.00	0.00	-125.42	1.00
Hw	3	258.39	15.23	0.00	0.00	-125.84	1.00
~	2	258.40	15.24	0.00	0.00	-127.03	1.00
Tt + Sf + Hw	5	258.81	15.65	0.00	0.00	-123.47	1.00
Depth	3	259.25	16.09	0.00	0.00	-126.27	1.00
Hw * Tt	5	259.62	16.46	0.00	0.00	-123.87	1.00
Tt + Sf + Hw + Depth	6	261.44	18.28	0.00	0.00	-123.37	1.00

Accounting for differences between sampling events by setting sampling event as the random effect, turtle sighting abundance is positively correlated with *T. testudinum* and *S. filiforme* abundance, but negatively correlated with *H. wrightii* abundance. The interactions between *S. filiforme* with *T. testudinum* and with *H. wrightii* are also significant (Table 15, Figure13). Although there are increases in turtle sightings with increasing abundance of both *T. testudinum* and *S. filiforme*, some of the highest turtle densities occurred where *S. filiforme* and *T. testudinum* were found in similar proportions (Figure 13).

Table 15. Results of generalized linear mixed effects best fit model for St. Martin; Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

Fixed effects:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-2.26	0.29	-7.93	<0.0001	***
Tt	0.95	0.22	4.24	<0.0001	***
Sf	0.76	0.22	3.44	0.0006	***
Hw	-1.23	0.46	-2.69	0.0071	**
Tt:Sf	-0.66	0.17	-3.95	0.0001	***
Sf:Hw	2.03	0.68	3.00	0.0027	**
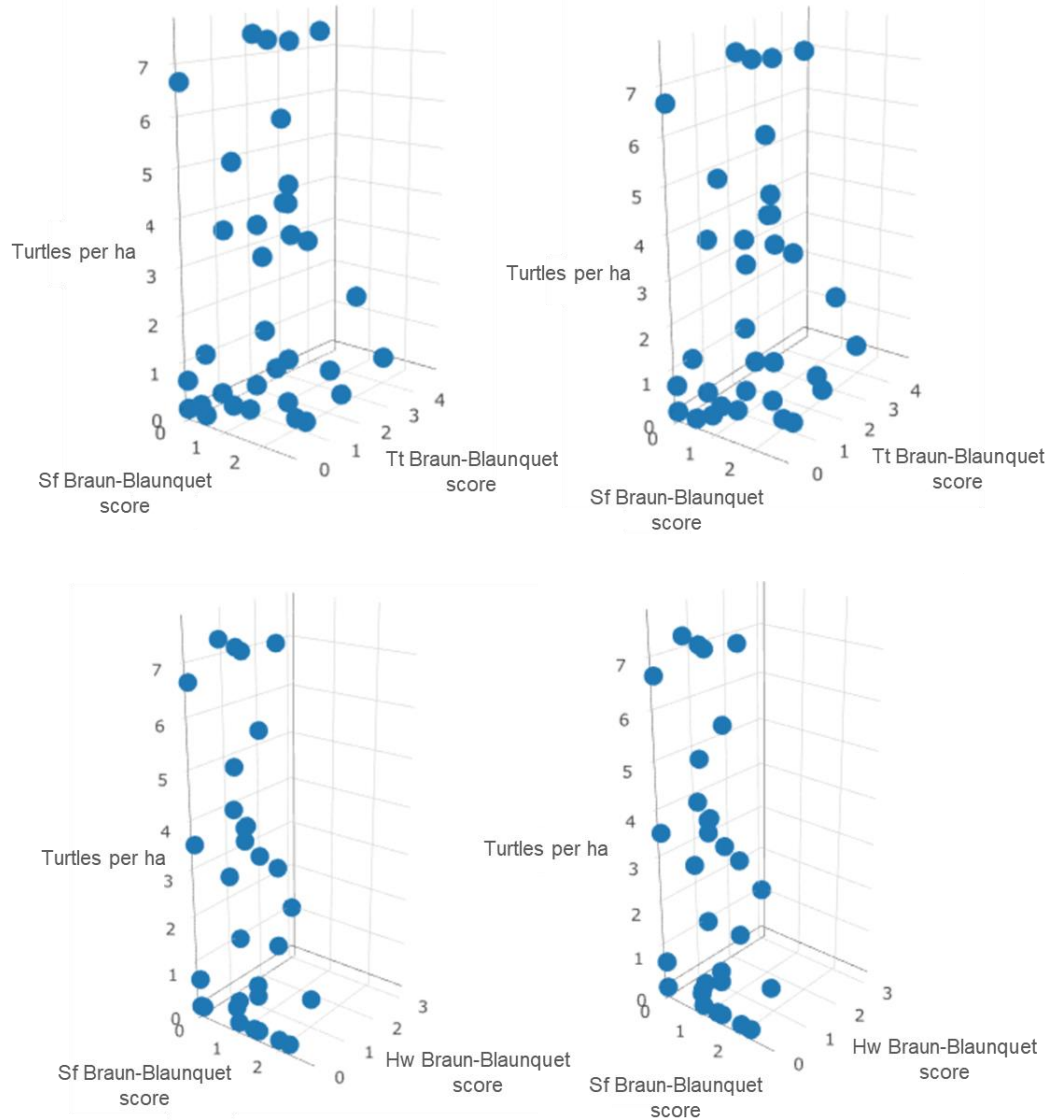
Figure 14. Relationships between turtle sighting densities (to account for effort) and Braun-Blanquet scores off St. Martin of; Top: the interaction of *S. filiforme* with *T. testudinum* and turtle sighting densities; Bottom: the interaction of *S. filiforme* with *H. wrightii* and turtle sighting densities. The shaded area represents the 95% confidence interval. Left panels include sum of Braun-Blanquet scores equal to zero. Right panels exclude sum of Braun-Blanquet scores equal to zero.
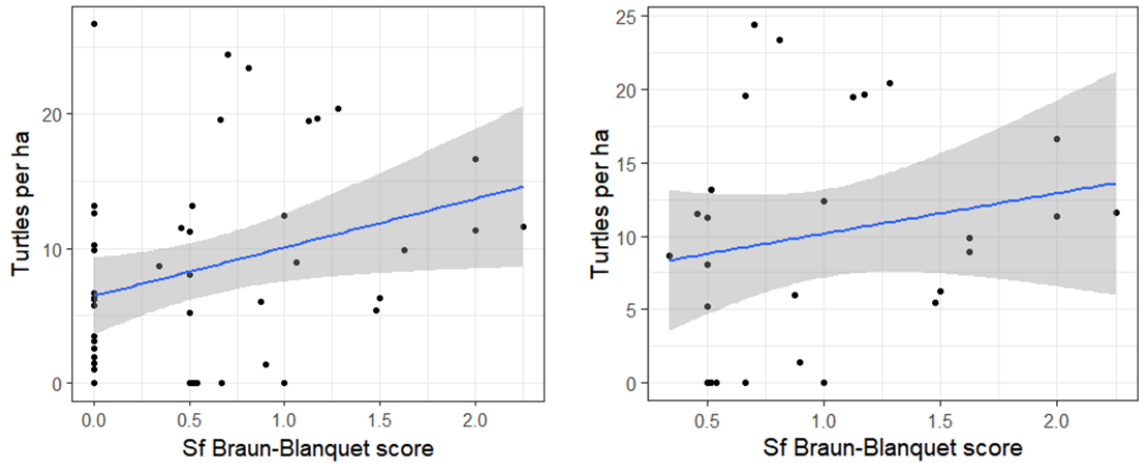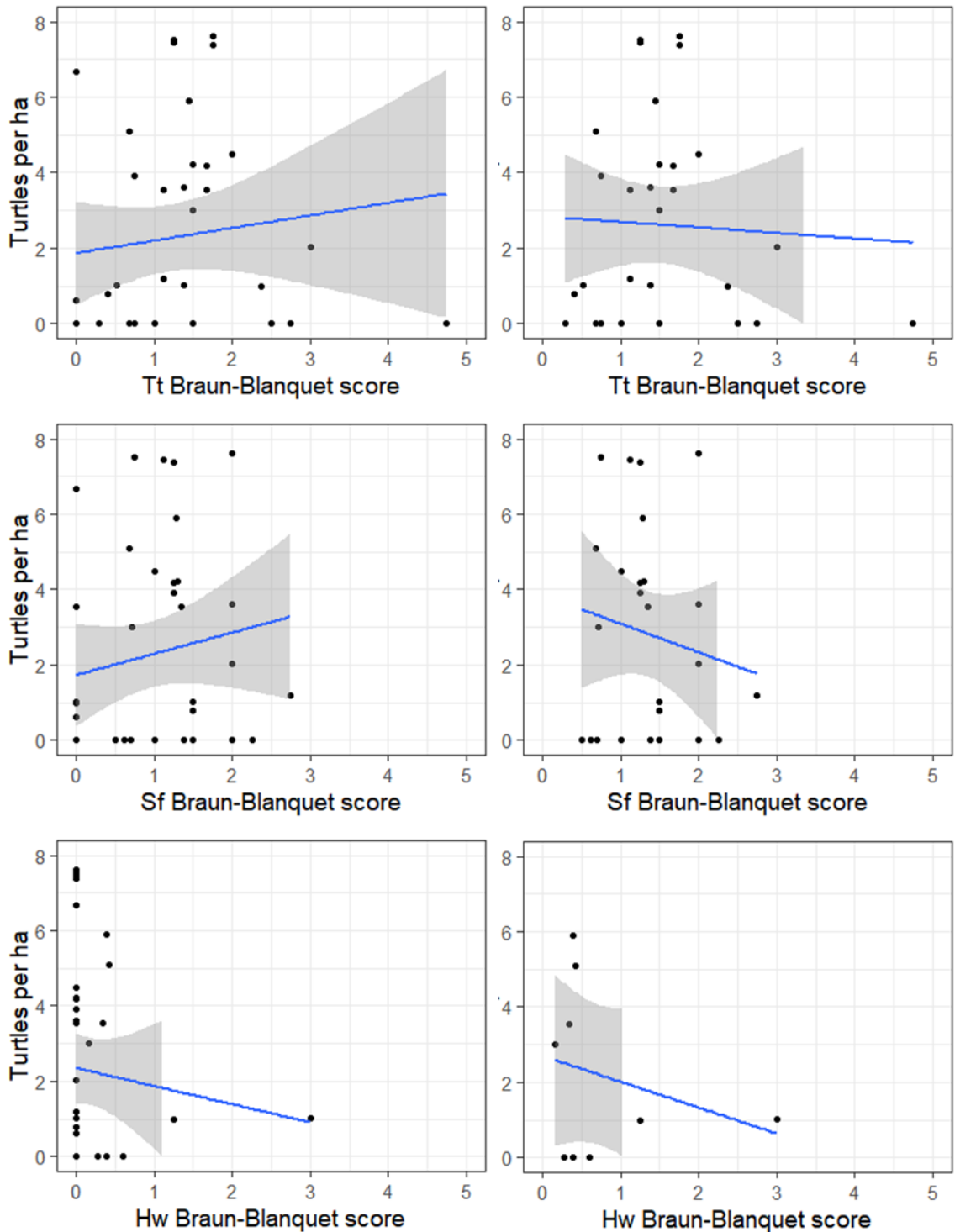
Figure 15. Relationships between turtle sighting densities (to account for effort) and Braun-Blanquet scores off St. Martin of; Top: *T. testudinum*, Middle: *S. filiforme*, and Bottom: *H. wrightii* Braun-Blanquet scores and turtle sighting densities. The shaded area represents the 95% confidence interval. Left panels include sum of Braun-Blanquet scores equal to zero. Right panels exclude sum of Braun-Blanquet scores equal to zero.

Resource selection

A total of 301 turtle sightings across all sites were included in the selectivity analysis. At the population level, green turtles across all sites had a strong significant preference for the native seagrasses *S. filiforme* and *T.testudinum* over the invasive seagrass *H. stipulacea* (*Khi2L* = 174, *df* = 12, *p* < 0.0001). Indeed, the mean selection ratios for *S. filiforme*, *T.testudinum*, and *H. stipulacea* were 1.39 ± 0.05 SE, 1.63 ± 0.11 SE, and 0.45 ± 0.04 SE, respectively (Figure 14). Turtles were observed in patches with an average of 1.8 ± 0.52 SD seagrass species at each sighting. However, green turtles showed a preference (visible foraging) for *S. filiforme* and *T.testudinum*, regardless of how many species they were foraging among. Turtles were occasionally observed foraging on the invasive *H. stipulacea* (see Chapter 5).
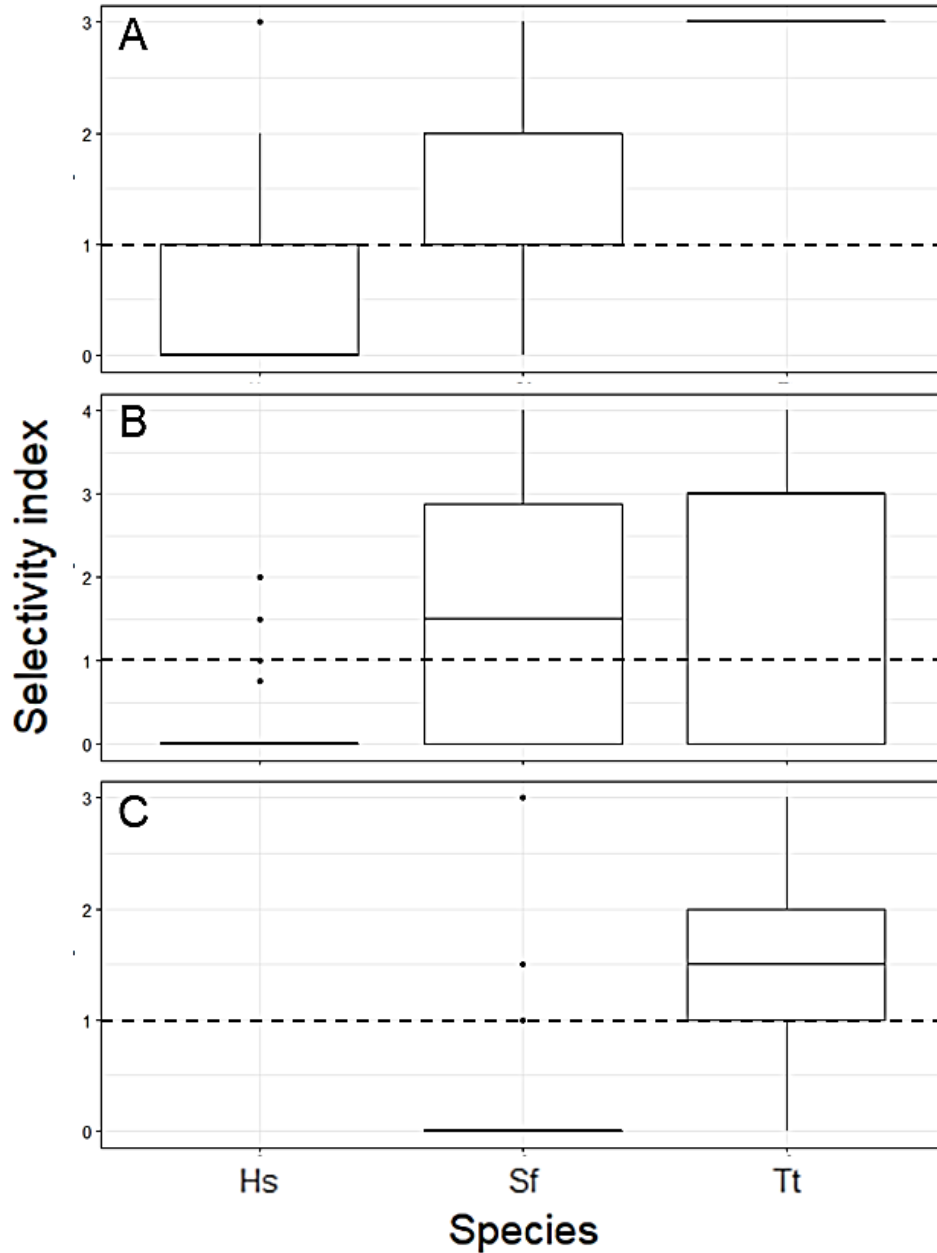
Figure 16. Selection ratios for *T. testudinum* (Tt), *S. filiforme* (Sf), and *H. stipulacea* (Hs) off A) Guadeloupe, B) Martinique, and C) St. Martin Each point represents the selection ratio at one turtle sighting; Values above 1.0 (dashed line) indicate positive selection, values below 1.0 indicate avoidance, and values near 1.0 indicate no apparent preference

Discussion

Understanding how large grazers select habitats and resources in the face of invasion fronts is important for determining both how the invasion is likely to affect individual foragers and their populations as well as how grazer populations might facilitate or attenuate the invasion. Here, I found that green turtles – large marine herbivores – across multiple sites, used areas where invasive species were found less often than expected, and when foraging in areas where invasives occurred, chose native species over the invasive species. Selective foraging occurred even when the invasive seagrass appeared to have similar nutrient content to native species. These observations, taken together, suggest that the non-native seagrass invasion of the Caribbean is likely to, at least in the short term, negatively affect energy or nutrient budgets of green turtles, and green turtles may be facilitating the invasion via their selective grazing.

While forage availability can affect the distribution of large bodied herbivores (Power, 1992; Massé and Côté, 2009; Sheppard *et al.,* 2010), some species of grazers are not limited by energy intake, and instead select foraging habitats and species on the basis the content of key nutrients (Murden and Risenhoover, 1993; Sheppard *et al.,* 2010; Christianen *et al.,* 2018). The elemental composition of seagrass leaves at each site provides clues to identify nutrients that may be particularly valuable to grazers. Low C:N and C:P ratios of seagrass leaves suggested that all FWI study sites were nutrient rich (Atkinson and Smith, 1983), and green turtles in other parts of the Caribbean will select for high quality forage with ample amounts of N, P, and soluble sugars (Bjorndal, 1997; Christianen *et al.,* 2018).

Each study site provided a unique combination of forage abundance and quality for green turtles. In Guadeloupe, native *S. filiforme* was the most abundant native seagrass, it was found at most survey plots and at the highest density within the plots. The invasive *H. stipulacea* was also encountered in most surveys and was more abundant than *S. filiforme* within plots. The nutrient content of the invasive seagrass *H. stipulacea* and the native seagrass *S. filiforme* had comparable C and N content and only differed in C content.

In Martinique, *H. stipulacea* was found at more sampling points than native species, had the highest abundance scores of any seagrass species, and contained nutrients at mid-range values compared to native species. Of the native species, *T. testudinum* was found most often in surveys and had higher Braun-Blanquet scores than the other native seagrasses (*S. filiforme* and *H. wrightii*). Patterns of nutrient composition among speicies were complex in this N-limited bay. The invasive *H. stipulacea* had significantly greater P content than the native seagrasses., and greater N content than the native seagrass *S. filiforme*. The native *T. testudinum*, however, had the highest N content. In St. Martin *T. testudinum* was found most often but was found in similar covers at sites as *S. filiforme*. Both *T. testudinum* and *S. filiforme* were found more often and in greater abundance than *H. wrightii*. At St. Martin, *H. stipulacea* was rare. *S. filiforme* had significantly lower N and C content than both *H. wrightii* and *T. testudinum* and lower P content than *T. testudinum*.

Within and across sites, green turtle distributions were correlated with the abundance of native seagrasses *S. filiforme* and *T. testudinum* and not correlated with the

abundance of the invasive seagrass *H. stipulacea*. One explanation for the pattern could be the relative quality of the available seagrasses. Results from Martinique and St. Martin were consistent with the hypothesis that turtles are driven by forage quality if turtles are selecting for N content. The abundances of turtles were most strongly associated with high abundances of the native *T. testudinum*, which had higher N content than the other seagrass species available. Turtles also showed positive selectivity for *T. testudinum* at the level of specific foraging locations. Green turtles in a study in Bonaire, Dutch Caribbean (Christianen *et al.,* 2018) also showed a preference for consuming native *T. testudinum* which had higher soluble sugars, N, and P content and a lower C:N ratio than the invasive *H. stipulacea*.

While their results would suggest that turtles avoid invasive species because it is lower forage quality, results from Guadeloupe suggest that nutrient content alone may not drive turtle foraging decisions. Indeed, off Guadeloupe, nutrient contents of native and invasive seagrasses were similar. If nutrient content alone were driving foraging decisions, turtles should have selected habitats based on seagrass abundance regardless of species and foraged indiscriminately. Instead, turtles selected habitats depending on the abundance of the native seagrass *S. filiforme*. Furthermore, turtles showed a preference for this species even when foraging in patches with high abundances of invasive *H. stipulacea* (Chapter IV).

Another possible explanation for why turtles may be selecting habitats relative to the availability of native seagrasses and not the invasive *H. stipulacea* is that turtles may not yet recognize it as a potential food source. Sea turtles from the Cheloniidae family are

believed to be use a combination of visual and chemical cues in forage selection, and green turtles have a greater ability to discriminate colors than pelagic fishes (Southwood *et al.,* 2008). In the FWI, green turtles often appear to visually assess forage options by tilting their head to the side to get a close view of the benthos prior to beginning to forage (*pers. obs.*). However, it is unlikely that green turtles are not recognizing the invasive as a food source because, although most individuals avoided *H. stipulacea*, some individuals were observed foraging on the invasive in both Guadeloupe and Martinique (Figure 15) where it was more abundant than any native seagrass. Green turtles in Hawaii, have demonstrated diet plasticity, and incorporated invasive macrophytes as major components of their diets (Russell and Balazs, 2009, 2015). The studies in Hawaii lacked data on resource availability, but the authors suggested that the proportion of the diet of the green turtles made up of invasive species increased with time since invasion and with the relative abundance invasive species. The highly invasive seagrass *H. stipulacea* has been present in the Caribbean since 2002 (Willette and Ambrose, 2009), however, the results from this study and cafeteria experiments conducted 3-6 years after the first record of *H. stipulacea* in Bonaire (Debrot *et al.,* 2012) suggest that green turtles selectively forage on native seagrasses even when the invasive is available equally or in greater abundance (Christianen *et al.,* 2018). In Guadeloupe, the *H. stipulacea* invasion began six and seven years prior to this study (Willette *et al.,* 2014), and green turtles may not yet have had to include greater proportions of the species in their diet in the manner Hawaiian turtles have.

Foraging habitat selection by large-bodied herbivores is likely context and species dependent (Redjadj *et al.,* 2014). Ungulates in terrestrial systems make habitat use

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decisions on the basis of multiple factors. Elk (*Cervus elaphus*) in northeastern Nevada, USA selected habitat based on forage availability and distance to water. In a study of a high-density white-tailed deer population, fine-scale habitat selection was mainly determined by forage abundance (Massé and Côté, 2009), but habitat selection was not significantly dependent on the biomass of preferred plant species. The high-arctic Avalbard reindeer (*Rangifer tarandus platyrhinchus*) provide perhaps the best parallel between green turtles in the FWI and a large-bodied herbivore in terrestrial habitats. They are non-gregarious, non-territorial, free from predation risk, and have no inter-specific competition (Hansen *et al.,* 2009). Reindeer in habitats with low forage availability and productivity selected home ranges and resource patches based on productivity, however, reindeer in habitats with relatively high forage availability and productivity selected habitats based on conditions supportive of high forage quality over forage biomass. White-tailed deer (*Odocoileus virginianus*) and Angora goats (*Capri hircus*) began feeding selectively for high-quality natural forage options when they were also provided with a high-quality diet supplement (Murden and Risenhoover, 1993). Marine herbivores also use multiple factors in their decision making over habitat utilization. Dugong (*Dugong dugong*) selected seagrass patches for high nitrogen concentrations, however, when habitat space was limited by low tides, their habitat use shifted to patches with high seagrass biomass (Sheppard *et al.,* 2010). Therefore, it is likely that green turtles base their habitat selection on multiple factors, and additional studies of forage biomass and productivity are warranted.

Selective grazing of green turtles may be facilitating the *H. stipulacea* invasion in the Caribbean and may be leading to a loss of macrophyte diversity as the invasive

spreads (Chapter V; Christianen *et al.,* 2018). At one site, Guadeloupe, both mean

seagrass species richness and mean *S. filiforme* decreased from Spring 2016 to Spring

2017. These results need to be interpreted with caution because sample sizes and point

locations differed across sampling events, but if this is in fact the trend, it is consistent

with surveys in other locations in the Caribbean (*e.g.*, Willette *et al.,* 2012; Scheibling *et*

al., 2018). Previous mapping of the benthos in Martinique between 2006 and 2010

surveys revealed new settlement of *H. stipulacea* in 58.2% of the surveyed area, whereas

new settlements of *S. filiforme* were found in only 7.46% of sites (Legrand *et al.,* 2012).

There are important long-term implications for the ecosystem if *H. stipulacea* is

outcompeting native species. Organisms that depend on native seagrasses for food or for

their physical structure, and who cannot adapt to the shift in the seagrass community will

find their available habitat decreasing. However, the spread of *H. stipulacea* may

positively affect fish communities by supporting more faunal species (richness) and large

fish (length in cm) (Willette and Ambrose 2012; Rogers, Willette, and Miller 2014).

Amphipod and crustacean abundances were also found to be significantly greater in

meadows of the invasive *H. stipulacea* than in the native *S. filiforme,* which may be

contributing factors to increases in fish metrics. So far, however, the invasion is most

likely detrimental or, at best, inconsequential for green turtles.

Bjorndal and Jackson (2003) used total area covered and productivity ranges of *T.*

testudinum in the Caribbean a proxy for food available to turtles to use in population

reconstructions, however, Heithaus *et al.* (2008) argued that herbivore populations are

also limited by direct predation and predation risk. Herbivores are faced with a food-risk

tradeoff may avoid especially risky areas if the less risky areas can support the individual

and population energy requirements. In a relatively pristine marine ecosystem of Shark Bay, Australia, dugongs change their habitat use and foraging behavior depending on seasonal patterns in risk from tiger shark encounters (Wirsing, Heithaus and Dill, 2007), and healthy green turtles preferentially foraged in seagrass meadow edge habitats where they are less likely to encounter predators (Heithaus *et al.,* 2007). Predators can constrain foraging site selection, but other factors could constrain their habitat such as human activity (Frid and Dill, 2002) and invasive forage species, and potentially further restrict carrying capacity (K) for the Caribbean. If green turtles continue to avoid *H. stipulacea*, their foraging habitat range will be reduced by invasion and potentially equate to less energy availability, lower intake rates, slower growth, or lower K. Moose (*Alces alces*) habitat selection in Norway at the landscape scale selected for high availability of forage, and within those habitats selected for higher quality forage most of the year, but when resources were depleted in the winter season moose site fidelity decreased and they selected lower quality forage (van Beest *et al.,* 2010). Should green turtles, like the moose, adapt to the depletion of their preferred resource (native seagrasses), they may exhibit decreased foraging site fidelity, costing them additional energy travelling among sites for forage.

In the FWI, I found that turtles may not avoid patches with invasive seagrass if native seagrasses are present, however, within the patch turtles are selecting for native seagrasses and avoiding the invasive and macroalgae (this chapter, Chapter IV). The results support the hypothesis that, like other large bodied herbivores, green turtles select foraging habitats on the basis of preferred forage abundance and select for high quality forage (where available) within patches. My analysis of green turtle foraging habitat and

resource selection in the FWI elucidates the importance of multi-level, multi-scale ecosystem management. The observation of grazers continuing to use habitat invaded by a non-native plant species is not sufficient to estimate its affect (or lack thereof) on the grazer.

Invasive plants are particularly successful when they benefit from a lack of enemies (Enemy Release Hypothesis; ERH; Cogni 2010; Keane and Crawley 2002), and are potentially more successful when the lack of enemies is coupled with a high-resource (nutrients) environment (Resource-Enemy Release Hypothesis; R-ERH; Blumenthal, 2005, 2006). The comparison of seagrass nutrient content to established seagrass Redfield ratios revealed that the sites in Guadeloupe, Martinique, and St. Martin are nutrient rich habitats, and a lack of interest by foraging green turtles may, at least in part, explain the successful invasion of *H. stipulacea* in the region.

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CHAPTER V

GREEN TURTLE FORAGING PREFERENCES FOR NATIVE SEAGRASSES
COULD FACILITATE THE *HALOPHILA STIPULACEA* INVASION OF THE
CARIBBEAN SEA: A TEST OF THE ENEMY RELEASE HYPOTHESIS

Abstract

Invasions may succeed because they are not controlled by natural enemies in a novel environment (Enemy Release Hypothesis; ERH). If local consumers preferentially feed on native species, they can facilitate invasions, while preferential or even non-selective feeding on an invader could minimize its impact. *Halophila stipulacea*, a seagrass native to the western Indian Ocean, has spread to the Mediterranean and Caribbean. Yet, little is known about the ecological consequences of the invasion or how local species might influence its persistence and spread. As locally abundant, large-bodied grazers, green turtles (*Chelonia mydas*) could either facilitate or attenuate the *H. stipulacea* invasion depending on their foraging patterns in the presence of native and invasive seagrasses. We tested *a priori* predictions about green turtle foraging behavior in the presence of *H. stipulacea* and native seagrasses off the west coast of Guadeloupe to investigate the ERH. Using turtle focal follows (n=70), we assessed individual and population level foraging preferences. Turtles foraged across a wide range of microhabitats including monospecific meadows and across a range of compositions in mixed-species seagrass beds. Green turtles showed a clear preference for native seagrass species, particularly *Syringodium filiforme*, over the invasive seagrass. Both *H. stipulacea* and macroalgae were generally avoided. However, *ca.* 12% of individuals foraged at rates above those predicted by availability on *H. stipulacea,* suggesting that turtle foraging preferences vary at the individual level. Our results provide the first support for the resource-enemy release hypothesis in a marine system and that green turtle foraging likely facilitates the *H. stipulacea* invasion at this stage of its spread.

Introduction

Across a wide array of ecosystem types, grazers of multiple body sizes can structure primary producer communities in ways that have profound consequences for other organisms and ecosystem dynamics (Jones, Lawton, & Shachak, 1994). In terrestrial ecosystems, large grazers can indirectly affect ecosystems by changing biomass through consumption or trampling, thus maintaining habitat heterogeneity that other plant and animal species depend on (see review by Dirzo *et al.,* 2015). Grazers can also affect invasion dynamics within ecosystems, but the nature of these effects can vary widely. Fundamental to the overall effect an invasive species has on an ecosystem is its ability to outcompete native species and spread widely. The Enemy Release Hypothesis posits that an invasive species' ability to proliferate in a new habitat is facilitated by a lack of enemies (Cogni, 2010; Keane & Crawley, 2002). In the case of invasive plants, if grazers preferentially feed on native species rather than invasive species, they can facilitate invasions by opening up space for the non-native plant to invade. The facilitation effect might be particularly pronounced if native species abundance and biomass is strongly shaped by herbivory (Gruner *et al.,* 2008). If, however, grazers forage indiscriminately, or even prefer to forage on invaders, an invasion may be slowed, minimized, or even halted.

In some cases, grazers can help prevent or attenuate invasions. For example, domesticated terrestrial grazers, such as goats, are being used as a means of invasive plant species control and removal (Silliman *et al.,* 2014). Native grazers also can mitigate plant invasions by limiting their spread or their performance (Parker, Burkepile, & Hay,

2006). In some grasslands, rodent herbivory on invasive species lessens the effects of invasions on community structure and productivity (Maron *et al.,* 2014). In contrast, Canada geese (*Branta canadensis moffitti*) preferentially feed on native cordgrass (*Spartina foliosa*) over an invasive *Spartina* hybrid grass (Grosholz, 2010). Grazing by the Canada geese reduced above ground biomass and stem hight of the native cordgrass but left the invasive hybrid untouched thereby facilitating the invasion of the hybrid. The variability of grazer impacts on habitats disturbed by invasive species suggests context-dependence upon both the characteristics of the invasive plant species and the foraging tactics of native grazers.

In marine ecosystems, herbivorous fish and invertebrates can alter community dynamics. In coral reef communities, this occurs through grazing on macroalgae that compete with hard corals for space (see review by McCook, Jompa, & Diaz-Pulido, 2001). Sea urchins can cause the collapse of kelp forest ecosystems when their natural predators, sea otters (*Enhydra lutris*), are removed (Estes & Palmisano, 1974). Similarly, large marine grazers (dugongs, *Dugong dugon*, and green turtles, *Chelonia mydas*) modify the structure (*e.g.,* biomass, species composition) and function (*e.g.,* nutrient cycling) of seagrass ecosystems (Burkholder, Heithaus, Fourqurean, Wirsing, & Dill, 2013; De Iongh, Kiswara, Kustiawan, & Loth, 2007; Preen, 1995; Thayer, Engel, & A. Bjorndal, 1982).

As adults, green turtles are mostly herbivorous but exhibit considerable variation within and among populations throughout their range (for a review see Jones & Seminoff, 2013). Some green turtle populations specialize on seagrasses and select for seagrass

blades that are high in protein (good nutritional value) and low in lignin content (easy digestibility) (Bjorndal, 1980; Fuentes, Lawler, & Gyuris, 2006). Other populations specialize on macroalgae (López-Mendilaharsu, Gardner, Seminoff, & Riosmena-Rodriguez, 2005; Santos *et al.,* 2011), and some forage on a mix that may even include invertebrates (Arthur & O'Neil, 2007; Burkholder, Heithaus, Thomson, & Fourqurean, 2011; Hatase *et al.,* 2002; Seminoff, Resendiz, & Nichols, 2002). Despite the strong support for specialization at the population level, most diet studies also include evidence of persistent variability among individuals (individual specialization *e.g.,* Burkholder *et al.,* 2011).

Of particular concern is how changes in large grazer abundances – both negative through overharvesting and positive through conservation coupled with the loss of predators on large turtles – might affect seagrass ecosystem structure and function (*e.g.,* Heithaus *et al.,* 2014; Heithaus *et al.,* 2008; Jackson, 2001). Also, of growing concern is the little-known potential role of green turtles and other large marine grazers in facilitating or attenuating marine plant invasions.

Halophila stipulacea, a seagrass native to the western Indian Ocean, the Persian Gulf and the Red Sea, has successfully spread to the Mediterranean and southern Caribbean. Possibly transported by pleasure yachts, it is one of only two seagrass species known to have transoceanic establishment (Ruiz & Ballantine, 2004). The invasive *H. stipulacea* is fast-growing, produces a large numbers of seeds, can spread quickly vegetatively, and can tolerate a wide range of salinities, temperatures, light levels, and disturbance regimes (Short *et al.,* 2010). These factors have contributed to its rapid

expansion in the Caribbean since its initial sighting in Grenada in 2002 (Ruiz &
Ballantine, 2004). As of 2017, it had been documented throughout the Lesser Antilles and
as far north as Puerto Rico (Ruiz, Ballantine, & Sabater, 2017). In its native range, *H.
stipulacea* is readily consumed by dugongs (Short *et al.,* 2010), but *H. stipulacea* could
be released from this 'enemy' pressure in the Caribbean if green turtles do not recognize
it as a potential food source or preferentially consume native seagrasses.

Given the observed plasticity in diets, green turtle feeding behavior might be
expected to change in the presence of novel species. Hawaiian green turtles, for example,
forage on the non-native *Halophila dicipiens* (Russell *et al.* 2003) and seven non-native
species of macroalgae that now make up the majority (64%) of their diets (Russell &
Balazs, 2015). Invasive species that quickly spread in Hawaii were incorporated into
turtle diets over *ca.* a decade, and those that took longer to become established entered
diets later (20-30 years). The incorporation of invasives into the diets of Hawaiian green
turtles over time suggests that green turtle dietary preferences are determined, at least in
part, by the abundances of forage species.

Because *H. stipulacea* is highly invasive and has been present in high abundances
in parts of the Caribbean for over a decade, it might be expected that Caribbean green
turtles would have incorporated *H. stipulacea* into their diets. However, 3-6 years after
the first documentation of *H. stipulacea* in Bonaire (Dutch Caribbean) (Debrot *et al.,*
2012), cafeteria experiments revealed that green turtles selectively feed on the native
seagrass *Thalassia testudinum* when presented with samples of each locally available
seagrass (native: *T. testudinum* and *Syringodium filiforme*, invasive: *H. stipulacea*) in

equal proportions (Christianen *et al.,* 2018). Despite the higher nutritional value observed in *T. testudinum*, two out of the 20 grazing green turtles did forage on the invasive *H. stipulacea*, and three foraged on *S. filiforme*. Additionally, satellite imaging revealed that green turtles expanded their grazing patches to include shallow, previously ungrazed *T. testudinum* after the local establishment of *H. stipulacea*. These results suggest that green turtles show individual variability with an overall preference for one nutrient-rich native seagrass. However, it is still unclear whether turtles preferentially forage on native or invasive seagrasses of similar nutritional value or forage indiscriminately across a range of forage species availability and composition.

Here, we used natural spatial variation in the relative abundance of native and invasive seagrasses within a nearshore green turtle foraging habitat to test *a priori* predictions about green turtle foraging preferences (Figure 1), and whether *H. stipulacea* might benefit from enemy release. Specifically, we used focal follows of individual green turtles to test whether 1) they prefer native seagrasses regardless of seagrass relative abundances (and, therefore, likely facilitate the invasion); 2) they prefer the invasive seagrass (and might attenuate the invasion); 3) they prefer most abundant seagrass (and may facilitate coexistence); or 4) show no obvious foraging preferences (which would favor the most herbivory-resistant species or coexistence of both species) (Figure 1).
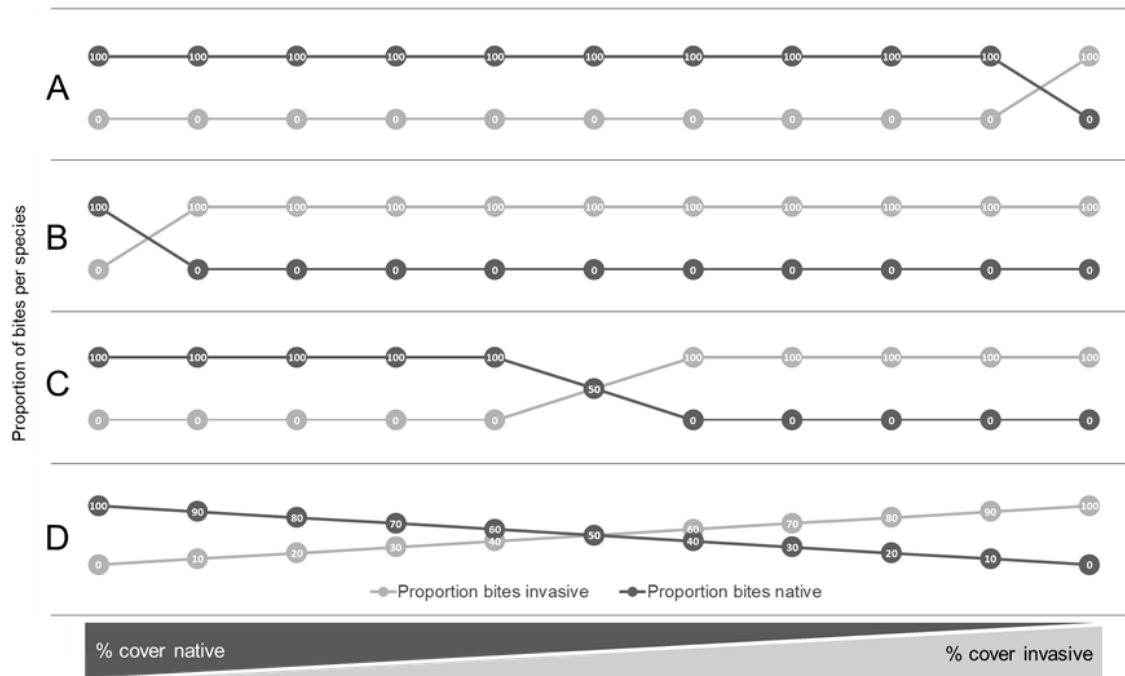
Figure 1. Conceptual diagram of predicted green turtle foraging behavior on two species if they A) prefer native seagrasses (dark circles), B) prefer invasive seagrass (gray circles), C) preferential to forage on the most abundant species, and D) display no foraging preference. Note, in (A) we assume that turtles would forage on the invasive species if it were the only forage available.

Methods

Study site

We conducted our study in Malendure Bay, along the western coast of Basse-terre, Guadeloupe, French West Indies (Figure 2). The mouth and widest width of the Bay spans *ca.* 750 m and a beach lines *ca.* 500 m of the inner coast. Seagrass is found between depths of 2-10 m and covers *ca.* 12 ha of the study area. Native seagrasses found in Malendure Bay include *S. filiforme*, *T. testudinum*, and *Halodule wrightii*. The

invasive seagrass *H. stipulacea* was first observed in Guadeloupe in 2010 (Kerninon, 2012).

Green turtles from multiple life stages – including juvenile, subadult and adult turtles, and nesting females – are found off Guadeloupe (Carr *et al.,* 1982; Meylan, 1983). The beach at Malendure Bay is not a regular nesting site (Rinaldi *et al.,* 2011), but an important foraging ground for juvenile and subadult green turtles. Malendure Bay is a popular tourist destination, in part because green turtles are abundant and highly acclimated to the presence of boats, snorkelers, and divers.
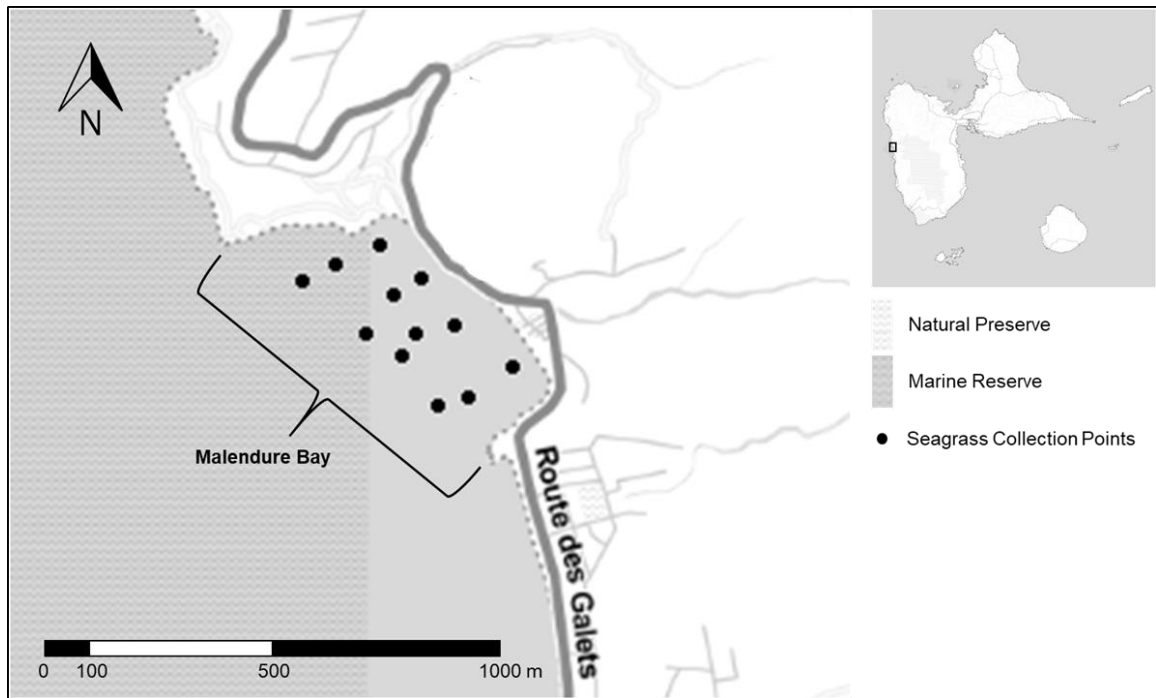
Figure 2. Malendure Bay lies on the west coast of Guadeloupe (inset). Seagrass nutrient content was measured at 12 locations within the study area (closed circles).

Focal follows

Focal follows were conducted on 10 days in 2015 (March: n = 5 days; April: n = 5 days) and 12 days in 2016 (June: n =3 days; July: n = 7 days; August: n = 2 days). During a follow, trained observers used GoPro® Hero 1+ video cameras attached to a 2m extendable pole at a 90° angle. Observers entered the water at predetermined, random starting points along the shoreline and swam for a predetermined, random, amount of time before actively searching for a turtle. Upon spotting a turtle, the video recording was initiated, the pole was extended to ~ 2 m, and the camera was oriented to record the turtle's head. If the turtle reacted to the presence of the observer or the camera, the observer moved 1-2 m further away from the turtle but continued recording. If the turtle resumed normal behavior (*e.g.,* foraging, resting) within a few minutes, the observer would re-approach and continue the recording; if not, the follow was terminated and another turtle was located. During follows, the observer attempted to record the species turtles were consuming and attempted to minimize their movements and noises. Observers remained at the surface throughout follows to minimize disturbance. We followed each turtle for 35 minutes or until human disturbance caused the turtle to flee or the turtle moved into areas that were unsafe to snorkel (*e.g.,* channels with high boat traffic). At the end of the follow, the observer marked a GPS point and began searching for another individual to follow.

Video data extraction

We excluded follows that contained less than 90 sec of foraging behavior and segments of follows where it was not possible to determine macrophyte species composition. Individuals were identified using a combination of carapace scute patterns and profile scale patterns. Turtle behaviors were classified as: 1) 'foraging' if the turtle was biting, chewing and swallowing; 2) 'surfacing' when swimming to and from the surface and time spent at the surface; 3) 'traveling' if swimming horizontally or if vertical movements were not associated with surfacing; and 4) 'resting' when stationary and not foraging. For each foraging bout (*i.e.,* time of continuous feeding, between surfacing or traveling events), we estimated the abundance of each macrophyte species present by averaging the percentage cover at observations taken every 60 seconds for both the full field of view and for the cover immediately available to the individual (Figure 3). We quantified foraging behavior using the number of bites taken within each foraging bout and classified the species consumed as macroalgae, *T. testudinum*, *H. stipulacea*, *S. filiforme*, mixed (*i.e.,* bite containing two or more macrophyte species), unknown (*i.e.,* targeted food item could not be identified), or other (*e.g.,* shells, garbage, gelatinous plankton). Although *H. wrightii* is present in Malendure Bay, it was not observed during our focal follows and is not included in the analysis. Videos were viewed in their entirety by one observer and subsections of the videos were viewed by an additional observer to validate macrophyte identification and abundance estimates.

Figure 3. Screen grab from a video of a green turtle during a focal follow. The outer box delineates the entire viewing area used for estimates of percent cover (*i.e.,* the entire field of view). The white dotted line, defined by a box extending from between the foreflippers to several cm in front of the turtle's head, delineates the area immediately available to the turtle for foraging and was used for the estimates of percent cover for each seagrass species that were used for analysis.

Nutrient content analysis

In 2016, we collected all macrophyte species present at each of 12 points throughout the Bay (Figure 2). Macrophyte samples were frozen immediately upon return to shore for storage until further processing. Samples were cleaned of epiphytes and dried in a food-grade dehydrator for a minimum of 24 hours within 48 hours of collection. After drying, samples were crushed using a mortar and pestle and stored in airtight vials for transport back to the laboratory. Total C and N were measured using a CE Flash 1112 elemental analyzer using standard procedures, and total P was analyzed colorimetrically

following modified methods from Solórzano and Sharp (1980) on a Shimadzu UV-2101PC spectrophotometer.

Data analysis

We compared foraging preferences using bite rates on each species both among individual turtles and across varying macrophyte community compositions. The mean percent cover of each macrophyte species present near the turtle and the total number of bites on each macrophyte taxa were calculated per foraging bout.

We used the R package (R Core Team, 2016) adehabitatHS (Calenge, 2006) design III selectivity analysis to test the effects of species composition (resource availability) on foraging (resource use). Because of the low occurrence of bites of mixed species, bites of unknown species, and feeding on marine debris and animal matter (*i.e.,* ctenophores, shells), these were not included in analyses. The native seagrass *T. testudinum* was also excluded from the selectivity analyses because it was only encountered once by each of two turtles. Only one of these turtles foraged on *T. testudinum*. Mean percent cover within each follow (defined by small box, Figure 3) was used as the resource availability input, and the mean number of bites $\ast$ min^{-1} for each foraging bout within each follow was used as the resource use input.

Assuming uniform use of habitats as the null hypothesis, resource use was tested for the population and for individuals using Chi-square goodness-of-fit tests. We calculated Manly's selection ratios (*Wi*) with Bonferroni confidence intervals with

resources defined by the categories *H. stipulacea* (Hs), *S. filiforme* (Sf), and Macroalgae (Calenge, 2015). Ratios (resource use to resource availability) >1 indicate selection and <1 indicate avoidance. Ratios near 1 or confidence intervals for the population overlapping 1 suggest no selectivity.

To test our four mutually exclusive hypotheses (Figure 1), we quantified the effects of seagrass community composition to our proxy for preference, proportion of bites taken of each species (per bout and cumulative). Data on relative abundance of each macrophyte (%) were tested for normality with Shapiro Wilk's tests. The inability to achieve a normal distribution after multiple transformation attempts and high dispersion of our data lead us to use generalized linear regression (quasipoisson). Akaike's Information Criterion (AIC) scores were used to determine best model fit.

We assed variation in %N, %C, and %P of dry weight and the C:N, C:P, and N:P ratios among macrophytes used in the selectivity analyses (*S. filiforme, H. stipulacea,* and macroalgae) with an ANOVA. All data were tested for normality using Shapiro-Wilk's tests. The non-normal distribution in %C and C:P of macroalgae and in N:P of *H. stipulacea* were rectified using a $\log_{10}$ transformation on all %C, C:P, and N:P data. Back transformations were performed for display of results. We used Tukey's HSD corrections, with alpha value set at 0.05, for all pairwise comparisons (Appendix I).

Results

In 2015, *H. stipulacea* was found at 22 of 23 (96%) haphazardly selected survey points distributed throughout Malendure Bay, and by 2016 it was found at 60 of 64 (94%) survey points from two sampling events. The %N and %P dry weight of *S. filiforme* and *H. stipulacea* were significantly greater than those of macroalgae (N: $F_{2,27} = 29.8$; $P < 0.0001$; P: $F_{2,27} = 83.3$; $P < 0.0001$), and all species varied significantly from one another in %C dry weight ($F_{2,27} = 101.0$; $P < 0.0001$). There were no significant differences among species for the ratio of C:N ($F_{2,27} = 1.71$; $P = 0.20$), but ratios of C:P and N:P were significantly higher in macroalgae than in the two seagrasses (C:P: $F_{2,27} = 49.7$; $P = < 0.0001$; N:P: $F_{2,27} = 37.3$; $P = < 0.0001$) (Figure 4). Both seagrass species were rich in nutrients relative to carbon, with C:P ratios <500 and C:N ratios <20, indicating nutrient-rich conditions (Atkinson & Smith, 1983; Johnson, Heck, & Fourqurean, 2006). Epiphyte loads were low on all samples collected, and so were unlikely to affect forage selection.
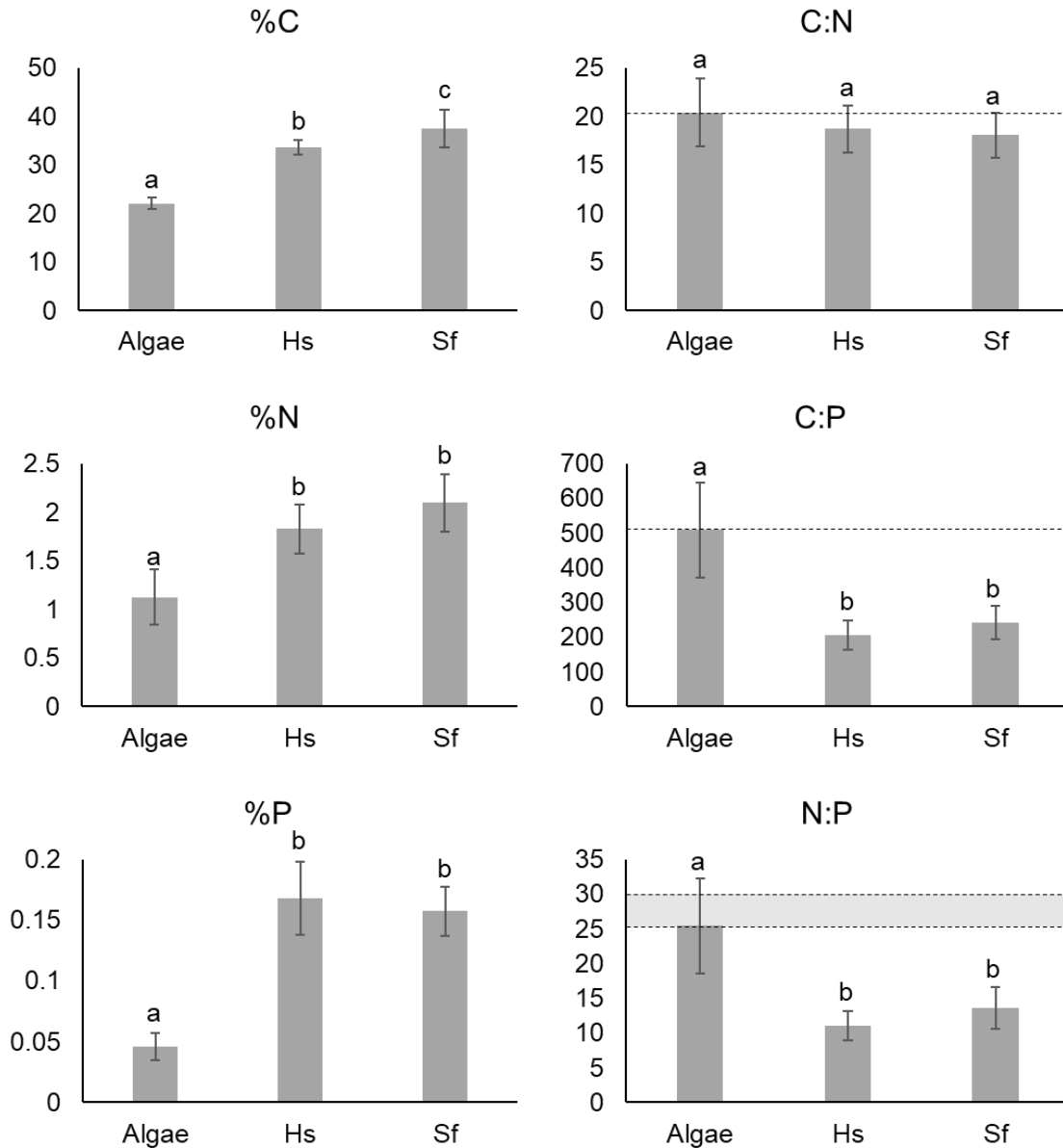
Figure 4. Left: Mean nutrient compositions (±SD) for macroalgae (Algae, *N=9*), *H. stipulacea* (Hs, *N=12*), and *S. filiforme* (Sf, *N=9*). Bars with different letters were significantly different from one another based on multiple post-hoc comparisons using the Tukey HSD test with alpha = 0.05; Right: Elemental ratios of macrophyte tissue, dotted lines indicate seagrass Redfield ratios

Throughout our study we only observed foraging juvenile and subadult green turtles. A total of 70 follows resulted in *ca.* 12.5 hours of video footage, including 7.3

hours of foraging activity from 125 total bouts. We identified 35 individuals from 45

focal follow videos (mean video length = 16 minutes) that we included in the analyses.

Four individuals were observed during two separate follows each, and two individuals

were observed during four separate follows each (Figure 5). To avoid pseudoreplication,

we pooled the multiple follows for these six turtles for population-level analyses. We

compared multiple follows within individuals to assess selectivity over time. The total

number of foraging bouts across all follows of individuals ranged from one to six.

Macrophyte abundance estimates for the full field of view differed significantly

from the cover immediately available to the individual (Wilcoxon Paired Signed-Rank

Test, *H. stipulacea*: $V = 36794$, $P < 0.0001$; *S. filiforme*: $V = 45674$, $P = 0.024$;

macroalgae: $V = 36748$, $P < 0.0001$). The mean relative abundance of the invasive *H.*

stipulacea was greater in the full field of view (43.76% ±1.03 SE) than in the area

immediately available to the turtle (36.55% ±1.24 SE), while the mean relative

abundance of the native *S. filiforme* was lower in the full field of view (15.79% ±0.66

SE) than in the area immediately available to the turtle (17.41% ±0.84 SE), and the mean

relative abundance of macroalgae was greater in the full field of view (13.53% ±0.46 SE)

than in the area immediately available to the turtle (11.21% ±0.70 SE). Because the

camera was focused on the turtle's head and the area in the field of view varied

depending on the water depth and our distance from the turtle, we chose to use the

relative abundance of macrophytes immediately available to the individual for the

selectivity analysis.
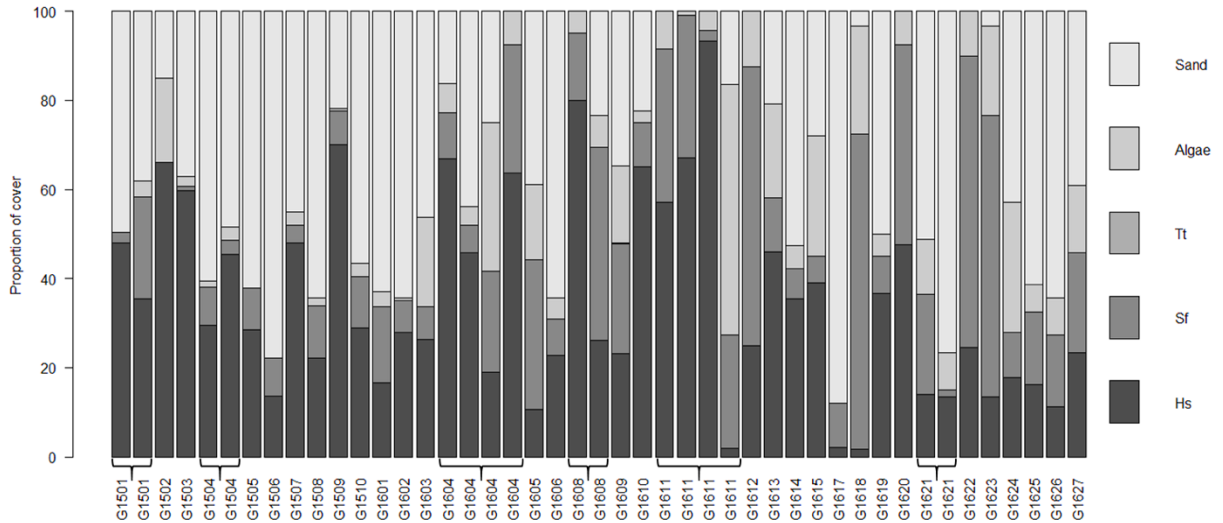
Figure 5. Mean macrophyte composition immediately available to each individual turtle during focal follows; area not covered by macrophytes (Sand), macroalgae (Algae), *T. testudinum* (Tt), *S. filiforme* (Sf), *H. stipulacea* (Hs); brackets indicate multiple follows of individuals

At the population level, green turtles in Malendure Bay had a strong and significant preference for the native seagrass (*S. filiforme*) over the invasive seagrass and macroalgae ($Khi2L$ = 708.45, df = 32, p = 0.000; Figure 6). Indeed, the mean selection ratios for *S. filiforme*, *H. stipulacea*, and macroalgae were 3.83 ± 0.35 SE, 0.23 ± 0.07 SE, and 0.09 ± 0.03 SE, respectively. Turtles encountered both seagrass species during every focal follow and macroalgae in 42 of the 45 follows (Figure 5). However, green turtles showed a preference (greater proportion of bites) for *S. filiforme* regardless of its relative abundance when in mixed meadows with *H. stipulacea* (McNemar's X^2 = 54.15, df = 1, $P < 0.0001$; Figure 7). Turtles occasionally foraged on the invasive *H. stipulacea,* primarily in monospecific meadows. When foraging in these monospecific meadows, however, the bite rates of turtles (mean = 9.70 bites * min^{-1}; Figure 8) were less than half

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those of turtles foraging in meadows composed exclusively of native seagrass (mean = 20.9 bites * min^{-1}, $t = 5.14$, $df = 18.7$, $P \leq 0.001$.
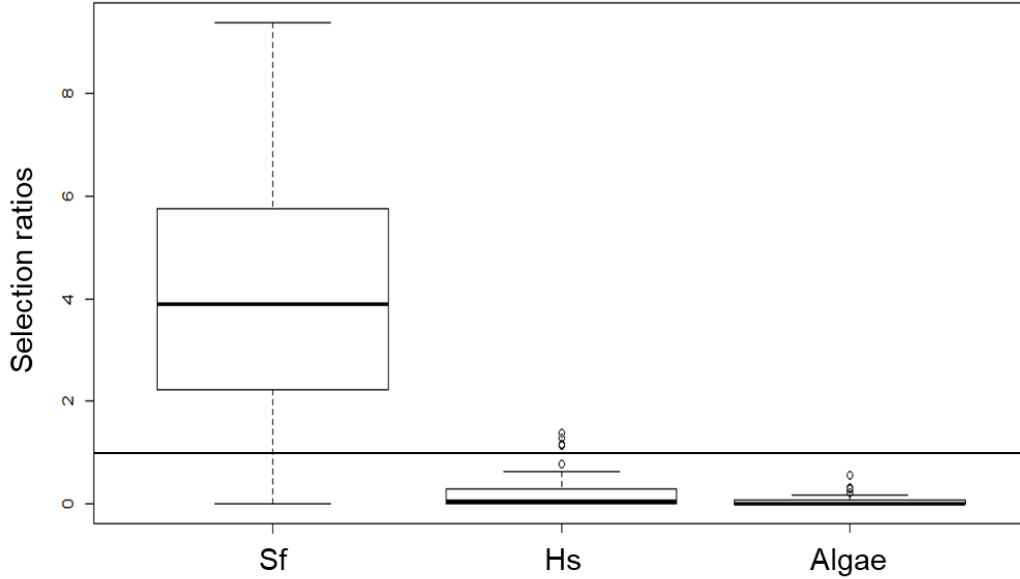
Figure 6. Selection ratios for *S. filiforme* (Sf), *H. stipulacea* (Hs), and macroalgae (Algae); Values above 1.0 indicate positive selection, values below 1.0 indicate avoidance, and values near 1.0 indicate no apparent preference
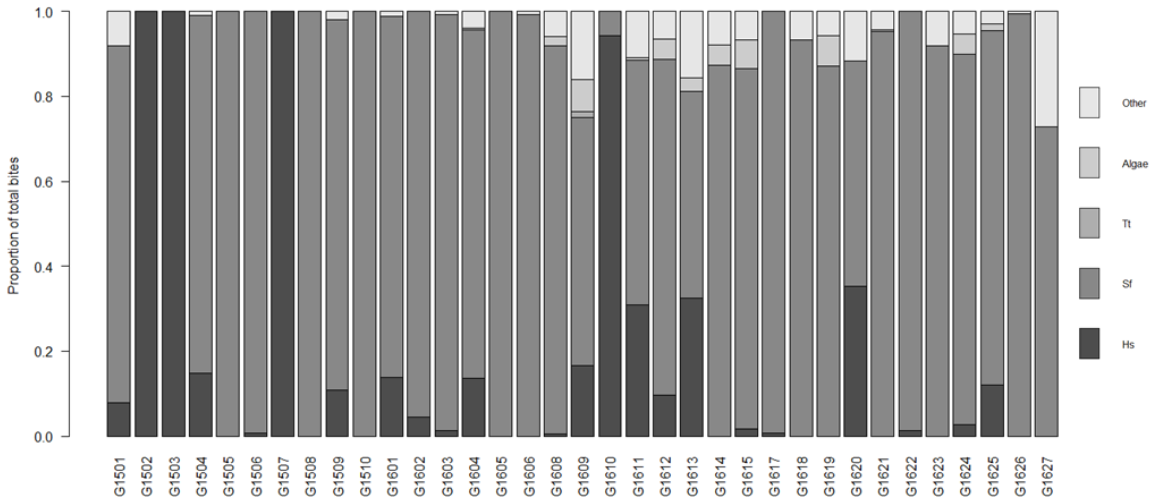
Figure 7. Proportion of total bites taken of each species for each turtle including macroalgae (Algae), *T. testudinum* (Tt), *S. filiforme* (Sf), *H. stipulacea* (Hs), and "other" (unknown, mixed species and non-flora combined)
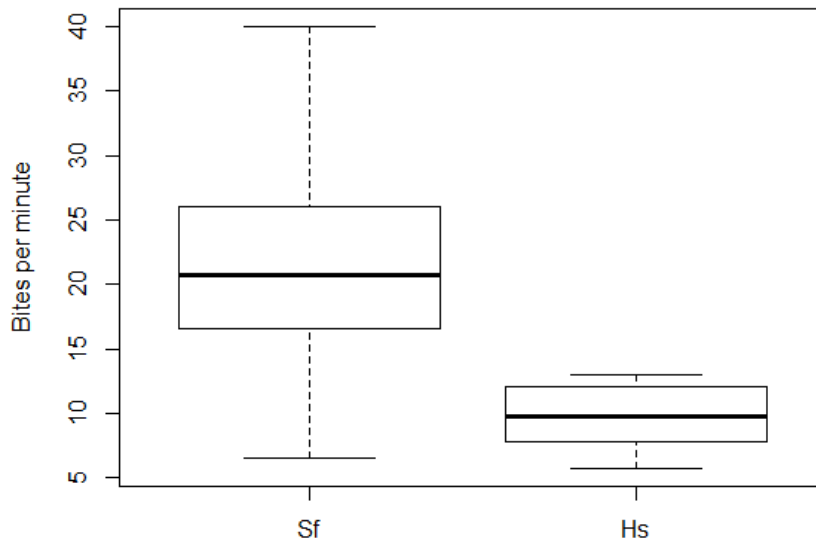
Figure 8. Bites per minute in monospecific meadows of *S. filiforme* (Sf) and *H. stipulacea* (Hs)

Individual-level selectivity was very similar to population-level patterns overall. Indeed, there was significant selectivity by 30 of 35 individuals (Appendix II), with 27 individuals positively selecting (*Wi* >1) for the native *S. filiforme*, three individuals positively selecting (*Wi* >1) for the invasive *H. stipulacea*, and all 35 individuals avoiding algae (*Wi* <1). Individual selectivity of resources was stable across multiple follows for four individuals that all positively selected for *S. filiforme*. Selection indices changed between follows for two turtles (Appendix III). One individual (G1608) positively selected macroalgae during the first follow, encountered and avoided it during the second follow, and overall (pooled follow data) avoided macroalgae and positively selected *S. filiforme*. Another individual (G1611) encountered and avoided the invasive seagrass *H. stipulacea* during the first, second, and fourth follows, neither selected nor

avoided it during the third follow ($Wi \approx 1$), and overall did not feed selectively. Turtle

G1611 also positively selected the native *S. filiforme* during the first, second, and fourth

follows, encountered and avoided it during the third follow, and overall selected for *S.*

filiforme.

The combination of predictor variables that produced the lowest AIC score for all

GLMs included the relative abundances (as percent macrophyte cover) of the native

seagrass *S. filiforme*, the invasive seagrass *H. stipulacea*, and macroalgae (Table 1). No

single predictor variable or combination of predictor variables significantly affected the

number of bites taken per bout of the invasive *H. stipulacea* (Table 1). The relative

abundance of *H. stipulacea* did significantly affect the number of total bites taken per

bout and the number of bites taken per bout of native *S. filiforme* were significantly

affected by the relative abundances of *H. stipulacea* and *S. filiforme* as well as the

interaction between the relative abundances of *H. stipulacea* and *S. filiforme*.

Table 1. *P* values from GLM testing the effect of relative abundance on the number of
bites taken (Factor); Hs (*H. stipulacea*), Sf (*S. filiforme*), and Algae (macroalgae) and all
possible interactions were tested; asterisks represent significant affects

Factor	df	Hs	Sf	Algae	Hs x Sf	Hs x Algae	Sf x Algae	Hs x Sf x Algae
Total bites	124	0.001*	0.160	0.685	0.120	0.811	0.334	0.501
Bites of Hs	124	0.370	0.866	0.234	0.995	0.350	0.270	0.457
Bites of Sf	124	<0.001*	<0.001*	0.662	0.016*	0.804	0.786	0.624

Using the number of bites taken, green turtle foraging behavior in Malendure Bay

is most consistent with a preference for native seagrasses regardless of its abundance

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relative to invasive seagrasses (Figure 9). Indeed, although turtles foraged on invasive

seagrasses, this occurred primarily in monospecific stands and they foraged preferentially

on native seagrasses even when it was present in low relative abundances.
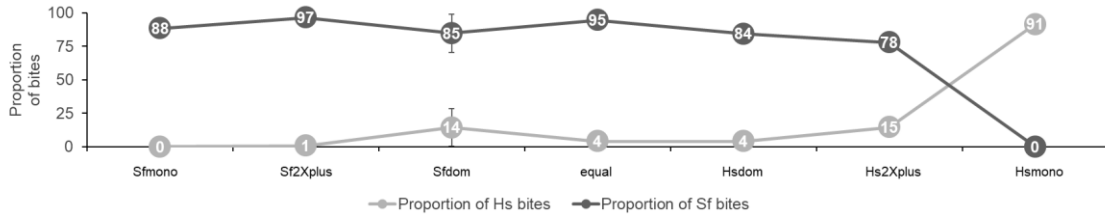
Figure 9. Mean percentage of bites (± SE) of Hs (orange) and Sf (blue) per bout across a range of relative availabilities. Total percentages less than 100 are due to bites of taxa other than seagrass. Error bars are SE, and are not visible when smaller than the size of the data point. Sfmono = 100% Sf, Sf2Xplus = Sf ≥ 2 x Hs = 75-99% Sf, Sfdom = 2 x Hs > Sf > Hs = 51-74% Sf, equal = Sf = Hs = 50% Sf + 50% Hs, Hsdom = 2 x Sf > Hs > Sf = 51-74% Hs, Hs2Xplus = Hs ≥ 2 x Sf = 75-99% Hs, Hsmono = 100% Hs

Discussion

Halophila stipulacea is spreading rapidly in the Caribbean (Rogers, Willette, &

Miller, 2014; Ruiz *et al.,* 2017; Willette *et al.,* 2014), making it important to understand

the factors that might facilitate or attenuate its spread. We found that the green turtles in

Malendure Bay show strong preferences (positive selection) for native seagrass over the

invader across a wide range of relative abundances. Although turtles foraged on *H.*

stipulacea when it was the only seagrass available, only three out of 35 individuals

showed a preference for this species while most preferred the native species. Together,

these data suggest that *H. stipulacea* is likely benefiting from the rare enemy effect, at

least from megagrazers, and that green turtles could be facilitating the invasion by allowing it to spread.

There are several possible explanations for why green turtles are not foraging widely on *H. stipulacea*. Turtles may not recognize it as a potential food source or be avoiding lower-quality forage. The former seems unlikely since turtles in Malendure grazed on *H. stipulacea* even if only three showed a preference for it, and *Halophila* spp. are part of the diet of green turtles in other parts of the world (*e.g., Halophila ovalis* in India, Agastheesapillai and Thiagarajan, 1979); *H. ovalis* and *Halophila ovata* in Oman, Ross, 2016); *H. ovalis* and *Halophila spinulosa* in Australia (Limpus *et al.,* 1994, 1985); *Halophila engelmanni* in Florida, Mendonça, 2016)]. Furthermore, green turtles in other locations have shifted their diets to include invasive taxa. Hawaiian green turtles, for example, shifted their foraging behavior to include non-native species, although the shift to include some invasive species in their diets occurred up to 30 years after their introductions (Russell & Balazs, 2009). The introduction of invasive species into the diets of Hawaiian green turtles may be related to their abundance in foraging habitats (Russell & Balazs, 2015; Russell *et al.,* 2003), but diet preferences have not been directly compared to resource availability in the Hawaiian population. While a similar degree of population-level dietary plasticity is not evident from our study of green turtles in Guadeloupe, some individuals foraged on the invasive seagrass and others switched preferences over time. The invasion is still relatively recent at this site (*c.a.* one decade). Thus, there may be enough native seagrass still available that turtles can afford to be selective, and shifts could occur at the population level over time if *H. stipulacea* proliferates to the point where *S. filiforme* becomes difficult for turtles to find.

It is unclear what role forage quality might play in the diet preferences we detected. Turtles demonstrated general negative selectivity for macroalgae, which is consistent with the lower N content in algae than in both seagrasses. In Bonaire, green turtles selectively foraged on the abundantly and nutritionally dominant native seagrass *T. testudinum* (Christianen *et al.,* 2018). However, if diet quality was driving differences in preferences for native over invasive seagrasses, it would have been expected that *S. filiforme* was higher in quality than *H. stipulacea*. My analyses did not reveal nutrient content as a clear driver for forage selection. Although *S. filiforme* did have a higher C content than *H. stipulacea* in Malendure, there were not statistically significant differences between the seagrasses in other measures of nutrient content. In a meta-analysis of seagrass nutrient content, *H. stipulacea* was found to have slightly greater, although still below average for all seagrasses, nitrogen content than *H. ovalis* and *H. spinulosa* (Duarte, 1990). *Halophila stipulacea* also had the widest range of nutrient content values reported for *Halophila* species, and our nutrient content results revealed that nitrogen content for *H. stipulacea* in Malendure Bay was at the high end of the range (1.83% ± 0.07 SE) and not significantly different than the nitrogen content of the Malendure native, *S. filiforme* (2.10% ± 0.10 SE). Compared to the seagrass Redfield ratio, the observed N:P ratios in Malendure were below 25, indicating N-limitation (Duarte, 1990; Fourqurean & Cai, 2001). Anthropogenic sources such as boats discharging their holding tanks while anchored in the bay and runoff from adjacent homes and businesses likely contribute to the increased seagrass nitrogen content that we observed. Similarly, Duarte (1990) also reported a wide range of values for carbon content of *H. stipulacea*, and the mean carbon content (33.59% ± 0.45 SE) in Malendure

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Bay was above the average reported in their meta-analysis. The reported mean carbon content was also significantly different than the mean carbon content of *S. filiforme* (37.39% ± 1.29 SE) in Malendure Bay. Given that green turtle diets in other regions do include *Halophila* spp., the nitrogen contents of *H. stipulacea* in Malendure Bay are greater than average for other *Halophila* species Both N and P contents of *H. stipulacea* are comparable to the contents of the native *S. filiforme* in the Bay, and the low N:P ratio suggests that the system is N limited, green turtles may eventually incorporate *H. stipulacea* into their diets more broadly. It is likely, because of the reaction of the Hawaiian green turtle population to invasive plant species (Russell & Balazs, 2009), that if *H. stipulacea* continues to spread, it will, by necessity, eventually become a major component in green turtle diets in the Caribbean. Invasive plant-herbivore interactions can be dynamic, and at the scale of whole meadows rather than patchworks, green turtles may be willing and able to switch to foraging on the invasive species. Continued monitoring of the *H. stipulacea* spread and green turtle foraging preferences will be necessary to understanding and predicting the broader ecosystem impacts of the invasion.

Previous studies of green turtle diets have shown that individual diets can vary over time (Brand, 1995; Fuentes *et al.,* 2006), while others reveal that despite diverse foraging options, diets varied considerably among individuals but were consistent over time within individuals (Burkholder *et al.,* 2011; Thomson *et al.,* n.d.). In Malendure, only one individual switched its preference between the native and invasive seagrasses between follows. The second individual that displayed diet preference shifts between follows encountered red drift algae rather than the more commonly encountered calcareous green algae. Despite this individual variability, the population showed a clear

preference for the native seagrass *S. filiforme* and clear avoidance of macroalgae and invasive seagrass *H. stipulacea*.

The spread of invasive species is not unique to the marine environment, and studies of the effects of large-bodied herbivores on plant invasions in terrestrial ecosystems reveal differences among systems and are dependent upon several factors. Some studies suggest that herbivores have little effect on plant invasions and other factors such as nutrients and disturbance play a bigger role in determining plant communities (Stohlgren, Schell, & Vanden Heuvel, 1999). Other studies present strong evidence that grazers mitigate the invasion of dense invasive grasses that can outcompete native grasses when grazers are removed and nutrients inputs increase (Weiss, 2009). Conversely, grazing by large populations of ungulate grazers is suggested to be required for the invasion of garlic mustard (*Alliaria petiolate*) (Kalisz, Spigler, & Horvitz, 2014). The conflicting results from studies in multiple terrestrial systems suggest that consideration of grazers alone is insufficient to explain the success of an invasive plant species. The resource-enemy release hypothesis (R-ERH) considers two of the most common factors credited with affecting plant invasions. The R-ERH suggests that high-resource plants are particularly successful invaders because of the interaction of a high resource environment and the release from their native enemies (Blumenthal, 2005, 2006). An explicit test of the predictions of R-ERH demonstrated that resource availability and vertebrate grazers did indeed jointly influence the success of a non-native plant invasion in a field undergoing secondary succession (Heckman, Wright, & Mitchell, 2016).

In Malendure Bay, we found nutrient-rich conditions indicated by ratios of C:N and C:P below the seagrass Redfield ratio in leaves from both the invasive and native seagrasses. The direct measurement of ambient nutrients is unnecessary because it is widely accepted that nutrient contents of seagrass leaves reflect relative nutrient availability (Atkinson & Smith, 1983; Duarte, 1990), and have even been used to identify sources of nitrogen inputs to the system (Fourqurean, Moore, Fry, & Hollibaugh, 1997). We also found that green turtles in this area, experiencing a *H. stipulacea* invasion, have a significant preference for native seagrass species, particularly *S. filiforme*. Green turtles in Malendure Bay are not feeding preferentially on the most abundant species or switching to prefer the most selection abundant species. Our results suggest that the spread of the invasion could be benefiting from the Enemy Release Hypothesis. When coupled with the high-nutrient resource availability found in Malendure Bay, our results provide the first support for the predictions of the R-ERH from a marine ecosystem.

We used natural spatial variation in the relative abundance of native and invasive seagrasses within Malendure Bay to test *a priori* predictions about green turtle foraging preferences and whether *H. stipulacea* might benefit from enemy release. Using focal follows of individual green turtles, we tested whether 1) they prefer native seagrasses; 2) they prefer the invasive seagrass; 3) they prefer most abundant seagrass; or 4) show no obvious foraging preferences. Our study reveals that the relative abundance of an invasive plant species does not always determine grazer diet preference, at least not in the initial stages of the invasion. In fact, *H. stipulacea* in Malendure Bay is likely benefiting from the Enemy Release Hypothesis, where native grazers play a critical role in determining how the invasion will change seagrass ecosystem functions. Similarly, in

terrestrial systems, white-tailed deer (*Odocoileus virginianus*), that are typically considered to be generalist ungulate grazers, preferentially graze on native species over exotics (Kalisz *et al.,* 2014), suggesting that large-bodied grazers across systems can facilitate plant invasions through selective feeding.

The nature of grazer-plant invasion interactions can be context-dependent and will require further studies across a diversity of ecosystems to understand the drivers of contingency of native grazer impacts on invasive species establishment and proliferation. However, our results are consistent with emerging patterns and suggest that the interaction of multiple factors, such as resource availability and enemy release, may further explain the success of an invasive marine plant species. The insights gained from our study echo those from studies from terrestrial habitats experiencing pressure from high ungulate populations (Heckman *et al.,* 2016; Kalisz *et al.,* 2014), and can be directly applied to ecosystems around the world where the foraging behavior of grazers – and thus their ecosystem role – can affect the success of an invasive plant species.

Service), Reseau Tortue Guadeloupe (Sea Turtle Network - Guadeloupe), DEAL

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Appendix I.

Table A. Post-hoc comparisons among macrophytes using the Tukey's test (alpha = 0.05) for %C, %N, C:N, C:P, and N:P.

| Dependent Variable	(I) Species	(J) Species	Mean Difference (I-J)	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
%N	*H. stipulacea*	macroalgae	0.70	<0.0001	0.39	1.01
%N	*S. filiforme*	macroalgae	0.98	<0.0001	0.64	1.32
%N	*S. filiforme*	*H. stipulacea*	0.28	0.09	-0.04	0.60
%C	*H. stipulacea*	macroalgae	1.52	0.00	1.41	1.65
%C	*S. filiforme*	macroalgae	1.70	0.00	1.56	1.85
%C	*S. filiforme*	*H. stipulacea*	1.11	0.01	1.03	1.21
%P	*H. stipulacea*	macroalgae	0.12	0.00	0.10	0.15
%P	*S. filiforme*	macroalgae	0.11	0.00	0.08	0.14
%P	*H. stipulacea*	*S. filiforme*	0.01	0.54	-0.01	0.04
C:N	macroalgae	*H. stipulacea*	0.63	0.87	-2.54	3.80
C:N	macroalgae	*S. filiforme*	2.29	0.23	-1.08	5.67
C:N	*H. stipulacea*	*S. filiforme*	1.66	0.38	-1.40	4.73
C:P	macroalgae	*H. stipulacea*	2.44	0.00	3.07	1.00
C:P	macroalgae	*S. filiforme*	2.07	<0.0001	2.65	1.00
C:P	*S. filiforme*	*H. stipulacea*	1.18	0.20	1.48	1.59
N:P	macroalgae	*H. stipulacea*	1.22	<0.0001	1.55	1.32
N:P	macroalgae	*S. filiforme*	2.26	0.00	2.87	1.00
N:P	*S. filiforme*	*H. stipulacea*	1.85	0.12	2.39	1.00

Appendix II. Individual selectivity; 30 of the 35 turtles foraged selectively, three selected for the invasive seagrass (*H. stipulacea*) and 27 positively selected for the native seagrass (*S. filiforme*); test of habitat selection:

> **Table B.** Selectivity test statistic (Khi2Lj), degrees of freedom (df), *P*; Selection Ratios (*Wi*) for each resource: *H. stipulacea* (Hs), *S. filiforme* (Sf), macroalgae (Algae); Resource with positive selection: NA indicates turtles that did not feed selectively

TurtleID	Test of habitat selection			Selection Ratios (*Wi*)			
	Khi2Lj	df	pvalue	Hs	Sf	Algae	Selection
G1501	32.02	1	0	0.11	4.63	0	Sf
G1502	1.12	0	0	1.13	NaN	0	Hs
G1503	1.7	0	0	1.17	0	0	Hs
G1504	31.8	1	0	0.19	8.79	0	Sf
G1505	47.13	0	0	0	6.96	0	Sf
G1506	32.37	1	0	0.01	5.68	0	Sf
G1507	2.2	0	0	1.27	0	0	Hs
G1508	41.16	0	0	0	5.75	0	Sf
G1509	29.05	1	0	0.14	7.09	0	Sf
G1510	34.44	0	0	0	5.11	0	Sf
G1601	23.07	1	0	0.22	4.23	0	Sf
G1602	31.83	1	0	0.06	5.76	0	Sf
G1603	41.15	1	0	0.02	8.07	0	Sf
G1604	20.44	2	0	0.24	5.09	0.02	Sf
G1605	25.11	0	0	0	3.75	0	Sf
G1606	34.85	0	0	0	6.02	0	Sf
G1608	13.52	2	0.0012	0.02	2.35	0.13	Sf
G1609	5.47	2	0.065	0.51	2.22	0.31	NA
G1610	5.75	1	0.0165	1.39	1.43	0	Sf
G1611	5.52	2	0.0634	0.48	4.05	0.05	NA
G1612	4.83	2	0.0893	0.35	1.86	0.21	NA
G1613	15.01	2	0.0005	0.64	3.57	0.15	Sf
G1614	47.67	1	0	0	7.56	0.28	Sf
G1615	20.69	2	0	0.03	9.39	0.29	Sf
G1617	16.57	1	0	0.02	1.98	NaN	Sf
G1618	2.7	0	0	0	1.78	0	Sf
G1619	27.54	1	0	0	4.07	0.56	Sf
G1620	0.97	1	0.3259	0.78	1.46	0	NA
G1621	18.43	1	0	0	3.52	0.01	Sf
G1622	2.31	1	0.1282	0.08	1.47	0	NA
G1623	10.63	0	0	0	2.56	0	Sf
G1624	27.13	2	0	0.05	5.24	0.18	Sf
G1625	14	2	0.0009	0.22	3.53	0.08	Sf
G1626	24.13	0	0	0	2.77	0	Sf
G1627	16.14	0	0	0	3.41	0	Sf

Appendix III.

Figure A. Selectivity indices for *H. stipulacea* (Hs), *S. filiforme* (Sf), and macroalgae (Algae) during multiple follows of individual turtles; G1501, G1504, G1608, and G1621 were followed twice each; G1604 and G1611 were followed four times each; asterisk denotes differences in selection among follows of the same individual
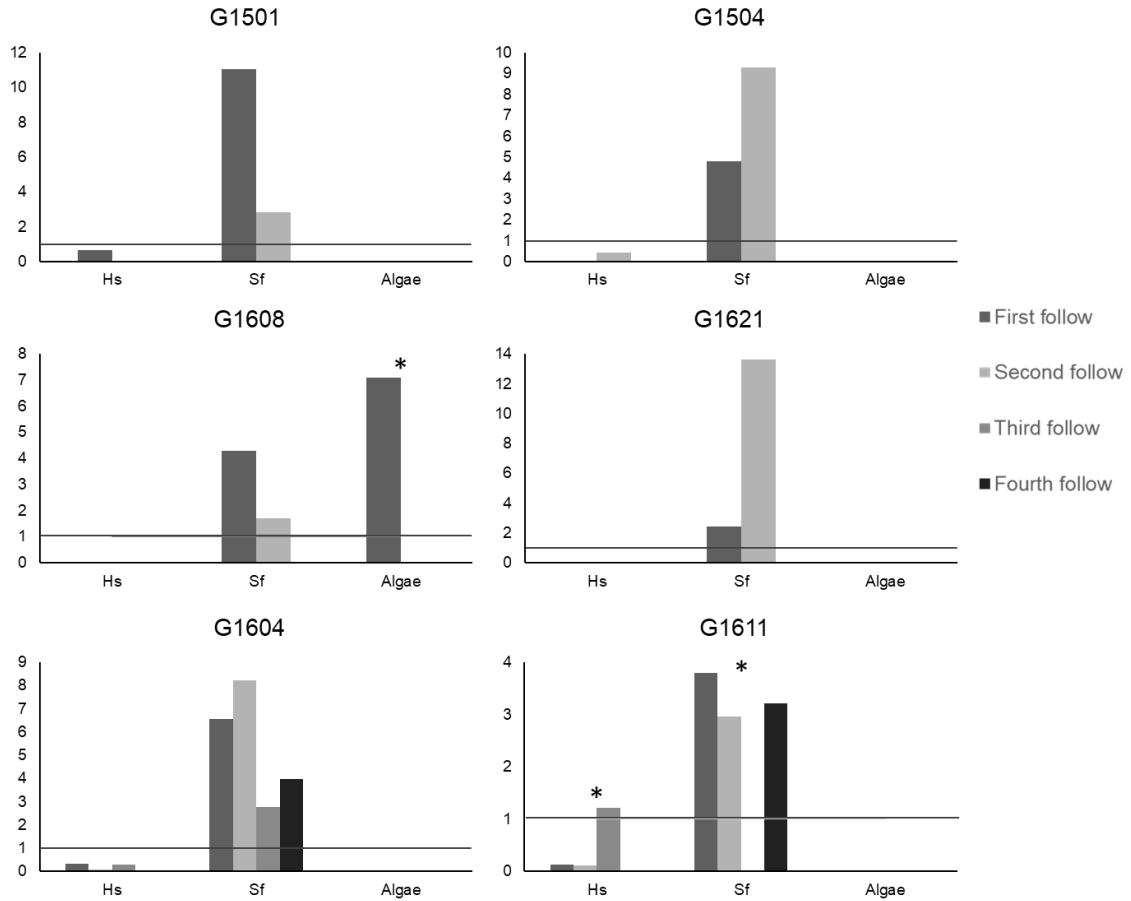
VI. GENERAL CONCLUSIONS

Understanding factors affecting habitat use and resource selection of herbivores at multiple scales is critical for understanding their potential roles in ecosystems and predicting how they, and their ecosystems, might respond to environmental or anthropogenic disturbance (Binzer *et al.,* 2016; Mougi and Kondoh, 2016; Augustine and Frank, 2017). For green turtles, and countless other species across virtually all ecosystem types, such an understanding is important because of the major changes occurring in ecosystems from climate change to apex predator overharvesting and species invasions. In this dissertation, I used existing variation in conditions across the Caribbean Sea to investigate hierarchical habitat and resource selection by a model marine herbivore to better understand how they respond to variation in their habitats.

In Abaco, The Bahamas, I quantified spatial variation in the relative abundance of potential turtle predators within one of the world's few shark sanctuaries (Chapter 2) and used these data and surveys of primary producer abundance and quality to explore resource selection at multiple scales and levels by green turtles (Chapter III). Using IFD theory I developed testable predictions to help elucidate factors driving space use at the landscape scale and patch selection (third order). In Chapter II, I found that shark species richness was high in both reef and seagrass-dominated bay habitats, although shark diversity and species-level occurrence differed between habitat types and even among reef sites in Abaco. I identified nine shark species (*Carcharhinus acronotus*, *Carcharhinus limbatus*, *Carcharhinus perezi*, *Galeocerdo cuvier*, *Ginglymostoma cirratum*, *Negaprion brevirostris*, *Rhizoprionodon* spp., *Sphyrna mokarran*, and *Sphyrna tiburo*). The species most likely to prey on sea turtles, *G. cuvier* (tiger sharks), were observed nearly exclusively in the seagrass lagoons, but never in creek habitats.

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In Chapter III, I found that at the site level (third order selection), green turtles did not conform to a basic Ideal Free Distribution (IFD) based on food abundance alone. Indeed, at broad spatial scales it appears that turtles are not using foraging habitats with the most abundant food resources. Turtles were rarely seen in dangerous open waters where seagrass was most abundant. Instead, turtles appear to conform to the foraging arena hypothesis (Walters and Juanes, 1993), with habitat use restricted to safer habitats, but space use within these habitats positively correlated with nitrogen content (*i.e.,* higher quality). Therefore, it is likely that turtles, historically, did not use all available seagrass habitats when predator presence region-wide was higher (Ward-Paige *et al.,* 2010) and, as suggested by Heithaus *et al.* (2008), reconstructions of Caribbean turtle populations that assume equal use of all seagrass habitats may overestimate historical populations. Within foraging habitats, however, turtles do appear to select high quality seagrass patches relative to nutrient content. In Abaco, their forage selection may be partially driven by the presence of allochthonous nutrient inputs and foraging dynamics of turtles likely reflect a dynamic interplay of biotic and abiotic drivers. Tidal creeks may be particularly critical habitats for rebuilding sea turtle populations. The protected shark populations in Abaco may be preventing unchecked grazing by green turtles, and the exchange of individuals from the invulnerable (creek) to the vulnerable (open water) population components could signal that the preferred habitat has reached carrying capacity.

In Chapters IV and V, I explored another potential factor that could constrain turtle use of apparent foraging resources in the shape of invasive seagrasses. In Chapter IV, Investigated both third order habitat selection of green turtles off the French West

Indies islands of Guadeloupe, Martinique, and St. Martin. At all sites, turtles selected for areas with abundant native seagrasses (*Thalassia testudinum*, *Syringodium filiforme*) and avoided areas typified by macroalgae and the invasive seagrass *H. stipulacea*. In Chapter V, I investigated fourth order resource selection and found that turtles showed a clear preference for native seagrass species, particularly *Syringodium filiforme* and *T. testudinum* and avoided *H. stipulacea* and macroalgae. While most individual turtles preferred native species, *ca.* 12% of individuals in Guadeloupe fed primarily on *H. stipulacea* during follows. Analysis of seagrass CN content did not reveal significant differences among the species, suggesting that turtles likely are not recognizing the invasive species as potential forage rather than selectively foraging on higher quality seagrasses. Together, the work in Chapters IV and V suggest that the green turtle-invasive seagrass interaction conforms to the Rare Enemy Hypothesis and that green turtles likely facilitate the invasion of *H. stipulacea* since they tend to avoid foraging on this species even when it is at high relative abundance. Furthermore, the spread of invasive seagrasses may result in decreases in habitat area that turtles perceive as quality foraging habitat, restricting energy flow into the turtle population and potentially reducing carrying capacities of habitats.

Green turtles in the Caribbean currently face tradeoffs (quantity-quality and energy-risk) in their foraging habitat use, and their ability to adapt to changing ecosystem conditions will affect the growth trajectory of their populations. If turtles have access to habitats such as the tidal creeks in Abaco that offer both adequate forage and refuge from predation, they can afford to forage selectively for high quality forage. At the population level, green turtles are not selecting to forage on the highly invasive seagrass *H.*

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stipulacea. The continued avoidance of an abundant forage option would mean turtles are self-imposing a foraging habitat constraint that could lead to lower energy intake and lower K. However, should green turtles incorporate *H. stipulacea* into their diets in the manner that Hawaiian green turtles incorporated invasive macrophytes into their diets (Russell and Balazs, 2015), they would have greater foraging habitat and the potential to increase their energy intake and K.

I investigated the foraging habitat use of green turtles in the broad context of a relatively intact shark population and abundant forage in Abaco, and in the context of a seagrass invasion in the FWI. However, these contexts are dynamic and there are likely interactions with factors not studied here that drive, at least in part, foraging habitat use. Shark conservation efforts could lead to increased risk and further habitat constraints. The interaction of increased predation risk with the *H. stipulacea* invasion could go one of two ways. If turtles do not incorporate invasive seagrass into their diets their populations may especially vulnerable when their available habitat is constrained by both predation risk and the invasion. If turtles do incorporate *H. stipulacea* into their diets, the interaction of the invasion with increased predation risk could mean that the constraint of predation risk is mitigated by the increased forage available. Further research is needed to elucidate the implications of the interactions between factors affecting large herbivore habitat use and given that predation risk and invasive species are not unique to the marine environment, the results from research into green turtle foraging habitat use can be directly applied to management strategies of similar ecosystems.

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