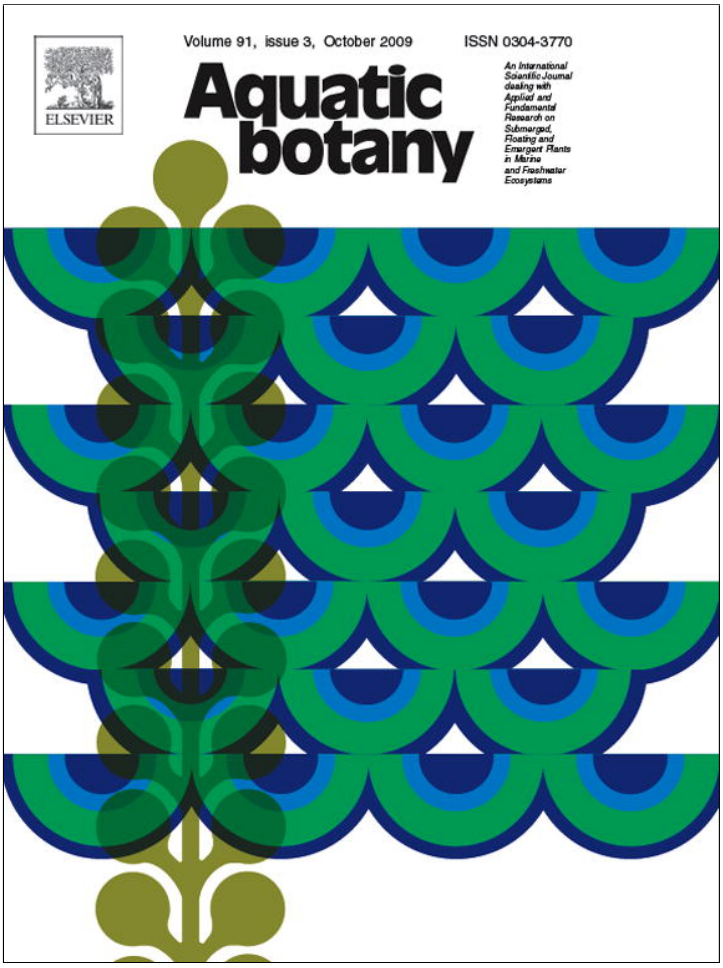
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The distribution and expansion of the invasive seagrass *Halophila stipulacea* in Dominica, West Indies, with a preliminary report from St. Lucia

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ABSTRACT

The seagrass *Halophila stipulacea* Forsskål, native to the Red Sea, is an invasive species in the Mediterranean that was recently observed offshore Grenada, in the Caribbean. Here, we document the presence of this seagrass in Dominica and St. Lucia, demonstrating it has spread across part of the eastern Caribbean. *H. stipulacea* in Dominica was present in seven locations along the west coast covering more than 22.9 ha of the benthos, at depths from 2 to 18 m. Populations were concentrated in or adjacent to bays frequented by recreational or commercial boats, likely vectors for the introduction. Morphological features varied from bed to bed, with depth being the predominant driving factor. *H. stipulacea* had a rapid mean lateral bed expansion rate of 0.5 cm d^{-1}, with a maximum rate of >6 cm d^{-1}. *H. stipulacea* patches often occurred exclusive of the otherwise dominant seagrasses of the Caribbean. The potential for the expansion of *H. stipulacea*, combined with its tolerance for a wide spectrum of environmental conditions, positions it as a potential threat to local and regional biodiversity.

1. Introduction

The ecological consequences of invasive species in marine environments can be severe (Carlton et al., 1990; Boudouresque et al., 1995; Shiganova, 1998; Casas et al., 2004). The loss of biological diversity and the impact on human activities are central concerns with the proliferation of an invasive species. In coastal seagrass habitats algae, cnidarians, mollusks, polychaetes, arthropods, and to a lesser degree allochthonous seagrasses have all been introduced, and in many instances have become invasive organisms. Two seagrass species, *Zostera japonica* Aschers and Graebn and *Halophila stipulacea* Forsskål, have extended their native range via human activities to become invasive (Williams, 2007). The temperate seagrass *Z. japonica* was introduced to the Pacific coast of North America from Japan in the early 1900s and has since become established in estuaries, where it competes with the native seagrass *Zostera marina* and has significantly altered the previously bare tidal flats (Harrison and Bigley, 1982; Baldwin and Lovvorn, 1994; Bando, 2006; Short et al., 2007).

H. stipulacea is a tropical seagrass with a native range east to India, west to eastern continental Africa, south to Madagascar, and north to the Red Sea and Persian Gulf (Den Hartog, 1970). The opening of the Suez Canal in 1869 facilitated the expansion of *H. stipulacea* into the Mediterranean Sea. From the mid-1800s *H. stipulacea* migrated west through the Mediterranean Sea, reaching Malta in 1970 (Schembri and Lanfranco, 1996), the Ionian Sea in 1992 (Van der Velde and Den Hartog, 1992), and the north coast of Sicily in 1997 (Procaccini et al., 1999). In 2002 *H. stipulacea* became only the second seagrass to make a transoceanic migration with the discovery of a 300 m^2 mono-culture of *H. stipulacea* in a single bay on the Caribbean coast of Grenada, West Indies (Ruiz and Ballantine, 2004).

The success of *H. stipulacea* as an invasive in the Mediterranean Sea can be attributed to its rapid vegetative expansion (Marbá and Duarte, 1998), habitat flexibility (Coppejans et al., 1992; Pereg et al., 1994), tolerance of a wide salinity range (Por, 1971), adaptation to high irradiance (Schwarz and Hellblom, 2002), and ability to grow at depths from the intertidal zone to greater than 50 m (Beer and Waisel, 1981). The rapid growth and pervasiveness of *H. stipulacea* is similar to another aggressive invasive macrophyte, *Caulerpa taxifolia* (Boudouresque and Verlaque, 2002; Anderson, 2005).

Here the seagrass *H. stipulacea* is documented for the first time in Dominica and St. Lucia. This second report in the Caribbean Sea occurs only a few years after its initial discovery in Grenada

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(Ruiz and Ballantine, 2004). A description verifying the species' identification, estimate of coverage, and a comparison of morphometric variation between stands occurring on the west coast of Dominica is presented.

2. Methods

2.1. Distribution

Following the initial identification of *H. stipulacea*, 48 of the 103 km (46%) of the north, west and south coastlines in Dominica, West Indies (15°30′N, 61°20′W) were surveyed in 0.5–4 km stretches. The surveyed area represents approximately 90% of potential seagrass habitat. The benthos from 0 to 18 m was searched systematically for *H. stipulacea* by snorkeling in a zigzag fashion along the coastline. This seagrass has been reported to grow as deep as 50 m; however, for this study it was surveyed only to the depth feasible for surveying by snorkeling. Upon encountering the seagrass, a map of the specific location was sketched, area (m^2) of the patch was estimated, and depth, substrate type, and co-occurring species were noted. An estimate of percent cover of *H. stipulacea* for each patch was assigned using a visual ranking: 1 = <25% cover, 2 = 25–75% cover, and 3 = >75% cover. Voucher specimens were taken from several sites, photographed, then preserved in 70% ethanol and archived at the Institute for Tropical Marine Ecology, Dominica.

To assess if *H. stipulacea*'s presence in the Caribbean was restricted to Dominica and Grenada, preliminary surveys were made at the nearby islands of St. Lucia (14°0′N, 61°0′W) and Antigua (17°5′N, 61°50′W). Using satellite images and guide books, sites were selected based on access, popularity for anchoring, and likelihood of supporting seagrasses. Surveying was conducted by snorkeling in a zigzag fashion along the coastline with a depth limit of 18 m using the same field protocol for mapping, describing and estimating features of *H. stipulacea* as used in Dominica.

2.2. Morphometric variation

Specimens of *H. stipulacea* were sampled from each location where the plant was found. The depth of each sampled bed was recorded and assigned to one of the three categories: shallow (<5 m), intermediate (5–10 m) and deep (>10 m). Specimens were sampled from the center of each patch (<200 m^2) or bed (≥200 m^2). Ten rhizome fragments with complete vertical shoots were collected by hand and blade height, blade width, scale height, folded scale width, internode length (rhizome length between consecutive vertical shoots), and rhizome diameter were measured. The means of each feature were contrasted using MANOVA to determine if *H. stipulacea* plants varied by depth or patch size.

2.3. Lateral bed expansion rate

Changes in bed dimensions were measured by monitoring the dimensions of four *H. stipulacea* patches at three locations on the west coast of Dominica. The maximum length along the patch's north–south and east–west axis was determined using a measuring tape. White-painted stones were placed along the boundary of the patch to facilitate subsequent locating and measurements. Changes in bed dimensions were determined by re-measuring each patch at 25–40 day intervals and noting the increase or decrease of the horizontal rhizomes along the margin of the patch. Distance in centimeters was then divided by the number of days to express mean daily lateral bed expansion rate for each interval.

3. Results

3.1. Species verification

The presence of *H. stipulacea* in Dominica was verified by examining the characteristic features of the species based on the description of Den Hartog (1970). Rhizome diameter measured 1–2 mm with a single root at each node and an internode distance of 7–50 mm (Fig. 1a). Leaf scales were folded and elliptic in shape with a length of 6–18 mm and width of 2–6 mm. Blades were elliptic, oblong to linear, and pale to dark green in color with a length of 22–57 mm and width of 5–9 mm. The surface of each blade had a distinct mid-rib originating at the petiole and ended near the apex of the blade where it merged with the circumventing intramarginal nerve (Fig. 1b). Serrations were present along the lateral margin and at the apex of the blade (Fig. 1b). Additionally, the blades had numerous and often paired cross-veins extending from the mid-rib to the intramarginal nerve at a 30–60° angle. Blade dimensions of samples (n = 78) taken from six beds along the west coast of Dominica were measured and yielded similar values reported in other studies (Table 1).

3.2. Distribution

In total, *H. stipulacea* was found along 9 km of the 103 km of coastline surveyed in Dominica. The invasive seagrass was not ubiquitous on the island, but rather concentrated on the northwest coast near the island's primary anchorage at depths of 2 to ≥18 m (Table 2, Fig. 2), and was most common at depths ≥6 m. In the northwest, *H. stipulacea* covered approximately 22.9 ha to depths of 18 m; however, the actual cover was higher given that the seagrass occurred at depths greater than 18 m that were observed, but not surveyed. For the most part, *H. stipulacea* was found in mono-specific assemblages (Fig. 1c), although small patches or the edges of large patches were occasionally intermixed with *Syringodium filiforme* Kütz. For example, in Prince Rupert Bay a 12 m × 12 m patch of *H. stipulacea* occurred within an area of *S. filiforme*. The density of the invasive seagrass was highest in the center of the patch (strictly *H. stipulacea*, percent cover was estimated at >75%) and decreased towards the margins (percent cover was estimated between 25 and 75%); within approximately 3 m of the margin, *S. filiforme* shoots increased in density and eventually were the sole seagrass beyond the invasive patch. Repeated monthly measurements of this patch showed *H. stipulacea*'s gradual expansion into space previously occupied by *S. filiforme*.

Along the southwest coast, *H. stipulacea* was limited to a single bay in two small, mono-specific patches with a total area of approximately 120 m^2. The two patches occurred 100 m offshore at a depth of 7 m, were roughly 10 m apart from each other and were completely surrounded by sand. The center of each patch had a percent cover >75% whereas the margins covered <25%. Small patches of the native *Halophila decipiens* Ostenfeld and scattered shoots of *S. filiforme* occurred closer to shore. This small bay, which also hosts an oil tanker depot, was the only location outside Prince Rupert Bay area where the invasive seagrass occurred.

The scattered distribution of *H. stipulacea* in Dominica was also found in St. Lucia. Roughly 4 km of coastline was surveyed in six St. Lucian bays, three of which supported patches of the invasive seagrass. Two of the bays (Marigot Bay and Labrelotte Bay) provide anchorage for recreational yachts, while the third bay (Anse La Raye) harbors a small fishing village. Preliminary surveying estimated a total area of 50 m^2 in St. Lucia.

A comparable effort was made searching for *H. stipulacea* in Antigua, yet the invasive seagrass was not found within any of the six bays frequented by recreational and fishing boats surveyed along this Leeward Island.

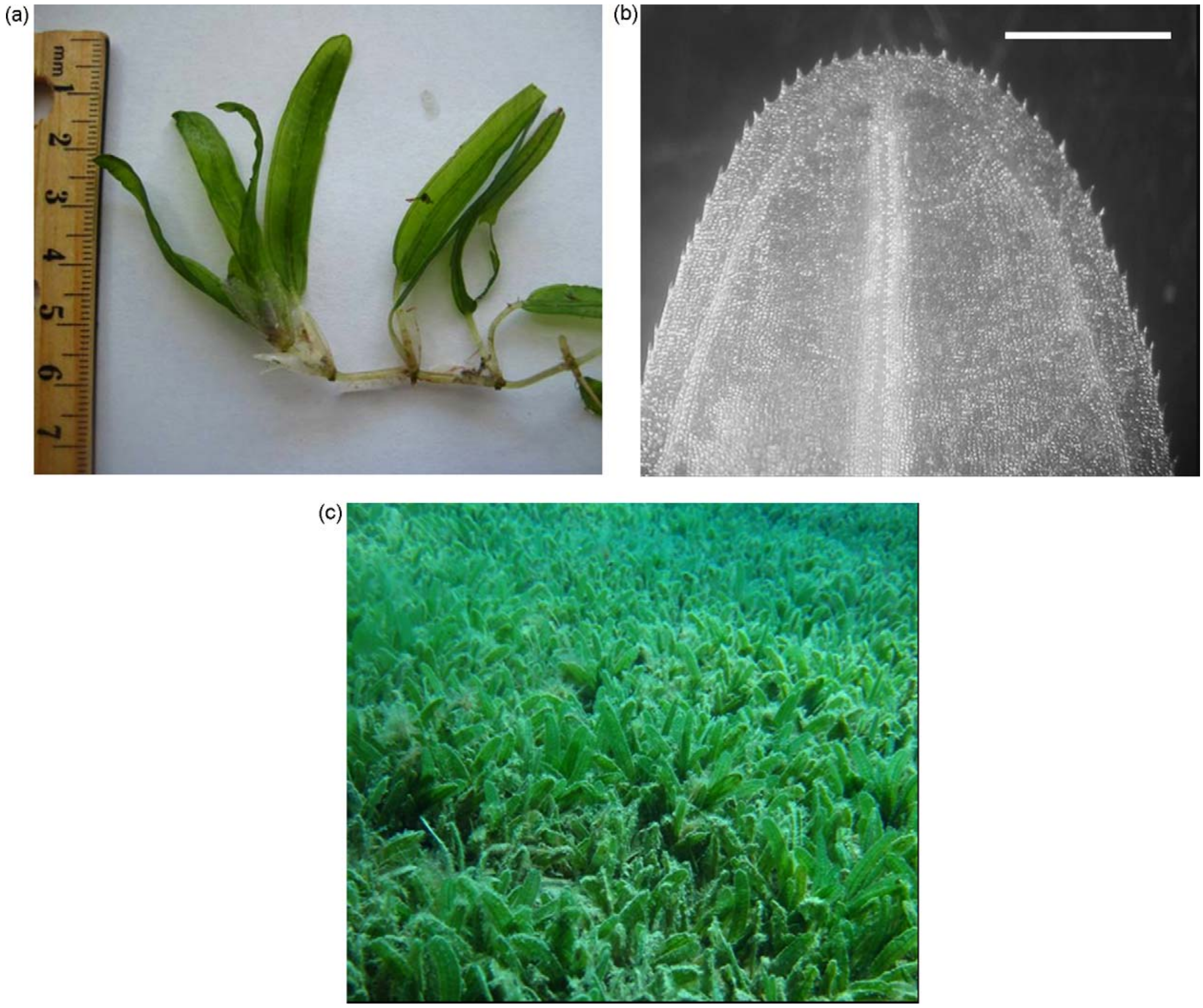

Fig. 1. (a) Intact *Halophila stipulacea* fragment displaying leaves (=blades), leaf scales, petiole, and horizontal rhizome; ruler shown for scale. (b) *H. stipulacea* apex blade region showing pronounced mid-rib terminating just prior to the tip of the leaf and merging with the circumventing intramarginal nerve; serrations along the apex margin also visible. Scale bar = 1 mm. (c) *H. stipulacea* patch, 10 m depth, Lamothie Bay, Dominica. Approximate field of view = 50 cm.

3.3. Morphometric variation

H. stipulacea occurring in Dominica at depths from 2 to 18 m had varied morphologies. The longest blades and scales, widest blades, and thickest diameter rhizomes were found at intermediate depths (5–10 m) (Fig. 3). *H. stipulacea* from depths less than 5 m had the lowest value for all of the aforementioned measures, but had the longest internode length. Specimens from deep sites (>10 m depth) had intermediate values for all plant features. All plant measures varied significantly with depth, but only blade length and internode length varied significantly with patch size (two-factor MANOVA; for depth: blade length $F_{2,62}$ = 125.4, blade width $F_{2,62}$ = 27.6, scale length $F_{2,62}$ = 48.6, rhizome diameter $F_{2,62}$ = 12.2, internode length $F_{2,62}$ = 17.4, all $P < 0.001$; for patch size: blade length $F_{1,62}$ = 8.3, internode length $F_{1,62}$ = 8.3, both $P = 0.005$).

Variation in plant features within a single patch or bed was qualitatively observed. Along the margin of most stands, individual rhizomes radiated outward from the patch in every direction and consistently had long internodes between vertical shoots with short leaves (<25 mm in length). In contrast, rhizomes in the

Table 1

Comparison of *Halophila stipulacea* plant measurements from three locations. Blade length, blade width, scale length, scale width, internode length (distance between consecutive vertical shoots), and rhizome diameter are reported in millimeters, mean and standard deviation in parenthesis (n = 78). Samples were collected from Prince Rupert Bay, Toucari Bay (2 locations), Fond Cole, Douglas Bay, and Pointe Ronde from 2 to 18 m depth. Native range specimens from Den Hartog (1970) are from the Red Sea and Indian Ocean.

Location	Blade height	Blade width	Scale height	Scale width	Internode length	Rhizome diameter
Dominica[a]	22–57 mm (44.1 ± 9.0 mm)	5–9 mm (7.2 ± 1.0 mm)	6–18 mm (12.4 ± 3.1 mm)	2–6 mm (4.4 ± 1.0 mm)	7–50 mm (17.8 ± 10.1 mm)	1–2 mm (1.3 ± 0.3 mm)
Grenada[b]	48 mm	8 mm	10–15 mm	5 mm	20–22 mm	2 mm
Native range[c]	30–60 mm	2.5–8 mm	12–17 mm	6–10 mm	10–40 mm	0.5–2 mm

[a] Current study.
[b] Ruiz and Ballantine (2004).
[c] Den Hartog (1970).

Table 2
Locations where *H. stipulacea* was found in Dominica, West Indies. Data includes name of specific location and region of the Dominica coastline, latitude and longitude coordinates, approximate area of *H. stipulacea* at location, depth of center of bed/patch, co-occurring native seagrasses within close proximity to the invasive, and whether or not *H. stipulacea* is found as a mono-culture or mixed with native species of seagrass within the bay.

Bay	Region	Latitude	Longitude	Estimated area (m^2)	Depth of bed (m)	Other seagrasses in bay	Occurs in mono-culture	Occurs in mixed assemblage
Lamothie Bay	Northwest	15°37′8.09″N	61°27′59.81″W	9,375	7-18+	Sf, Hd	Yes	No
Toucari Bay	Northwest	15°36′32.08″N	61°27′51.79″W	36	2, 18	Sf, Hd, Hw	Yes	Yes
Douglas Bay	Northwest	15°35′57.30″N	61°27′56.33″W	37,500	7-18+	Sf, Hd, Tt	Yes	Yes
Prince Rupert Bay	Northwest	15°34′58.92″N	61°28′2.47″W	181,600	5-18+	Sf, Hd, Tt	Yes	Yes
Pointe Ronde	Northwest	15°32′21.66″N	61°28′53.82″W	4	15	Sf	Yes	No
Ti Bay	Northwest	15°32′49.83″N	61°28′22.32″W	80	10	Sf, Hd, Hw	Yes	No
Pringles Bay	Southwest	15°19′36.06″N	61°23′47.50″W	120	7	Hd	Yes	No

Sf = *Syringodium filiforme*, Hd = *Halophila decipiens*, Hw = *Halodule wrightii*, Tt = *Thalassia testudinum*.

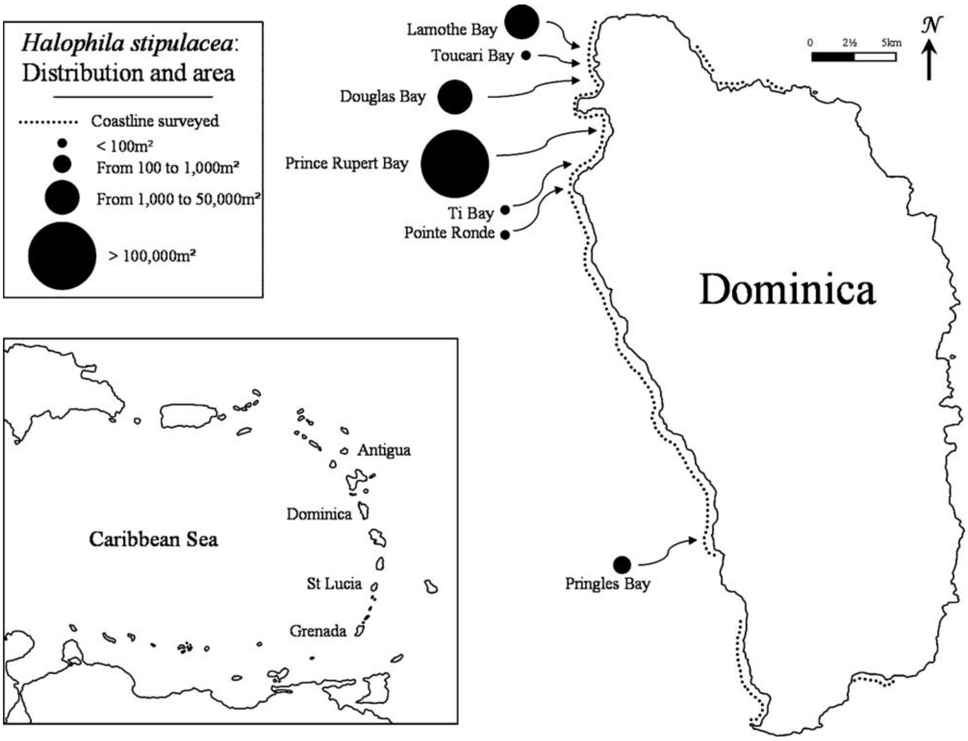

Fig. 2. *H. stipulacea*'s distribution and estimated area at the seven locations along the west coast (Caribbean) of Dominica, West Indies as of February 2008. Black circles represent the estimated number of m^2 that the invasive seagrass covered within each specified bay.

center of these patches had short internodes with tall blades (41–51 mm in length). This differentiation of plant measures is also reported for *H. stipulacea* in the Mediterranean (Procaccini et al., 1999).

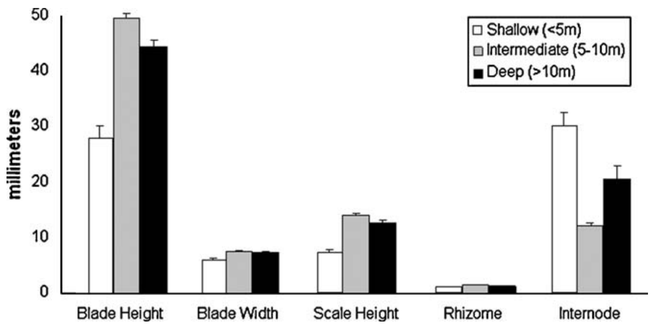

Fig. 3. *H. stipulacea* morphometrics compared by depth. Plant measures of blade height, blade width, scale height, rhizome diameter and internode length (all in mm) are significantly different (ANOVA, $P < 0.01$) when compared by bed depth (shallow <5 m, intermediate 5–10 m, deep >10 m). Error bars represent standard error.

3.4. Lateral bed expansion rate

Dimensions of four *H. stipulacea* patches were monitored for one to three months between December 2007 and February 2008. Mean lateral expansion across all patches during this period was 0.5 cm d^{-1}. This estimate includes lateral retreats experienced by some patches after a strong wave disturbance in February. Considering only sites and months of positive growth, mean lateral expansion was 1.1 cm d^{-1}. A maximum lateral expansion of 6.7 cm d^{-1} was recorded along one portion of the South Cabrits' patch in December 2007, although other regions of the patch showed slower expansion and overall the patch had an average lateral expansion of 1.0 cm d^{-1} for that month. Patches had positive lateral bed expansion 71% of the time.

4. Discussion

4.1. H. stipulacea in Dominica and the Caribbean

H. stipulacea was first recorded in Dominica in June 2007, although surveying did not begin until September 2007. Within three months of the survey's onset, *H. stipulacea* was documented in seven bays stretching along 9 km of coastline and covering a total survey area of over 22.9 ha. *H. stipulacea* occurred predominantly along the northwest coast of the island in the vicinity of Prince Rupert Bay. Prince Rupert Bay is Dominica's largest and most protected harbor and supports the island's primary recreational anchorage (Honeychurch, 1995). The only other location where *H. stipulacea* has been found was in Pringles Bay, the site of an oil tanker depot. *H. stipulacea*'s close proximity to anchorages for foreign vessels suggests these sites may have served as a corridor for the introduction of this species to Dominica. Ruiz and Ballantine (2004) first reported the occurrence of *H. stipulacea* in the Caribbean and drew a similar conclusion, suggesting that recreational yachts brought the seagrass to Grenada from the Mediterranean Sea. Given the added discoveries of the invasive seagrass in Dominica and St. Lucia it seems likely that *H. stipulacea* is spreading throughout in the region.

4.2. Implications of H. stipulacea in Dominica

It is unclear how the invasion of *H. stipulacea* will influence the Dominica's near-shore ecosystem. The island's steep, narrow shelf and high output from fluvial outfalls (Steiner, 2003) limits the viable habitat for the native seagrasses. The presence of a seagrass that is tolerant to a wide range of environmental factors could occupy open space and thus re-shape the local marine resources, such as near-shore fisheries. Differences in *H. stipulacea*'s structural morphometrics at different depths, and to some degree different patch sizes, highlights the seagrass's plasticity when growing in a broad range of conditions in Dominica. A higher cover of seagrasses may be beneficial as submerged aquatic vegetation has been often cited to support higher populations of marine fish and invertebrates than bare substrate, as was the case for *Z. japonica* (Lubbers et al., 1990; Ferrell and Bell, 1991; Baldwin and Lovvorn, 1994; Jenkins and Wheatley, 1998; Gillanders, 2006). Additionally, herbivorous fish have shown a grazing preference towards pioneering species, such as *H. stipulacea*, over climax seagrass species (Mariani and Alcoverro, 1999).

On the other hand, if *H. stipulacea* expands into existing seagrass beds, it may result in the loss of biodiversity. In hurricane-prone areas like Dominica, the rapid colonization of recently disturbed habitats by *H. stipulacea* could interfere with natural seagrass succession. Likewise, if *H. stipulacea* is displacing native seagrasses in Dominica, a loss of seagrass diversity may occur. The displacement of an indigenous species may not only compromise that species (for examples, see Race, 1982; Fogarty and Facelli, 1999), but may also having a cascading effect on any organisms supported by that species (for examples, see Spencer et al., 1991; Levin et al., 2006; Khan et al., 2003; Byrnes et al., 2007; Daskalov et al., 2007). Further studies of *H. stipulacea* will be needed to resolve the question of its ecological impacts in the Caribbean basin.

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