

Effect of seagrass nutrient content and relative abundance on the foraging behavior of green turtles in the face of a marine plant invasion

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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. As locally abundant large-bodied grazers, green turtles *Chelonia mydas* could either facilitate or attenuate the *H. stipulacea* invasion depending on their foraging patterns. 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, French West Indies, to investigate the ERH. Using video-assisted individual focal follows (n = 45), we assessed individual- and population-level foraging preferences. Turtles foraged across a wide range of microhabitats including monospecific seagrass meadows and a range of compositions within mixed-species meadows. Green turtles showed clear preference for native *Syringodium filiforme* over the invasive seagrass. Both *H. stipulacea* and macroalgae were generally avoided. However, individual turtle foraging preferences varied with ca. 12% of individuals foraging on *H. stipulacea* at rates above those predicted by availability. No differences in nutrient content were observed between the native and invasive seagrass, suggesting that other factors can drive forage selection. The preference shown by most green turtles in Guadeloupe for native over invasive seagrass suggests green turtle foraging likely facilitates the *H. stipulacea* invasion at this stage of its spread, regardless of relative abundance and nutritional value.

KEY WORDS: Exotic species · *Chelonia mydas* · Megagrazers · Enemy release hypothesis · Guadeloupe · French West Indies · Sea turtle

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1. INTRODUCTION

Across a wide array of ecosystems, grazers can structure primary producer communities in ways that have profound consequences for other organisms and ecosystem dynamics (Jones et al. 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 Ripple et al. 2015). Grazers can also affect invasion dynamics, but the nature of these effects can

vary widely (Maron & Vila 2001). 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 (ERH) posits that the ability of an invasive species to proliferate in a new habitat is facilitated by a lack of predators (Keane & Crawley 2002, Cogni 2010). 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 prefer to forage on invaders, an invasion may be slowed or even halted.

In some cases, grazers can help prevent or attenuate invasions. For example, domesticated terrestrial grazers, such as goats, show potential as a means of invasive species control and removal (Silliman et al. 2014). Native grazers also can mitigate plant invasions by limiting their spread or their performance (Parker et al. 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 height 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 decisions of native grazers.

In marine ecosystems, large grazers (dugongs *Dugong dugon*, and green turtles *Chelonia mydas*) can modify the structure (e.g. biomass and species composition) and function (e.g. nutrient cycling) of seagrass ecosystems (Preen 1995, Burkholder et al. 2013). Green turtles are mostly herbivorous as adults but exhibit considerable variation within and among populations throughout their range (for a review, see Jones & Seminoff 2013). Some 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 et al. 2006). Other populations specialize on macroalgae (López-Mendilaharsu et al. 2005, Santos et al. 2011), and some forage on a mix that may even include invertebrates (Seminoff et al. 2002, Arthur & O'Neil 2007, Burkholder et al. 2011, Shimada et al. 2014). Despite 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).

In the context of changes to marine ecosystems, of particular concern is how changes in large grazer abundances might affect seagrass ecosystem structure and function (e.g. Jackson 2001, Heithaus et al. 2008, 2014). Grazing by green turtle populations that have benefitted from successful conservation measures and declines in predator populations in some regions have led to changes in seagrass productivity (Kelkar

et al. 2013) and the collapse of local seagrass meadows (Fourqurean et al. 2010, Christianen et al. 2014). 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 was only the second seagrass species known to have transoceanic establishment (Ruiz & Ballantine 2004). The invasive *H. stipulacea* is fast-growing, produces a large number of seeds, can rapidly spread 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 et al. 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 native large-bodied grazers do not recognize it as a potential food source or preferentially consume native seagrasses competing for space. To date, *H. stipulacea* in the Caribbean has only been reported in seagrass habitats used by green turtles, and it is unknown how manatees *Trichetus manatus*, another large-bodied Caribbean grazer, will react when the invasion reaches their habitat.

Because *H. stipulacea* is highly invasive and has been present in high abundance in parts of the Caribbean for over a decade, it might be expected that green turtles would have incorporated *H. stipulacea* into their diets. However, 3 to 6 yr after the first documentation of *H. stipulacea* in Bonaire (Dutch Caribbean) (Debrot et al. 2012), cafeteria experiments revealed that turtles selectively fed 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 (Becking et al. 2014, Christianen et al. 2019). Despite the higher nutritional value observed in *T. testudinum*, 2 of the 20 grazing turtles did forage on the invasive *H. stipulacea* and 3 foraged on *S. filiforme* during the Bonaire experiment. 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* (Christianen et al. 2019). These results suggest that green turtles show

individual variability with a preference for one nutrient-rich native seagrass at the population level. 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.

Here, we used natural spatial variation in the percent cover of native and invasive seagrasses within a near-shore green turtle foraging habitat off Guadeloupe (French West Indies) to test *a priori* predictions about green turtle foraging preferences (Fig. 1) and whether *H. stipulacea* might benefit from enemy release. Specifically, we used video-assisted focal follows of individuals to test whether they (1) prefer native seagrasses regardless of seagrass relative percent covers (and, therefore, likely facilitate the invasion), (2) prefer the invasive seagrass (and might attenuate the invasion), (3) prefer the 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) (Fig. 1).

2. MATERIALS AND METHODS

2.1. Study site

We conducted our study in Malendure Bay, along the western coast of Basse-terre, Guadeloupe,

French West Indies (Fig. 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, the dominant benthic biota, is found between depths of 2 to 20 m and covers ca. 12 ha of the study area. Malendure Bay is bordered by a sandy beach and rock coastline on the east, rock and coral reef habitat on the north and south, and the Cousteau Underwater Reserve on the west. Native seagrasses found in Malendure Bay include *Syringodium filiforme*, *Thalassia testudinum*, and *Halodule wrightii*. The non-native seagrass *Halophila stipulacea* was first observed in Guadeloupe in 2010 (Kerninon 2012). At the time of our study, *H. stipulacea* was found throughout the bay both among the native seagrasses in mixed patches and in dense monospecific patches.

Green turtles *Chelonia mydas* from multiple life stages—including juvenile, subadult and adult turtles, and nesting females—are found off Guadeloupe (Carr et al. 1982, Maylan 1983). The beach at Malendure Bay is not a regular nesting site (Rinaldi et al. 2011), and no mature turtles were observed during our study. However, the bay is an important foraging ground for juvenile and subadult green turtles. Malendure Bay is also a popular tourist destination, in part because turtles are abundant and highly acclimated to the presence of boats, snorkelers, and divers.

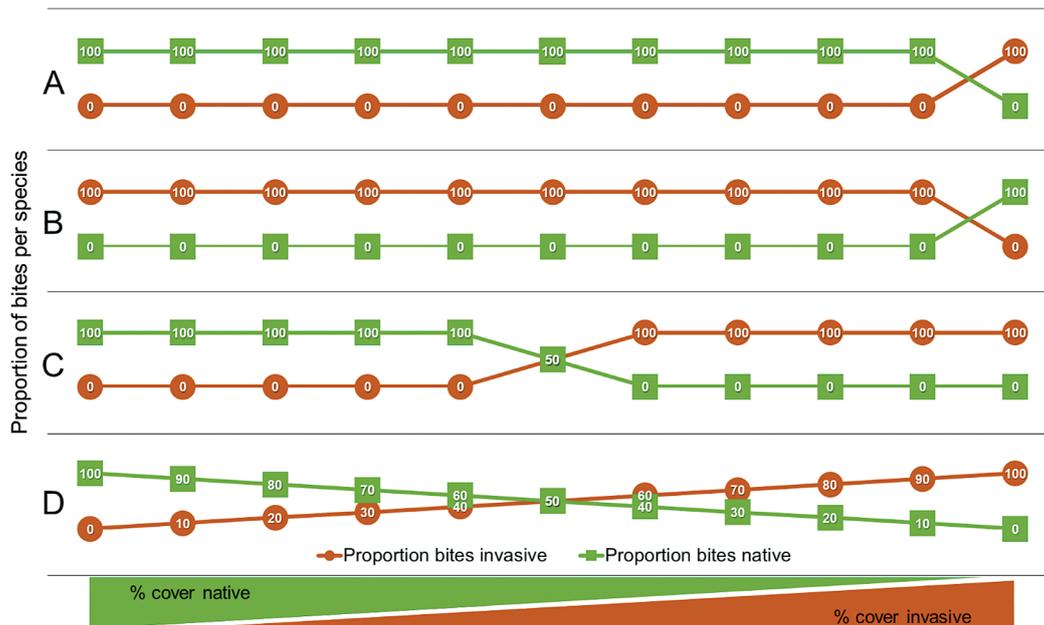


Fig. 1. Conceptual diagram of predicted green turtle *Chelonia mydas* foraging behavior on 2 species if they (A) prefer native seagrasses (green squares), (B) prefer invasive seagrass (orange circles), (C) prefer to forage on the most abundant species, and (D) display no foraging preference. Note: in (A), we assume that turtles would forage on the invasive species if it were the only food available

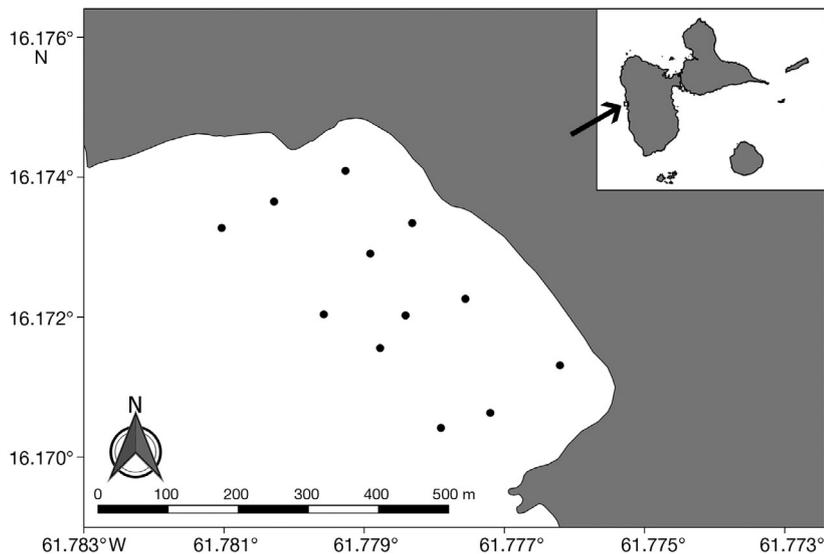


Fig. 2. Malendure Bay (16.172324° N, 61.778399° W) lies on the west coast of Guadeloupe (inset). Seagrass nutrient content was measured at 12 locations within the study area (closed circles)

2.2. Seagrass availability and nutrient content

We conducted surveys of seagrass and macroalgae occurrence in March 2015 and April 2016 at 23 and 122 haphazardly selected points, chosen to sample across depth and distance-to-shore gradients throughout Malendure Bay, respectively. At each sampling point, each macroalgae and seagrass species observed in 50 × 50 cm quadrats was assigned a score according to the Braun-Blanquet scale for rapid vegetation assessments (Fourqurean et al. 2001). The abundance for each species per point was calculated as the mean score from 4 haphazardly placed (within a ca. 4 m² area) quadrats. In April 2016, we also collected all macroalgae and seagrass species present at each of 12 haphazardly selected survey points throughout Malendure Bay (Fig. 2) to assess the nutrient content of each species during the season when most follows occurred. Macroalgae and seagrass 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 h within 48 h 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 & Sharp (1980) on a Shimadzu UV-2101PC spectrophotometer.

2.3. Focal follows

We conducted video-assisted focal follows (detailed methods in Text S1 in the Supplement at www.int-res.com/articles/suppl/m628p171_supp.pdf) over 10 d in 2015 (March: n = 5 d; April: n = 5 d) and 12 d in 2016 (June: n = 3 d; July: n = 7 d; August: n = 2 d). A total of 45 follows (mean video length = 16 min) resulted in ca. 12.5 h of video footage, including 7.3 h of foraging activity. Videos were viewed in their entirety by one observer, and a second observer, familiar with the study site, was consulted for subsections of the videos to validate macroalgae and seagrass species identification and percent cover estimates. Throughout our study, we only observed foraging juvenile and sub-adult green turtles. We identified 35 individuals using a combination of carapace scute patterns, profile scale patterns, and scars or other physical damage.

Segments of follows for which it was not possible to determine seagrass community composition were also excluded from analyses. Four turtles were observed during 2 separate follows each, and 2 individuals were observed during 4 separate follows each (Fig. 3). To avoid pseudoreplication, we pooled the multiple follows for each of these 6 turtles for population-level analyses. We also compared multiple follows within individuals to assess selectivity over time.

2.4. Video data extraction

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 visually estimated the percent cover of macroalgae and each seagrass species present by averaging the percent cover for both the full field of view and within the area reachable with only head movement by the turtle from the paused video at 60 s intervals. 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 percent-

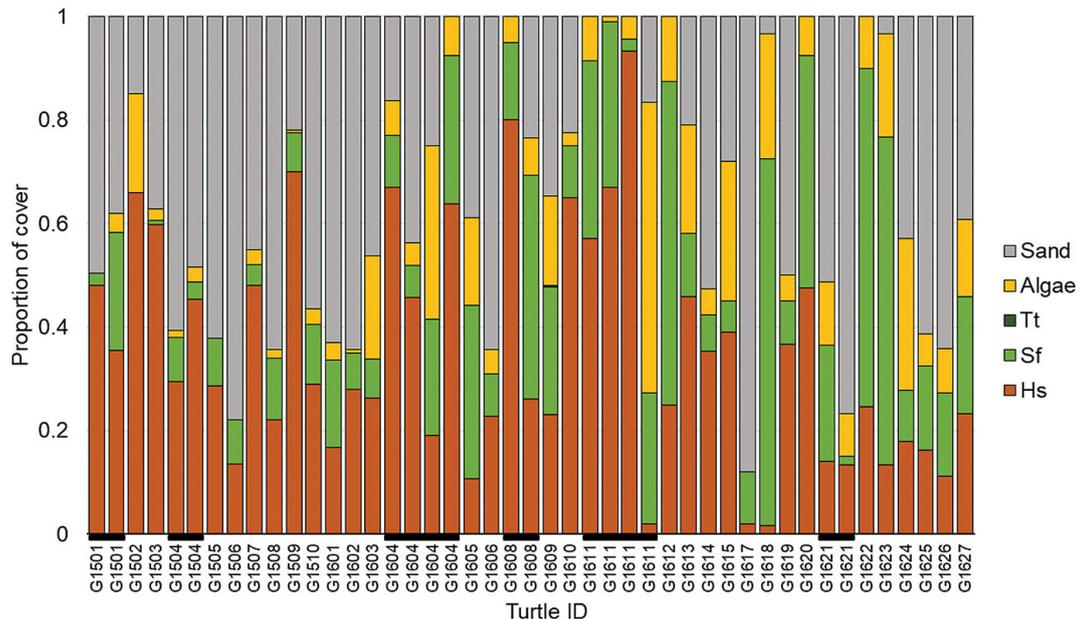


Fig. 3. Mean macroalgae and seagrass species composition immediately available to each individual turtle during focal follows; area not covered by macroalgae or seagrass (Sand), macroalgae (Algae), *Thalassia testudinum* (Tt), *Syringodium filiforme* (Sf), *Halophila stipulacea* (Hs). Black bars on x-axis indicate multiple follows of individual turtles

age cover of algae and seagrasses immediately available to the individual for the selectivity analysis.

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 ≥ 2 species), unknown (i.e. targeted food item could not be identified), or other (e.g. shells, garbage, gelatinous plankton). Macroalgae species were grouped to obtain the most conservative estimate of turtle preference relative to macroalgae. 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 2 turtles. Only one of these turtles foraged on *T. testudinum*. Combined bites from the categories not included in the analyses (*T. testudinum*, mixed, unknown, and other) accounted for 5.5% of the total number of bites and a mean (± 1 SD) of $4.6 \pm 6.1\%$ of bites by individuals. Although *H. wrightii* is present in Malendure Bay, it was not observed during our focal follows and is not included in the analysis.

To estimate the straight carapace length (SCL) of turtles, we measured both the length of the turtle carapace and the width of *H. stipulacea* leaves from multiple still frames of each follow in Microsoft Power Point (Text S2 in the Supplement). We converted the

measurements to SCL using the median width of 374 *H. stipulacea* leaves from samples collected for nutrient content analysis. Because of the relatively coarse nature of this method, we binned estimated turtle lengths into <40 , 40–60, and >60 cm SCL.

2.5. Data analysis

We assessed variation in %N, %C, and %P of dry weight and the molar C:N, C:P, and N:P ratios among seagrass and algae species used in the selectivity analyses (*S. filiforme*, *H. stipulacea*, and macroalgae) (Text S3 in the Supplement).

We compared foraging preferences using bite rates on each species both among individual turtles and across a gradient of seagrass and macroalgae community composition. The mean percentage cover of macroalgae and each seagrass species present near the turtle and the total number of bites of macroalgae and each seagrass species were calculated per foraging bout. We used the R package (v.3.4.1, R Core Team 2016) adehabitatHS (Calenge 2006) design III selectivity analysis to test the effects of species composition (resource availability) on foraging (resource use). Mean percentage cover of macroalgae and each seagrass species were used as the resource availability input, and the mean number of bites per minute for each foraging bout within each follow was used as the resource use input (see Text S1 for justification).

Assuming resource consumption relative to availability as the null hypothesis, resource use was tested for the population and for individuals using chi-squared goodness-of-fit tests. We calculated Manly's selection ratios (W_i) (Manly et al. 2002) with Bonferroni confidence intervals with resources defined by the categories *H. stipulacea* (Hs), *S. filiforme* (Sf), and macroalgae (Calenge 2011). Ratios (resource use to resource availability) >1 indicated selection, and ratios <1 indicated avoidance. Ratios near 1 or confidence intervals for the population overlapping 1 suggested no selectivity. A generalized linear model was used to test the effects of macroalgae and each seagrass species abundance on the number of bites taken per bout (details and results in Text S4 in the Supplement).

To test for the effect of turtle size on forage selection, we used a chi-squared test of independence of forage selection by the 3 size classes of turtles.

3. RESULTS

3.1. Seagrass availability and nutrient content

In 2015, *Halophila stipulacea* was found at 22 of 23 (96%) haphazardly selected survey points, and in 2016, it was found at 118 of 122 (97%) survey points. *Penicillus* spp., a calcareous green algae, was the only macroalgae found at the haphazardly selected collection points. The %N and %P dry weight of *Syringodium filiforme* and *H. stipulacea* were significantly greater than those of macroalgae (N: $F_{2,27} = 34.9$; $p < 0.001$; P: $F_{2,27} = 83.3$; $p < 0.001$), and all species varied significantly from one another in %C dry weight ($F_{2,27} = 148.4$; $p < 0.001$) (Fig. 4). Both seagrass species had N:P ratios similar to seagrass-specific Redfield ratios, indicating sufficient N and P availability and likely light limitation (Atkinson & Smith 1983, Ferdie & Fourqurean 2004, Johnson et al. 2006). Epiphyte loads were low on all samples collected, and so were unlikely to affect forage selection.

Analysis of data pooled from all videos revealed the percent cover estimates for macroalgae and each seagrass species within the full field of view differed significantly from the cover immediately

available to the individual (Wilcoxon paired signed-rank test, *H. stipulacea*: $V = 36794$, $p < 0.001$; *S. filiforme*: $V = 45674$, $p = 0.024$; macroalgae: $V = 36748$, $p < 0.001$). The mean (± 1 SE) percent cover of the invasive *H. stipulacea* was greater in the full field of view ($43.76 \pm 1.03\%$) than in the area immediately available to the turtle *Chelonia mydas* ($36.55 \pm 1.24\%$), while the mean percent cover of the native *S. filiforme* was lower in the full field of view ($15.79 \pm 0.66\%$) than in the area immediately available to the turtle ($17.41 \pm 0.84\%$), and the mean percent cover of macroalgae was greater in the full field of view ($13.53 \pm 0.46\%$) than in the area immediately available to the turtle ($11.21 \pm 0.70\%$).

3.2. Green turtle foraging

We observed green turtles across a total of 125 foraging bouts with a mean (± 1 SD) of 3.85 ± 2.44 min observed foraging time per bout. Turtles foraged dur-

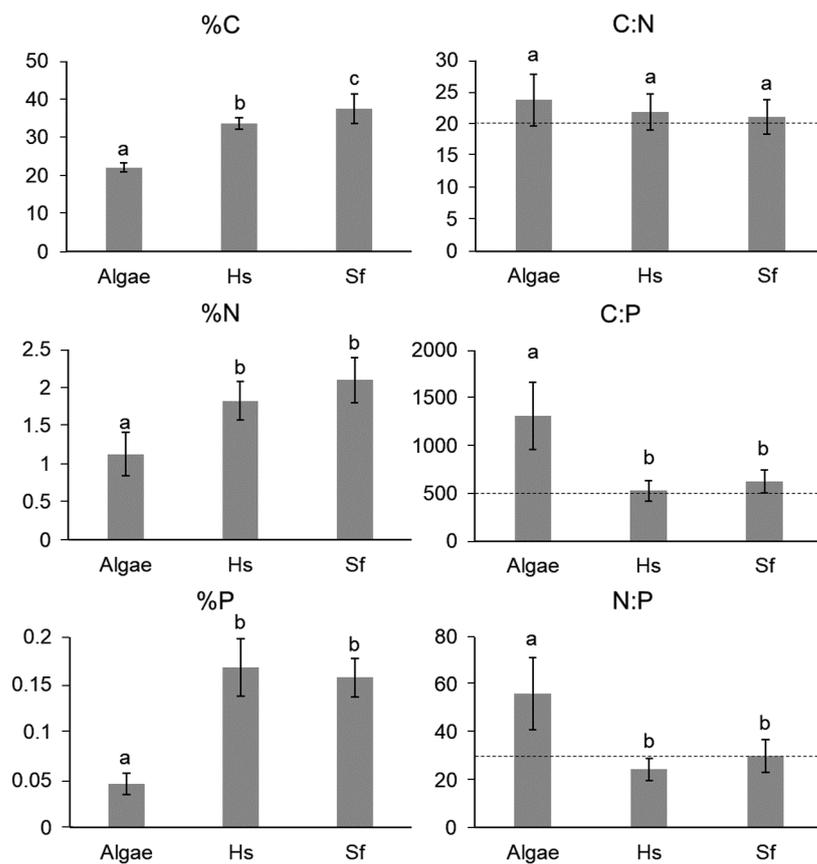


Fig. 4. Left: Mean nutrient compositions (± 1 SD) for macroalgae (Algae, $n = 9$), *Halophila stipulacea* (Hs, $n = 12$), and *Syringodium filiforme* (Sf, $n = 9$). Bars with different letters were significantly different from one another based on multiple post-hoc comparisons using the Tukey HSD test with $\alpha = 0.05$. Right: Elemental ratios of macroalgae and seagrass tissue; dotted lines indicate seagrass-specific Redfield Ratios

ing an average of 2.78 ± 1.43 bouts (range: 1 to 6 bouts) per follow.

At the population level, green turtles had a strong and significant preference for the native seagrass (*S. filiforme*) over the invasive seagrass and macroalgae (*Khi2L* [log-likelihood statistic] = 708.45, $df = 32$, $p < 0.001$; Fig. 5). Indeed, the mean (± 1 SE) selection ratios for *S. filiforme*, *H. stipulacea*, and macroalgae were 3.83 ± 0.35 , 0.23 ± 0.07 , and 0.09 ± 0.03 , respectively. Turtles encountered both seagrass species during every focal follow and macroalgae in 42 of the 45 follows (Fig. 3). However, green turtles showed a preference (greater proportion of bites) for *S. filiforme* regardless of its percentage cover when in mixed meadows with *H. stipulacea* (McNemar's $\chi^2 = 54.15$, $df = 1$, $p < 0.001$; Fig. 6). 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 = $9.70 \text{ bites min}^{-1}$) were less than half those of turtles foraging in meadows composed exclusively of native seagrass (mean = $20.9 \text{ bites min}^{-1}$, $t = 5.14$, $df = 18.7$, $p \leq 0.001$).

Individual-level selectivity was similar to population-level patterns. Indeed, there was significant selectivity by 30 of 35 individuals (see Text S5 in the Supplement), with 26 individuals positively selecting ($Wi > 1$) for the native *S. filiforme*, 3 individuals positively selecting ($Wi > 1$) for the invasive *H. stipulacea*, 1 individual positively selecting ($Wi > 1$) for both the native and invasive seagrass, and all 35 individuals avoiding algae ($Wi < 1$). Individual selectivity of resources was stable across multiple follows for 4 indi-

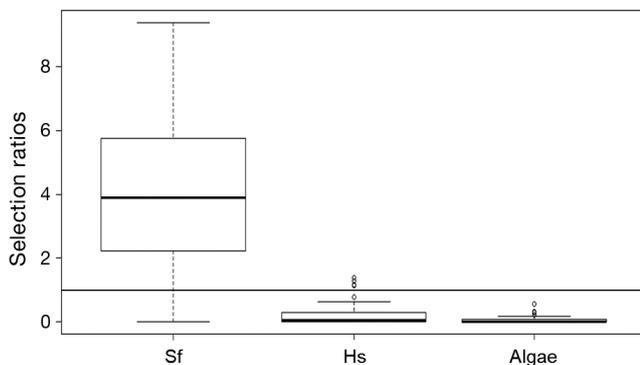


Fig. 5. Selection ratios for *Syringodium filiforme* (Sf), *Halophila stipulacea* (Hs), and macroalgae (Algae). Values >1.0 indicate positive selection, values <1.0 indicate avoidance, and values near 1.0 indicate no apparent preference. Box and whisker plots where the midline is the median, upper and 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 displayed as open circles (possibly outliers)

viduals that all positively selected for *S. filiforme*. Selection indices changed between follows for 2 turtles (Text S6 in the Supplement). 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*.

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 percentage cover relative to invasive seagrasses (Fig. 7). Indeed, although turtles foraged on invasive seagrasses, this foraging occurred primarily in monospecific stands, and they foraged preferentially on native seagrasses even when it was present in low percentage covers.

Foraging decisions varied among size classes ($\chi^2_4 = 13.74$, $p < 0.01$). Turtles <40 cm SCL selected the invasive *H. stipulacea* more often than expected; however, the sample size of individuals <40 cm SCL was small ($n = 4$) (Fig. 8).

4. DISCUSSION

Halophila stipulacea is spreading rapidly in the Caribbean (Rogers et al. 2014, Willette et al. 2014, Ruiz et al. 2017), making it important to understand the ecological drivers of its spread. The foraging patterns we observed in Malendure Bay strongly support our first *a priori* prediction that green turtles *Chelonia mydas* prefer native seagrasses regardless of seagrass relative percentage covers (and, therefore, likely facilitate the invasion) (Fig. 9). We found that the green turtles show strong preferences (positive selection) for native seagrass over *H. stipulacea* across a wide range of percentage covers. Although turtles foraged on *H. stipulacea* when it was the only seagrass available, only 3 of 35 individuals showed a preference for the invasive over the native species, while most preferred the native species. Together, these data suggest that *H. stipulacea* is likely benefiting from the lack of interest as a forage option from green turtles. Therefore, our results suggest that the

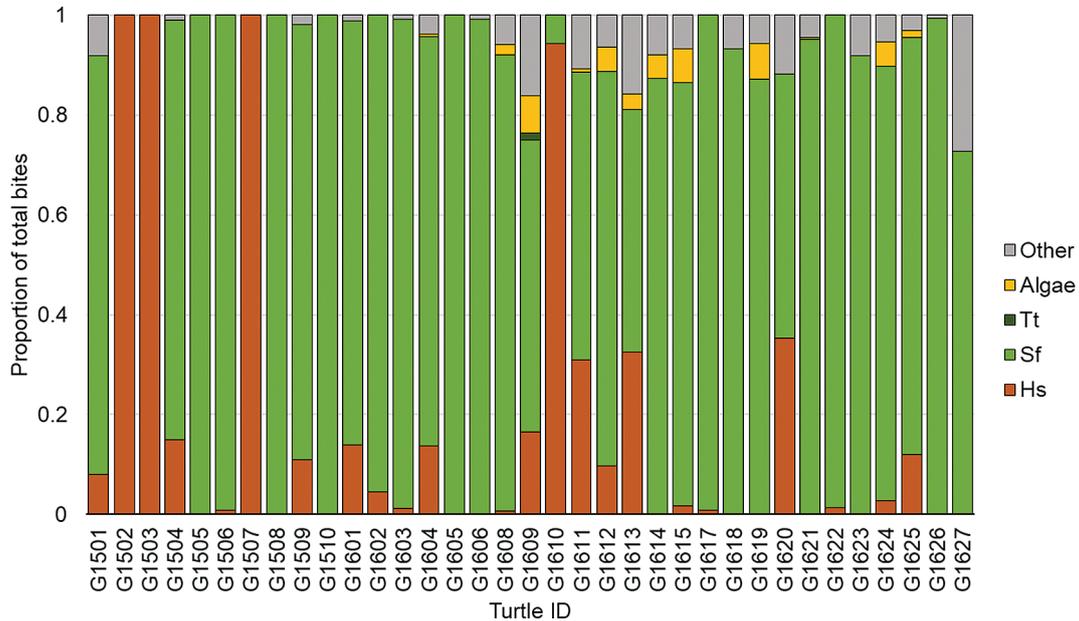


Fig. 6. Proportion of total bites taken of each species for each turtle including macroalgae (Algae), *Thalassia testudinum* (Tt), *Syringodium filiforme* (Sf), *Halophila stipulacea* (Hs), and 'other' (unknown, mixed species, and non-flora combined)

green turtles are not slowing the invasion of *H. stipulacea* and, consistent with observations in Bonaire (Christianen et al. 2019), could be facilitating the invasion by allowing it to spread into spaces where their grazing prevents the growth of thick canopies of native seagrasses.

There are multiple, non-mutually exclusive, explanations for why green turtles are not foraging heavily on *H. stipulacea*. Turtles may not recognize it as a potential food source and/or be avoiding lower-quality foods. Adoption of novel foods is likely highly context-dependent, and the drivers are not well understood. However, it is unlikely that turtles do not recognize the invasive species as a potential food source because some turtles in Malendure grazed on *H. stipulacea*, even if only 3 showed a preference for it over a native seagrass, and *Halophila* spp. are part of the diet of green turtles in other parts of the world, e.g. *H. ovalis*

in India (Agastheesapillai & Thiagarajan 1979), *H. ovalis* and *H. spinulosa* in Australia (Limpus et al. 1994, Reed & Limpus 2002), *H. engelmanni* in Florida (Mendonça 1983) and *H. ovalis* and *H. ovata* in Oman (Ross 1985). Furthermore, green turtles in other locations have shifted their diets to include invasive taxa. In Hawaii, USA, green turtles shifted their foraging behavior to include non-native species, although the shift to include some invasive species in their diet occurred up to 30 yr after the introduction of the invasive species (Russell & Balazs 2009). The introduction of invasive species into the diets of green turtles in Hawaii may be related to their abundance in foraging habitats (Russell et al. 2003, Russell & Balazs 2015), but feeding 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

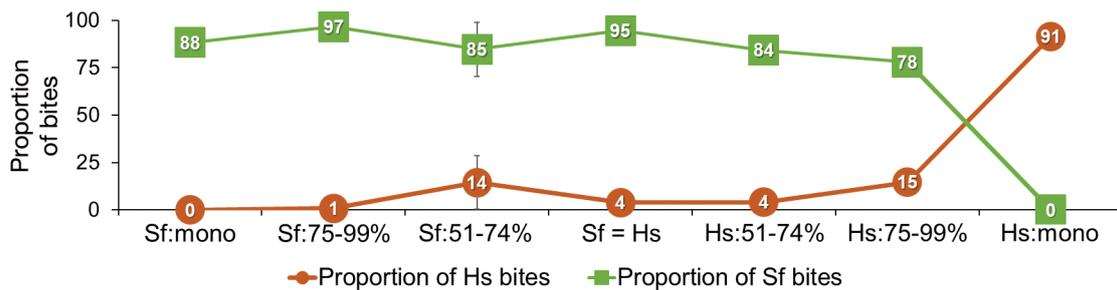


Fig. 7. Mean percentage of bites (± 1 SE) of *Halophila stipulacea* (Hs) (orange circles) and *Syringodium filiforme* (Sf) (green squares) per bout across a range of relative availabilities. Total percentages <100 are due to bites of taxa other than seagrass Error bars (SE) are not visible when smaller than the size of the data point

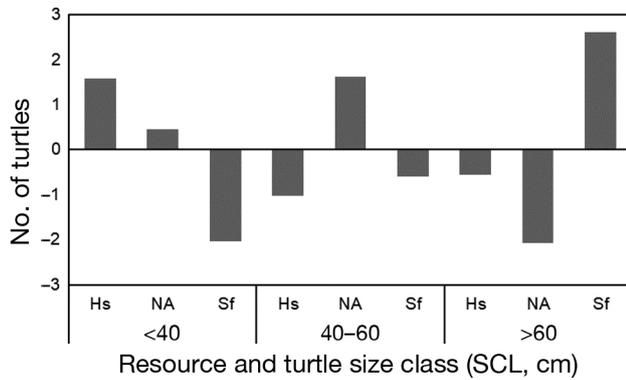


Fig. 8. Observed - expected number of turtles within each size class selectively foraging on *Halophila stipulacea* (Hs), not foraging selectively (NA), or selectively foraging on *Syringodium filiforme* (Sf). SCL: straight carapace length

Guadeloupe, some individuals foraged on the invasive seagrass and others switched preferences among follows. The invasion is still relatively recent at this site (<1 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 native seagrasses becomes difficult for turtles to find (see Fig. 9).

It is unclear what role forage quality might play in the feeding preferences we found off Guadeloupe, and our analyses did not reveal nutrient content as a clear driver for forage selection. Turtles demonstrated negative selectivity (avoidance) of macroalgae, which is consistent with the lower N content found in macroalgae relative to that found in either seagrass. In Bonaire, the green turtle population selectively foraged on the abundantly and nutritionally dominant native seagrass *Thalassia testudinum* (Christianen et al. 2019). However, if nutrient content, one component of forage quality, was driving differences in preferences for native over invasive seagrasses off Guadeloupe, we would have expected *Syringodium filiforme* to have higher content of the limiting nutrient than *H. stipulacea*. While *S. filiforme* did have higher C content than *H. stipulacea* in Malendure, there were no statistically significant differences between the seagrasses in other measures of nutrient content that are often considered important in driving herbivore foraging patterns (e.g. Bjorndal 1997). In a meta-analysis of seagrass nutrient content, *H. stipulacea* was found to have slightly greater N content than *H. ovalis* and *H. spinulosa* (Duarte 1990). *H. stipu-*

lacea also had the widest range of nutrient content values among the *Halophila* species included in the meta-analysis. Our nutrient content results revealed that N content for *H. stipulacea* ($1.83 \pm 0.07\%$, mean \pm SE) in Malendure Bay was at the high end of the range reported for *Halophila* spp. and not significantly different from the N content of the Malendure native, *S. filiforme* ($2.10 \pm 0.10\%$). Duarte (1990) also reported a wide range of values for C content of *H. stipulacea*, and the mean C content ($33.59 \pm 0.45\%$) in Malendure Bay was above the average (ca. 29%) reported in their meta-analysis. The mean C content of *S. filiforme* ($37.39 \pm 1.29\%$) in Malendure Bay was significantly greater than the mean C content of all seagrass ($33.6 \pm 0.31\%$) reported by Duarte (1990). Compared to the seagrass-specific Redfield ratio, the observed N:P ratios across seagrass species in Malendure were close to 30, indicating sufficient nutrients and a system likely limited by light (Duarte 1990, Burkholder et al. 2013). 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 relatively high seagrass nutrient content that we observed.

Given that green turtle diets in other regions include *Halophila* spp., and both N and P contents of *H. stipulacea* are comparable to the contents of the native *S. filiforme* in the Bay, green turtles may eventually incorporate *H. stipulacea* into their diets more broadly. If green turtles in Malendure react to invasive plant species similarly to green turtles in Hawaii (Russell & Balazs 2009), the continued spread or persistence of *H. stipulacea* should lead to it becoming a major component of local green turtle diets. Invasive plant-herbivore interactions can be dynamic, and at the scale of whole meadows rather than patchworks,

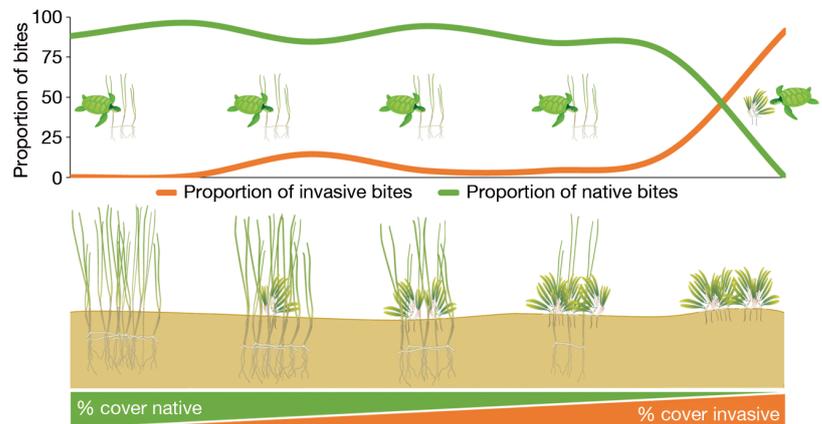


Fig. 9. Foraging pattern reveals that green turtles show strong preferences for native seagrasses regardless of seagrass relative abundance and similarities in nutrient composition, facilitating a seagrass invasion

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 understand and predict 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. 2018). In Malendure, only one individual switched its preference for native or 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*, suggesting that the invasive may be benefiting from the ERH.

We found that relatively small turtles (<40 cm SCL) selectively foraged on *H. stipulacea* more often than expected. However, caution is warranted in the interpretation of the results because of the small sample size ($n = 4$) of turtles within the <40 cm size class. The invasive seagrass is more likely to have been well established in Malendure Bay during the ontogenetic shift from the pelagic stage to neritic stage of turtles within the small size class (<40 cm SCL) than for the turtles in the larger size classes (40–60 and >60 cm SCL). Here we have presented a snapshot of the foraging behavior of green turtles in the face of a seagrass invasion. However, if the diet of individuals is determined by food availability when they shift to neritic foraging, we would expect the abundance of the invasive seagrass to be correlated with a population-level shift towards adoption of the invasive seagrass into the diet over time.

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 differences dependent upon several factors. Some studies suggest that herbivores have little effect on plant invasions and that other factors such as nutrients and disturbance play a bigger role in determining plant communities (Stohlgren et al. 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 1999). Conversely, grazing

by large populations of ungulate grazers is suggested to be required for the invasion of garlic mustard *Allyria petiolate* (Kalisz et al. 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 2 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 (e.g. nutrients) 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 et al. 2016). In Malendure Bay, we found nutrient-sufficient conditions indicated by ratios of C:N and C:P near the seagrass-specific Redfield ratios in leaves from both the invasive and native seagrasses. 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 always feeding preferentially on the most abundant species or switching to prefer the most abundant species. Although we did not explicitly test the R-ERH in Malendure, our results suggest a study comparing the effects of turtle grazing on the proliferation of *H. stipulacea* between our site and a nutrient-poor site could help elucidate whether the R-ERH could explain the course of the invasion.

We used natural spatial variation in the percent cover 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. Our study reveals that the percent cover of an invasive plant species does not always determine grazer diet preference, at least not at this stage of the invasion. *H. stipulacea* in Malendure Bay may be benefiting from the ERH, 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*, which are typically considered to be generalist ungulate grazers, prefer native species over exotics (Kalisz et al. 2014), suggesting that large 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 in-

vestigation across a diversity of conditions to understand the drivers of possible 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 of terrestrial habitats experiencing pressure from large ungulate populations (Kalisz et al. 2014, Heckman et al. 2016) and provide a likely early-stage response scenario for ecosystems around the world where the foraging behavior of grazers—and thus their ecosystem role—can affect the success of an invasive plant species.

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