

Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiota communities in the Eastern Caribbean

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ABSTRACT

The invasion and expansion of the Indian Ocean seagrass *Halophila stipulacea* into the Eastern Caribbean raises the question of how local seagrass communities respond to this fast-growing, ecologically flexible species. An in situ transplant experiment examining the effect of *H. stipulacea* within beds of the dominant native seagrass *Syringodium filiforme* found the invasive seagrass capable of rapid expansion, with the displacement of the native seagrass beginning in 10–12 weeks. Fish traps placed in monocultures of the invasive seagrass yielded statistically similar fish measures as traps in the native seagrass, except for *H. stipulacea* supporting larger fish and *S. filiforme* supporting twice the proportion of juvenile-stage fish. The invasive seagrass supported significantly more epibiotic invertebrates than the native seagrass. Evidence suggests *H. stipulacea* had a negative effect on *S. filiforme* via displacement, yet supported equal or higher abundances of different trophic groups relative to the native seagrass. Furthermore, the formation of *H. stipulacea* fragments by locally used fish traps reached 100% frequency when traps were submerged for 7+ days, suggesting local fishing can increase dissemination of the invasive species.

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1. Introduction

The planet's aquatic environments are experiencing an extraordinary transformation via the pervasive spread of non-indigenous species due to human activities (Mooney and Cleland, 2001; Naylor et al., 2001; Byrnes et al., 2007; Williams and Smith, 2007), many of which have negative impacts on ecological communities. Understanding how invasive species interacts with native macrophytes and how the indigenous fauna respond to the arrival of an invader are central in determining how the new species will fit into the existing system and what degree of eradication efforts are warranted.

The invasion of a non-indigenous macrophyte has resulted in the loss or decline of native macrophytes. For example, the invasion of *Zostera japonica* along the Pacific Northwest coast of North America has directly contributed to the decline of congener *Z. marina* via the invasive species' ability to out-competing the native species when

co-occurring in soft-bottom habitats, and ability to out-perform the native species after disturbances (Jun Bando, 2006). This one-two, competition-recovery advantage of the invasive species helps to explain the broad success of this invasive macrophyte. In this case, the native species is largely displaced but is still present in the shared habitat (Baldwin and Lovvorn, 1994; Jun Bando, 2006); yet in other interactions the invasive species completely replaces the native. For example, after the removal of the invasive kelp *Undaria pinnatifida* in Patagonia, indigenous seaweed diversity and richness increased significantly, suggesting the invasive species was competitively excluding natives (Casas et al., 2004), and congeners *Caulerpa taxifolia* and *C. racemosa*, two of the best studied invasive macrophytes, have been reported to overwhelm native floral communities, turning them into low diversity, alien algal beds (Meinesz and Hesse, 1991; Piazzini et al., 2001; Meinesz et al., 2001; Klein and Verlaque, 2008).

Invasive macrophytes also imposed changes on native communities via mechanisms that modify the habitat and vary indigenous faunal composition. *Caulerpa taxifolia* altered fish and infaunal communities in the Mediterranean by creating a physical barrier for fish consuming benthic food sources, thus increasing search time for fish and sheltering infauna from predators (Levi and Francour, 2004; Longepierre et al., 2005). Further, *C. taxifolia* was believed to enhance invertebrate infaunal recruitment to densities higher

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than native vegetation or bare mud (Gribben and Wright, 2006), yet it was subsequently concluded that the invasive species created a sub-optimal environment, with recruits and adults experiencing reduced survivorship, growth, and fitness after the initial surge (Gribben et al., 2009). Houston and Duivenvoorden (2002) found an invasive macrophyte to support a 30-fold increase in vegetation biomass and substantially alter the structural complexity of the aquatic habitat, while lowering native plant diversity and simultaneously decreasing and shifting epibiota and fish assemblage composition. These changes in tropic structure and feeding preference of epibiota and fishes are observable after the arrival of invasive macrophytes as a result of either bare mudflats or native vegetation being replaced by a new palatable species (Baldwin and Lovvorn, 1994; Levin et al., 2006; Lorenti et al., 2011) or due to changes in macrophyte substrate availability and biomass for prey items (Stoner, 1983; Edgar and Robertson, 1992). Likewise, the morphology of a macrophyte, such as differences in available surface area, influences epibiota abundance, diversity, and preference (Stoner, 1980; Bell and Westoby, 1986; De Troch et al., 2001; Schmidt and Scheibling, 2006). The abundance and distribution of prey can subsequently have influence on the density and distribution of larger predators (Bologna, 2007), thus creating higher tropic level changes in the system.

After alien macrophytes are established, formation and dissemination of vegetative propagules may be created through natural processes such as waves or storms (Macreadie et al., 2011), or by anthropogenic activities occurring in or over the invaded habitat. Correlations between the location of new infestations of invasive macrophytes and popular boating or fishing locations suggest these activities facilitate spreading (Meinesz et al., 2001; Casas et al., 2004; Gambi et al., 2009; Willette and Ambrose, 2009). Indeed, empirical studies have shown bottom trawling, the casting of fishing nets, the removal of boat anchors, the passing of boat propellers over and through the invaded habitat, and even recreational swimming can create fragments (Relini et al., 2000; West et al., 2007, 2009). Bottom trawlers and anchor lockers can potentially carry propagules tens of kilometers from where they originated (Relini et al., 2000; Meinesz et al., 2001; Gambi et al., 2009). Macrophyte propagules can survive for weeks in the water column, settle and re-root (Hall et al., 2006), with the likelihood of successful colonization increasing as fragment abundance increases (Ceccherelli and Cinelli, 1999; Smith and Walters, 1999). Further, fragment size influences viability of propagules (West et al., 2007) with different activities creating different size fragments (Relini et al., 2000). Familiarity with how local anthropogenic activities may increase fragment formation and dispersal can aid in predicting future spread and developing more comprehensive management strategies of the invasive species.

The expansion of *Halophila stipulacea*, which is indigenous to the Red Sea and parts of the Indian Ocean (den Hartog, 1970), has been extensive, spanning from the Suez Canal in the Mediterranean Sea in 1869 (Por, 1971) to the Eastern Caribbean by 2002 (Ruiz and Ballantine, 2004). *H. stipulacea* forms monocultures as well as multi-species assemblages throughout its native and extended range (Ruiz and Ballantine, 2004; Short et al., 2007) and can be found exposed at low tides (den Hartog, 1970) down to depths of 50 m (Beer and Waisel, 1981), making it one of the deeper living seagrass (Lipkin et al., 2003). Additional attributes facilitating its invasion success are a tolerance to low and high light intensity (Beer and Waisel, 1981; Schwarz and Hellblom, 2002), wide salinity range (Por, 1971), adaptability to sediment quality (Coppejans et al., 1992; Pereg et al., 1994), and rapid vegetative expansion (Marbá and Duarte, 1998). Because of its potential and realized impact on biodiversity and socioeconomic losses, *H. stipulacea* has been assigned to the 100 Worst Invasives in the Mediterranean by Streftaris and Zenetos (2006), yet other studies report that *H. stipulacea* has had

no impact in the Mediterranean (Duarte, 2002; Williams, 2007). Little is known of *H. stipulacea*'s effects in its recently discovered Caribbean locations.

H. stipulacea was first documented in the Caribbean in Grenada in 2002 (Ruiz and Ballantine, 2004), then in Dominica and St. Lucia in 2007 (Willette and Ambrose, 2009). In these locations it grows predominantly as mono-specific stands, though occasionally mixing with native seagrass *Syringodium filiforme* at the bed margins. *H. stipulacea* and *S. filiforme* are both considered pioneer species based on their reduced longevity and high turnover rates (Gallegos et al., 1994); however, they differ in various parameters including *H. stipulacea* being more tolerant of lower light levels (Lee et al., 2007), having shorter leaf lifespan (Hemminga et al., 1999); and having a more profuse leaf production rate (Duarte, 1991). Further, *Halophila* species has roughly twice the rhizome horizontal elongation rate of *Syringodium* species (Duarte, 1991), and have a highly differentiated shoot system with orderly meristem growth; whereas *Syringodium* shoots proliferate unregulated and grow with a higher sensitivity to environmental disturbances (Tomlinson, 1974).

This paper addresses the ecological concerns of Eastern Caribbean marine resource users and gaps in our current knowledge of *H. stipulacea* as an invasive species. We conducted in situ experiments and field observations to assess the interaction of the invasive *H. stipulacea* in a native Caribbean seagrass bed. Our goals were to determine (1) the effects of *H. stipulacea* on *S. filiforme*; (2) the effects of *H. stipulacea* on seagrass fish and epibiota communities; and (3) whether local fishing activities such as the use of fish traps facilitate the spread of the invasive seagrass.

2. Methods

2.1. Study site

Field experiments were conducted in Prince Rupert Bay (15°34'N, 61°28'W), a 3.8 km wide bight along the northwest coast of Dominica, West Indies. *H. stipulacea* covers more than 100,000 m² of the benthos, which is the largest identified population of the invasive seagrass in the Caribbean (Willette and Ambrose, 2009). *H. stipulacea* grows primarily as mono-culture beds in the bay's southern region, but is also found throughout the bay interspersed with the native seagrasses *S. filiforme* and *Halodule wrightii* (Willette and Ambrose, 2009). *Thalassia testudinum* also occurs in Dominica but is rare along the northwest coast. Prince Rupert Bay serves as the island's primary recreational anchorage, a port of entry for foreign vessels, and the site of multiple near-shore fishing activities (Honeychurch, 1995).

2.2. Transplant experiment

To assess the effect of *H. stipulacea* in *S. filiforme* beds, a transplant experiment was conducted for 85 d from May to August 2008. The seagrass *S. filiforme* was chosen as the host bed for this study because it is the dominant seagrass species along Dominica's west coast where *H. stipulacea* is found and *S. filiforme* was present at every site where *H. stipulacea* has been reported (Steiner and Willette, 2010; Willette and Ambrose, 2009). Ten-cm diameter by approximately 20-cm long plugs of the invasive seagrass were removed from an established *H. stipulacea* bed and transplanted in an adjacent *S. filiforme* bed with a comparable profile and a depth of three to five meters. Plugs began with greater than 80% cover and included 8–16 shoots. A total of twenty-five plugs were transplanted at a distance of 20 cm apart in a single line, and each plug was marked with a neon tag tied to a steel nail. Five *H. stipulacea* control plugs were removed and then replanted in the same location to assess the effect of coring. Weekly to tri-weekly assessments

of lateral expansion of transplanted plugs were taken by measuring the maximum distance between the two shoots that were the furthest apart for each plug. Growth of *H. stipulacea* plugs was often haphazard with runners stretching along one or two axes rather than a symmetrical and consistent growth outward in all directions. Distance in centimeters was then divided by the number of days since transplanting to express mean daily lateral expansion.

We selected the plug experimental unit over individual seagrass fragments for several reasons.

First, preliminary observations indicated that *H. stipulacea* fragments generated by locally used fish traps included 2–4 shoots and approximately 8 cm long rhizomes with roots and sediments still attached. The plug unit served to include all of these dispersal structures in the transplant. Further, fragments were often interwoven in the fish trap mesh and upon re-casting the newly created fragments would be in contact and pressed into the substrate. Based on these criteria the plug unit was a better mimic than individual shoots. Lastly, rhizome apical meristems (RAMs) RAMs were abundant in even a small sample of *H. stipulacea* (i.e. a 10 cm plug) and this design allowed for a good representation of *H. stipulacea* to expand under natural conditions.

In regards to the bio-security risk of this study, all transplants were moved only within Prince Rupert Bay, a bay already heavily invaded by *H. stipulacea* (Willette and Ambrose, 2009) and no transplants were placed in un-invaded habitats. Additionally, physical removal of all transplanted plant material was planned for December 2008, 200 days after the initial planting; however, a powerful hurricane (Hurricane Omar) in October 2008 eliminated all transplants and markers (and native seagrass beds) from the study site. No evidence of transplants was observed in November 2008 or June 2009, indicating no bio-security risk.

2.3. Fish catch comparison between seagrass species

To compare fish species composition and biomass between the invasive seagrass *H. stipulacea* and the native seagrass *S. filiforme*, locally used fish traps (double-funnel West Indian Z-type fish traps) were baited with the traditional bait of green papaya and bread and set in adjacent mono-culture beds and allowed to fish for four to sixteen days from May 30 to July 29, 2008. Three pairs of fish traps (90 cm by 190 cm by 250 cm) were built and covered on all sides with wire mesh (2.54 cm diameter mesh). Fish traps were placed within Prince Rupert Bay at depths where each seagrass species had the highest percent cover, 8.5–11.5 m for *H. stipulacea*, and 6.5–9 m for *S. filiforme*. The difference in depth placement of fish traps was dictated by where the two species occurred in proximity to one another. Further, the steep bathymetry of the bay meant that a half meter change in depth could occur in just several meters of lateral distance off-shore (Steiner et al., 2010). Paired traps (one trap for each seagrass species) were placed roughly 50 m apart from each other in their respective seagrass bed with three pairs of traps spaced approximately 1 km apart along the bay's shoreline. All traps were between 150 m and 300 m offshore. These parameters were within the typical zone selected by local fishermen using the West Indian Z-type fish trap. Fifty-four trap samplings, 27 for each seagrass, were attempted during the study, although three *H. stipulacea* and eight *S. filiforme* samples were unusable due to damage from boat anchors or loss due to weather or theft. After the allotted fishing period, traps were removed from the bed, emptied of their contents, re-baited, and re-deployed in the same location. Individual fish were identified to species, photographed, weighed, measured for standard and total length. For the five most commonly caught species from each bed, life stage (juvenile or adult) was recorded based on maturation size classes in Munro (1983), Mueller et al. (1994), Martinez-Andrade (2003), Bilgin and Celik (2009) and Froese and Pauly (2009). A two-sample *t*-test was used

to assess if differences existed between fish catches in *H. stipulacea* and *S. filiforme* beds. Statistical power was calculated using Lenth's Java applet (Lenth, 2009).

2.4. Epibiota community structure on the seagrasses

The availability of epibiotic food resources for fish within the two seagrass mono-cultures was estimated by gently lowering a 500 mL plastic beaker with the base removed and a nylon mesh stocking attached at the upper end over upright shoots of seagrass, then cutting entire blades at the sediment level. The beaker was then inverted, the net slid off and tied, and the contents preserved in a 70% ETOH and Rose Bengal solution until sorted. A total of 12 epibiota samples were taken from each seagrass species. Samples were collected from native and invasive seagrass beds co-occupied by the fish traps. Placement of beaker was selected by haphazardly dropping the sampling beaker from the water surface and extracting a sample from where the beaker landed, so long as it was within the seagrass bed. Samples were individually rinsed through a 500 μ m filter and then sorted under a microscope, with all mobile epibiota enumerated and identified to lowest practicable taxonomic level. After sorting, seagrass shoots/blades were counted and dried to obtain the biomass of each sample. A two-sample *t*-test was used to compare epibiont abundances between seagrass species.

2.5. Fragment generation by fish traps

West Indian Z-type fish traps are commonly and repeatedly used in the seagrass beds along Dominica's Caribbean coast. The mesh composition of the traps combined with *H. stipulacea*'s shallow, creeping rhizome system (den Hartog, 1970) and high above-ground to below-ground biomass ratio (Wahbeh, 1988) create a favorable situation for fragment generation. Hall et al. (2006) demonstrated that not only are fragments of *Halophila* able to survive for several days in the water column and disperse over short distances, but also that that vegetative fragments have the ability to settle to the substrate and root. To quantify the frequency of new fragment production, fish traps cast in *H. stipulacea* beds for the fish trap experiment were inspected for rhizomal fragments upon each removal from the seagrass bed. All fragments were collected, measured for total fragment length, number of shoots, and then dried in the lab to obtain biomass. A two-sample *t*-test was used to compare the number and biomass of fragments created when fish traps were allowed to fish for 6 or fewer days versus 7 or more days.

3. Results

3.1. Transplant experiment

Survival after the initial transplanting was high for *H. stipulacea*, with 23 of 25 plugs (92%) surviving at least one week. All five of the control plugs (100%) survived the initial transplanting and were indistinguishable from the surrounding bed at the end of the experiment.

Between Week 1 and Week 12, *H. stipulacea* plugs increased by 186% on average (8.2 ± 0.9 cm to 25.2 ± 5.7 cm [mean \pm SE]) (Fig. 1). Over the entire time period, *H. stipulacea* expressed a mean positive growth rate of 0.13 cm d^{-1} . Shoots from the host *S. filiforme* bed were observed to be loosely intermixed with the laterally expanding *H. stipulacea* plants both within the transplant plug and in the host bed as the invasive species expanded. Towards the end of the study, surviving *H. stipulacea* plugs were densely populated with new shoots and blades and had begun to displace *S. filiforme* shoots near the transplanted plugs. *H. stipulacea* plugs largely remained isolated units, though those with the most extensive expansion did

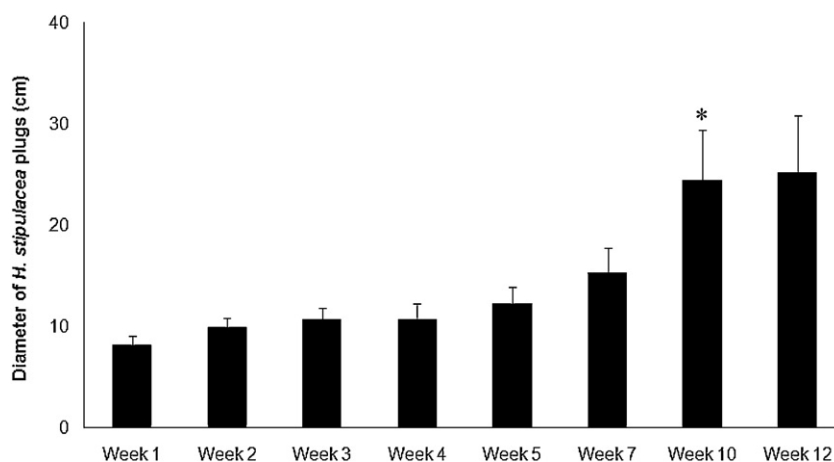


Fig. 1. Mean diameter (\pm SE) of *Halophila stipulacea* plugs transplanted into *Syringodium filiforme* bed measured weekly, bi-weekly, or tri-weekly. $n = 25$ transplant plugs. * indicates significant difference between weeks 7 and 10.

begin to merge and form a single plug. The 20 cm distance between plugs did not appear to have any effect on which plugs survived, expanded, or died out. At the conclusion of the transplant experiment a total of 17 *H. stipulacea* plugs (78%) and all control plugs had survived the entire 12 weeks while all other plugs either died out or were displaced by the host bed.

3.2. Epibiota community structure on the seagrasses

Epibiota abundances were significantly higher on *H. stipulacea* than on *S. filiforme* for total abundance of all taxa, for the most numerous epibiont group, Crustacea, and for the most abundant group within Crustacea, Amphipods, despite no significant differences in mean seagrass dry weight per sample (Table 1). Abundance of other taxa was not significantly different.

3.3. Fish catch comparison between seagrass species

H. stipulacea supported significantly larger fish than native *S. filiforme* (Table 1). Other comparisons of fish trap data between the two seagrasses were not significantly different, yet the invasive seagrass tended to capture more fish, a greater total species richness of fish, but smaller mean species richness per catch than those in the native seagrass (Table 1).

Lutjanidae was the most common fish family caught in traps placed in both *H. stipulacea* and *S. filiforme* (63% and 57% respectively; Table 2). Likewise, Lutjanidae made up the largest percentage of total fish biomass caught in traps placed in the seagrasses (*H. stipulacea* 72%, *S. filiforme* 60%, Table 2). The most abundant species within the family Lutjanidae in traps placed in *H. stipulacea* was yellowtail snapper *Ocyurus chrysurus*, whereas lane snapper *Lutjanus synagris* was most abundant in traps placed in *S. filiforme*. The next most frequently caught fish families in traps placed in the invasive seagrass were scorpion fish Scorpaenidae (12%) and porcupinefish Diodontidae (11%), while Diodontidae (10%), seabass Serranidae (9%), and jacks Carangidae (7%) were the next most common in traps placed in the native seagrass. No other family made up more than 5% of total fish abundance. Four of the five most commonly caught fishes in traps placed in *S. filiforme* and all of the top five species from *H. stipulacea* were seagrass-associated fish species (Bohlke and Chaplin, 1968) (Table 2).

Twenty percent of the most commonly caught fishes captured in *H. stipulacea* beds were juvenile-stage, which is much lower than the 55% found in *S. filiforme* (Fig. 2 and Table 2). At the species level, juveniles of the most commonly caught fish in *H. stipulacea* beds, the yellowtail snapper *Ocyurus chrysurus*, were never observed, whereas the majority of balloonfish *Diodon holocanthus* (>65%) and mahogany snappers *Lutjanus mahogoni* (>90%) in both *H. stipulacea* and *S. filiforme* beds were juveniles (Fig. 2). In

Table 1

Epifaunal and fish abundances and values from measures taken in *Halophila stipulacea* and *Syringodium filiforme* seagrass beds. Average and standard error values are shown for all measures, except total fish species richness. Paired (epifauna) and unpaired (fish) t -test values and p -values between seagrasses are shown with values below 0.05 indicating statistical significant difference.

| | <i>Halophila stipulacea</i> | | <i>Syringodium filiforme</i> | | t -Value | P -value |
|--|-----------------------------|----------|------------------------------|----------|------------|------------|
| | Average | \pm SE | Average | \pm SE | | |
| <i>Epifauna measures</i> | | | | | | |
| Total epifaunal abundance ^a | 16716.0 | 2456.6 | 8523.8 | 1580.4 | 2.4 | 0.04 |
| Amphipod abundance ^a | 8457.5 | 1517.2 | 2835.8 | 530.5 | 3.0 | 0.01 |
| Crustacean abundance ^a | 13250.1 | 2127.0 | 5240.3 | 823.5 | 3.1 | 0.01 |
| Annelid abundance ^a | 2326.3 | 421.5 | 2272.9 | 721.4 | -3.8 | 0.60 |
| Mollusk abundance ^a | 332.7 | 123.3 | 464.1 | 107.7 | -1.1 | 0.28 |
| Nematode abundance ^a | 332.7 | 151.7 | 514.3 | 195.1 | -0.7 | 0.50 |
| Dry blade biomass ^b | 93.0 | 21.6 | 91.8 | 11.9 | -61.1 | 0.97 |
| <i>Fish measures</i> | | | | | | |
| Average no. fish captured per sample | 7.0 | 0.9 | 5.1 | 0.2 | 0.6 | 0.52 |
| Average total fish length (cm) | 27.8 | 0.6 | 22.7 | 0.4 | 7.1 | 0.01 |
| Mean fish species richness per sample | 2.3 | 0.1 | 3.1 | 0.1 | -1.5 | 0.15 |
| Total fish species richness | 21.0 | | 17.0 | | | |

^a Individual per m² of seagrass.

^b Grams per m² of seagrass.

Table 2

Fish species captured in fish traps placed within *Halophila stipulacea* and *Syringodium filiforme* seagrass beds. For each fish species the family name, total number of fish captured, ranking in terms of abundance for the seagrass type, and proportion of total biomass of all fish captured the species represents within the said seagrass type. Proportion of total biomass adds sums to more than 100% due to rounding. * signifies non-seagrass-associated fish, all other species are seagrass-associated based on Bohllke and Chaplin (1968) (ND = no data due to lack of complete length measurements, escaped fish).

| <i>Halophila stipulacea</i> | | | | | <i>Syringodium filiforme</i> | | | | |
|----------------------------------|-----------------|---------------------|------|-----------------------------|-------------------------------|-----------------|---------------------|------|-----------------------------|
| Species | Family | Total fish captured | Rank | Proportion of total biomass | Species | Family | Total fish captured | Rank | Proportion of total biomass |
| <i>Ocyurus chrysurus</i> | Lutjanidae | 62 | 1 | 39% | <i>Lutjanus synagris</i> | Lutjanidae | 28 | 1 | 33% |
| <i>Scorpaena plumieri</i> | Scorpaenidae | 18 | 2 | 14% | <i>Lutjanus mahogoni</i> | Lutjanidae | 15 | 2 | 18% |
| <i>Diodon holocanthus</i> | Diodontidae | 17 | 3 | ND | <i>Lutjanus analis</i> | Lutjanidae | 13 | 3 | 9% |
| <i>Lutjanus mahogoni</i> | Lutjanidae | 13 | 4 | 7% | <i>Diodon holocanthus</i> | Diodontidae | 10 | 4 | ND |
| <i>Lutjanus analis</i> | Lutjanidae | 10 | 5 | 16% | <i>Epinephelus fulvus</i> * | Serranidae | 9 | 5 | 9% |
| <i>Lutjanus synagris</i> | Lutjanidae | 10 | 5 | 9% | <i>Caranx ruber</i> * | Carangidae | 7 | 6 | 12% |
| <i>Dactylopterus volitans</i> | Dactylopteridae | 5 | 6 | 6% | <i>Scorpaena plumieri</i> | Scorpaenidae | 4 | 7 | 5% |
| <i>Epinephelus fulvus</i> * | Serranidae | 2 | 7 | 1% | <i>Lactophrys triqueter</i> * | Ostraciidae | 4 | 7 | ND |
| <i>Haemulon carbonarium</i> | Pomadasyidae | 2 | 7 | 1% | <i>Sparisoma chrysopteron</i> | Scaridae | 2 | 8 | 3% |
| <i>Chaetodipterus faber</i> * | Ephippidae | 2 | 7 | 2% | <i>Sparisoma viride</i> | Scaridae | 1 | 9 | 1% |
| <i>Pomacanthus paru</i> | Pomacanthidae | 2 | 7 | ND | <i>Scarus vetula</i> | Scaridae | 1 | 9 | 1% |
| <i>Sparisoma chrysopteron</i> | Scaridae | 2 | 7 | 2% | <i>Scarus guacamaia</i> | Scaridae | 1 | 9 | 2% |
| <i>Sparisoma viridae</i> | Scaridae | 1 | 8 | 1% | <i>Ocyurus chrysurus</i> | Lutjanidae | 1 | 9 | 1% |
| <i>Lutjanus apodus</i> | Lutjanidae | 1 | 8 | 1% | <i>Dactylopterus volitans</i> | Dactylopteridae | 1 | 9 | 2% |
| <i>Anisotremus surinamensis</i> | Pomadasyidae | 1 | 8 | 1% | <i>Haemulon album</i> | Pomadasyidae | 1 | 9 | 1% |
| <i>Mulloidichthys martinicus</i> | Mullidae | 1 | 8 | 1% | <i>Haemulon carbonarium</i> | Pomadasyidae | 1 | 9 | 1% |
| <i>Caranx ruber</i> * | Carangidae | 1 | 8 | 1% | <i>Calamus proridens</i> | Sparidae | 1 | 9 | 5% |
| <i>Lactophrys triqueter</i> * | Ostraciidae | 1 | 8 | ND | | | | | |
| <i>Myripristis jacobus</i> * | Holocentridae | 1 | 8 | ND | | | | | |
| <i>Aulostomus maculatus</i> | Aulostomidae | 1 | 8 | 1% | | | | | |
| Total | | 153 | | | Total | | 100 | | |

addition, more than 70% of mutton snappers *Lutjanus analis* captured in *S. filiforme* beds were juvenile-stage while only mature fish of these species were found in traps placed in *H. stipulacea* beds (Fig. 2).

3.4. Fragment generation by fish traps

Fish trap removal from *H. stipulacea* beds generated fragments 72% of the time. Traps submerged for 6 or fewer days ($n = 12$) had a lower frequency of fragment generation (42%) than traps submerged for 7 or more days (100%) ($n = 13$). The average number of fragments created and average biomass fragments per sampling were not significantly different between the two time periods (t -values > -1.2 , p -values > 0.20), likely due to a single outlying value. Upon exclusion of this value, the longer fishing period produced significantly more fragments ($t = -4.0$, $p < 0.01$) and significantly larger fragments (total dry weight, $t = -3.7$, $p < 0.01$). Fragments were created when the traps were removed from the bed by either (a) a dragged fish trap hooking and liberating protruding rhizomes and shoots, or (b) severing complete segments that had grown through the mesh of the fish trap. Created fragments were observed to have one of three fates, with larger fragments falling back to the sea floor, smaller fragments floating to the water surface or in the water column, and complete segments with rhizomes and sediment interwoven into the mesh transported along with the fish trap to a different location. A total of 197 fragments were generated from the 18 times the fish traps were removed from the

H. stipulacea beds. The mean length of generated fragments was 101.7 ± 30.1 mm [mean \pm SE] having 2.8 ± 1.4 shoots per fragment, with an average of 11.4 ± 3.0 mm pieces formed per trap with a mean biomass of 1.6 ± 0.4 g per trap. The removal of West Indian Z-traps from seagrass beds was also destructive in the adjacent *S. filiforme* beds, with blades and rhizomes often liberated from the sea floor.

4. Discussion

4.1. Effects of *H. stipulacea* on a native Eastern Caribbean seagrass bed

This study provides the first in situ experimental data on effects of the invasive seagrass *H. stipulacea* on the native seagrass *S. filiforme*. *H. stipulacea* demonstrated the capacity to expand rapidly into transplanted host *S. filiforme* beds with observations at the end of the study indicating eventual overtaking of the indigenous seagrass. The experimental design using plugs is a good representation of how *H. stipulacea* may arrive to un-invaded habitats in Dominica and similar environments elsewhere in the Caribbean. Despite the limited duration of the transplant experiment, patterns of rapid expansion and competitive displacement of the native seagrass are characteristic of other invasive macrophyte scenarios in seagrass beds (Williams, 2007). Algal species *Sargassum muticum*, *Caulerpa ollivieri*, *C. prolifera*, *C. taxifolia*, *C. racemosa*, the cordgrass *Spartina alternifolia*, and the seagrass

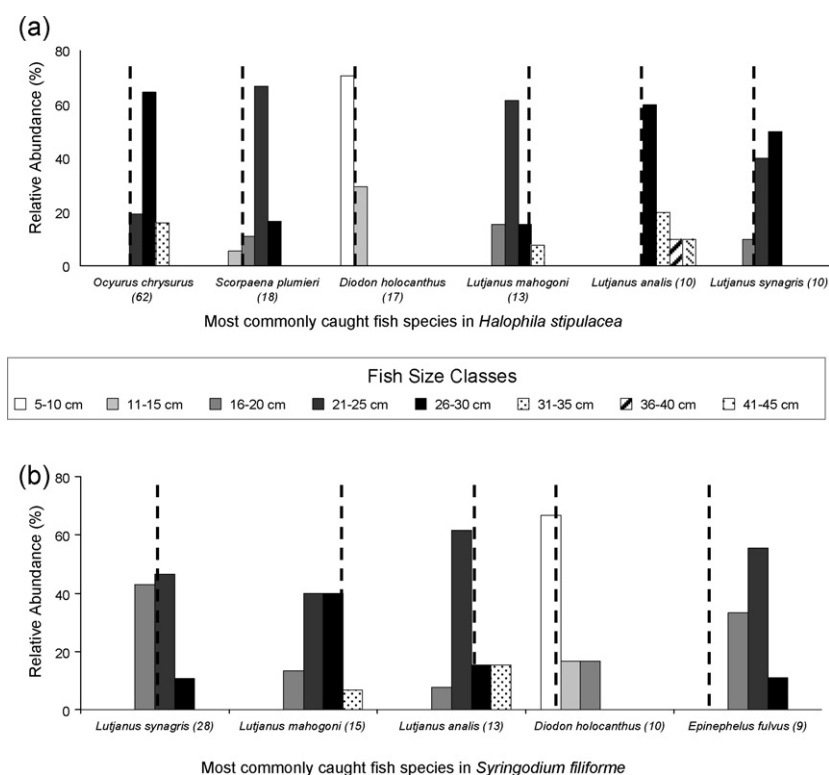


Fig. 2. Relative abundance of the most abundant fish divided into size classes in (a) *Halophila stipulacea*, and (b) *Syringodium filiforme* beds. Total number of specimens caught in parentheses. Vertical dotted line indicates size class cut-off of maturation size (to right of line is mature size) based on Bohlke and Chaplin (1968).

Zostera japonica have all been shown to compete, overtake, and/or displace indigenous seagrass species (Ceccherelli and Cinelli, 1999; den Hartog, 1997; Smith et al., 2002; Lapointe et al., 2005; Stafford and Bell, 2006; Jun Bando, 2006). Interestingly, the success of the aforementioned *C. prolifera* over the Caribbean seagrass *Halodule wrightii* was mediated by sediment disturbances (Stafford and Bell, 2006). Observations after two hurricane disturbances near our study sites in November 2008 and June 2009 found *H. stipulacea* occupying areas where *S. filiforme* previously occurred, as surveyed in 2007 by Steiner and Willette (2010). Disturbances, both natural and anthropogenic, can increase the susceptibility of a habitat to invasive species (Cohen and Carlton, 1998). This is in part because disturbances open up bare ground and the availability of bare ground is strongly correlated to invasion vulnerability of indigenous communities (Burke and Grime, 1996). Further, invasions are highest in scenarios where resources, including space, are available and where propagule pressure, the number of non-indigenous fragments arriving to a habitat, is high (Catford et al., 2011). Thus here, where the ecosystem is prone to tropical storms, local fishing methods increase the frequency of invasive propagules (discussed below), and the non-native species has a capacity for rapid expansion and quick recovery in the native habitat (this study, Marbá and Duarte, 1998; Willette and Ambrose, 2009), *H. stipulacea* has a negative effect on the native *S. filiforme* seagrass beds. It is, however, worth reiterating that the Caribbean's dominant seagrass *Thalassia testudinum* is rare where *H. stipulacea* occurs in Dominica and St. Lucia (Willette and Ambrose, 2009), and in Dominica these sites are largely dominated by *S. filiforme* or bare sand (Steiner et al., 2010; Steiner and Willette, 2010). Although high species diversity does not necessarily correlate with a habitat's ability to resist invasion (Keeley et al., 2003), high density may (Capers et al., 2007; Catford et al., 2011). Thus, the success of *H. stipulacea* may be a result of a more complex combination of factors than those examined to date.

4.2. Effects of *H. stipulacea* on fauna in a native Caribbean seagrass bed

Mensurative comparisons of fauna associated with the invasive seagrass *H. stipulacea* and native Caribbean seagrass *S. filiforme* indicate clear change occurring in the invaded ecosystem. For fish, the significantly larger fish size, and tendency towards higher abundance and richness, of fish caught in *H. stipulacea* beds hint at the invasive seagrass being a more productive assemblage than the native seagrass. The comparison in fish catch between the invasive and native seagrasses was not significant but had low power to detect a difference (only 27% power to detect a 50% difference at $\alpha=0.05$), so at this point we do not know whether *H. stipulacea* has changed the near-shore fish community. The likelihood of eventual changes in fish assemblages is supported, however, by the significant differences in epibiota abundances, particularly the crustaceans and amphipods that are preferred food items by some predatory fish (Stoner, 1983). How native fish and epibiont faunal community responds to a habitat-forming invasive species depends in part on its suitability for ecological functions such as those associated with foraging. For example, the introduction of *Zostera japonica* onto bare mud flats increased local faunal richness and density (Posey, 1988), whereas the colonization of *Caulerpa taxifolia* onto bare sand acted as a chemical deterrent and physical barrier to fish food resources and led to the decline in fish faunal densities (Levi and Francour, 2004). A clear response to *H. stipulacea* is not as apparent in our study as it supports higher epibiont abundances (particularly Crustacea) than *S. filiforme* but statistically indistinguishable fish abundances, except for total fish length. The limited number of locations with mono-cultures of the two seagrasses growing in similar conditions may partly explain the comparable fish measurements as fish found on seagrass beds do not segregate into specific habitats or meadows, but rather use them as a spatial continuum that is partitioned by animal age or nutritional

requirements (Weinstein and Heck, 1979; Middleton et al., 1984). Thus, the movement of fish between adjacent *H. stipulacea* and *S. filiforme* beds could blur the broad scale effect of different availability of food resources.

For epibiont fish prey, *H. stipulacea* supported significantly higher abundances of total epifaunal and crustaceans than the native *S. filiforme*, a result that may be influenced by attributes of the host seagrass species. For example, *Zostera capricorni* and *Posidonia australis* seagrasses in Australia both shared a number of epibiota species and supported other species exclusively, with the abundance of epibionts varying greatly in response to local changes in the seagrass blade height and density (Bell and Westoby, 1986). De Troch et al. (2001) found a higher diversity of epibiota on the structurally similar long, thin-bladed *Syringodium isoetifolium* and *Halodule wrightii* than elliptic, oblong bladed *H. stipulacea* and *Halophila ovalis*. The conclusions of De Troch et al. (2001) differ from our study's findings, which showed *H. stipulacea* supporting a higher abundance of total epibionts than the long, thin-bladed *S. filiforme*. We attribute the differences in epibiotic abundances to the architectural differences of the seagrass blades, yet with the opposite conclusion from De Troch et al. in that the flat, elliptic *H. stipulacea* support more epibiota than the thin, cylindrical *S. filiforme*. Our conclusion is further supported by Stoner (1980), who similarly found seagrass surface area rather than biomass as the driving factor in epibiota abundances. Predation and seagrass structural complexity also influence epibiont abundances with low fish abundances and dense, convoluted seagrass beds supporting higher epibiont counts (Nelson, 1979; Nelson et al., 1982; Edgar and Robertson, 1992). Thus *H. stipulacea*'s thick, creeping formation may act as better refugia for epibiota than the *S. filiforme* upright and solitary blade morphology.

Another key difference between the invasive and native seagrasses was the relative abundance of juvenile fish, with the native *S. filiforme* supporting more than twice the proportion of juveniles as *H. stipulacea*. Because the beds (and paired traps) were in close proximity, it is difficult to determine how well *H. stipulacea* could provide a nursery function for Dominican fish species, but the differences in juvenile proportions suggest that *S. filiforme* may be a better nursery. Some fish life-stage dynamics from Dominican seagrass beds differed from other Caribbean reports. For example, only adult yellowtail snapper *Ocyurus chrysurus* were captured in seagrass beds in Dominica, yet *O. chrysurus* is typically found in the juvenile stage, not as adults, in these seagrass beds elsewhere in the Caribbean (Nagelkerken et al., 2000, 2001). It is worth noting that mangroves, an important fish nursery habitat (Baelde, 1990; Mumby et al., 2004), do not occur in Dominica (Steiner, 2003). Hence in Dominica, seagrasses, native or invasive, may be the only nursery habitat available for juvenile fish prior to their migration to coral reefs or the open ocean.

4.3. Involuntary dispersal of *H. stipulacea* by local fishing gear

Local fishing methods may increase the dissemination of *H. stipulacea* propagules and the likelihood of the invasive seagrass expanding to new habitat. Seagrasses naturally form vegetative propagules (Cambridge et al., 1983; Alberte et al., 1994), but here, locally used fish traps also, with the exclusion of a single outlying data point, create significantly more propagules and larger propagules with increased fishing period. It is note-worthy that in Dominica, fish traps are typically emptied and retrieved once a week, given trap fishing is supplemental to more frequent fishing techniques such as line and net fishing (personal observations). The probability of an adult macrophyte forming from a fragment is very low, yet these odds are improved as the number of fragments increases (Smith and Walters, 1999). Additionally, the survivorship of a fragment improves with increased clump size (West

et al., 2007) and *H. stipulacea*'s rapid growth (Marbá and Duarte, 1998) through fish trap mesh may contribute to the formation of larger clumps with increased submergence time. The average size of fragments created by the fish traps were comparable to what has been observed naturally for *Halophila* and *Halodule* in Florida (Hall et al., 2006). Hence, in addition to the spread of *H. stipulacea* by pleasure boats and anchoring (Ruiz and Ballantine, 2004; Gambi et al., 2009), sustenance fishing via fish traps may be directly contributing to the expansion of *H. stipulacea* in Dominica.

4.4. Threats and benefits of *H. stipulacea*

The rapid expansion and observed displacement capability *H. stipulacea* is a potential threat to local seagrass diversity and may create unknown shifts in trophic structure, as has been the case with many other invasive macrophytes including *Caulerpa taxifolia*, *C. racemosa*, *Undaria pinnatifida*, *Caulerpa racemosa*, and *Spartina* spp. (Meinesz and Hesse, 1991; Verlaque et al., 2000; Grevstad et al., 2003; Casas et al., 2004). The combination of *H. stipulacea*'s aggressive growth (Willette and Ambrose, 2009) along with its potential capacity to disperse both short-range via fragments created by fish traps and long-range via ship traffic (Ruiz and Ballantine, 2004) put this invasive species in a position to alter the seagrass community in Dominica, St. Lucia, Grenada, and elsewhere in the Caribbean. Furthermore, the current worldwide decline in seagrass health and coverage (Duarte, 2002; Orth et al., 2006; Waycott et al., 2009) is being driven by disturbances such as coastal development (Cambridge and McComb, 1984), wasting disease (den Hartog, 1987), overfishing (Jackson et al., 2001), and eutrophication (Burkholder et al., 2007), disturbances that may make the expansion of an invasive species even more likely (Byrnes et al., 2007).

Invasive species are frequently reported as having devastating ecological impacts with implications ranging from the local loss of key species to the widespread decline in ecosystem functions and services (Carlton et al., 1990; Spencer et al., 1991; Shiganova, 1998; Lowe et al., 2000; Boudouresque and Verlaque, 2002). One of the most visible changes with the arrival of a submerged macrophyte is the loss of open mud and the mudflat's associated fauna, which proceed to have profound effects at multiple trophic levels (Posey, 1988; Baldwin and Lovvorn, 1994; Neira et al., 2005; Ayres et al., 2004; Levin et al., 2006; Burfeind et al., 2009). It is unclear whether the loss of unvegetated sediments, with their distinct biodiversity and functional role, can be substituted ecologically by an invading macrophyte. Still, some non-indigenous species can have "positive" ecological impacts in invaded habitats (Sax et al., 2007; Davis et al., 2011). Invasive species have been reported to facilitate native species through mechanisms including pollination, habitat modification, and predatory release (see Rodriguez, 2006 for review). In seagrass beds where the invasion of *Zostera japonica* into native *Z. marina* habitats along the Pacific Northwest coast resulted in competition between the plants, vegetated benthic cover increased overall and supported higher productivity within invaded bays (Posey, 1988; Baldwin and Lovvorn, 1994; Ruesink et al., 2006). Optimistically then, the expansion of *H. stipulacea* into unvegetated or low-density seagrass assemblages in Dominica and the Caribbean may lead to a greater availability of trophic resources such as epibiota prey, and may support an increased number of both seagrass and non-seagrass associated fish. In Dominica particularly, present seagrass acreage is limited and *H. stipulacea* may increase coverage by expanding into areas not currently inhabited by seagrass. Thus, the consolation of decreased local seagrass biodiversity may be the creation of new seagrass habitat and its own associated resources.

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