







RESEARCH ARTICLE

Seagrass ecosystem metabolic carbon capture in response to green turtle grazing across Caribbean meadows

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Abstract

1. Increasing green turtle abundance will lead to increased grazing within seagrass habitats—ecosystems that are important for carbon sequestration and storage. However, it is not well understood how carbon dynamics in these ecosystems respond to grazing and whether a response differs among meadows or locations.
2. We measured seagrass ecosystem metabolism in grazed and ungrazed areas of *Thalassia testudinum* meadows with established green turtle foraging areas across the Greater Caribbean and Gulf of Mexico. We sampled meadows from five locations that differed in seagrass and environmental characteristics. Established meadows of the invasive seagrass *Halophila stipulacea* were also present at two of these locations, and we measured ecosystem metabolism in these meadows for comparison to grazed and ungrazed areas of the native *T. testudinum*.
3. Across all individual sites, rates of net ecosystem production (NEP) ranged from 56% to 96% lower in grazed areas than ungrazed areas of *T. testudinum* meadows. Rates of NEP were also strongly, positively correlated with above-ground seagrass biomass across sites. While metabolic carbon capture rates were lower in grazed areas, heterotrophic respiration was not stimulated, and grazing therefore did not result in significant metabolic remineralization of carbon in these meadows. NEP in *H. stipulacea* meadows was similar to rates in *T. testudinum* meadows at all three sites, suggesting that metabolic carbon capture may remain similar in Caribbean meadows where this invasive seagrass is replacing native species.
4. *Synthesis*. Our results show that there is a consistent response in metabolic carbon dynamics to green turtle grazing in *T. testudinum* meadows across the Greater Caribbean region. An increase in grazing will not likely stimulate remineralization of carbon as these important habitats are returned to a natural grazed state.

KEYWORDS

carbon dynamics, grazing, green turtle, *Halophila stipulacea*, invasive, metabolism, plant-herbivore interactions, *Thalassia testudinum*

1 | INTRODUCTION

Seagrasses form some of the most productive ecosystems on the planet (Duarte & Chiscano, 1999). High rates of metabolic carbon capture, and subsequent biomass production, is one of the main processes by which seagrasses contribute to carbon sequestration (known as 'blue carbon' in seagrass habitats; Duarte et al., 2010; Kennedy et al., 2010). Among seagrass meadows globally, about half of the total carbon stored in a meadow on average may be derived from seagrass biomass (Kennedy et al., 2010). Meadows also export large amounts of biomass annually, contributing to carbon storage in peripheral habitats (Duarte & Cebrián, 1996; Duarte & Krause-Jensen, 2017). Coupled with the ability to store carbon for centuries to millennia through the creation of a hypoxic sedimentary environment (Mateo, Romero, Pérez, Littler, & Littler, 1997; Serrano, Mateo, Renom, & Julià, 2012; Terrados et al., 1999), highly productive seagrass meadows form efficient natural carbon sinks (Duarte, Kennedy, Marbà, & Hendriks, 2013), and their protection has been suggested as a climate change mitigation strategy (Macreadie et al., 2017; Murdiyarso et al., 2015).

There is an estimated 150,000 km² of seagrass habitat across the Caribbean Sea, Gulf of Mexico and The Bahamas (Green & Short, 2003; Jackson, 1997; Wabnitz, Andrefouet, Torres-Pulliza, Muller-Karger, & Kramer, 2008). These meadows provide important foraging habitat for numerous species (Hemminga & Duarte, 2000; Ogden, 1976; Scott et al., 2018), including green turtles (*Chelonia mydas*), which were historically abundant in this region prior to overexploitation by humans (Jackson, 1997; Jackson et al., 2001). Green turtle abundance is currently increasing in areas such as the Caribbean (e.g. nest numbers roughly tripled 1970–2005 at the Caribbean's largest rookery) as a result of successful conservation efforts (Chaloupka et al., 2008; Mazaris, Schofield, Gkazinou, Almpnidou, & Hays, 2017). This will lead to more seagrass areas being returned to a natural grazed state (Figure 1a). Green turtles in the Greater Caribbean region normally forage by creating grazing plots within seagrass meadows in which they crop the blades to short heights above the sediment surface, and continually re-graze these areas to consume new tissue growth (Bjorndal, 1980; Ogden, 1980). This grazing strategy leads to a reduction of the photosynthetic biomass in a meadow. At high densities, green turtles are capable of grazing an entire meadow and have been recorded consuming 100% of new seagrass growth daily (Christianen et al., 2012). Given the desire to conserve seagrasses for their ability to sequester and store carbon (Macreadie et al., 2017), and the expectation that more seagrass will return to a natural grazed state in the future, it is necessary to understand how metabolic carbon capture (carbon fixed through photosynthesis or mineralized through respiration) is affected by grazing across seagrass meadows.

Much of the research on seagrass metabolic carbon dynamics to date has focused on differences among species (Lindeboom & Sandee, 1989; Murray & Wetzel, 1987; Pollard & Moriarty, 1991) or between seagrasses and unvegetated sediments (Barrón, Duarte, Frankignoulle, & Borges, 2006; Rheuban, Berg, & McGlathery, 2014;

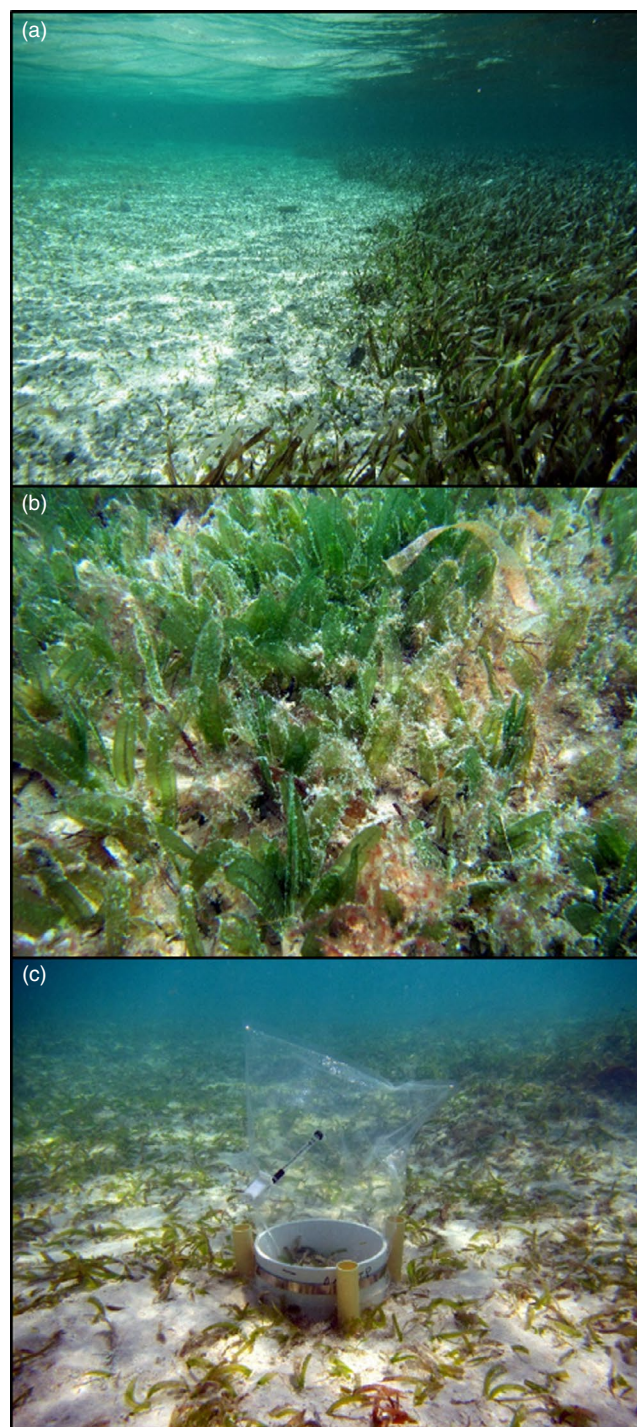


FIGURE 1 A *Thalassia testudinum* seagrass meadow with an area grazed by green turtles (panel a, left side) and an adjacent ungrazed area (panel a, right side) in Eleuthera, The Bahamas. The invasive seagrass *Halophila stipulacea* in St. Croix, US Virgin Islands (b). A light incubation chamber deployed in a grazed area in Bonaire (c). Photos: R. Johnson

Stutes, Cebrian, Stutes, Hunter, & Corcoran, 2007), with little attention being given to grazed areas. In a Caribbean *Thalassia testudinum* meadow grazed by green turtles, rates of metabolic carbon capture were found to be lower compared to ungrazed seagrass (Johnson, Gulick, Bolten, & Bjorndal, 2017). However, long-term

grazing (greater than a year) did not lead to a proportional increase in benthic respiration and remineralization of carbon stored in the meadow, possibly due to lack of a significant heterotrophic community. These results are from a single Caribbean location (Little Cayman, Cayman Islands) that has some of the highest recorded metabolic rates among seagrass meadows (Johnson et al., 2017). It is not known if grazing has similar effects across seagrass meadows in other locations or under different environmental conditions. A better understanding of the variability among meadows in response to grazing is needed to understand how increasing green turtle abundance and increased grazing will affect seagrass carbon capture in the Greater Caribbean region.

In addition to increased grazing, seagrass meadows in the Caribbean are also being invaded by the seagrass *Halophila stipulacea* (Figure 1b). This seagrass species—native to the Indian Ocean—has invaded the meadows of many Caribbean islands following its introduction to the region in 2002 (Ruiz & Ballantine, 2004; Willette et al., 2014). Initial research suggests that green turtles avoid grazing this invasive seagrass in favour of native species and that *H. stipulacea* may spread more rapidly within areas of meadows grazed by green turtles compared to areas left ungrazed (Christianen et al., 2018). Little is known about how invasion by *H. stipulacea* may affect carbon dynamics or ecosystem functioning in Caribbean meadows, however (Viana, Siriwardane-de Zoysa, Willette, & Gillis, 2019). Given this interaction between grazing and *H. stipulacea*, it is critical to understand how carbon dynamics are affected in meadows where invasion by this species is occurring in addition to grazing.

Our primary objective in this study was to evaluate the hypothesis that effects of green turtle grazing on metabolic carbon capture rates are consistent across seagrass meadows. We also evaluate variation in the strength of the response to grazing among meadows and how rates of metabolic carbon capture in invasive *H. stipulacea* meadows compare to native meadows where turtles graze. We compared rates of net ecosystem production (NEP) between grazed and ungrazed areas of *T. testudinum* seagrass meadows in four locations around the Greater Caribbean (definition from Petuch, 2013; Robertson & Cramer, 2014) and Gulf of Mexico with established green turtle grazing populations (in addition to those previously sampled in Little Cayman). The five total locations encompassed a wide geographical area and spanned a range of environmental and seagrass meadow characteristics representative of green turtle foraging areas in this region. The seagrass *H. stipulacea* had established at two of these locations, and we compared rates of NEP in meadows of this invasive species to those measured in both grazed and ungrazed areas of native meadows at these locations.

2 | MATERIALS AND METHODS

2.1 | Study sites

We sampled grazed and ungrazed areas of *T. testudinum* seagrass meadows at five locations across the Greater Caribbean and Gulf of Mexico where green turtles had established foraging areas (Figure 2).

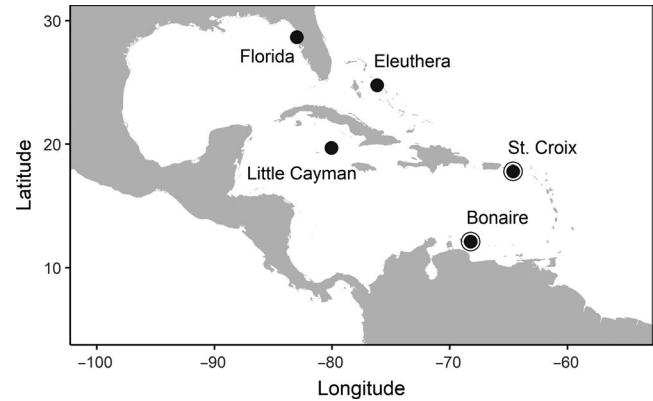


FIGURE 2 Map of seagrass meadow sampling locations. Two sites were sampled in each of Bonaire and Eleuthera, and one site was sampled at each of the other three locations. Circled symbols for St. Croix and Bonaire denote locations where *Halophila stipulacea* meadows were also sampled

One of these locations, Little Cayman, Cayman Islands, was sampled three times during June and July 2016 as part of a previous study (Johnson et al., 2017). The remaining four locations were sampled in 2018: St. Croix, US Virgin Islands (February); west coast of Florida (Gulf of Mexico side), USA (May); Bonaire, Caribbean Netherlands (July); Eleuthera, The Bahamas (August). We opportunistically sampled two separate sites in both Bonaire and Eleuthera, and one site at all other locations (time and/or weather conditions did not allow sampling additional sites at these locations). Established meadows of the seagrass *H. stipulacea* were present at two of the locations—St. Croix and Bonaire—and these meadows were also sampled for comparison to nearby grazed and ungrazed areas of native *T. testudinum* meadows (one of the sites in Bonaire only had nearby grazed *T. testudinum* for comparison). Coordinates and general environmental characteristics (daylight hours, water depth, salinity, temperature and irradiance) for all sites are given in Table 1.

The meadows sampled in this study varied greatly in size, from relatively small (<150 m²) for the grazed *T. testudinum* area at the northwest Lac Bay site in Bonaire, to very large (several square kilometres of unbroken seagrass habitat) for the ungrazed *T. testudinum* meadow at the North Rack site in Florida (west coast). Meadows at other sites encompassed a range of sizes between these two, such as ~350 m² each for the grazed and ungrazed *T. testudinum* areas in Little Cayman, and ~600 m² for the grazed area and >50,000 m² for the ungrazed *T. testudinum* meadow at the Arvida Bay site in Eleuthera, The Bahamas. At each site, a grazed area and adjacent ungrazed area were selected for sampling that were representative of the meadow. Samples (Sections 2.2 and 2.3) were collected within several metres of the border between the grazed and ungrazed areas to avoid possible edge effects while ensuring similar environmental conditions.

All sampled grazed areas (natural green turtle grazing plots) were nearly uniformly grazed. The proportion of grazed *T. testudinum* blades ranged from 95% to 100% in all grazed areas. Evidence of grazing by green turtles was not observed in ungrazed areas, except

TABLE 1 Coordinates of each sampling site and environmental parameters measured in the seagrass meadows on days of metabolic incubations

| Site | Latitude Decimal degrees | Longitude | Daylight hours | Depth M | Salinity ‰ | Temperature °C | Irradiance Lux |
|----------------|-----------------------------|------------|-------------------|------------|---------------|-------------------|-------------------|
| Bonaire | | | | | | | |
| Lac Cai Beach | 12.104417 | -68.223183 | 12.75 | 1.0 | 35 | 30.0 | 32451.8 |
| NW Lac Bay | 12.108546 | -68.231562 | 12.75 | 1.4 | 36 | 31.1 | 43221.7 |
| St. Croix | | | | | | | |
| BIRNM | 17.784612 | -64.624566 | 11.5 | 4.5 | 35 | 27.9 | 21190.4 |
| Little Cayman | | | | | | | |
| Grape Tree Bay | 19.696518 | -80.059652 | 13 | 1.0 | 36 | 31.9 | 55184.0 |
| | 19.696518 | -80.059652 | 13 | 1.0 | 37 | 31.7 | 46573.2 |
| | 19.696518 | -80.059652 | 13 | 1.0 | 38 | 33.6 | 60071.5 |
| Eleuthera | | | | | | | |
| Arvida Bay | 24.722297 | -76.190644 | 12.5 | 2.4 | 39 | 32.2 | 26764.8 |
| Half Sound | 24.936641 | -76.153420 | 12.5 | 0.6 | 36 | 34.4 | 71721.5 |
| Florida | | | | | | | |
| North Rack | 28.564760 | -82.779335 | 13.75 | 2.0 | — | 29.2 | 40980.1 |

Note: Temperature and irradiance data are mean values measured during incubations. The Little Cayman site was sampled three times in 2016. All other sites were sampled once in 2018. Sampling times are given in Section 2.1.

Abbreviation: BIRNM, Buck Island Reef National Monument site.

for in St. Croix, where ~3% of *T. testudinum* blades showed signs of grazing (cropped blade tips). Some fishes also graze on seagrass, and evidence of fish grazing (e.g. bite marks) was observed in ungrazed *T. testudinum* meadows at some sites. Biomass removal from fish grazing was minor compared to turtle grazing, however, and was not quantified. No evidence of green turtle grazing was observed in any *H. stipulacea* meadows.

We sampled seven areas from *T. testudinum*-dominated seagrass meadows that displayed signs of active green turtle grazing (hereafter grazed areas), six areas from *T. testudinum*-dominated meadows that were not grazed (hereafter ungrazed areas) and three meadows that were dominated by the invasive seagrass *H. stipulacea* (hereafter *H. stipulacea* meadows). These meadows were spread across a wide area of the Greater Caribbean and Gulf of Mexico regions and varied in their biotic and abiotic characteristics. Some of the sampled seagrass meadows, such as the *T. testudinum* meadows in Bonaire, were largely monospecific, whereas others were dominated by one species (*T. testudinum* or *H. stipulacea*) with interspersed *Syringodium filiforme* or *Halodule wrightii* seagrasses and various macroalgae (Table S1). The substrate in all meadows was primarily calcium carbonate sand. Additional meadow characteristics are provided in Results (Section 3.1). Data from the Little Cayman site have been reported previously (Johnson et al., 2017), and are presented again here for comparison to the other sites.

2.2 | Sampling seagrass meadow characteristics

Seagrass meadow and environmental characteristics were sampled at each site at the time metabolic incubations were conducted

(Section 2.3). Environmental temperature and irradiance were measured during metabolic incubations at seagrass canopy height (5-min intervals) at each site with a HOBO Pendant data logger (Onset Computer Corporation). A water sample was collected at canopy height and salinity was measured with a handheld AgTec Salinity Refractometer that was calibrated with freshwater each day before sampling (Agriculture Solutions, Strong, ME; no sample was collected at the Florida site). Meadow depth was measured at each location with either a tape measure or a scuba diver's depth gauge (accuracy ± 10 cm).

Seagrass species composition, shoot density, blade morphometry (length, width and surface area) and above-ground biomass were determined in all sampled areas (grazed, ungrazed, *H. stipulacea*) within 1 metre of where incubation chambers were placed. Shoot densities were measured using 25 \times 25 cm quadrats (0.0625 m² area) in *T. testudinum* meadows. Due to the high densities of *H. stipulacea*, 10 \times 10 cm quadrats (0.01 m² area) were used to measure shoot densities in meadows dominated by this species. Above-ground biomass samples were collected using 10 \times 10 cm quadrats (all meadows) by clipping all blades at the sediment surface with scissors. Six replicate quadrats (for both shoot density and biomass) were collected from all sampled areas at each site, except for the St. Croix ($n = 5$) and Florida ($n = 3$) sites (Table 2). Blade length and width were measured for the dominant species (*T. testudinum* or *H. stipulacea*) from 30 randomly selected seagrass blades from these biomass samples for each area. Blade surface area (i.e. photosynthetic area per blade) was calculated as two times the product of blade length and width (for each species). Following measurement, all blades were gently scraped clean of sediments and epiphytes (low epiphyte loads at all

TABLE 2 Seagrass characteristics of grazed and ungrazed areas of *Thalassia testudinum* meadows and *Halophila stipulacea* meadows measured at each sampling site

| Site | Meadow | n | Seagrass density | Canopy height | Blade surface area | AG biomass |
|----------------|----------------------|---|-----------------------|---------------|--------------------|---------------------|
| | | | shoots/m ² | cm | cm ² | g DM/m ² |
| Bonaire | | | | | | |
| Lac Cai Beach | Grazed | 6 | 741.3 ± 126.3 | 4.7 ± 2.2 | 6.3 ± 3.2 | 27.1 ± 7.6 |
| | Ungrazed | 6 | 954.7 ± 93.7 | 9.6 ± 3.9 | 21.4 ± 11.6 | 130.9 ± 54.4 |
| | <i>H. stipulacea</i> | 6 | 3850.0 ± 806.8 | 2.1 ± 0.6 | 1.9 ± 0.9 | 36.4 ± 13.3 |
| NW Lac Bay | Grazed | 6 | 237.3 ± 44.6 | 2.8 ± 1.4 | 2.8 ± 1.4 | 4.8 ± 2.8 |
| | <i>H. stipulacea</i> | 6 | 3483.3 ± 549.2 | 2.0 ± 0.4 | 1.8 ± 0.6 | 17.1 ± 5.9 |
| St. Croix | | | | | | |
| BIRNM | Grazed | 5 | 1964.8 ± 226.1 | 4.0 ± 2.3 | 4.4 ± 2.7 | 27.4 ± 10.2 |
| | Ungrazed | 5 | 2406.4 ± 250.1 | 8.1 ± 3.1 | 9.7 ± 4.5 | 51.6 ± 11.0 |
| | <i>H. stipulacea</i> | 5 | 3733.6 ± 1249.4 | 2.8 ± 0.5 | 3.2 ± 0.9 | 63.0 ± 24.0 |
| Little Cayman | | | | | | |
| Grape Tree Bay | Grazed | 6 | 957.3 ± 148.5 | 2.0 ± 0.9 | 2.3 ± 1.2 | 12.3 ± 3.7 |
| | Ungrazed | 6 | 1018.7 ± 210.2 | 14.9 ± 8.5 | 30.7 ± 20.4 | 183.2 ± 94.8 |
| Eleuthera | | | | | | |
| Arvida Bay | Grazed | 6 | 1648.0 ± 392.7 | 3.5 ± 1.9 | 4.2 ± 2.2 | 41.8 ± 13.9 |
| | Ungrazed | 6 | 2053.3 ± 329.9 | 15.2 ± 4.6 | 25.8 ± 8.8 | 202.2 ± 34.8 |
| Half Sound | Grazed | 6 | 1674.7 ± 316.7 | 1.8 ± 0.7 | 1.4 ± 0.6 | 8.8 ± 2.0 |
| | Ungrazed | 6 | 1784.0 ± 284.7 | 9.4 ± 2.0 | 10.8 ± 3.1 | 96.5 ± 16.2 |
| Florida | | | | | | |
| North Rack | Grazed | 3 | 1322.7 ± 444.1 | 2.5 ± 1.1 | 1.6 ± 0.8 | 9.3 ± 2.4 |
| | Ungrazed | 3 | 1386.7 ± 161.9 | 8.9 ± 2.7 | 7.8 ± 2.9 | 70.7 ± 23.3 |

Note: n is number of replicates at each site. Values are means ± SD. Canopy height is measured from mean blade length. Blade surface area is per blade of seagrass.

Abbreviations: AG, above-ground; BIRNM, Buck Island Reef National Monument site; DM, dry mass.

sites), rinsed in freshwater and dried to a constant weight at 60°C before weighing for dry mass.

2.3 | Ecosystem metabolism measurements

Metabolic carbon dynamics of the seagrass ecosystems were measured using benthic incubation chambers (Figure 1c), similar to previous studies (Barrón, Marbà, Terrados, Kennedy, & Duarte, 2004; Calleja, Barrón, Hale, Frazer, & Duarte, 2006; Johnson et al., 2017; Olivé, Silva, Costa, & Santos, 2015). Chambers were constructed by inserting a PVC cylinder (16 cm diameter, 0.02 m² area) ~7.5 cm into the sediment (attempting to avoid severing horizontal rhizomes), and attaching a flexible, gas-tight polyethylene bag with sampling port to the top (Hansen, Thamdrup, & Jørgensen, 2000). The use of flexible, gas-tight bags in chamber construction allows the propagation of wave turbulence to the chamber's interior to more closely simulate environmental conditions. Incubation chamber volume was measured in the laboratory to be 5.5–6 L. On sampling days, chambers were set up in the meadows between 10:30 and 11:30, and incubations were run for 2.5–3 hr. This incubation length was chosen because saturation effects can occur within chambers during longer

incubations and have been shown to underestimate metabolic rates (Olivé et al., 2015). Metabolic dynamics were measured three times at 2-week intervals in Little Cayman as part of a previous study and shown to be relatively stable among sampling events (Johnson et al., 2017). Incubations were therefore conducted once at each additional site in the present study.

We set up three light (clear) and three dark (opaque) chambers in each area (grazed or ungrazed *T. testudinum*, or *H. stipulacea*) to measure ecosystem metabolic rates ($n = 3$ for all areas). Light chambers were used to measure rates of NEP and dark chambers were used to measure rates of ecosystem respiration (R_E). Metabolic rates were estimated from changes in dissolved oxygen (DO) concentration inside the chambers between the beginning and end of the incubation period. Three water samples were collected from the chamber, via the sampling port, in 60-ml plastic syringes at the beginning and end of the incubation. Upon collection, syringes were capped with a silicon cap and brought to the surface where DO concentration was measured directly in the syringe with an optical DO probe (Vadeboncoeur, 2011; YSI ProODO, Yellow Springs, Ohio). The DO probe was calibrated at the beginning of each sampling day with water-saturated air.

To measure only metabolic rates of the seagrass/benthic components of the system (those affecting carbon storage), we corrected rates measured from incubation chambers for water column metabolism. We measured water column metabolism using biological oxygen demand (BOD) bottles at the same time as benthic chamber incubations. Three clear 300-ml glass BOD bottles and three opaque 300-ml glass BOD bottles were used to measure water column production and respiration, respectively. Bottles were filled with water at seagrass canopy height, anchored to the bottom and incubated under in situ conditions in the seagrass meadow. Water column samples were collected at the beginning of incubations in 60-ml syringes at canopy height, and DO concentration was measured in the same manner as samples from incubation chambers. Following the incubation period, bottles were collected and returned to the surface, one sample was collected from each bottle with a syringe, and DO concentration was measured.

Hourly metabolic rates were calculated from the difference in DO concentration within light (NEP) and dark (R_E) incubation chambers between the beginning and end of the incubation period. Water column metabolic rates measured from BOD bottles were subtracted from rates measured in chambers. Hourly gross primary production (GPP) was then calculated as the sum of hourly NEP and R_E . Daily rates of GPP were calculated by multiplying hourly GPP by the length of the photoperiod multiplied by 0.75 (to account for lower metabolic rates at dawn and dusk; Johnson et al., 2017; Olivé et al., 2015) and daily rates of R_E were calculated by multiplying hourly R_E by 24 hours. Daily NEP was calculated as the difference between daily GPP and R_E . There were a few occasions when an increase in DO concentration was measured within a dark chamber or the dark BOD bottles during an incubation, suggesting an error. These measured increases were small, usually within the probe's margin of error (0.1 mg O_2 /L), and we assumed respiration to be zero during these times. Correcting for these respiration errors had minor effects on daily metabolic rates in the meadows (Tables S2 and S3). Measured DO concentrations were converted from mg O_2 to mmol O_2 , and then to carbon units (mmol C) assuming photosynthetic and respiratory quotients of one (Barrón & Duarte, 2009).

2.4 | Data analyses

Net ecosystem production was the metabolic variable of primary interest, as it accounts for both carbon capture and loss and can be used as an indicator of whether a system is currently a metabolic carbon sink or source. Therefore, NEP is the metabolic variable for which statistical results are presented.

Our aim was to evaluate whether green turtle grazing has a consistent effect on metabolic rates across seagrass ecosystems—that is, to evaluate whether at any given site, at any given time, rates of NEP are lower in grazed areas than in ungrazed areas. We evaluated differences in rates of NEP between areas of grazed and adjacent ungrazed *T. testudinum* from each site with paired *t* tests. *T* tests were used because the comparison of interest was the difference between grazed and ungrazed areas (effect of

grazing) within a given site, not differences in NEP among sites. For sites where the invasive seagrass *H. stipulacea* was present, we used one-way ANOVAs to test for significant differences in rates of NEP between *H. stipulacea* meadows and nearby grazed and ungrazed *T. testudinum* areas (St. Croix site and Lac Cai Beach site, Bonaire). For the northwest site in Lac Bay, Bonaire, where only a grazed area of *T. testudinum* and an invasive *H. stipulacea* meadow were compared, an unpaired *t* test was used. If ANOVA results were significant, a Tukey's post-hoc test was used to identify significant comparisons. We tested for differences in seagrass meadow parameters between grazed and ungrazed *T. testudinum* areas and *H. stipulacea* meadows at sites using paired *t* tests and ANOVAs in the same manner as for NEP. We used linear regression to test relationships between NEP and explanatory variables (e.g. seagrass biomass, environmental temperature). Mean values for NEP and explanatory variables from each meadow were used for linear regressions tests, so there was a single data point for each grazed and ungrazed *T. testudinum* area or *H. stipulacea* meadow at each sampling site.

All analyses were performed in R version 3.4.3 (R Core Team, 2018). Data were processed using the 'dplyr' package (Wickham, Francois, Henry, & Müller, 2017) and post-hoc analyses were performed using the 'agricolae' package (de Mendiburu, 2017). All data met the assumptions for these analyses and data are presented as mean \pm SD.

3 | RESULTS

3.1 | Seagrass meadow characteristics

Total seagrass shoot densities varied widely among meadows and locations (Table 2), though shoot densities were always highest in *H. stipulacea* meadows. The lowest shoot density observed (237.3 ± 44.6 shoots/m²) was in a grazed area (NW site in Lac Bay, Bonaire), but there was no clear trend for higher or lower seagrass densities between grazed and ungrazed areas across the sampled sites. *Thalassia testudinum* density in Little Cayman was greater in the grazed area than ungrazed area (paired *t* test, $p = .02$), while *T. testudinum* density at the Lac Cai Beach site in Bonaire was greater in the ungrazed area (paired *t* test, $p = .02$). *Thalassia testudinum* density did not differ between grazed and ungrazed areas at the remaining sites (paired *t* tests, $p > .05$). Shoot density of *H. stipulacea* was not significantly different between any of the three *H. stipulacea* meadows measured (ANOVA, $F_2 = 0.09$, $p = .92$).

Halophila seagrasses typically grow short blades. Canopy height of the *H. stipulacea* meadow was similar to that of the nearby grazed area in St. Croix and was shorter than the nearby grazed areas at both sites in Bonaire (Table 2). *Halophila stipulacea* blade length was greater in St. Croix than Bonaire (ANOVA, $F_2 = 24.13$, $p < .01$). Areas of *T. testudinum*-dominated seagrass meadows grazed by green turtles had significantly shorter blades, and therefore canopy height, than adjacent ungrazed areas at all sampled sites (paired *t* tests, $p < .05$ for all comparisons; Table 2).

Green turtles, by cropping seagrass blades near the sediment surface and reducing canopy height, greatly reduce the above-ground seagrass biomass of meadows within their grazing areas. Above-ground biomass ranged from 4.8 ± 2.8 to 41.8 ± 13.9 g DM/m² among grazed areas (Table 2), and from 51.6 ± 11.0 to 202.2 ± 34.8 g DM/m² among ungrazed areas. Biomass was always lower in grazed areas than adjacent ungrazed areas ($p < .05$ for all comparisons). Biomass among the three sampled *H. stipulacea* meadows ranged from 17.1 ± 5.9 to 63.0 ± 24.0 g DM/m². The *H. stipulacea* meadow in St. Croix had significantly greater above-ground biomass than either of the *H. stipulacea* meadows sampled in Bonaire (ANOVA, $F_2 = 12.02$, $p < .01$). Evidence of green turtle grazing was only observed in *T. testudinum*-dominated meadows in this study, not *H. stipulacea* meadows, and grazing resulted in a >79% decrease in biomass in grazed compared to ungrazed areas at all sites, except St. Croix (47%; Table 3).

3.2 | Ecosystem metabolic rates

Rates of NEP differed among meadow types (grazed, ungrazed, *H. stipulacea*) across the studied locations (Figures 3 and 4; see Table S2 for data). Across all sites, NEP ranged from 4.2 ± 7.0 to 51.7 ± 11.0 mmol C m⁻² day⁻¹ among grazed areas, and from 52.3 ± 5.7 to 225.3 ± 19.1 mmol C m⁻² day⁻¹ among ungrazed areas. The large standard deviations on some of the ungrazed area NEP estimates from Little Cayman were a result of one incubation chamber producing rates much different from the other two. Across all sites, NEP was

TABLE 3 Per cent difference in metabolic rates and above-ground (AG) seagrass biomass between grazed and adjacent ungrazed *Thalassia testudinum* areas

| Site | GPP % difference | R _E | NEP | AG Biomass |
|----------------|---------------------|----------------|------|------------|
| Bonaire | | | | |
| Lac Cai Beach | 81.8 | 90.9 | 65.6 | 79.3 |
| St. Croix | | | | |
| BIRNM | 60.4 | 78.3 | 56.0 | 46.9 |
| Little Cayman | | | | |
| Grape Tree Bay | 92.2 | 95.5 | 89.1 | 93.3 |
| | 89.9 | 79.6 | 96.0 | 93.3 |
| | 88.5 | 87.0 | 90.0 | 93.3 |
| Eleuthera | | | | |
| Arvida Bay | 54.3 | 39.5 | 62.9 | 79.3 |
| Half Sound | 80.1 | 88.9 | 67.9 | 90.8 |
| Florida | | | | |
| North Rack | 61.5 | 41.3 | 91.9 | 86.8 |

Note: The Little Cayman site was sampled three times in 2016. All other sites were sampled once in 2018. Sampling times are given in Section 2.1.

Abbreviations: BIRNM, Buck Island Reef National Monument site; GPP, gross primary production; NEP, net ecosystem production; R_E, ecosystem respiration.

consistently lower in grazed areas than ungrazed areas (Figure 3). Differences in NEP between grazed and ungrazed areas were significant at four of the six sites where ungrazed *T. testudinum* was present: St. Croix, Little Cayman (all three measurement times), the Arvida Bay site in Eleuthera and Florida (paired *t* tests, $p < .05$ for all comparisons).

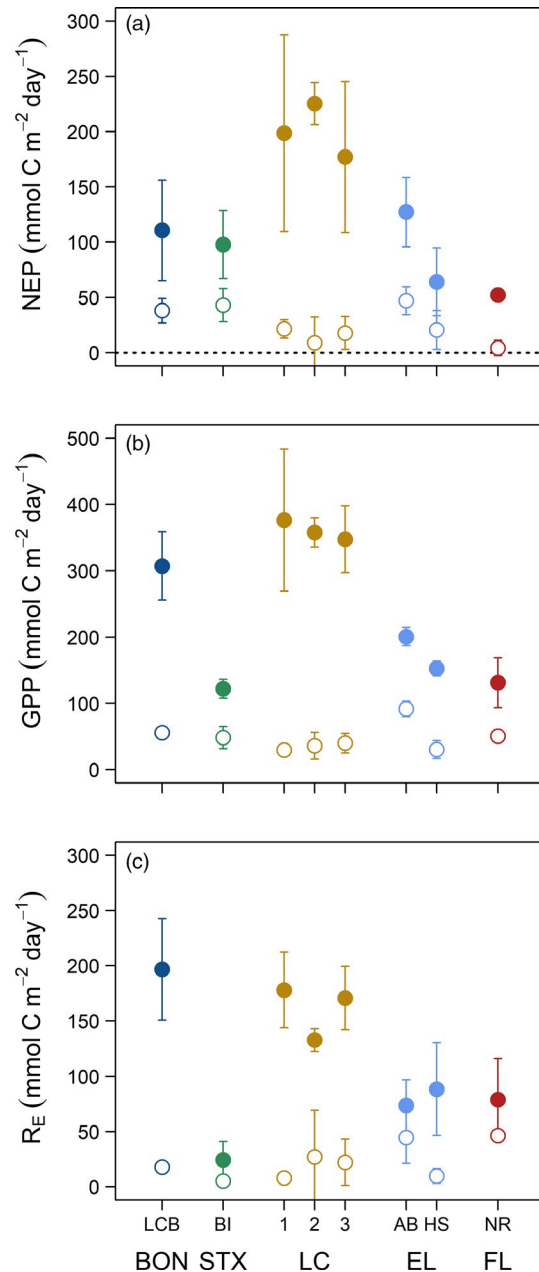


FIGURE 3 Rates (mean \pm SD) of net ecosystem production (a), gross primary production (b) and ecosystem respiration (c) from grazed (open points) and adjacent ungrazed (solid points) areas of *Thalassia testudinum* seagrass meadows. Rates of Net ecosystem production (NEP) were significantly lower in grazed areas than ungrazed areas at all sites except at Lac Cai Beach, Bonaire, and Half Sound, Eleuthera (Section 3.2). Sites ordered south to north. BON: Bonaire (LCB: Lac Cai Beach site); STX: St. Croix; LC: Little Cayman; EL: Eleuthera (AB: Arvida Bay site; HS: Half Sound site); FL: Florida. Dashed line in (a) denotes metabolic balance (NEP = 0). Values above line represent net metabolic carbon capture

At the Lac Cai Beach site in Bonaire and the Half Sound site in Eleuthera, differences in NEP between grazed and ungrazed areas were nearly significant (paired t tests, $p = .08$ and $p = .09$, respectively).

Though NEP was significantly lower in grazed than ungrazed areas at most sites, rates of NEP were almost always positive, as ecosystem respiration was not stimulated in relation to primary production even with considerable reduction of photosynthetic seagrass biomass by grazing (>79% biomass reduction at all sites except St. Croix; Table 3). NEP ranged from 56% to 96% lower in grazed areas than ungrazed

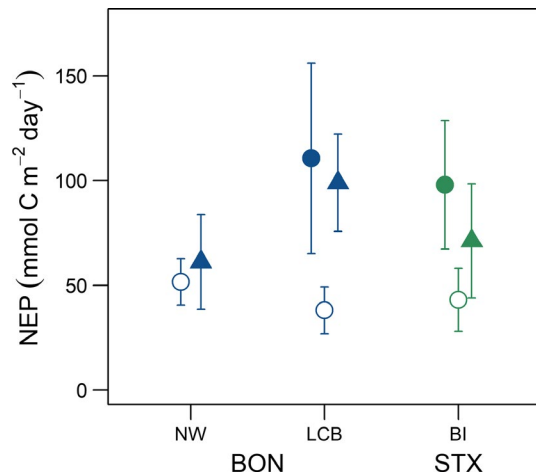


FIGURE 4 Rates (mean \pm SD) of net ecosystem production in meadows dominated by the invasive seagrass *Halophila stipulacea* (triangles) compared to nearby grazed (open circles) and ungrazed (solid circles) areas of *Thalassia testudinum* meadows. BON: Bonaire (LCB: Lac Cai Beach site; NW: northwest Lac Bay site); STX: St. Croix

areas (Table 3). A similar range in the difference between grazed and ungrazed areas was measured for gross primary production (54%–92% lower in grazed) and ecosystem respiration (40%–96% lower in grazed).

Halophila stipulacea meadows were present at three sites, and rates of NEP in these invasive seagrass meadows were compared to nearby native *T. testudinum*-dominated meadows. NEP in the *H. stipulacea* meadows was compared to nearby grazed and ungrazed areas of *T. testudinum*-dominated meadows at two of the sites (St. Croix and the Lac Cai Beach site in Bonaire). Within each site, rates of NEP in the *H. stipulacea* meadow were between those of the grazed and ungrazed areas (Figure 4), but the differences were not significant (ANOVA, $p > .10$ for all post-hoc comparisons within each site). An ungrazed area was not available for comparison at the third site at which *H. stipulacea* was present (NW Lac Bay site in Bonaire), as all *T. testudinum* at this site was grazed by green turtles, and rates of NEP did not differ between the invasive- and native-dominated areas at this site either (t test, $p = .56$; Figure 4). *Halophila stipulacea* meadow NEP ranged from 61.2 ± 22.6 to 98.9 ± 23.3 mmol C m⁻² day⁻¹ (Table S2), and did not differ significantly among the three sites at which it was present (ANOVA, $F_2 = 1.92$, $p = .23$), even though the establishment of *H. stipulacea* seagrass meadows in St. Croix was relatively recent (A. Gulick, unpublished data) compared to those in Bonaire (Willette et al., 2014).

3.3 | Drivers of metabolic rates

Variation in rates of seagrass ecosystem metabolism across grazed and ungrazed areas appeared to be driven by some characteristics of the seagrass meadows, but not by environmental factors. Meadow NEP was strongly, positively related to above-ground seagrass biomass across sites (linear regression, $R^2 = .82$, $p < .01$; Figure 5a). NEP

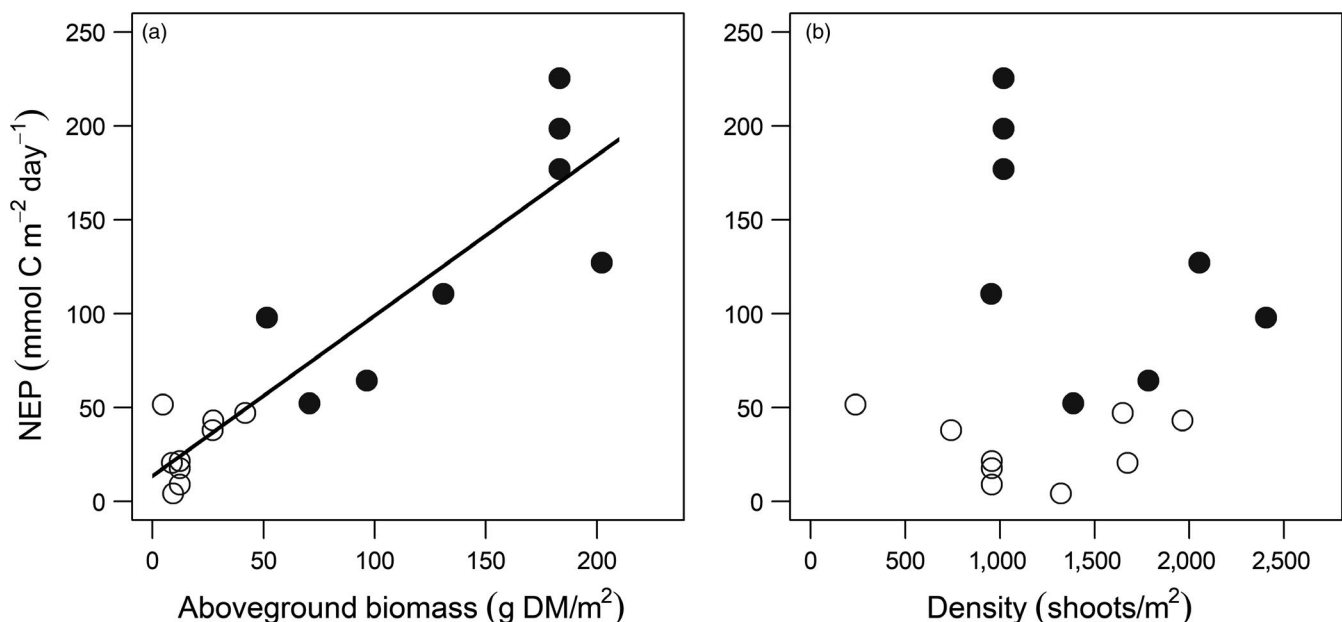


FIGURE 5 Relationship between net ecosystem production and above-ground seagrass biomass (a) and total seagrass shoot density (b) from grazed (open points) and ungrazed (solid points) areas of *Thalassia testudinum* meadows. Solid line in (a) is the significant linear regression ($R^2 = .82$, $p < .01$) between net ecosystem production (NEP) and biomass. NEP was not related to seagrass shoot density across meadows

was also positively correlated with seagrass meadow canopy height ($R^2 = .84$, $p < .01$) and blade surface area ($R^2 = .92$, $p < .01$). Above-ground biomass is likely the more useful predictor of meadow NEP however, as biomass is influenced by both canopy height and blade surface area and a change in either of these variables results in a change in biomass. NEP was not related to seagrass shoot density across meadows (linear regression, $R^2 < .01$, $p = .96$; Figure 5b), nor were there relationships between NEP and environmental temperature ($R^2 = .01$, $p = .70$), irradiance ($R^2 < .01$, $p = 1.0$) or meadow depth ($R^2 < .01$, $p = .77$) across sites (Figure S1).

4 | DISCUSSION

Through a comparative study of seagrass meadows—grazed and ungrazed—across a wide area encompassing sites in the Greater Caribbean and Gulf of Mexico, we found that green turtle grazing has a consistent effect on the metabolic carbon capture rates of *T. testudinum*-dominated seagrass meadows. Rates of metabolic carbon capture were always lower in areas grazed by turtles than ungrazed areas of meadows—up to 96% in Little Cayman—but rates of NEP were always near or above metabolic balance. Ecosystem respiration was not stimulated in relation to primary production within areas grazed by green turtles regardless of the amount of above-ground seagrass biomass removed through grazing or other differences in biotic and abiotic factors among sites. These findings lend additional support to the hypothesis that future rates of metabolic carbon capture may be lower in areas grazed by turtles, but grazing will not stimulate ecosystem respiration and result in a large remineralization of carbon currently stored in these seagrass habitats (Johnson et al., 2017).

The similarity in results between St. Croix (a winter measurement) and the other four locations in the present study (all summer measurements) strengthens our conclusion that grazing results in a consistent response in metabolic carbon capture across meadows. However, we were not able to address potential temporal dynamics within sites that may affect net carbon capture over an annual cycle in these systems. Future studies measuring carbon capture over longer temporal scales (i.e. seasonal) may be beneficial to our understanding of the effects of grazing on within-system carbon dynamics.

Though the response in metabolic rates to grazing was consistent across meadows, the strength of this response varied among individual sites. Some sites, such as Little Cayman, had considerably lower rates of NEP in grazed areas than ungrazed areas (mean 91.7%), whereas the response to grazing (difference in NEP between grazed and adjacent ungrazed areas) was less pronounced at other sites, such as St. Croix (Table 3). Seagrass meadow characteristics such as shoot density, canopy height and above-ground biomass are likely to be more variable among ungrazed areas than grazed areas, as green turtle grazing results in similar canopy morphology across meadows in the Greater Caribbean region (e.g. Bjørndal, 1980; Hernández & van Tussenbroek, 2014; Williams, 1988). Given

the strong relationship between NEP and above-ground biomass (Figure 5a), high variability in NEP would be expected across ungrazed meadows (e.g. Figure 3a). Indeed, the range in rates of NEP among ungrazed areas was nearly three times greater than the range measured across grazed areas in this study. As sites were specifically chosen that differed from each other in meadow characteristics, variation in the strength of the metabolic response to grazing would be expected.

Variability in the strength of the metabolic response to grazing resulted in the lack of a significant difference between grazed and ungrazed areas at two sites—Lac Cai Beach in Bonaire and Half Sound in Eleuthera (Figure 3a). It is possible that other factors not accounted for here, such as local environmental factors or green turtle grazing history (e.g. intensity, longevity of plot use), may have led to higher variability in metabolic rates at some sites and lack of a statistical difference. In addition, metabolic rates may exhibit within-meadow variation (patchiness) similar to below-ground carbon storage in meadows (Oreska, Mcglathery, & Porter, 2017), leading to higher variability in estimates and helping to explain the lack of a significant difference in NEP at these two sites. This could be driven in part by within-meadow spatial heterogeneity in above-ground biomass, given the strong relationship between biomass and NEP. High within-meadow variability in metabolic rates, if present, may also help explain the large variability measured in the ungrazed area in Little Cayman. Future studies using the eddy correlation technique (Berg et al., 2003) to measure ecosystem metabolism may be able to overcome some of this within-meadow variability; however, the great expense of this method makes it prohibitive for many studies.

Seagrass ecosystem metabolism is commonly estimated using oxygen dynamics measured with benthic incubation chambers (e.g. Barrón et al., 2004; Gacia et al., 2005; present study); however, there are some limitations to this method. Benthic chambers may sever below-ground rhizomes and release carbon that could affect metabolic estimates. Intact rhizomes, on the other hand, can affect the diffusive oxygen loss from the seagrass to the rhizosphere (Borum, Sand-Jensen, Binzer, Pedersen, & Greve, 2006) and may result in an underestimate of gross primary production (and therefore NEP). This may be minimized using shorter incubation times, as in this study. Incubation length also strongly affects metabolic rates estimated from oxygen dynamics (Olivé et al., 2015), with longer incubation times biasing estimates towards net heterotrophy. In addition to oxygen metabolism, other processes such as carbonate dynamics (Van Dam, Lopes, Osburn, & Fourqurean, 2019) play important roles in total ecosystem carbon dynamics without affecting the measured productivity of a meadow.

Caribbean *T. testudinum* meadows are highly productive (e.g. Johnson et al., 2017; Koch & Madden, 2001) and the relationship between biomass and NEP observed in this study suggests that meadows may maintain positive productivity as long as photosynthetic biomass remains. A threshold biomass below which Caribbean meadows may become net heterotrophic cannot be directly addressed here but could be predicted to be near zero. This is in contrast to a previously suggested above-ground biomass

threshold (41 g DM/m²) below which meadows may become heterotrophic (Duarte et al., 2010). However, that threshold was calculated for seagrasses globally and included less productive species. Additional studies of the relationship between biomass and meadow NEP from seagrass species and regions other than those in the present study would be beneficial to further generalize how grazing affects metabolic carbon capture across seagrass ecosystems.

Environmental temperature and irradiance are strong drivers of seagrass meadow productivity (Calleja et al., 2006; Lee & Dunton, 1997; Lee, Park, & Kim, 2007; Pérez & Romero, 1992); however, previous studies examining controls on seagrass metabolism have focused on ungrazed seagrasses (e.g. Apostolaki, Holmer, Marbà & Karakassis, 2010; Gacia et al., 2005). Meadow metabolic productivity correlates strongly with above-ground seagrass biomass (Johnson et al., 2017; Figure 5a) that can be greatly affected by green turtle grazing (Bjorndal, 1980; Cebrián & Duarte, 1998; Christianen et al., 2012; Fourqurean, Manuel, Coates, Kenworthy, & Smith, 2010; Williams, 1988). Above-ground biomass explained 82% of the variation in NEP across grazed and ungrazed *T. testudinum* meadows in this study, but NEP was not correlated with either environmental temperature or irradiance (Figure S1). We therefore investigated whether the lack of an observed relationship between NEP and temperature and irradiance was perhaps due to a larger effect from differences in biomass caused by grazing masking any effect of these environmental variables. We scaled metabolic rates to the above-ground biomass in each grazed and ungrazed area (unit metabolism per unit biomass) and compared them to temperature and irradiance. Accounting for differences in above-ground biomass did not reveal an underlying relationship between NEP and these environmental parameters across meadows (grazed, ungrazed or all areas combined; Figure S2). The lack of a relationship between NEP and environmental parameters in this study may be due in part to the relatively limited range of temperature and irradiance in seagrass meadows grazed by green turtles in the Greater Caribbean. All meadows in this study were located in relatively shallow, warm tropical and subtropical environments receiving high levels of incident sunlight.

4.1 | Effects of *Halophila stipulacea* invasion on meadow carbon capture

In addition to the new metabolic carbon capture estimates we contribute from grazed areas in *T. testudinum* meadows, we also present the first estimates of NEP from meadows dominated by *H. stipulacea* seagrass. Having been first reported in the Caribbean in 2002 (Ruiz & Ballantine, 2004), *H. stipulacea* has spread rapidly among islands and become invasive in this region (Christianen et al., 2018; Willette et al., 2014). *Halophila stipulacea* may also spread more quickly within areas of seagrass grazed by green turtles than in ungrazed areas (Christianen et al., 2018), suggesting that grazing may inadvertently facilitate the spread of this invasive species once it has become established in

an area. In Lac Bay, Bonaire, green turtles have begun to expand their grazing plots into areas of previously ungrazed *T. testudinum* as *H. stipulacea* slowly takes over the historically grazed areas within the bay (Christianen et al., 2018; Smulders, Vonk, Engel, & Christianen, 2017). If this relationship between green turtles, native seagrasses and invasive seagrass exists in other areas, it could have implications for total ecosystem carbon dynamics and carbon storage as well as other ecosystem functions within these meadows.

Our results demonstrate that rates of metabolic carbon capture may be similar between *H. stipulacea* meadows and the native *T. testudinum* meadows that they are replacing (Figure 4). However, given the limited number of *H. stipulacea* meadows, we were able to sample in this study ($n = 3$), caution is warranted in extrapolating these findings widely to other locations facing invasion by *H. stipulacea* seagrass. While rates of NEP in *H. stipulacea* meadows were similar to both grazed ($n = 3$) and ungrazed ($n = 2$) areas of *T. testudinum*-dominated meadows in St. Croix and Bonaire (within-site comparisons), multiple factors affect these rates that may differ and affect this relationship in other locations (e.g. dominant species of native seagrass, density and biomass of *H. stipulacea* vs. the native species, blade epiphyte coverage). For example, this relationship may differ in areas such as Dominica (eastern Caribbean), where the meadows undergoing *H. stipulacea* invasion are dominated by *S. filiforme* seagrass (Willette & Ambrose, 2012). Measurements from additional locations will greatly aid in understanding the spatial extent of the similarity in metabolic carbon capture rates between *H. stipulacea* and native seagrass meadows seen here. However, the comparable metabolic rates between the invasive and native seagrasses measured in this study suggest some benefits of seagrass presence may be retained in meadows following invasion by *H. stipulacea*, such as local mitigation of ocean acidification (through metabolic buffering of pH; Camp et al., 2016; Hendriks et al., 2014; Unsworth, Collier, Henderson, & McKenzie, 2012).

It is not yet known whether comparable rates of metabolic carbon capture will translate to comparable carbon sequestration or storage in meadows dominated by invasive *H. stipulacea*. Unlike *T. testudinum* (van Tussenbroek et al., 2006), seagrass species within the genus *Halophila* do not form a deep below-ground rhizome mat (Fonseca, 1989). Robust rhizome mats formed by some seagrass species contribute to higher below-ground carbon storage (Christianen et al., 2013), and the lack of a similar rhizome mat may result in lower sediment carbon storage in *H. stipulacea* meadows. *Halophila* tissues also decompose quickly in sediment (Josselyn, Fonseca, Niesen, & Larson, 1986), and this may affect seagrass-derived carbon input to the sediments in invaded meadows compared to native species with higher refractory organic matter content (Trevathan-Tackett et al., 2017). Further studies on carbon dynamics in *H. stipulacea* meadows will be needed to form a better understanding of how the continued invasion by this species will affect total ecosystem carbon dynamics in seagrass meadows in the Caribbean.

4.2 | Greater global assessment of grazed meadows needed

Ungrazed areas of *T. testudinum*-dominated seagrass meadows from this study exhibited rates of NEP (median 104.0 mmol C m⁻² day⁻¹) near the upper end of those reported in the literature for seagrass ecosystems, and grazed areas in this study exhibited rates (median 38.1) near the median value of NEP for all reported ungrazed seagrass meadows (median 27.1; Figure 6). Measurements of seagrass metabolic carbon capture are relatively geographically limited however, with the majority of measurements—mostly from ungrazed *T. testudinum*-dominated meadows—coming from the Greater Caribbean and Gulf of Mexico regions. The Caribbean and Gulf of Mexico are ecologically important grazing regions, but only a single estimate of seagrass metabolism from a grazed area existed prior to this study (Johnson et al., 2017).

All meadows in the present study exhibited a consistent response of metabolic carbon capture to green turtle grazing; however, our study was limited to the effects of grazing in tropical and subtropical *T. testudinum*-dominated meadows. It is possible that meadows in other regions of the world, perhaps dominated by different seagrass species and under different environmental conditions, will not exhibit the same response to grazing in terms of metabolic carbon dynamics. We are aware of only one other study in which this was investigated. In a tropical *Thalassia hemprichii* meadow (Tanzania), NEP was reduced as a result of experimental clipping to simulate grazing (Dahl et al., 2016); however, only hourly rates of daytime NEP were measured. Without corresponding rates of respiration, we cannot evaluate if NEP remained

positive in this *T. hemprichii* meadow over a diel cycle and if the response to experimental clipping in Tanzania was similar to the response to grazing measured in our study. Further studies on effects of grazing on seagrass meadow metabolic carbon dynamics would be particularly beneficial in (a) additional areas where grazer abundance is increasing and (b) meadows dominated by species other than *T. testudinum*.

5 | CONCLUSION

Given the importance of seagrass meadows as blue carbon ecosystems (Fourqurean et al., 2012) and their role in carbon sequestration and potential climate change mitigation, it is necessary to understand how meadow carbon dynamics are affected by grazing. Our study adds critical information on the effects of grazing on seagrass metabolic carbon dynamics and how these processes may be affected with increasing green turtle abundance and grazing. We demonstrate that the response in metabolic carbon capture to green turtle grazing is consistent across seagrass ecosystems in the Greater Caribbean and Gulf of Mexico regions—an area that supports vast expanses of seagrass (Green & Short, 2003; Jackson, 1997; Wabnitz et al., 2008). This is an ecologically important grazing region for green turtle populations, and given increasing green turtle abundance across the globe (Chaloupka et al., 2008; Mazaris et al., 2017), it is expected that more seagrass area will return to a natural grazed state. Our results suggest that increased grazing will translate to lower rates of metabolic carbon capture but will not stimulate respiration and the metabolic loss of carbon from these meadows.

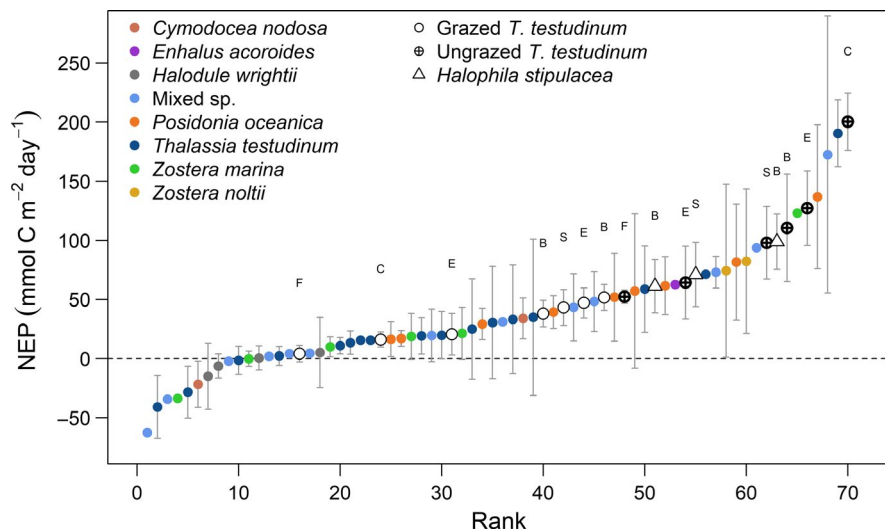


FIGURE 6 Rates (mean \pm SD) of net ecosystem production from meadows of various seagrass species collected from the literature. Open circles, 'crossed' circles and open triangles are grazed *Thalassia testudinum* ($n = 7$), ungrazed *T. testudinum* ($n = 6$) and *Halophila stipulacea* ($n = 3$) meadows, respectively, from the present study. Filled circles are previously published estimates of ungrazed seagrass meadow net ecosystem production (NEP) and come from various locations around the world. Criteria for literature collection and data inclusion are described in Johnson et al. (2017). Rates of NEP from ungrazed *T. testudinum* and *H. stipulacea* meadows from the present study are near the upper end of published values. Median NEP from grazed *T. testudinum* areas (present study) is similar to the median NEP of ungrazed seagrass meadows globally (Section 4.2). Figure modified from Johnson et al. (2017) to include additional estimates. Letters above points denote sites from the present study – B: Bonaire; C: Little Cayman; E: Eleuthera; F: Florida; S: St. Croix

There are many different fluxes, in addition to metabolism, that contribute to total ecosystem carbon dynamics in seagrass meadows (Mateo, Cebrián, Dunton, & Mutchler, 2006). To fully understand the effects of green turtle grazing on total carbon capture and storage in seagrass ecosystems, a better understanding is needed on how other carbon fluxes and stocks also respond to grazing. In addition to reducing above-ground biomass, green turtle grazing also led to reduced below-ground rhizome carbohydrate reserves in a meadow in Bermuda (Fourqurean et al., 2010). However, a better understanding of temporal dynamics of carbon stored in seagrass tissues is needed among naturally grazed areas. The majority of carbon in seagrass meadows is stored in below-ground sediments (Fourqurean et al., 2012), and the trapping of organic particles is an important process by which seagrasses accumulate sediment carbon (Gacia, Granata, & Duarte, 1999). Recent research has shown that green turtle grazing may not directly lead to increased erosion of sediments from coastal meadows in this region (Johnson, Gulick, Bolten, & Bjorndal, 2019), but further research is needed to understand how long-term (e.g. decadal) grazing may affect sediment carbon stocks. Future studies on additional carbon fluxes and stocks will be beneficial and complementary to our results on metabolic carbon dynamics, which show that an increase in green turtle abundance and grazing pressure is not expected to result in a large remineralization of carbon from these important ecosystems.

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AUTHORS' CONTRIBUTIONS

R.A.J., A.B.B. and K.A.B. conceived of and designed the study. All authors contributed to planning field sampling at the various locations. R.A.J., A.G.G. and N.C. collected the data. R.A.J. analysed the data. All authors contributed to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

Data are archived in the Environmental Data Initiative repository: <https://doi.org/10.6073/pasta/c2ba534cb03a7d1ef203a3af63bfe6bc>. (Johnson, Gulick, Constant, et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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