



## Growth and recovery after small-scale disturbance of a rapidly-expanding invasive seagrass in St. John, U.S. Virgin Islands

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### ABSTRACT

Seagrass meadows evolved in the presence of disturbances and have a wide variance in recovery rate that largely follow a trajectory of re-colonization and succession to pre-disturbance levels. Invasive species may gain a foothold within native seagrass beds after space is opened by disturbances that reduce seagrass cover. Here we use shoot density monitoring data to describe growth of the invasive seagrass *Halophila stipulacea* in Caribbean bays over a 5-year period and conduct a series of experiments using a combination of mesocosm, seagrass removal plots, and field measurements to quantify vegetative fragment survivorship and recovery after benthic disturbance. Shoot density increased rapidly in invaded bays, reaching average densities of approximately 600 shoots/m<sup>2</sup> within 5 years of establishment. Seagrass cover was estimated to recover to pre-disturbance level 17–31 weeks after removal from vegetative propagation of neighboring plants outside the treatment plot. Mesocosm experiments found floating and settled fragments as small as 2 cm in length and containing at least one vertical shoot survived the 4-day trial and increased in both length and biomass. Empirical evidence here demonstrates that *H. stipulacea* is highly resilient to small-scale disturbance which we suggest is having a transformative impact on Caribbean seagrass communities.

### 1. Introduction

Seagrass ecosystems can be resilient to disturbance. Disturbances may damage or remove seagrass biomass yet can also induce rapid regrowth and subsequent expansion of seagrasses after the perturbation subsides (O'Brien et al. 2018). For example, hurricane disturbance in native Caribbean *Syringodium filiforme* beds enhanced the dispersal of seeds and seagrass fragments thus facilitating local expansion of the species (Kendall et al. 2004). Likewise, Caribbean *Halophila decipiens* recovered to its pre-disturbance levels of biomass and cover within 6 months after a hurricane via vegetative expansion and sexual reproduction (Williams 1988). Recovery after anchor scarring was slower, taking 7 months–4 years for *Halodule wrightii* (Dawes et al. 1997; Williams 1990) and 2–8 years for *Thalassia testudinum* (Dawes et al. 1997). Habitats like seagrass beds have evolved in the presence of disturbances (White 1979) and recovery from such events have a wide variance in recovery rate yet typically follows a trajectory of re-

colonization and succession to a community comparable to pre-disturbance states (Dayton 1971; Fonseca et al. 2000; Kenworthy et al. 2002; O'Brien et al. 2018).

Understanding how aquatic macrophytes spread into suitable habitats is of long-standing interest in plant biology (Leakey 1981; Silvertown 2008; Bornette and Puijalon 2011), and of increasing importance in the restoration of native marine plants (Orth et al. 1984; Di Carlo et al. 2005) and control of invasive marine species (Smith and Walters 1999; Wang et al. 2014). The dispersal and colonization capability of plants, including non-native species, is important as global changes in the natural environment will have profound effects on current and forecasted species distributions (Birchenough et al. 2015; Lenoir and Svenning 2015). Disturbance is one mechanism to explain the establishment and spread of non-native species into seagrass beds (Williams 2007), and the increasing frequency of natural and anthropogenic disturbances foreshadow growing challenges for native Caribbean seagrass habitats (Waycott et al. 2009; Unsworth et al. 2018).

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Invasive species may gain a foothold within native seagrass meadows after physical disturbances open space by eliminating or thinning seagrass cover (Williams 2007). For example, sparse *Posidonia oceanica* meadows were readily invaded by an invasive macroalga from the genus *Caulerpa* whereas *P. oceanica* beds with high shoot density were resistant to invasion (Meinesz and Hesse 1991; Klein and Verlaque 2008). Likewise, interactions between native *S. filiforme* and invasive *Halophila stipulacea* along the Caribbean island of Dominica demonstrated that *S. filiforme* beds with  $\geq 45\%$  benthic cover were able to resist invasion, yet less dense *S. filiforme* beds were replaced with *H. stipulacea* over a five-year period that included multiple storm disturbances that opened benthic spaces (Steiner and Willette 2015). *Halophila stipulacea* has also been reported to grow over dead mats of *P. oceanica* where it has invaded in the southern Mediterranean Sea (Sghaier et al. 2011). Invasions by members of the genus *Halophila* are particularly remarkable as this group has some of the highest rhizome extension rates, leaf turnover times, and maximum seed densities of all seagrasses (O'Brien et al. 2018). Further, its fragments have among the farthest dispersal potential of seagrasses (Weatherall et al. 2016).

The Indo-Pacific seagrass *H. stipulacea* is the first globally-invasive marine angiosperm and is driving major restructuring of seagrass ecosystems (Willette and Ambrose 2012; Sghaier et al. 2014; Olinger et al. 2017). This tropical, euryhaline seagrass is native to the Indian Ocean, Red Sea, and Persian Gulf (Den Hartog 1970). It was first reported in the Mediterranean Sea in the late-1800s, likely the result of dispersal of fragments in fishing nets on vessels moving through the Suez Canal (Lipkin 1975). It was first observed in the southeastern Caribbean Sea along the island of Grenada in 2002, potentially introduced by recreational boats sailing between the Mediterranean and Caribbean Seas (Ruiz and Ballantine 2004). In the Caribbean Sea, this seagrass has thrived and spread rapidly in the 17 years since it was first reported, now occurring on at least 25 islands and along the coast of South America (Vera et al. 2014; Willette et al. 2014; Ruiz et al. 2017). *Halophila stipulacea* fragments are created when the plant is disturbed by natural (storms, animal grazing) or human (anchoring, dragging of fishing gear) activities (Ruiz and Ballantine 2004; Willette and Ambrose 2012; Steiner and Willette 2015). These fragments can float and may prompt local asexual spread of the seagrass (Willette et al. 2014; Steiner and Willette 2015). Local spread is believed to be driven solely by vegetative fragments, as *H. stipulacea* found in the Caribbean has a low flowering percentage compared to other seagrasses (Den Hartog 1970) and only recently have male flowers (Vera et al. 2014, Chiquillo et al. 2019) been found. But, to date, no female flowers have been observed in the region.

Seagrass habitats are regularly disturbed systems that recover over time using natural successional processes (Fonseca et al. 2000). In this study we evaluate if the invasive seagrass *H. stipulacea* has growth traits that take advantage of open spaces created by disturbance, helping to explain why the species' Caribbean invasion has been so effective. We use shoot density monitoring data to describe growth of the seagrass in four bays over a 5-year period and conduct a series of experiments using a combination of mesocosm, seagrass removal plots, and field measurements to quantify rates of vegetative fragment survivorship and recovery after benthic disturbance.

## 2. Methods

Field work was conducted within the Virgin Islands National Park, St. John, United States Virgin Islands. *Halophila stipulacea* was first reported on the island in 2012 (Willette et al. 2014) at Mennebeck Reef and has since spread to multiple bays (Fig. 1).

### 2.1. Monitoring of *H. stipulacea* shoot density at mooring sites

*Halophila stipulacea* shoot density was recorded beneath mooring buoys in four locations (Fig. 1): Hawksnest Bay (18° 21'N, 64° 46'W),

Maho Bay (18° 21'N, 64° 44'W), Frances Bay (18° 21'N, 64° 44'W), and Leinster Bay (18° 21'N, 64° 43'W). These mooring buoys were installed by the National Park Service (NPS) in 1999 and 2000 and the NPS maintained regular monitoring of seagrass cover below these moorings between 2000 and 2016. Five mooring buoys were selected within each bay (except four in Frances Bay) where seagrasses were known to occur based on historical NPS maps. At each buoy four 25-m transects were placed extending out from the mooring anchor along four fixed headings of 33°, 87°, 124°, and 205°, and ten 20 cm × 20 cm quadrats were placed at randomly chosen positions along the transect line (the same quadrat locations were monitored in subsequent monitoring events). The monitored seagrass meadows and transects were between 3 and 15 m depth. Total short shoot counts of *H. stipulacea* were recorded. Measurements were taken once a year in April or May, and a second time when resources permitted in November or December, from 2012 to 2016. Shoot counts were normalized to density per m<sup>2</sup> and averaged by year and by bay. A linear mixed model was fit to *H. stipulacea* shoot counts between 2012 and 2016 to estimate the yearly rate of increase with bay as the random variable and year as the fixed effect. The linear mixed model was conducted in R version 3.5.1 (R Core Team, 2018) using the “lmer” function (from the lme4 package, Bates et al. 2015) and statistical significance was calculated with the “summary. merModLmerTest” function from the lmerTest package (Kuznetsova et al. 2017) using the Satterthwaite method for approximating degrees of freedom to calculate *p*-values.

### 2.2. *Halophila stipulacea* lateral expansion

We estimated the lateral rhizome expansion rate for *H. stipulacea* to compare to rates measured elsewhere in the Caribbean (sensu Willette and Ambrose 2009). To incorporate potential spatial variability in expansion rate, lateral expansion measurements were taken at multiple locations in three *H. stipulacea* beds (total *n* = 13) in Great Lameshur Bay (GLB) in July 2014. The monospecific *H. stipulacea* beds were surrounded by bare sand. Expansion rates were quantified by placing 10 cm garden staples (Jobe's Company, Texas) with colored flagging tape at the growing end of horizontal rhizomes at the margins of the patches and measuring the distance the rhizome extended past the staple after seven days. Mean daily expansion rate was expressed by dividing the growth (in cm) by the number of days.

### 2.3. Growth of floating *H. stipulacea* fragments

The viability of floating *H. stipulacea* fragments was determined by creating experimental fragments from whole plants dug up by hand from GLB, gently shaken of sediment, and immediately taken in plastic bags to the Virgin Island Environmental Research Station (VIERS) outdoor lab. Seagrass was cleaned of epiphytic material, and rhizomes inclusive of at least one vertical shoot were cut into fragments of 1 cm, 2 cm, 5 cm, and 10 cm lengths (*n* = 5 per length) and weighed to obtain an average biomass per length. Lengths were selected based on previous work which reported *H. stipulacea* fragments generated by fish traps were of similar length and included at least one vertical shoot (Willette and Ambrose 2012). Fragments were placed in a 75 l tank with flow-through ocean water. Five cm of sand was placed at the bottom of the tank and observations were made twice daily for fragments which settled in the sand. After 4 days, which was the amount of time floating fragments remained viable reported by Hall et al. (2006) for a native Caribbean *Halophila* congener, fragments were removed, re-measured for length, re-weighed for biomass, and fragment growth was calculated as change from initial.

### 2.4. Growth of settled *H. stipulacea* fragments

We conducted a second experiment to evaluate the ability of fragments of different sizes to establish and grow. Fragments of 1 cm, 2 cm,

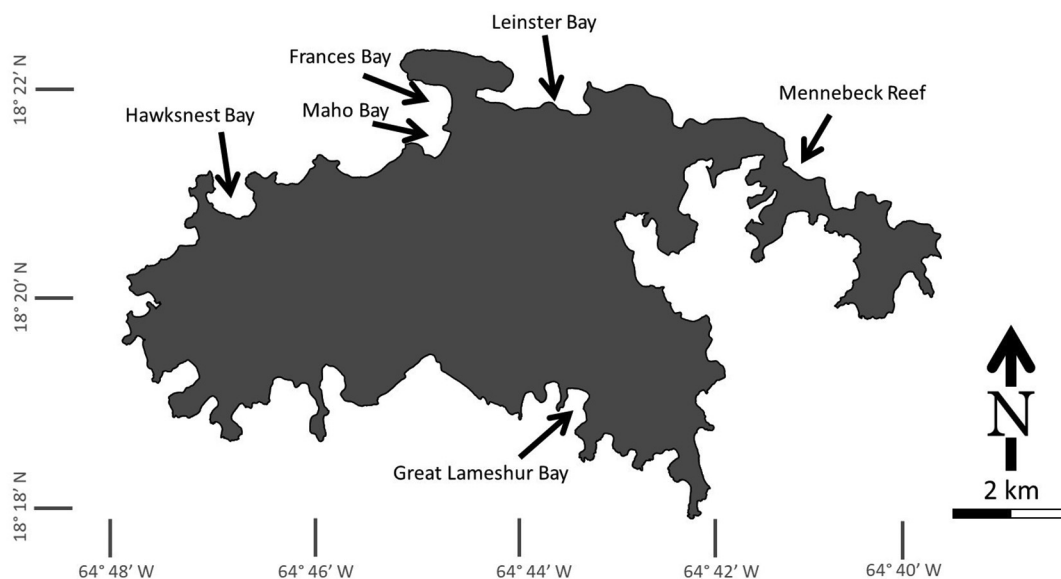


Fig. 1. Map of St. John Island, indicating location of mooring buoy monitoring sites of Hawksnest Bay, Maho Bay, Frances Bay, and Leinster Bay, the experimental research site of Great Lameshur Bay (GLB), and Mennebeck Reef where *H. stipulacea* was first reported in 2012.

5 cm, and 10 cm length ( $n = 10$  per length) were prepared as above with at least 1 vertical shoot. Fragments were gently pressed into 3 cm of sediment in grow trays, and trays were placed in a circulating ocean water wet table at the VIERS outdoor lab. Seagrass fragments grew for 4 days, then were re-measured for length and re-weighed for biomass to determine if fragments survived and what, if any, were the growth rates of each fragment length. A One-way ANOVA was used to test for significant differences in growth rates among fragment lengths.

### 2.5. Removal and recovery rate of *H. stipulacea*

To evaluate the recovery of *H. stipulacea* after a disturbance, ten 1 m<sup>2</sup> plots of the invasive seagrass were removed from an invasive seagrass bed in GLB by hand-pulling using SCUBA in January 2017. All plots were at depths between 4 and 6 m and appeared to have similar initial shoot density and substrate type. Each 1 m<sup>2</sup> plot was initially defined by pressing a 1 m<sup>2</sup> aluminum cutting frame into a pure *H. stipulacea* stand and the frame hammered down to a depth of 10 cm to sever rhizomes and roots (Pereg et al. 1994). All above and below sediment seagrass biomass within the cut area was dug out with a small trowel or pulled by hand, placed in a large mesh bag, removed from the site, and weighed. Removal of each 1 m<sup>2</sup> plot took approximately 1 person-hour. To ensure all seagrass biomass was completely extracted, a first pass taking ~30–45 min removed most seagrass, followed by a ‘fine cleaning’ for approximately 15–20 min. Loose floating blades were also removed from the plots to the best of our ability. After clearing seagrass, the frame was removed, and steel rebar markers and plastic tags were placed at the corners to relocate the plots.

Removal plots and nearby control plots (2–3 m away, rhizomes not cut, but markers placed to assist in re-locating) were photographed immediately after and 1, 2, 4, 6, and 14 weeks after removal. High-resolution photographs were taken with a GoPro Hero 5 camera equipped with an underwater light filter and mounted on a PVC stand to maintain a consistent distance from the plot. Four photos of 0.25 m<sup>2</sup> sections were taken per plot to provide better resolution images. Digital photos were analyzed by creating area polygons using ImageJ software to quantify the percentage of seagrass cover at each time interval. A two-way ANOVA was used to compare the change in percent cover of seagrass week to week, between removal and control plots, and the interaction of these two factors. The percent of cover at monitoring intervals was fit with linear and exponential non-linear regressions to

explore the best fit, and to estimate time (weeks) until removal plots would recover to the percent cover of the control plots.

## 3. Results

### 3.1. Monitoring of *H. stipulacea* shoot density at mooring sites

*Halophila stipulacea* was observed in Leinster Bay in 2012, followed by Frances Bay and Hawksnest Bay in 2014, and Maho Bay in 2015 (Fig. 2). *Halophila stipulacea* shoot density increased from 0 shoots m<sup>2</sup> prior to 2012 to an overall average ( $\pm$  SE) of  $599.2 \pm 122.3$  shoots m<sup>2</sup> by 2016. *Halophila stipulacea* shoot density initially reported in Leinster Bay was very high and continued to increase in count, whereas shoot density at Hawksnest Bay and Frances Bay were first counted below 35 shoot m<sup>2</sup> and increased severalfold in subsequent samplings (Fig. 2). Shoot density in Maho Bay was similar in both years observed (150 shoot m<sup>2</sup>). *Halophila stipulacea* shoot count in 2016 was highest in Leinster Bay at 2108 shoots/m<sup>2</sup>, followed by 800 shoot m<sup>2</sup> in Hawksnest Bay, 320 s shoots/m<sup>2</sup> in Francis Bay, and 150 shoot m<sup>2</sup> in Maho Bay. Results from the linear mixed model based on the 2012–2016 monitoring data indicated a statistically significant increase in shoots per quadrat ( $t = 28.7$ ,  $DF = 421$ ,  $p < 0.0001$ ).

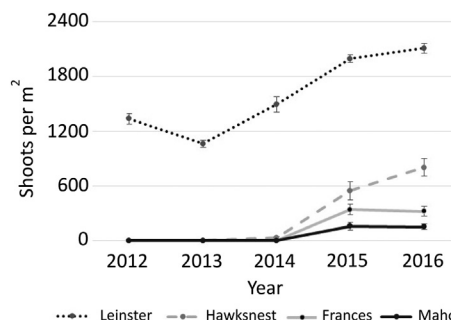
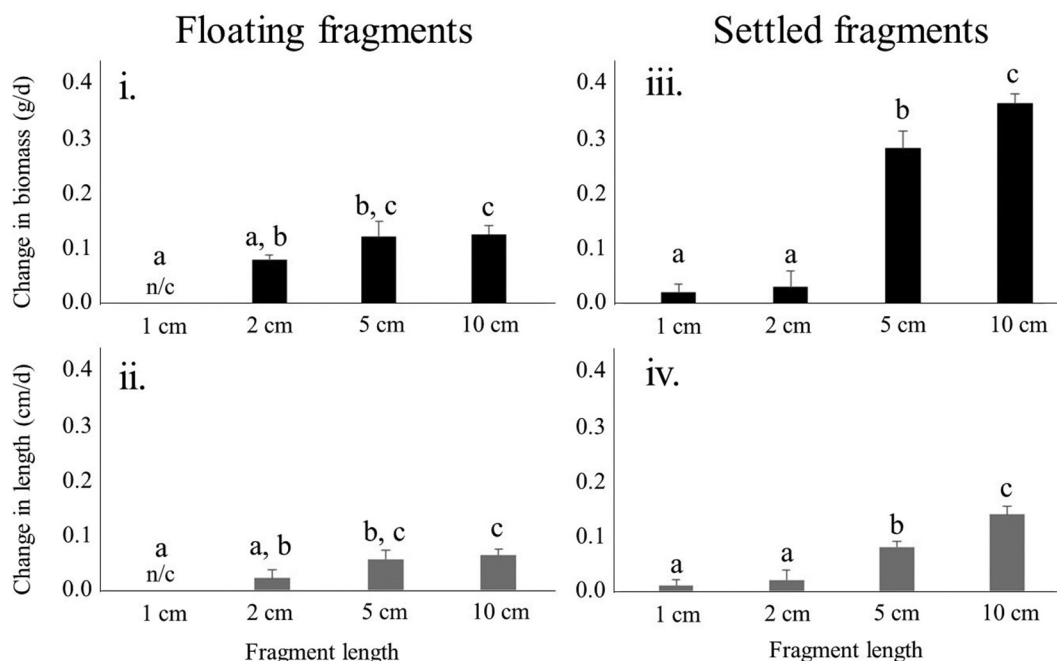
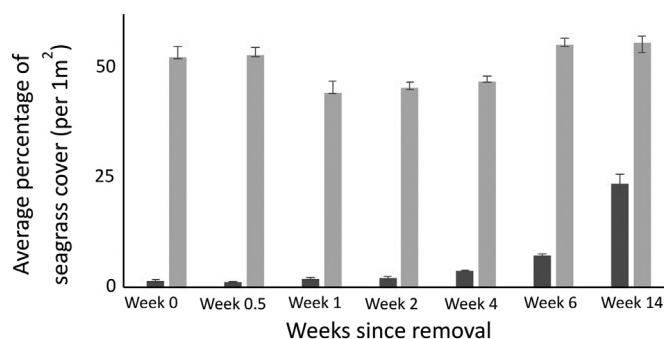


Fig. 2. Shoot count (shoot m<sup>2</sup>  $\pm$  SE) for *Halophila stipulacea* by location, Leinster Bay (black dotted, first observed in 2012), Hawksnest Bay (grey dash, first observed in 2014), Frances Bay (grey line, first observed in 2014), and Maho Bay (black line, first observed in 2015). Shoot counts obtained using 20 cm  $\times$  20 cm quadrats.



**Fig. 3.** Change in biomass (grams per day) for floating (i) and settled (iii) fragments; and change in length (centimeters per day) for floating (ii) and settled (iv) fragments (Average change  $\pm$  SE). Sample size was 5 per length for floating fragments and 10 per length for fragments. Fragments with no change in growth indicated by n/c. Letters indicate significant difference between fragment lengths based on one-way ANOVA with post-hoc Tukey test.



**Fig. 4.** Average percent cover ( $\pm$  SE) of *H. stipulacea* within the ten 1 m<sup>2</sup> control (grey) and ten 1 m<sup>2</sup> removal (black) plots measured after initial removal event. A two-way ANOVA was conducted to compare control versus treatment, time, and the interaction of these factors.

### 3.2. *H. stipulacea* lateral expansion

We observed a lateral expansion rate of  $1.6 \pm 0.4$  cm/d (avg  $\pm$  SE). The maximum daily lateral expansion rate measured among the tracked rhizomes was 5.5 cm/d, with growth of all rhizomes except two with no change.

### 3.3. Growth of floating *H. stipulacea* fragments

All floating fragments survived the duration of the study, yet only the 2 cm, 5 cm, and 10 cm sizes increased in both average biomass and length (Fig. 3i, ii). While the 1 cm fragments survived, we did not observe growth. The 5 cm fragments had the greatest increase in length and biomass, though this was not statistically different from other lengths (Length - one-way ANOVA, DF = 3, F = 9.58,  $p < 0.001$ ; biomass DF = 3, F = 12.80,  $p < 0.001$ ). No floating fragments settled into the tank's sand substrate. New growth on floating fragments manifested as combinations of new shoots, new roots from new or existing shoots, and new lateral growth of the horizontal rhizome.

### 3.4. Growth of settled *H. stipulacea* fragments

All settled fragments survived the 4 days of the study and all demonstrated some growth in both average length and biomass (Fig. 3 iii, iv). The 10 cm fragments had the greatest increase in length and biomass. Growth of shoots, roots and rhizomes displayed similar patterns to growth of floating fragments. Fragment length and biomass for 1 cm and 2 cm increased at a comparable rate, whereas increases were significantly larger for 5 cm and 10 cm fragments (Length - one-way ANOVA, DF = 3, F = 24.02,  $p < 0.0001$ ; biomass DF = 3, F = 54.86,  $p < 0.0001$ ). (Fig. 3).

### 3.5. Removal and recovery rate of *H. stipulacea*

The average ( $\pm$  SE) biomass of seagrass removed from individual plots was  $798.7 \pm 336.9$  g.

At the beginning of the experiment but post seagrass removal (Week 0), *H. stipulacea* cover averaged 52.8% in the control plots and 1.6% in the removal plots (Fig. 4). The presence of small amounts of plant cover in the removal plots is largely from loose blades captured in the photographs, and blades of plants outside the 1 m<sup>2</sup> plot bending into the area (Fig. 5). Control plot seagrass cover averaged 50.9% over the study period yet fluctuated between 44% and 56% across weeks. Removal plot seagrass cover remained below 10% during the first six weeks and expanded to approximately half of the original cover by Week 14 (Fig. 5). Percentage of cover differed significantly between the removal plots and controls (treatment), week to week (time), and significantly in the interaction between treatment and time (Table 1). Change in percent of cover in removal plots was best fit by an exponential non-linear regression ( $R^2 = 0.98$ ) and tracked until removal plots reached the average cover of the control plots (~50%), approximately 17 weeks after removal (Fig. 6). Data was also fit to a linear regression ( $R^2 = 0.96$ ) with comparable recovery to control plots in approximately 31 weeks. Male flowers were found in several removal plots as described in Chiquillo et al. (2019).

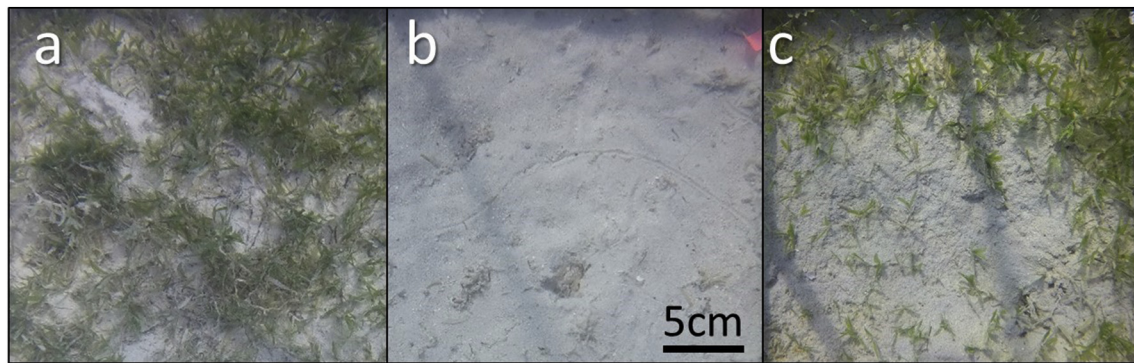


Fig. 5. Photographs of (a) a representative control plot at Week 0, (b) a representative removal plot at week 0, and (c) a representative removal plot at week 14. Scale bar equals 5 cm.

**Table 1**  
Two-way ANOVA table for *Halophila stipulacea* seagrass removal experiment.

	DF	Sum Sq	Mean Sq	F-Value	P-Value
Removal/control plot (Treatment)	1	7.14	7.14	4028.67	0.0001
Week since removal (Time)	6	0.46	0.08	43.45	0.0001
Treatment:time	6	0.15	0.02	13.71	0.0001

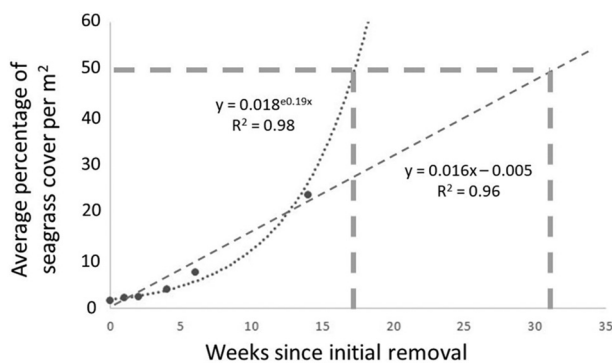


Fig. 6. Average percent cover of seagrass recovery (per m<sup>2</sup>) after removal. An exponential function (dotted line) provided the best fit for the data indicating recovery comparable to control plots expected after 17 weeks post removal (dashed line); and a linear function (small dash line) provided a comparable recovery expected 31 weeks after removal (dashed line).

#### 4. Discussion

Disturbances open space in seagrass beds, initiating a process of recovery that may take years (Williams 1990; Rasheed 2004). In contrast, we estimate that if recovery of the invasive *H. stipulacea* continued to follow an exponential trajectory it could match the control condition in as little as 17 weeks, approximately 1.5–30 times faster than reported for native Caribbean species (Fourqurean et al. 1995; Williams 1988; Kenworthy et al. 2002). The recovery time may take twice as long, an estimated 31 weeks, if regrowth occurs at a linear rate (Fig. 6), but our observed pattern of larger seagrass fragments gaining more biomass in the mesocosm experiments hint at an exponential growth rate for *H. stipulacea* may be more realistic. Kenworthy et al. (2002) examined the recovery of multiple small-scale plots (0.25 m<sup>2</sup>–2.25 m<sup>2</sup>) with a 100% removal treatment of all seagrass material to 10–25 cm depth, and consistent with the seagrass successional paradigm (Fonseca et al. 2000), the pioneering species *Halodule wrightii* recovered quickly (1.7 years) and utilized vegetative reproduction to opportunistically-colonize plots containing the slower recovering *Thalassia testudinum*. Species does matter in seagrass recovery as illustrated by O'Brien et al. (2018) with dominant species such as *Thalassia* having a high resistance

capacity and low recovery capacity. The opposite is true for *Halophila* whose principle threat to recovery is not growth but barriers to dispersal and recruitment.

*Halophila stipulacea*'s recovery occurred via vegetative propagation of neighboring plants as evident from the photographs and the absence of *H. stipulacea* female flowers or seeds within the removal plots. Only *H. stipulacea* flowers, but not seeds, have been found in the Caribbean (Vera et al. 2014; Chiquillo et al. 2019). Although regrowth may occur via sexual reproduction, recovery through rhizome growth from the surrounding bed is more common for native Caribbean seagrasses (Kenworthy et al. 2002; Rasheed 2004), and thus the fast rhizome elongation rate reported here for *H. stipulacea* may provide an advantage after disturbance.

Mesocosm data demonstrated *H. stipulacea* fragments as small as 2 cm in length with at least one shoot are viable in the water column and in the sediment, capable of increasing in both biomass and rhizome length. Floating fragments do become established plants as demonstrated by Smulders et al. (2017) who saw in situ settlement within 10 days. Smulders et al. (2017) did not report changes in fragment length but did report gains in biomass that were slightly lower than gains observed in our study. Smulders et al. (2017) also reported rapid plant production rates of ~1 new shoot/d and ~1.5 new leaves/d. Results from our study add to earlier evidence (Steiner and Willette 2015; Sghaier et al. 2014; Scheibling et al. 2018; Christianen et al. 2019) that *H. stipulacea* fragments are viable and have the potential to disperse in the water column, a pattern consistent with described mechanisms for dispersal and recruitment of native *Halophila* seagrasses in the Caribbean (Herbert 1986; Hall et al. 2006).

High numbers of floating fragments of *H. stipulacea* have become common in Caribbean bays where the seagrass has colonized (Vera et al. 2014; Willette et al. 2014), and it was the observation of floating fragments that lead Ruiz and Ballantine (2004) to find and first report established *H. stipulacea* in the Caribbean Sea in 2002. In our study, fragments were found floating in and washed up along the shore of GLB. *Halophila stipulacea* fragments are created from a range of natural and anthropogenic disturbances to the habitat including storms, wave action, sea turtle grazing, boat anchoring and fishing (Willette and Ambrose 2012; Steiner and Willette 2015; Scheibling et al. 2018; Christianen et al. 2019). For example, numerous hurricanes in 2004 were proposed as a key mechanism that lead to the northern range limit expansion of native *Halophila johnsonii* and *Halophila decipiens* in the Indian River Lagoon, Florida (Virmstein and Hall 2009). Large hurricanes have also facilitated the spread of invasive macrophytes 100 s of km along the U.S. Gulf and Atlantic coasts (Bhattarai and Cronin 2014). Such a possibility is particularly salient given that recent Caribbean hurricanes mobilized massive seagrass rafts and raised concerns that future events could introduce *H. stipulacea* propagules to Florida (Fonseca 2017), a location still over one thousand km north of the seagrass's present-day northern range limit. Recent and increasingly

regular massive blooms of drifting *Sargassum* that span from West Africa through the eastern Caribbean to the Gulf of Mexico (Wang et al., 2019) may be yet another vehicle to spread *H. stipulacea* that can intertwine with floating algae (Willette, Per. Obser).

*Halophila stipulacea* has become established across most of the Eastern Caribbean and part of the Southern Caribbean since its discovery in 2002, a spread that has likely been facilitated by the creation of viable vegetative fragments from natural and anthropogenic disturbances. Anthropogenic dispersal of *H. stipulacea* fragments is proposed as the means in which the seagrass moved from the Red Sea to the Mediterranean Sea (Lipkin 1975) and from the Mediterranean Sea to the Caribbean Sea (Ruiz and Ballantine 2004). This possible explanation is consistent with human-mediated spread of invasive algae across large geographic distances in a short time (Lyons and Scheibling 2009). *Halophila stipulacea*'s spread and colonization may be problematic for native Caribbean species (Willette and Ambrose 2012; Van Tussenbroek et al. 2016), including threatened green turtles (*Chelonia mydas*) which have shifted their grazing behavior after the introduction of the invasive seagrass (Christianen et al. 2019). Alternatively, given the long-standing and accelerating loss of seagrasses in the Caribbean (Waycott et al. 2009), the damages of the rapidly-spreading *H. stipulacea* could be outweighed by this invasive species' potential benefits of creating habitat where native seagrasses are no longer able to grow due to disturbance and supporting a robust, albeit altered diversity of marine species (Viana et al. 2019). Our data provides empirical support that *H. stipulacea* is highly resilient to small-scale disturbances. We believe this capacity for rapid recovery is already having a profound effect on reshaping the Caribbean seagrass communities and is an important component of the invasiveness of *H. stipulacea*.

#### Declaration of Competing Interest

All authors state they have no interests to declare.

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