

Short communication

Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the Eastern CaribbeanDemian A. Willette^{a,*}, Julien Chalifour^b, A.O. Dolfi Debrot^c, M. Sabine Engel^d, Jeff Miller^e, Hazel A. Oxenford^f, Frederick T. Short^{g,h}, Sascha C.C. Steinerⁱ, Fabien Védie^j^a Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095, United States^b Julien Chalifour, Réserve Naturelle Nationale de Saint-Martin, Antenne du Conservatoire du Littoral Saint-Martin, 803 Résidence les Acacias, Anse Marcel 97150, Saint Martin (French Part)^c Institute for Marine Research and Ecosystem Studies, Wageningen UR, P.O. Box 57, 1780AB, Den Helder, The Netherlands^d STINAPA, P.O. Box 368, Bonaire^e US National Park Service, South Florida/Caribbean Inventory and Monitoring Network, 1300 Cruz Bay Creek, St. John, VI 00830, United States^f Center for Resource Management and Environmental Studies, University of the West Indies, Cave Hill Campus, BB 11000, Barbados^g Aquatic Resources Division, Washington State Department of Natural Resources, Olympia, WA 98504, United States^h Jackson Estuarine Laboratory, University of New Hampshire, Durham, NH 03824, United Statesⁱ Institute for Tropical Marine Ecology, Dominica^j Direction de l'Environnement de l'Amenagement et du Logement, Pointe de Jaham, 97274 Schoelcher Cedex, Martinique

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ABSTRACT

Halophila stipulacea (Hydrocharitaceae) is reported for the first time from Aruba, Curaçao, Grenadines (Grenada), St. Eustatius, St. John (US Virgin Islands), St. Martin (France), and St. Vincent and the Grenadines, bringing the total number of known occurrences from eastern Caribbean islands to 19. Native to the Red Sea and western Indian Ocean, *H. stipulacea* spread to the Mediterranean Sea in the late 1800s and became established in the eastern Caribbean in 2002. The species has dispersed north and south of its first sighting in Grenada and now spans a latitudinal distance of 6° (>700 km), most likely facilitated by a combination of commercial and recreational boat traffic. The continuing range expansion of *H. stipulacea* indicates the species has successfully acclimated to surviving in the Caribbean environment, warranting further investigation into its ecological interactions with the indigenous seagrasses.

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1. Introduction

Invasions of non-indigenous species into marine habitats are increasingly common and often troublesome (Cohen and Carlton, 1998; Williams and Smith, 2007; Molnar et al., 2008). Further, some invasive species have expanded globally, across a wide range of environmental parameters and into diverse native communities. To date, two marine angiosperms have shown recent trans-oceanic range expansions; *Zostera japonica* from the northwest to the north-east Pacific Ocean, and *Halophila stipulacea* from the Indian Ocean to the Mediterranean Sea and the Caribbean Sea (Williams, 2007).

H. stipulacea Fosskal is a tropical, euryhaline marine angiosperm in the family Hydrocharitaceae. The genus *Halophila* is composed of ten species. Five species (*H. beccarii*, *H. decipiens*, *H. minor*, *H. ovalis* and *H. stipulacea*) are native to the Red Sea and western Indian Ocean and five are native to the Caribbean Sea (*H. baillonii*,

H. decipiens, *H. engelmanni*, *H. johnsonii*, and *H. ovalis*) (Green and Short, 2003; Short et al., 2010a). There are no *Halophila* in the Mediterranean except *H. stipulacea*; however, *H. decipiens* does occur along the Atlantic northwest coast of Africa and around the Canary Islands (Green and Short, 2003).

The native range of *H. stipulacea* includes the Red Sea and Persian Gulf, as well as the coastal islands of eastern Africa and the southeast coast of the Indian subcontinent (den Hartog, 1970). *H. stipulacea* was first reported in the Mediterranean in 1894 and is believed to have arrived from the Red Sea after the opening of the Suez Canal in 1869 (Lipkin, 1975; notably this reference to the invasive *H. stipulacea* appears in the very first issue of Aquatic Botany). The species first became established along the eastern Mediterranean coastlines of Egypt, Greece, and Lebanon (den Hartog, 1970; Lipkin, 1975) with subsequent expansion northward to Turkey and Albania (Alpinar, 1987; Kashta and Pizzuto, 1995) and westward to Italy, Libya and Tunisia (Gambi et al., 2009; Sghaier et al., 2011).

H. stipulacea was first reported in the Caribbean in Grenada in 2002 (Ruiz and Ballantine, 2004), followed by reports from Dominica and Saint Lucia in 2007 and 2008, respectively (Willette

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and Ambrose, 2009). Since then, the seagrass has been found in Bonaire, Guadeloupe, Les Saintes, Martinique and St. Maarten (Netherlands) (DEAL, 2011; Debrot et al., 2012; Kerninon, 2012; Debrot et al., in review; Table 1). The invasive seagrass was not observed in Antigua in 2008 or 2010 during seagrass surveys (Willette and Ambrose, 2009; Short et al., 2010a). Here we provide first reports of *H. stipulacea* from eleven additional islands, and summarize the geographic distribution in the eastern Caribbean one decade after its first report.

2. Methods

To determine the geographic extent of the seagrass *H. stipulacea* beyond published reports, inquiries were made to institutes and colleagues located throughout the eastern Caribbean. A description of the habitat, diagnostic features and photographs of *H. stipulacea* were provided in the initial communication. To verify the presence of the seagrass, collaborators were requested to collect specimens and photograph the putative *H. stipulacea* seagrass for identification via diagnostic characteristics (den Hartog, 1970). Five indigenous *Halophila* species occur in the Caribbean; however, most are clearly distinguishable from *H. stipulacea*. *Halophila bailonii* Ascherson and *H. engelmanni* Ascherson are morphologically distinct with four to eight blades at the tip of a pronounced petiole (den Hartog, 1970). *Halophila ovalis* (R. Brown) Hooker f. and *H. johnsonii* Eiseman are geographically restricted to Antigua and Florida, respectively; typically have petioles longer than blades, a smooth blade surface and leaf margin, and blade scales less than 6 mm (den Hartog, 1970; Eiseman and McMillan, 1980; Short et al., 2010a). *Halophila decipiens* Ostenfeld is the most widespread and abundant native Caribbean *Halophila* and co-occurs with *H. stipulacea* in Dominica (Willette and Ambrose, 2009). *H. decipiens* has paddle-shaped, translucent blades (1–2½ cm long) with 6–9 pairs of cross veins. Blades extend in pairs from non-sheathed petioles growing from the rhizome. *H. decipiens* and *H. stipulacea* both have serrated leaf margins and minute hairs on the leaf surface. *H. stipulacea* is distinguished from *H. decipiens* by its long, linear and occasional bullate blades (3–6 cm long) with 10–20 pairs of cross veins. Further, at each rhizome node of *H. stipulacea*, a large, lopsided leaf sheath covers the short petioles, of which each has two blades.

Where *H. stipulacea* was confirmed to be present, site data including coordinates, depth of the seagrass, visual estimation of abundance and distribution, conspicuous presence of associated flora and fauna, conspicuous presence of flowers or seed pods, if the invasive seagrass occurred in a Marine Protected Area (MPA)/marine reserve, and if the location was the site of frequent anchoring (i.e. a harbor or anchorage) were collected.

3. Results

H. stipulacea was reported as present along the coastlines of Aruba, Bonaire, Curaçao, Grenada, the Grenada Grenadines, Dominica, Guadeloupe, Les Saintes, Martinique, St. Eustatius, St. Vincent and the Grenadines, St. John (US Virgin Islands), St. Martin (France) and St. Maarten (Netherlands) (Table 1 and Fig. 1). Species identification was confirmed using diagnostic morphological features of *H. stipulacea* (Fig. 2). Descriptions from Aruba, Curaçao, the Grenadines of Grenada, St. Eustatius, St. John, St. Martin, St. Vincent and five of the St. Vincent Grenadine islands represent new sightings. The invasive seagrass was reported as “not present” in Barbados and South Caicos (Turks and Caicos Islands), and inconclusive evidence precludes us from confirming *H. stipulacea* in St. Kitts and Nevis.

Table 1 Reported *H. stipulacea* in eastern Caribbean islands. Site descriptions include island name, location where seagrass was first observed, year of first observation, latitude and longitude, approximate depth of seagrass, abundance (rare, common, abundant), substrate type, presence/co-occurrence of native seagrasses (Sf – *Syringodium filiforme*, Tt – *Thalassia testudinum*, Hd – *Halophila decipiens*, Hd – *Halodule wrightii*), if *H. stipulacea* occurs in a Marine Protected Area (MPA) on the island, and whether the location is or near fishing or recreational boat anchorage.

Island	Year first observed	Location	Latitude	Longitude	Depth	Abundance	Substrate	Other seagrasses	<i>H. stipulacea</i> in MPA?	Anchorage	Reference
Grenada	2002	Flamingo Bay	12° 05' N	61° 45' W	4 m	Rare	Sand	None	No	Yes	Ruiz and Ballantine (2004)
Martinique	2006 ^a	Fort-de-France Bay	14° 36' N	61° 05' W	30 m	Abundant	Sand	Tt, Sf, Hd, Hw	No	Yes	DEAL (2011), This report
Dominica	2007	Lamothe Bay	15° 37' N	61° 27' W	7–18 m	Common	Sand	Sf, Hd	Yes	No	Willette and Ambrose (2009)
St. Lucia	2008	Marigot Bay	13° 57' N	61° 01' W	1 m	Rare	Sand	None	No	Yes	Willette and Ambrose (2009)
Bonaire	2010	Lac Bay	12° 05' N	68° 14' W	<1–5 m	Abundant	Sand	Tt, Sf, Hw	Yes	No	Debrot et al. (2012)
Guadeloupe	2010	Anse du petit Malendure	16° 10' N	61° 46' W	n/d	n/d	Sand	n/d	No	Yes	Kerninon (2012)
Les Saintes	2010	Terre-de-Haut	15° 51' N	61° 37' W	7–15 m	Common	Sand	Tt, Sf	No	Yes	Kerninon (2012)
St. Vincent	2011	Villa	13° 08' N	61° 12' W	3–6 m	Abundant	Sand	None	No	Yes	This report
Curaçao	2012	St. Jorisybay	12° 07' N	68° 49' W	2 m	Abundant	Sand	Tt	No	No	This report
St. Maarten (Dutch)	2012	Simpson Bay	18° 01' N	63° 05' W	5 m	Abundant	Sand	None	Yes	Yes	Debrot et al. (in review)
St. John USVI	2012	Mennebeck Reef	18° 21' N	64° 41' W	16 m	Abundant	Sand	Sf, Tt	Yes	No	This report
St. Martin (French)	2012	Baie du Cul-de-Sac	18° 06' N	63° 01' W	3 m	Rare	Sand	Sf, Tt	No	Yes	This report
St. Eustatius	2012	Jenkins Bay	17° 30' N	63° 00' W	16–26 m	Common	Sand	Sf	Yes	No	This report
Aruba	2013	San Nicolas	12° 27' N	69° 55' W	10 m	Abundant	Sand	None	No	Yes	This report
Grenadines (St. Vincent)	2013	Admiralty Bay, Bequia	13° 0' N	61° 14' W	1–8 m	Abundant	Sand	None	Yes	Yes	This report
	2013	Salt Whistle Bay, Mayreau	12° 39' N	61° 23' W	3–4 m	Common	Sand	Tt, Sf	No	Yes	This report
	2013	Tobago Cays	12° 38' N	61° 21' W	3–5 m	Rare	Sand	Sf	Yes	Yes	This report
	2013	Richmond Bay, Union Is.	12° 36' N	61° 26' W	1–3 m	Common	Sand	Tt	No	No	This report
	2013	Petit St. Vincent	12° 32' N	61° 23' W	4–8 m	Abundant	Sand	None	No	Yes	This report
Grenadines (Grenada)	2013	Sandy Island, Carriacou	12° 29' N	61° 28' W	1–4 m	Common	Sand	None	Yes	Yes	This report

^a Martinique first report in 2006, table data from 2010 by F. Védie as summation of island-wide survey. N/d indicates no data available.

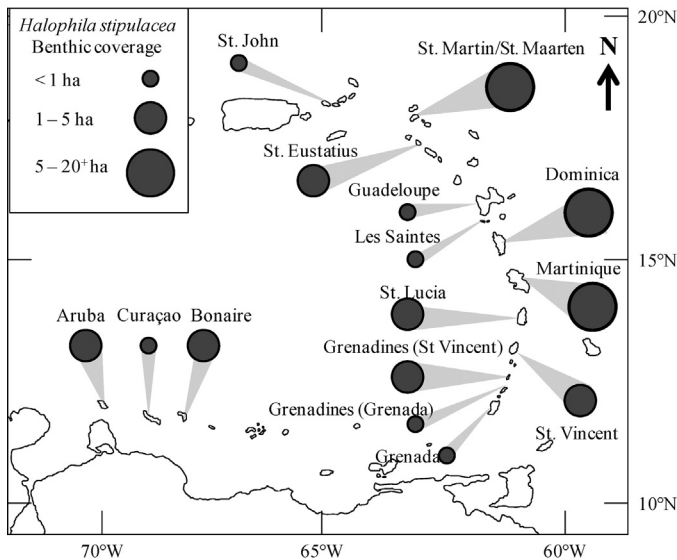


Fig. 1. Geographic distribution of *Halophila stipulacea* in the Caribbean with annotation of estimated benthic cover (ha).

The invasive seagrass *H. stipulacea* occurred in popular anchorages frequented by commercial and recreational boats, however, the distribution of the seagrass was not confined to these locations. The seagrass is also reported from four marine protected areas including the Virgin Islands National Park and Virgin Islands Coral Reef National Monument in St. John, the Tobago Cays Marine Park in St. Vincent and the Grenadines, Sandy Island Marine Park in Grenadines (Grenada), Lac Bay Marine Protected Area in Bonaire, and the Northern Marine Park Reserve in St. Eustatius. *H. stipulacea* inhabited sandy substrate as pure, monospecific beds or in mixed assemblages with the native Caribbean seagrasses *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii* and congener *H. decipiens*. The depth range of the invasive seagrass was as shallow as 0.25 m (Curaçao) and as deep as 30 m (Martinique). Flowers or seedpods were not observed at any location.

Notable features and descriptions from each new report are detailed below:

Aruba – *H. stipulacea* was found in a lagoon near the settlement of San Nicolas, close to a local oil refining plant. The seagrass formed extensive and pure beds at approximately 10 m depth. No other seagrass species were found co-occurring with the invasive species.

Curaçao – *H. stipulacea* was found along more than 500 m of the northwestern shore of St. Jorisbay, a shallow, protected bay along the east coast. The seagrass formed dense, pure beds from 0.25 to 2 m depth in between beds of *T. testudinum*. The two seagrasses were found intermixed in some areas, with *H. stipulacea* occurring at very low densities. The bay is poorly accessible and has little to no motorboat traffic and negligible fishing activity.

Grenadines (Grenada) – *H. stipulacea* was identified within a popular day-charter anchorage at Sandy Island Marine Park, Carriacou. The seagrass was found in dense, pure beds over the sand substrate. The seagrass occurred at depths between 1 and 4 m, with no other flora or fauna conspicuously present.

St. Eustatius – *H. stipulacea* was identified in a single location, Jenkins Bay, during a survey of benthic habitats around the island in 2012. Jenkins Bay is located within the Northern Marine Park Reserve and supports several recreational dive sites. The site is also in close to a crude oil refinery and depot. The seagrass grew predominantly as dense, monoculture beds at 16 to 26 m depth, but

also co-occurred occasionally with *S. filiforme*, *Penicillus pyriformis* and *Udotea cyathiformis* (Chlorophyta).

St. John (US Virgin Islands) – *H. stipulacea* was first observed along the northeast coast of the island along the offshore Mennebeck Reef at a depth of 16 m (Table 1). The seagrass occurred in a mixed seagrass bed with *T. testudinum* and *S. filiforme* on sand adjacent to the reef. No conspicuous associated organisms were observed with *H. stipulacea*. Encroachment of *H. stipulacea* into the sand “halo” area, a typical zone of bare sand between reefs and seagrass beds, was noted during repeated visits to the site. The invasive seagrass has also been identified at the adjacent Haulover Reef, along the western shore at Lind Point, and within the southwest shoreline of Leinster Bay; all four locations are within the boundaries of the Virgin Islands National Park. Additionally, sightings have occurred in very shallow water (<2 m) between Otter and Water Creek in the Hurricane Hole area; within the boundary of Virgin Islands Coral Reef National Monument.

St. Martin (France) – *H. stipulacea* was found along the northeastern coastline in small patches within Baie de Cul-de-Sac, as well as at several sites within a 4 km radius including Anse Marcel, Ilet Tintamarre, and Baie de L’Embouchure. The seagrass occurred within extensive meadows of *T. testudinum* and *S. filiforme* at a depth of 1–10 m. *H. stipulacea* has also been reported from the Dutch portion of Simpson Bay Lagoon (Debrot et al., 2012), and here is reported from the French side. *Penicillus* spp. and *Caulerpa* sp. (Chlorophyta), and *Astichopus multifidus* (Holothuroidea) occurred alongside the invasive seagrass. Both Baie de Cul-de-Sac and Simpson Bay Lagoon are popular anchorages that receive high levels of boat traffic.

St. Vincent and the Grenadines – *H. stipulacea* occurs along at least six islands within St. Vincent and the Grenadines spanning 70 km and including St. Vincent, Bequia, Mayreau, the Tobago Cays, Union Island and Petit St. Vincent. Almost all locations are anchorages, with or without permanent moorings. The invasive seagrass was found between 1 and 8 m depth. *H. stipulacea* formed pure beds along St. Vincent, Petit St. Vincent and Bequia, and occurred in mixed assemblages with *T. testudinum* and *S. filiforme* at Mayreau and Union Island, and with *S. filiforme* in the Tobago Cays. *Tripaneustes ventricosus* (Echinoidea) was abundant at most locations, with observations of *Myrichthys breviceps* (Actinopterygii), *Pinna carnea* (Bivalvia), *Oreaster reticulatus* (Asteroidea), *Strombus gigas* (Gastropoda), *Chelonia mydas* (Reptilia) and various sponges and juvenile fishes at one or more sites (Fig. 2).

Martinique – Although *H. stipulacea* has been previously reported in Martinique (DEAL, 2011), limited information was available regarding its habitat. Here we provide such details from ongoing benthic habitat surveys around the island. At present, *H. stipulacea* occurs within the east coast bays of Galion, Sans-Souci, Francois and Anglais; the west coast bays of Anse Caritan and Fort-de-France, the southern shore section from Le Diamant to Trois Ilets and widely along the northern west shore of the island. It has been observed as deep as 30 m, and occurs both as pure beds and as mixed assemblages with the native seagrasses of *T. testudinum*, *S. filiforme*, *H. wrightii*, and *H. decipiens*. The seagrass grows adjacent coral reefs (no “halo”) and in small sand patches within the reef system. *T. ventricosus*, *S. gigas*, *C. mydas*, and various burrowing invertebrates and juvenile fishes occur in the invasive seagrass beds.

4. Discussion

From the first Caribbean sighting reported as a single 300 m² monospecific patch in Flamingo Bay, Grenada, in 2002, to its current distribution across at least 19 islands with coverage of hundreds of hectares, *H. stipulacea* is unquestionably now well established in

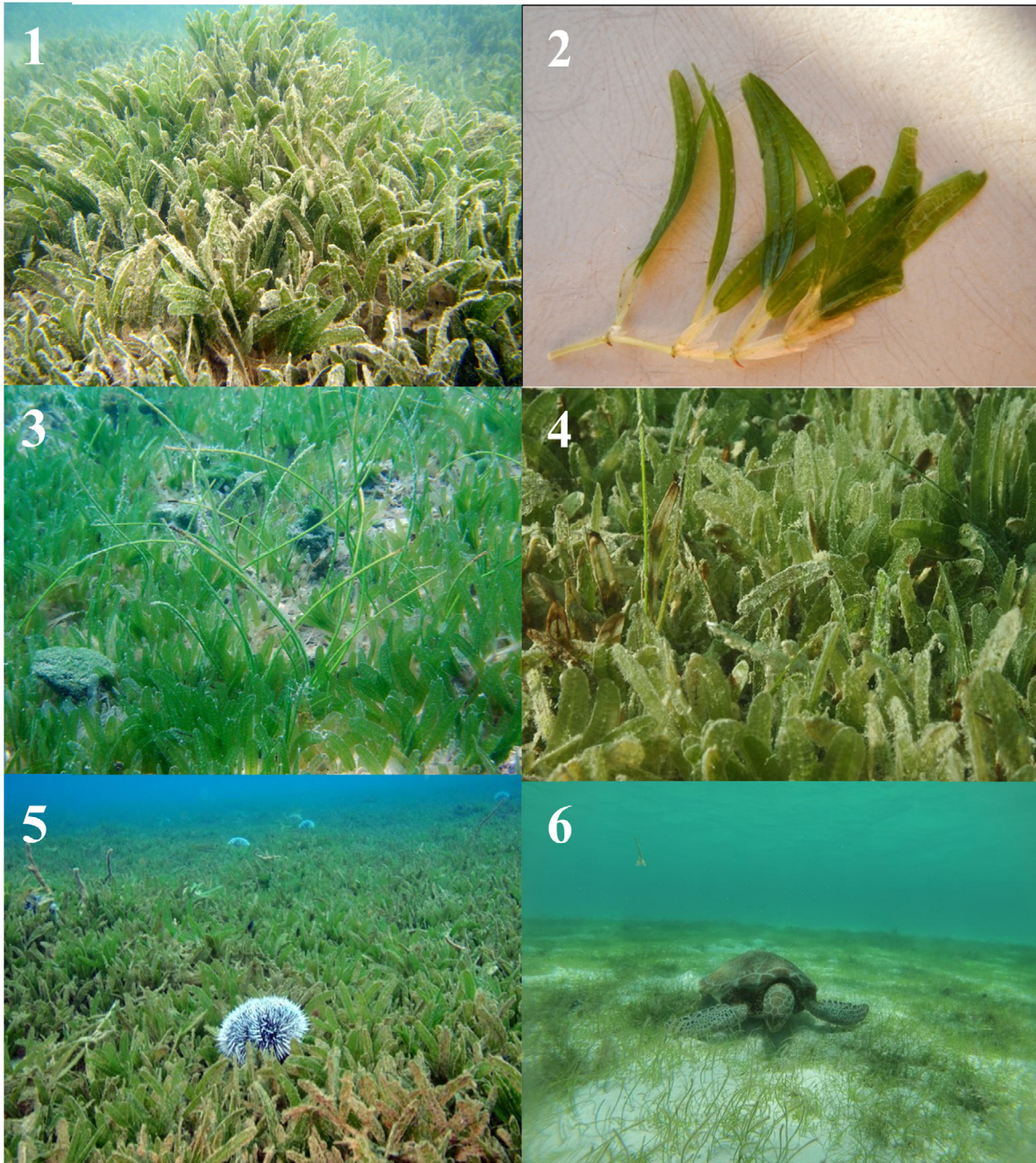


Fig. 2. Photographs of *H. stipulacea* and mixed with *Syringodium filiforme* (3,4,6) from Grenadines (Grenada) (1), St. Eustatius (2), St. John (3), St. Martin (France) (4), St. Vincent (5), and the Grenadines (St. Vincent) (6).

the eastern Caribbean. Consistent with previous reports from both the Caribbean and Mediterranean Seas, *H. stipulacea* continues to frequently, although not exclusively, invade anchorages used by commercial and recreational boats, establish beds at a range of depths, in a variety of salinity conditions (i.e. saltier eastern Mediterranean Sea, Simpson Bay, St. Martin, and Lac Bay Curaçao) and appears to be hospitable to indigenous flora and fauna (Lipkin, 1975; Rindi et al., 1999; Calvo et al., 2010; Steiner et al., 2010; Sghaier et al., 2011). Female reproductive structures and seeds have yet to be reported from either Sea; however, male flowers have been sampled from the coast of Italy (Gambi et al., 2009) although not in the Caribbean. Therefore, the apparent mechanism of dissemination of *H. stipulacea* in the Caribbean and Mediterranean Seas continues to be via fragmentation and vegetative propagation. Dissimilar to Mediterranean reports (Gambi et al., 2009; Sghaier

et al., 2011), *H. stipulacea* does compete with the native Caribbean seagrass *S. filiforme* for space and has empirically been shown to alter the abundance and composition of seagrass-associated organisms and the local seagrass community (Willette and Ambrose, 2012); however, further investigation of this interaction is needed.

Based on the growing number of new reports of *H. stipulacea* in the eastern Caribbean, we do not believe that this species is a case of an “overlooked” remnant species that has been missed by previous benthic habitat surveys (see DEAL, 2011; Debrot et al., 2012; Kerninon, 2012; for examples of monitoring programs). In contrast, *H. stipulacea* appears to be spreading broadly in the Caribbean although no flowers have been found. *H. stipulacea* (sampled from the Mediterranean) was genetically distinct from any other *Halophila* species, separated by a minimum of 15 mutational changes (Waycott et al., 2002); genetics investigations of

the *H. stipulacea* from the Caribbean are needed to determine its similarity to the Indian Ocean and Mediterranean populations.

H. stipulacea has demonstrated exceptional ecological flexibility in salinity, depth and habitat in its invasive range and a high potential for dissemination to new locations as exemplified by the present and previous reports of the species in the Caribbean. Given the seemingly rapid island-to-island spread of this invasive species in the past decade, it is reasonable to assume that additional first reports will be published in the coming years, particularly at more western and northern sites. Further, we anticipate and encourage more investigations on the interaction of *H. stipulacea* with native Caribbean seagrass, including those with other *Halophila* species that inhabit ecologically similar habitats. Particular attention is warranted in the case *H. stipulacea*'s possible negative interactions with *H. engelmanni* and *H. baillonii*, both of which are geographically limited and listed by the IUCN as "vulnerable" (Short et al., 2010b). Additionally, *H. stipulacea* could adversely affect *H. johnsonii*, listed in the United States as "endangered" (NMFS, 2002).

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