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Sascha C.C. Steiner and Demian A. Willette

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Cover Photograph: *Halophila stipulacea* meadow at Espagnol Bay, a site previously densely covered by Dominica's widest *Syringodium filiforme* meadow. Photograph © Demian Willette.

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The Expansion of *Halophila stipulacea* (Hydrocharitaceae, Angiospermae) is Changing the Seagrass Landscape in the Commonwealth of Dominica, Lesser Antilles

Sascha C.C. Steiner[1,*] and Demian A. Willette[2]

Abstract - The seagrass *Halophila stipulacea*, alien to the Caribbean, was first reported from Dominica in 2007, where its rapid growth and ability to supplant native species, as well as the profiles of native seagrasses meadows, were established in 2008. In 2013, we reexamined 27 meadows and observed a highly altered underwater landscape along Dominica's west coast (leeward) and unchanged seagrass beds along the northeast (windward). On the western sublittoral, pure stands of *H. stipulacea* replaced most *Syringodium filiforme* meadows and *Halodule wrightii* in depths greater than 4 m, as well as all *Halophila decipiens* stands and meadows. Fauna and flora occurring within seagrasses was concentrated in the remaining native seagrass stands. We identified three scenarios of increasing impact by *H. stipulacea*: "native strongholds" of pure native stands, "invasive takeovers" where native seagrasses were completely replaced, and "new meadows" in areas previously free of seagrasses. The area covered by Dominica's seagrasses doubled from an estimated 316 ha in 2008 to 773 ha in 2013; driven exclusively by the spread of the alien seagrass. Benefits and losses of the recent angiosperm invasion are unforeseeable, yet the remaining strongholds and the unchanged north coast meadows point at ecological limitations in the invasibility of native seagrasses and environmental circumstances that foster refugia for some native species. However, based on the increasing number of sightings *H. stipulacea* in the Lesser Antilles, we predict large-scale alterations in the architecture and species composition of seagrass meadows throughout the Caribbean within the next decade, and the demise of *H. decipiens*.

Introduction

Biological invasions in marine environments have caused the displacement of native species (Piazzi et al. 2001), structural changes in their habitats (Boudouresque and Verlaque 2002, Williams 2007), and alterations in biodiversity and food-webs (Bax et al. 2003, Byrnes et al. 2007, Klein and Verlaque 2008). Despite heightened international awareness on the topic (Delaney et al. 2008, Ricciardi et al. 2000), the incidence of species introductions grows with global trade (Gibson et al. 2005). The vulnerability of a region, habitat, or species to alien species often only becomes evident after a successful invasion. Indentifying this vulnerability may facilitate a proactive control of future species introductions. Such identification requires an understanding of the stages of expansion of an introduced species from the point where it reproduces or spreads vegetatively in its new habitat to

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where it out-competes native species. Essential for this process are an early detection of the alien species and baseline information on the distribution of native species within well-defined areas.

The distribution and benthic cover of Dominica's seagrasses were first assessed in 2007 by Steiner and Willette (2010) during the only island-wide mapping of sublittoral habitats to date. During the survey, D.A. Willette identified the alien Hydrocharitaceae *Halophila stipulacea* (Forsskål) Ascherson (Halpohila Seagrass) (Willette and Ambrose 2009). This was its second detection in the region, following the initial sighting from 2002 in Grenada by Ruiz and Ballentine (2004). *Halophila stipulacea* is a globally successful invasive species. Originally described with specimens from the Red Sea by Forsskål (1775), *H. stipulacea* is native to the Indian Ocean, from East Africa to Madagascar, the Persian Gulf, and the southwestern coast of India (Ascherson 1906; den Hartog 1970; Ostenfeld 1914, 1926). It spread to the Mediterranean Sea via the Suez Canal, which opened in 1869. Lipkin (1975a, b) reviewed the history of its subsequent dispersal from the first plant fragments collected in Rhodes by Johann Nemetz in 1894 and later identified as *H. stipulacea* by Fritsch (1895), to reports of living plants and meadows at multiple locations in the eastern Mediterranean as far as Malta in 1970 (den Hartog 1972). Over a decade later, *H. stipulacea* was documented in the Tyrrhenian Sea (Acunto et al. 1997, Gambi et al. 2009, Procaccini et al. 1999), the Ionian coasts of Sicily (Alongi et al. 1992, Bilotti and Abdelahad 1990) and Greece (Van der Velte and den Hartog 1992), and most recently from Turkey (Valera-Alvarez et al. 2011) and Tunisia and Libya (Sghaier et al. 2011).

To date, no stepping-stone locations in the dispersal of *H. stipulacea* between the central Mediterranean and the Lesser Antilles have been reported. Although limited to isolated patches in Dominica in 2007 (Figs. 1, 2a), Willette and Ambrose (2009, 2012) demonstrated its rapid lateral expansion and ability to supplant the native *Syringodium filiforme* Kützing (Manatee Grass; Cymodoceaceae) in situ. Incited by the looming spread of *H. stipulacea,* Steiner et al. (2010) established a bathymetric and horizontal distribution baseline of native seagrasses in 2008, while Willette and Ambrose (2009) identified *H. stipulacea* in St. Lucia the same year. Sightings of *H. stipulacea* have since been reported from 18 additional islands across the Lesser Antillean archipelago (DEAL 2011, Debrot et al. 2012, Kerninon 2012, Mège 2013, Vedie 2013, Willette et al. 2014). By 2012, *H. stipulacea* had infiltrated and replaced native meadows and colonized areas previously devoid of seagrasses throughout most of Dominica's west coast (S.C.C. Steiner, pers. observ.).

With the purpose of assessing the alterations in native seagrass meadows, we repeated the 2008 surveys by Steiner et al. (2010) in March 2013. Our objectives were to determine the extent to which *H. stipulacea* had (a) infringed on the distribution of native seagrass species, (b) altered the morphology of seagrass meadows, (c) augmented Dominica's benthic seagrass cover, and (d) exhibited a distribution pattern on the island similar to that reported by other studies from the Lesser Antilles.

Field-Site Description

Dominica's narrow sublittoral provides limited space suitable for seagrass meadows, and the majority were within 300 m from the western (leeward) shores between 15º37'47"N, 61º27'52"W, and 15º14'42"N, 61º22'25"W. In 2008, seagrasses inhabited most sandy environments north of Roseau in 4 to at least 24 m depth with negligible spatial overlap among species (Steiner et al. 2010). *Syringodium filiforme* formed mono-specific or pure meadows with shoots covering up to 80% of the benthos (Willette 2010) and isolated patches along its shallow-depth distribution limit. Its meadows shaped the contour of the seafloor in depths of 5–12 m where multiple rhizome layers stabilized sediments. A sharp, 20–40-cm step-down separated the shallow boundary of such *S. filiforme* meadows from their sandy shore-ward surroundings (Steiner et al. 2010). A smoother step-down was common in depths of >12 m, from where the benthic cover of *S. filiforme* decreased with increasing depth until it ended abruptly at 18 m. We define meadows with the step-down feature as consolidated beds, to underline their relative longevity and topographic influence on the seafloor vis-à-vis other seagrass meadows in Dominica.

Halophila decipiens Ascherson (Paddle Grass) and *H. stipulacea* were restricted to the west. *Halophila decipiens* grew below 4 m depth. In the absence of *H. stipulacea* it grew in patches and vast pure stands with consistently low benthic cover (<10%), but never intermixed with *S. filiforme*. It was common along and below the deep boundaries of *S. filiforme* meadows. *H. stipulacea* was spreading in Prince Rupert's and Pringle's bays and had rooted in 8 additional locations (Steiner et al. 2010), partially within stands of *H. decipiens*. Occasionally, it also intermixed with *S. filiforme* along the latter's deep boundary. *Halodule wrightii* Ascherson (Shoal Grass) had a depth range of 2 to 15 m, consistently grew in patches, and was widespread along the near-shore boundaries of *S. filiforme* (Steiner et al. 2010).

Northeastern (windward) seagrass meadows were exclusively established on the back reef flats (0.5 m depth) of fringing reefs, characterized by mixed stands of *Thalassia testudinum* Bank ex König (Turtle Grass) and *S. filiforme*, and mostly found in coves between 15º35'43"N, 61º23'00"W and 15º35'45"N, 61º19'52"W. *Thalassia testudinum* was limited to the windward side of Dominica and had the widest distribution within the reef flats due to its ability to root on coral rubble close to the reef crests. *Syringodium filiforme* was restricted to sandy areas closer to shore. *Halodule wrightii* grew sparsely and occupied near-shore margins of seagrass beds and sandy blowouts, as it did along the west coast (Steiner et al. 2010).

Methods

The benthic habitat maps by Steiner and Willette (2010) are based on in situ surveys from 2007, covering 1815 ha along 90% of Dominica's coastline (99% of the west coast). In 2008, seventeen seagrass meadows, representative of the island were selected and surveyed by Steiner et al. (2010). Between the 6th and 22nd of March 2013, we replicated the survey protocol at 16 of the previously studied meadows, and examined seagrasses at 8 additional sites to determine *H. stiplacea*'s spatial impact on native species (Table 1, Fig. 1).

Field studies were conducted with SCUBA or by snorkeling across seagrass meadows to profile the seagrass species composition, mean benthic cover and blade height, as well as associated fauna and flora. At the 16 reexamined sites, transect headings followed the contour of the seafloor's slope and were typically perpendicular to the shoreline. Transect lengths depended on the distance between the intertidal and the offshore end of the examined seagrass meadows, or where our 18-m depth limit was reached, whichever came first. On the "outbound" leg of the survey, away from shore, we made qualitative observations of the meadows' margins (intact or eroded, species composition, and height and benthic cover of

Table 1. Location and transect features of quantitatively and qualitatively surveyed sites. Transect lengths and maximum depths are given for the years 2008 and 2013. Staring points are located in the intertidal. Headings for the 24 sites are in reference to magnetic North as they are read in the field and not grid North. Sites 1–14 and 17–22 are on the west coast (leeward). Sites 15, 16, 23, and 24 are on the northeastern coast (windward).

	Transect				
	Starting point			Length (m)	Max. depth (m)
Site	Latitude	Longitude	Heading	2008 / 2013	2008 / 2013
Quantitatively surveyed sites					
1 Toucari	15°36'32.07"N	61°27'50.87"W	290°	190 / 275	15 / 18
2 Douglas Bay	15°35'27.86"N	61°27'56.16"W	340°	230 / 230	12 / 12
3 Espagnol Bay	15°31'52.35"N	61°28'31.21"W	240°	300 / 360	16 / 18
4 Bioche	15°30'29.54"N	61°28'01.26"W	290°	190 / 205	15 / 18
5 Anse à Liane	15°29'20.73"N	61°27'56.71"W	235°	160 / 160	18 / 18
6 Colihaut (Anse Cola)	15°28'49.56"N	61°27'38.32"W	250°	155 / 180	18 / 18
7 Gueule Lion	15°27'44.40"N	61°27'15.23"W	240°	185 / 185	18 / 18
8 Salisbury Bay	15°25'57.17"N	61°26'10.52"W	235°	220 / 240	18 / 19
9 Mero North	15°25'08.93vN	61°25'48.89"W	270°	290 / 300	11 / 10
10 Layou	15°24'04.88"N	61°25'39.02"W	255°	290 / 190	15 / 11
11 Jimmit	15°22'38.95"N	61°24'27,04"W	240°	180 / 190	15 / 18
12 Mahaut	15°21'49.96"N	61°24'01.18"W	220°	200 / 210	18 / 18
13 Canefield	15°20'05.00"N	61°23'37.51"W	310°	180 /190	18/ 18
14 Pointe Michel	15°15'34.55vN	61°22'39.37vW	250°	240 / 220	18 / 15
15 Anse Soldat	15°35'39.56"N	61°22'58.79"W	20°	70 / 78	1
16 Calibishie	15°35'38.84"N	61°20'45.87"W	0°	120 / 120	1
				Length · width (m)	Depth range (m)
Qualitatively surveyed sites					
17 Prince Rupert's Bay	15°34'40.12"N	61°27'29.69"W	325°	250 · 100	2–5
18 Salisbury Cliffs	15°26'08.81"N	61°26'27.44"W	195°	100 · 60	6–15
19 Macoucheri	15°25'48.98"N	61°26'14.14"W	160°	300 · 40	5–7
20 Mero Central	15°25'04.50"N	61°25'52.47"W	225°	455 · 60	8–15
21 Mero South	15°24'57.11"N	61°25'45.91"W	215°	300 · 60	6–15
22 Scott's Head	15°12'47.08"N	61°22'07.60"W	280°	380 · 70	1–7
23 Hodges Bay	15°35'24.14"N	61°19'54.29"W	0 °	280 · 80	1–5
24 Middle Bay, Marigot	15°32'30.28"N	61°17'04.38"W	15°	130 · 130	1–4

leaf shoots) and their central sections (species composition, height and benthic cover of shoots, signs of endofauna, epiphytes, and sessile and vagile fauna). We

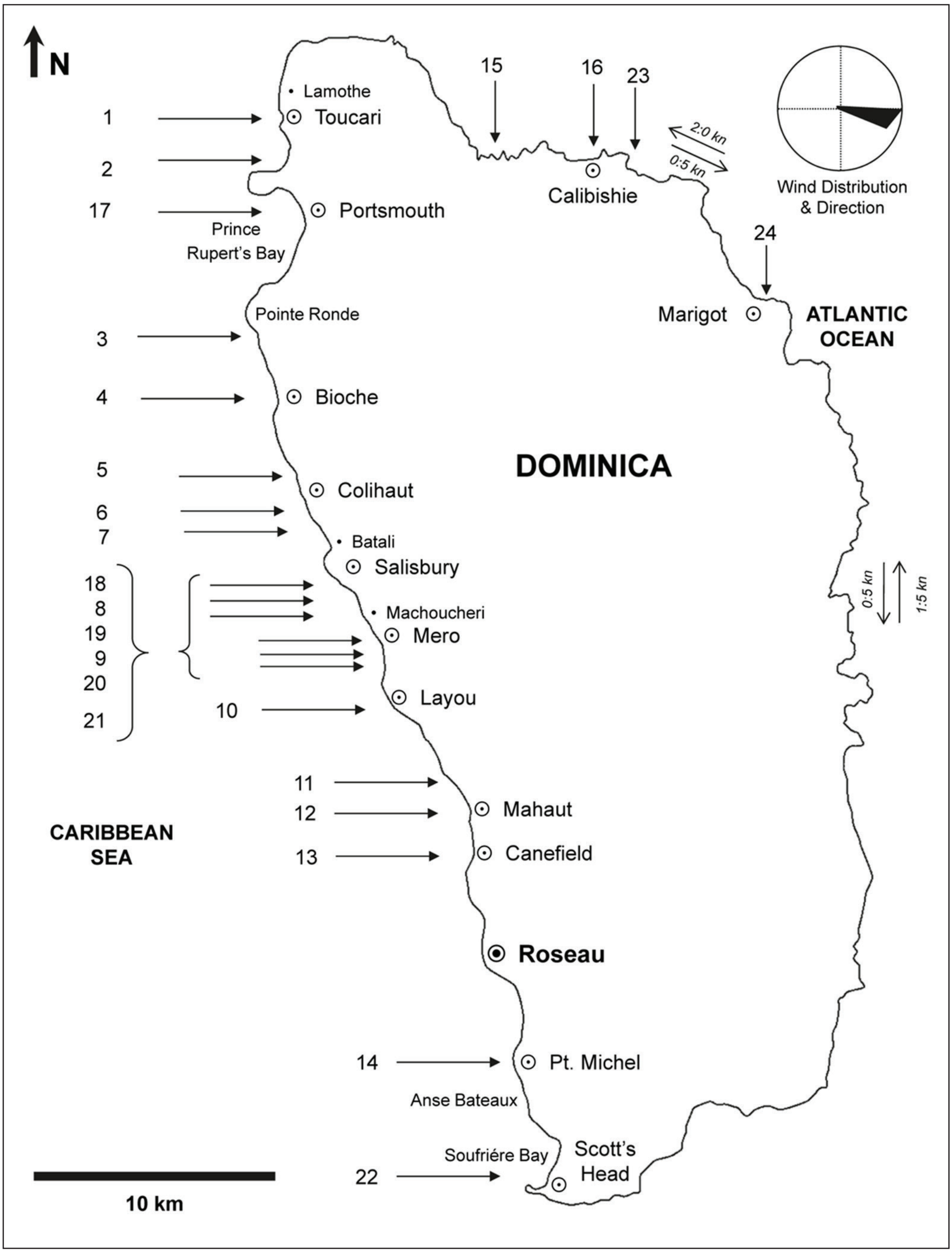

Figure 1. Location of survey sites (2013) in Dominica. Site numbers as in Table 1. Sites 1–16 were previously surveyed by Steiner et al. (2010), site 17 was monitored by Willette from 2007 to 2009 (unpublished information), and sites 18–24 were monitored by Steiner from 2000–2009 (unpubl. data). Surface currents are given in knots.

recorded seagrasses that grew below the deep end of each transect and estimated their benthic cover.

On the "inbound" leg of the survey, we quantified our observations within plots consisting of three 1-m^2 quadrats, perpendicularly aligned to the seafloor's slope and 1 m apart from each other. We set plots every 20 m along the transect. In cases where we encountered extensive pure stands of a single species with a homogenous benthic cover, we spaced plots at 40–60-m intervals. Within each plot, we estimated the area occupied by the shoots of each seagrass species to the nearest 5% (benthic cover), using a 1-m^2 quadrat subdivided into four 0.25-m^2 squares. Each estimate was derived from our consensus and was based on laboratory and in situ calibration of our estimates. For infield calibration only, we used a 1-m^2 quadrat with 100 square subdivisions of 100 cm^2. Such quadrats push down the canopy in tall and dense stands, obscuring the view of the open benthic spaces and hindering quick estimates of seagrass cover. In the laboratory, digital images of 1-m^2 seagrass areas with known benthic cover were used to attune visual estimates.

We then measured the height of shoots that were closest to five pre-marked spots within each quadrat (15 per plot) to the nearest cm and determined the mean blade height. Finally, we recorded the occurrence of conspicuous epiphytic and epibenthic macroalgae and invertebrates, signs of endofauna, and fishes. We identified the organisms to the lowest taxonomic level when possible. Depth was recorded at each plot.

For each of the 16 reexamined sites, we also expressed change in seagrass species distribution as the percent increase or decrease in the presence of *H. stipulacea* and combined native species along the transect. With the exception of Layou, *H. decipiens* and *H. wrightii* were thinly distributed in 2008, the former primarily below the deep end of our transects. Native species were thus dominantly *S. filiforme* along the western coast, and *T. testudinum* and *S. filiforme* along the northeast.

To further ascertain *H. stipulacea*'s expansion in Dominica, we executed 8 roving surveys that were laid out as belt transects and covered between 0.6 and 2.6 ha. We selected sites from the habitat maps of Steiner and Willette (2010) that included meadows in the vicinity of Dominica's large coral reef complexes (Mero-Central, Mero-South) and seagrass pockets in regions with limiting conditions for seagrasses (e.g., Scott's Head, Middle Bay near Marigot) (Fig. 1). We looked for *H. stipulacea*'s depth range during exploratory dives up to 30 m deep at Grande Savane, Salisbury, Mero, and the northern Sourfriére Bay, and received complementary reports on Grande Savane and Anse Bateaux from A. Madisetti. In addition, fishermen and SCUBA divers were interviewed and shown photographs of all reported seagrasses, as well as fresh specimens. Accounts of *H. stipulacea*'s distribution, abundance and its possible displacement of native species were compared to field data gathered between 2007 and 2008 for the entire west coast (Steiner and Willette 2010, Steiner et al. 2010, Willette and Ambrose 2009). Fishermen's in-water observations of seagrass cover came from artisanal spear fishing, seine netting, and the placement and retrieval of fish traps. SCUBA divers gave information on the depth range. Brief exploratory snorkeling surveys were necessary where information was unavailable or questionable. The distance of *H. stipulacea*'s expansion along the island, was determined with coastal-length measurements by Steiner and Willette (2009).

Results

The distribution of *H. stipulacea* ballooned in just four-and-a-half years from isolated patches in 2008 to a 55-km swath along the west coast (62 km) with few discontinuities in 2013 (Fig. 2), and radically changed the species composition and benthic cover of native seagrasses. The distinct northeastern seagrass landscapes remained free of *H. stipulacea*.

West coast

Pure, homogenously dense meadows of *H. stipulacea* dominated sandy areas between the depths of 3 to 30 m, with the leaf-canopy (4–5 cm) covering close to 100% of the benthos. In contrast, the remnants of the native seagrass meadows occurred intermittently, between Mero and Pointe Ronde (Fig. 1), at depths between 5 and 12 m. Across our linear transects, *H. stipulacea* expanded by a mean of 61%, and at the expense of the native seagrasses (Fig. 3). The width of *S. filiforme* beds was reduced by no less than 58%, and this area was replaced by *H. stipulacea*

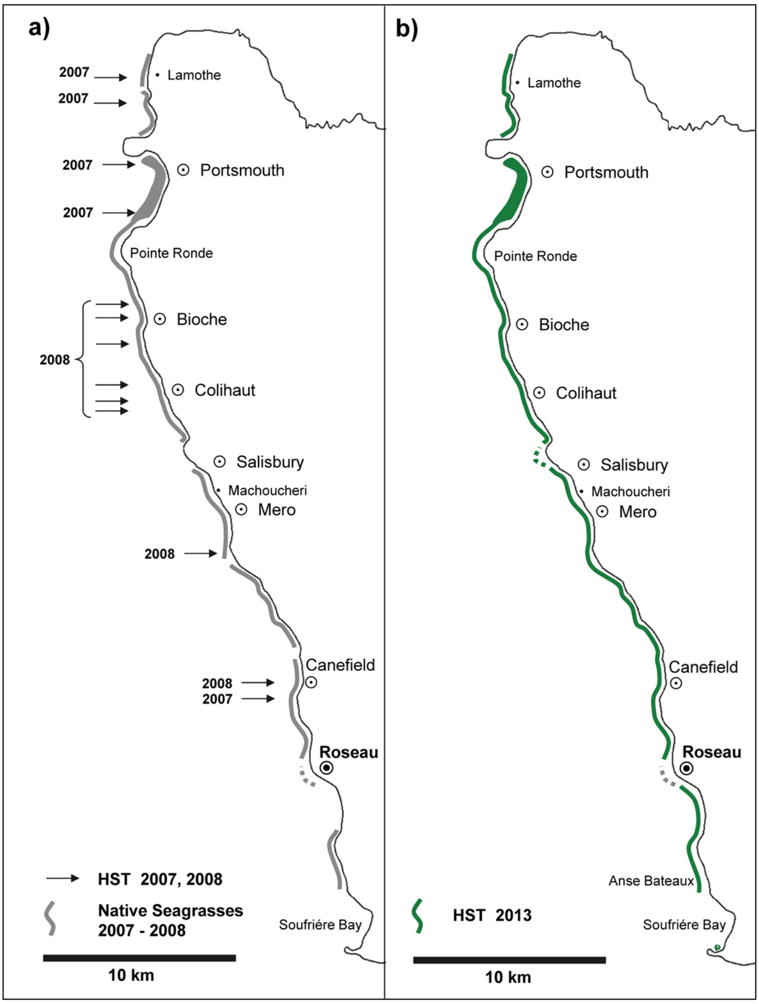

Figure 2. a) Distribution of native seagrasses (solid lines) and *H. stipulacea* (arrows) in late 2007 and 2008. b) Distribution of *H. stipulacea* in March 2013. The solid distribution lines are not to scale in terms of width. Dotted distribution line indicates the known interruption of seagrasses by the Grande Savane Reef complex near Salisbury and the unknown status of seagrasses around Roseau.

(Table 2). No specimens of *H. decipiens* were found at any of its 15 previously documented growing areas, which were covered by *H. stipulace* in 2013, nor anywhere else. *Halodule wrightii*'s 2008 depth range (2–15 m) and distribution was reduced to 2–4 m depth.

Within the observed changes, individual meadows fit one of three scenarios that we refer to as native strongholds, invasive takeovers, and new seagrass meadows. Native strongholds, exemplified by Bioche (Fig. 4), were the consolidated seagrass beds at Espagnol Bay, A. Liane, Colihaut, and Salisbury Bay (Fig. 1), where bands of pure *S. filiform*e still existed in 2013 at depths of 6–12 m and stretched parallel to shore. All were encircled by *H. stipulacea*. Espagnol Bay stood out with a 100-m-wide swath of pure *S. filiforme,* while the other locations had bands no more than 40 m wide (Table 2). In 2008, benthic cover within *S. filiforme* beds ranged from 6% on the deep end to 75% in the shallow third. Portions of native seagrass beds with less than 20% cover in 2008 were replaced by *H. stipulacea* in 2013. Where *S. filiforme* covered 20–45% of the benthos in 2008, it persisted but was intermixed with *H. stipulacea* by 2013. Stands where *S. filiforme* percent cover was 45% or greater in 2008 (~300 shoots per m^2 based on Willette [2010]) remained as pure stands in 2013. The characteristic step-down feature on the shallow margin of *S. filiforme* beds, as well as blowouts and other sediment-exposing scars, had been largely replaced by the alien species.

Invasive takeovers by *H. stipulacea* were evident at Toucari, Prince Rupert's, Bay Macoucheri, Mero N, Layou, Jimmit, Mahaut, Canefield, and Pt. Michel (Fig. 1), where *H. stipulacea* had replaced most or all of the native meadows (Table 2).

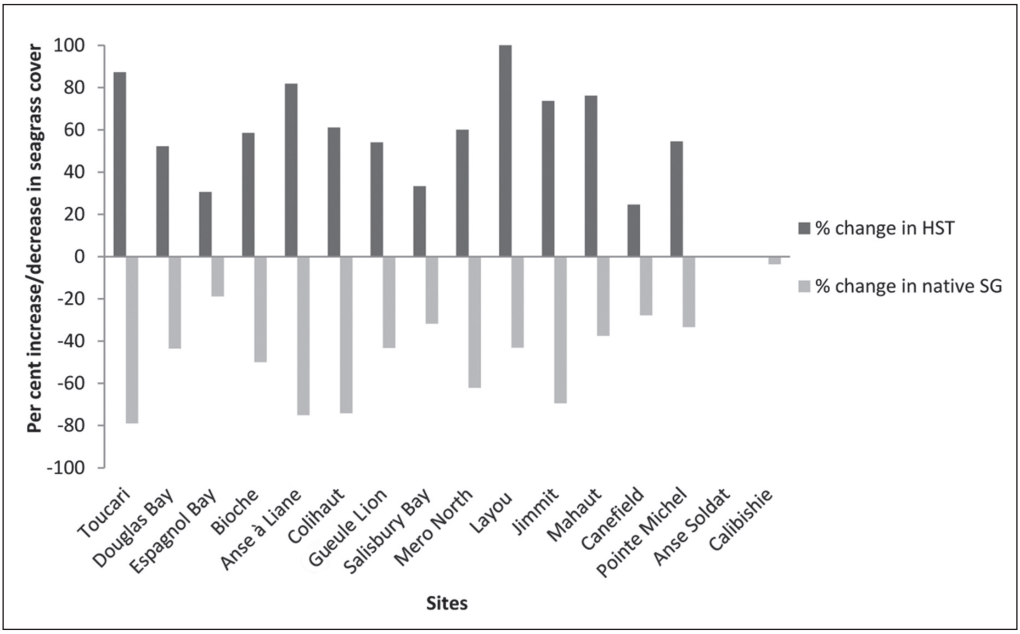

Figure 3. Change of distribution of *H. stipulacea* (HST) versus native seagrass species along transects. Native species (SG) were primarily *S. filiforme* on the west coast, and *T. testudinum* and *S. filiforme* along the northeast coast.

Remnants of *S. filiforme* meadows at Mahaut and Jimmit, contributed up to 5% and 20%, respectively, of the benthic cover within a narrow (<20 m) band in the vast *H. stipulacea* meadows. *Syringodium filiforme* was insignificant at Mero N, and absent at Macoucheri, Layou and Pt. Michel. At Layou the only previously known pure meadow of *H. decipiens* had disappeared, and *H. stipulacea* was in its place (Fig. 5). Similarly, *S. filiforme* beds at Prince Rupert's Bay and Mero Bay (Fig. 6) were almost completely replaced by *H. stipulacea*. The extensive *H. decipiens* zone between and along the Mero's reefs no longer existed in 2013. As a result of all these changes, *S. filiforme* was no longer present below 13 m depth anywhere in Dominica.

Table 2. Change in Seagrass species composition of meadows from 2008 to 2013. The spatial dominance of species is expressed as the extent (m) of pure stands along each transect. In 2008, *Halodule wrightii* (HWR), *Halophila decipiens* (HDE) and *H. stipulacea* (HST) were the marginal species. *Syringodium filiforme* (SFI) was occasionally intermixed (indicated by superscripted "1") and in isolated pure stands (indicated by superscripted "2") within *H. stipulacea* meadows. Removed or buried meadows due to the effects of Hurricane Omar in 2008 are marked with * and their pre-impact width is in parentheses. *Thalassia testudinum* (TTE) occurred only in the northeast. For site numbers 17–24, seagrass species composition of meadows and patches is based on habitat maps from 2007, observations between 1999 and 2009, and from 2013 surveys.

		Principal seagrasses and their meadow's width in m		Marginal, intermixed^{1}, and pure^{2} stands in decreasing benthic cover	
	Site name	2008	2013	2008	2013
1	Toucari	SFI 150	HST 240	HST, HDE, HWR	SFI^{1}
2	Douglas Bay	*None (SFI 100)	HST 120	None	SFI^{1}, HWR
3	Espagnol Bay	SFI 140	HST 110, SFI 100	HWR	SFI^{1}, HWR
4	Bioche	SFI 95	HST 120	HDE, HST	SFI^{2} 40, HWR
5	Anse à Liane	SFI 120	HST 180	HDE, HST, HWR	SFI^{2} 30, HWR
6	Colihaut	SFI 115	HST 110	HDE, HST	SFI^{2} 30
7	Gueule Lion	SFI 80	HST 100	HDE, HST	SFI^{1}
8	Salisbury Bay	*None (SFI 70)	HST 80	SFI	SFI^{2} 20
9	Mero North	*SFI 20 (180)	HST 180	HWR	SFI^{1}, HWR, HWR^{1}
10	Layou	SFI 65, HDE 60	HST 190	HST, HWR	none
11	Jimmit	SFI 125	HST 140	HDE, HWR	SFI^{1}, HWR
12	Mahaut	*SFI 45, HDE 30	HST 160	HWR	SFI^{1}, HWR
13	Canefield	*HST 60 (SFI 50)	HST 110	HWR	None
14	Pointe Michel	*HDE 20 (SFI 60)	HST 120	SFI, HWR	HWR
15	Anse Soldat	TTE 70, SFI^{1} 30	TTE 75 SFI^{1} 30	HWR	HWR
16	Calibishie	TTE 100, SFI^{1} 50	TTE 120, SFI^{1} 60	HWR	HWR
	Site name	2009	2013	2009	2013
17	P. Rupert's Bay	SFI 250	HST 250	HST	SFI^{1}
18	Salisbury Cliffs	SFI 100	HST 85	HDE	SFI^{1}
19	Macoucheri	SFI 300	HST 300	None	None
20	Mero Central	SFI 420	HST 440	HDE	SFI^{1,2}
21	Mero South	SFI 290	HST 280	HDE	SFI^{1,2}
22	Scott's Head	None	HST, HWR	HWR	HWR
23	Hodges Bay	SFI, HWR, TTE	SFI, HWR, TTE	None	None
24	Middle Bay	TTE	TTE	None	None

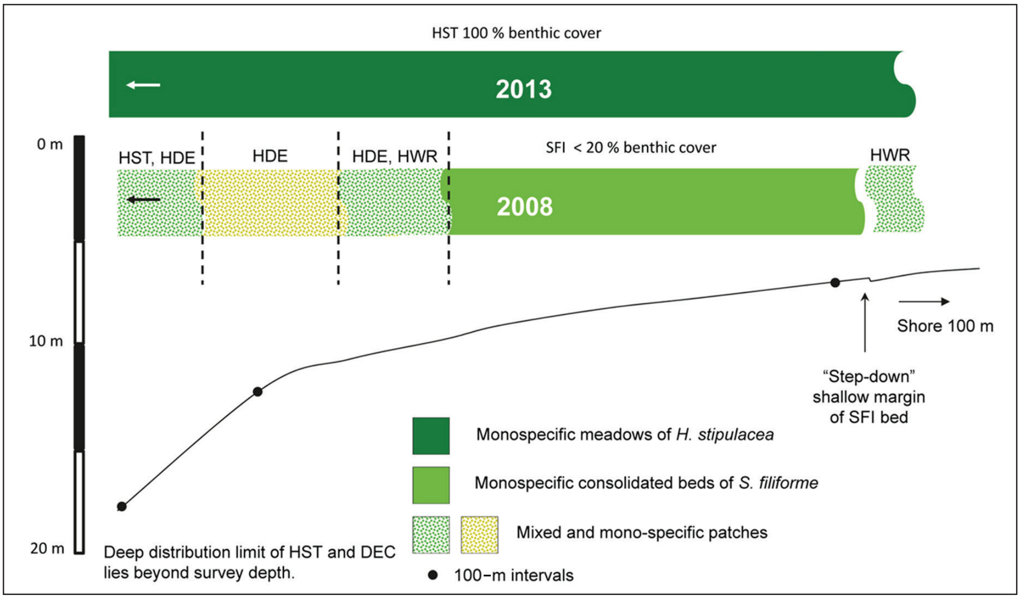

Figure 4. Seagrass profile at Layou: seagrass composition in 2008 and 2013. The invasive *Halophila stipulacea* replaced all native seagrasses. HWR = *Halodule wrightii*, HDE = *Halophila decipiens*, and HST = *H. stipulacea.*

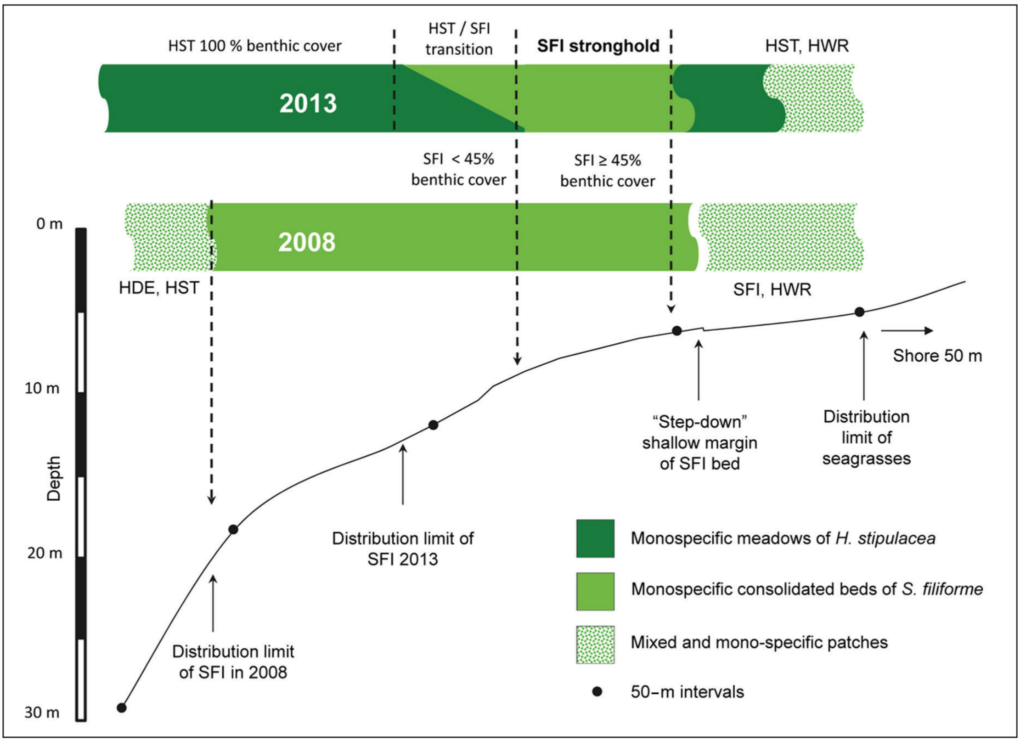

Figure 5. Seagrass profile at Bioche; seagrass composition in 2008 and 2013. The *S. filiforme* (SFI) stronghold is located within the shallow third of the 2008 seagrass bed. HWR = *Halodule wrightii*, HDE = *Halophila decipiens*, and HST = *H. stipulacea.*

Lastly of the three scenarios, new seagrass meadows of *H. stipulacea*, had established themselves at depths below the 2008 *S. filiforme* distribution limit (18 m) and in previously barren sandy areas up to a depth of 29 m, which we observed at Batali, Salisbury, and Mero (Figs. 1, 6). In its horizontal expansion, *Halophila stipulacea* also rooted in Scott's Head, the southernmost shallow-water habitat along the west coast and an area typically devoid of seagrasses. Unlike the native west coast species, *H. stipulacea* had grown up to coral reefs and into sand and rubble-laden depressions within the reefs at Douglas Bay (12–18 m depth) and Macoucheri (3–5 m depth). The sandy halos of these reefs were supplanted by *H. stipulacea*. At Scotts' Head, the shallow margins of dead reefs in 2–3 m depth were colonized by *H. stipulacea* and served as expansion corridors across unstable sandy environments. *Halophila stipulacea* had thus spread into shallower, but more stable rocky substrates. Leaves were 4–5 cm tall along the corridors and 2–3 cm tall along the expansion limits. Sandy halos around coral reefs were, however, maintained at Mero (9–18 m), where sediments were heavily bioturbated by macro-endofauna including the burrowing polychaete *Arenicola cristata* Stimpson and the echinoid *Meoma ventricosa* (Lamarck) (Red Heart Urchin), as well as fishes such as mullids and the burrow-building malacanthid *Malacanthus plumeri* (Bloch) (Sand Tilefish).

The architecture of seagrass meadows successfully invaded by *H. stipulacea* had changed. Vast areas that in 2008 were occupied by *S. filiforme* with a mean shoot height of 20 cm and a mean benthic cover under 45% were by 2013 covered with densely packed *H. stipulacea* leaves with a mean height of 4 cm. Open spaces

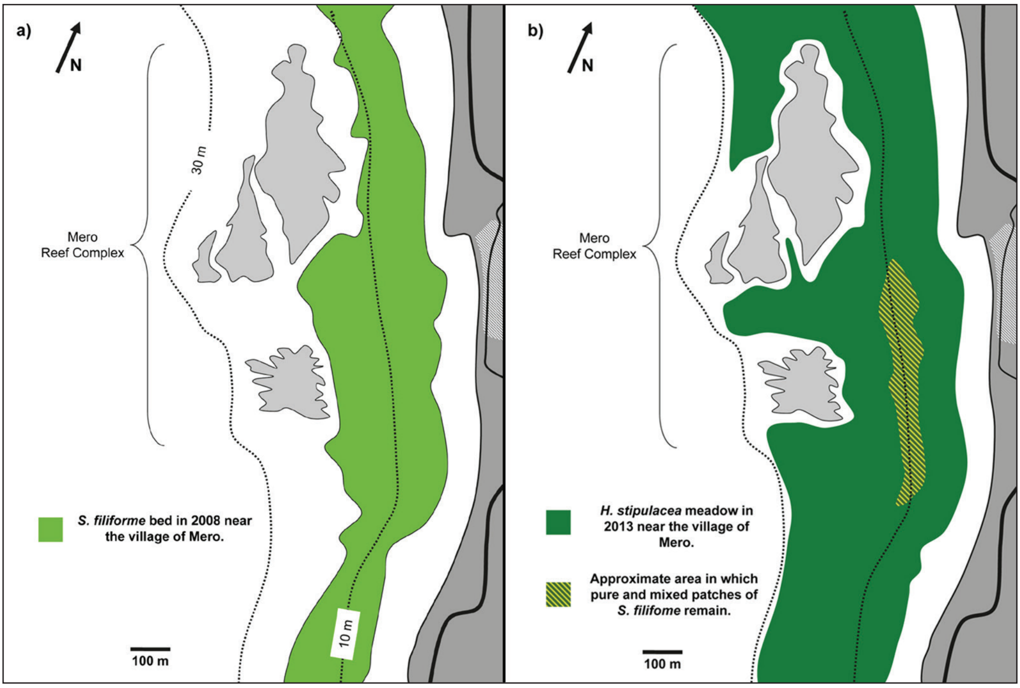

Figure 6. Expanse and composition of seagrass meadows in a) 2008 and b) 2013 at Mero.

between seagrass shoots and under the seagrass canopy were drastically reduced. This change was also evident in all former *H. decipiens* zones.

We observed 79 species along the transects and identified 11 macroalgae, 23 invertebrates, 22 vertebrates to the genus or species level (Steiner and Willette 2014:table A). The taxa with the highest numbers of species were Chlorophyta (6), Echinodermata (10), and Osteichtyes (19). Compared to 2008, we found fewer species of green algae (6 vs. 3), echinoderms (9 vs. 7), and fishes (14 vs. 10). Green algae documented in 2013 were also present in 2008; however, only 40% of the echinoderms and 32% of the fishes were the same for both years. The macroalgae observed in 2013 were confined to the spaces among and between the remaining *S. filiforme*. With few exceptions, the same was true for invertebrates and fishes. Cyanobacterial mats were exclusively found on sediments and covering *H. stipulacea* in circular patches up to 3 m in diameter.

The only reproductive structures documented were seedpods of *S. filiforme* in pure *S. filiforme* meadows and mixed *S. filiforme–H. stipulacea* beds. Seedpods occurred intermittently in densities up to 32 pods per m^2 in pure stands of *S. filiforme*.

Northeast coast

No changes were noted in the seagrass species composition of northeastern seagrasses. In 2013, as in 2008, meadows at Calibishie and Anse Soldat (Fig. 1) were comprised of intermixed *T. testudinum* and *S. filiforme*. *Thalassia testudinum* still dominated the seagrass beds with its wide distribution between calm and turbulent waters. Near the reef crest, shoots covered less than 1–5% of the benthos, with a mean shoot height of 5 cm due to chronic breakage. Taller (15 cm) stands covered up to 80% of the benthos in the calm waters of the bed's near-shore margin. *Syringodium filiforme* had a narrower distribution and was never rooted in pure coral rubble. Its mean benthic cover and blade height peaked at 30% and 20 cm, respectively, at 5 to 15 m from the shore-facing bed margin, which was always dominated by *T. testudinum*. *Halodule wrightii* grew near shore along the step-down feature, as well as in tidal channels and blowouts. In 2013, the occurrence of algae and invertebrates associated with the seagrasses at Calibishie and Anse Soldat was nearly identical to that found in 2008.

In the marginal and isolated pockets of seagrasses outside of the well-established seagrass meadows, the above-mentioned species never overlapped. *Syringodium filiforme* grew monospecifically in an area of approximately 0.5 ha in the southern half of Hodges Bay (Fig. 1) at a depth of 3 m. Along the southwestern margin of Hodges Reef, we observed the first and so far only monspecific consolidated bed of *H. wrightii*, with a benthic cover close to 20% and a total area of approximately 0.1 ha. A 10–15-cm step-down with exposed rhizomes lined the western margin of the bed. *Halodule wrightii* patches of 2–8 m^2 with a circummarginal step-down feature were located along the eastern fringes of the bay. *Thalassia testudinum* grew in small patches at less than 2 m depth on open sand and between rocks (eastern side of bay), and on coral rubble that was overgrown by macroalgae (east of Hodges Reef).

At Marigot (Fig. 1), which is the most turbulent site, *T. testudinum* was the only seagrass species present. Small patches (<20 m^2 max. diameter) were rooted in open sandy areas on the leeward side of patch reefs, where shoots covered up to 40% of the ground and were occasionally intermixed with green algae (*Penicillus lamourouxii* Decaisne, *Caulerpa* spp.). *Thalassia testudinum* also grew within the patch reefs where it was intermixed with algae-dominated beds that covered 100% of the substrate and included multiple calcareous red algae (*Galaxaura* spp.), brown algae (*Dictyota* spp., *Sargassum* sp.), and green algae (*P. lamourouxii*, *Caulerpa cupressoides* (West) C. Agardh, *C. serrulata* (Forsskål) J. Agardh, *Ventricaria ventricosa* (J. Agardh) J.L. Olsen & J.A. West, flabellate *Udotea* sp.). We found no specimens or fragments of *Halophila decipiens* or *H. stipulacea* along the northeast coast.

Discussion

The spread of the alien *H. stipulacea* in Dominica since 2007, illustrates the species' competitive advantage over the native *S. filiforme*, *H. wrightii*, and *H. decipiens* under the current environmental conditions of the island's leeward sublittoral. *Syringodium filiforme* and *H. wrightii* suffered substantial spatial niche reductions by being replaced throughout most of their depth range, and *H. decipiens* appears to have been extirpated from Dominica. Factors driving *H. stipulacea*'s success include rapid lateral expansion rates (Willette and Ambrose 2009) and its tolerance for a wide range of light levels (Beer and Waisel 1981, Schwarz and Hellblom 2002). Barren sandy areas favored the spread of *H. stipulacea*. Based on our observations from 2008, we suggest that *H. stipulacea* infiltrated west coast *S. filiforme* meadows along their deep margins where the benthic seagrass cover was consistently low (<5%; Steiner et al. 2010). *Halophila decipiens* was supplanted during this process, but a number of *S. filiforme* strong-holds have withstood the replacement by *H. stipulacea* thus far.

Storms probably accelerated the expansion of *H. stipulacea* by forming new horizontal expansion passages. During storms, Dominica's seagrasses are commonly uprooted to depths of up to 8 m and buried by redeposited sediments in depths of up to 15 m (Steiner et al. 2010). During the 4.5 years considered in this study, 14 tropical depressions and storms, including 3 hurricanes, disturbed the island's coastal waters. By 2013, *H. stipulacea* had colonized most open areas created by storms. Old and new blowouts located within pure *S. filiforme* strong-holds and colonized by *H. stipulacea* indicate that negatively buoyant clumps of this species can also take root (Willette and Ambrose 2012). In sum, the west coast sandy environments up to 30 m underwent a phase shift from intermittent open areas and seagrass meadows consisting of 3 species with minor spatial overlap, to a monospecific low-canopy carpet of *H. stipulacea,* remnants of 2 native species, and a notably reduced diversity and abundance of cohabiting macroalgae.

If the remaining strong-holds of *S. filiforme* on the west coast keep their ground over time, ecological limitations in *H. stipulacea*'s expansion related to structural or chemical thresholds by *S. filiforme* stands may become discernible. In addition, seasonal fluctuations in the biomass of roots, rhizomes, and leaves of *S. filiforme* need to also be considered as possible settlement windows for *H. stipulacea* (Dawes and Lawrence 1980, Gallegos et al. 1994, Van Tussenbroek 1994).

Contrasting *H. stipulacea*'s swiftly gained dominance along the west coast is its continued absence in the northeast. Compared to *S. filiforme* and *T. testudinum, H. stipulacea* has delicate unbranched roots, one at each node, along the rhizome (den Hartog 1970). It is readily uprooted in turbulent waters (S.C.C. Steiner, pers. observ.), during the retrieval of anchors and fish traps, or while dragging seine nets (Dominican fishermen, pers. comm.; Willette and Ambrose 2012). The near-shore turbulence regimes along the west coast have limited *H. stipulacea*'s advance into shallows of less than 3 m depth. Only in the most-protected coves and back-reef areas (e.g., Toucari, Macoucheri, Scott's Head) has *H. stipulacea* grown across coral rubble to depths as shallow as 1 m. Along the northeast, however, seagrass meadows are in less than 1 m depth and expand into back reefs, some of which are far less agitated than western shores. The absence of *H. stipulacea* in the northeast is hence not an effect of turbulence alone.

Ultraviolet radiation as a possible limiting factor for *H. stipulacea* is undermined by the species' ability of clumping chloroplasts, and thus protecting most of its chloroplast from high irradiance (Sharon et al. 2011). Instead, the compact rhizome layers and height of the benthic shoot cover in northern seagrasses beds may have prevented the settlement of *H. stipulacea* (see Cecherelli et al. 2000). *Thalassia testudinum,* is known as climax species (den Hartog 1970, Williams 1987), has the deepest live rhizome layers (den Hartog 1970, Duarte and Chiscano 1999) and the highest leaf and root productivity (Duarte et al. 1998) of the native seagrasses. Together with the intermixed *S. filiforme*, it restricts new settlement spaces within the meadows. *Halodule wrightii*'s many intermingled unidirectional rhizomes (Harnett 1983, Pangallo and Bell 1988) were evidently also good anchors in tidal channels and sandy margins of northeastern consolidated seagrass beds, where they may have further limited rooting opportunities for *H. stipulacea*.

Alternatively, Dominica's rough eastern seas and the prevailing easterly surface currents may have barred *H. stipulacea* from the northeast so far. Introductions of *H. stipulacea* fragments tangled in fishing gear might be possible, but fishing on or above seagrass meadows has traditionally only been carried out on the west coast. There is also no regular boat traffic between western and northern landing sites, and commonly used fishing boats there have no ballast tanks. However, an introduction could occur via fishing boats from the northeast that occasionally transport agricultural goods across the 50-km Dominica Passage to Guadeloupe, where *H. stipulacea* has been reported as of 2010 by Mége (2013), Kernion (2012), and DEAL (2011).

Given the aforementioned storm disturbances, annual expansion rates of *H. stipulacea* in Dominica are likely highly variable and not deducible with our observation points from 2008 and 2013. However, by overlaying *H. stipulacea*'s current distribution onto our habitat maps from 2008, we estimated the total seagrass cover to have increased from approximately 316 ha in 2008 to at least 773 ha in 2013, a change that has been driven largely by a minimum gain of 649 ha of *H. stipulacea* and a minimum loss of 150 ha of *S. filiforme*. Boundaries of seagrass meadows widened drastically and rapidly, and it is plausible that the first settlement of *H. stipulacea* in Dominica was only a few years before its initial sighting in 2007.

Investigations of factors inhibiting the settlement and growth of *H. stipulacea* among native Caribbean species will clarify the circumstances under which native meadows can be conserved in their original composition and functionality (e.g., nursery, habitat, shoreline protection). The comparison of locations where *H. stipulacea* has been documented in the Lesser Antilles shows the species' "preference" for leeward or sheltered areas (Steiner and Willette 2014:table B). Results from seagrass surveys covering multiple disturbance regimes (Mège 2013, Vedie 2013) follow this pattern in indicating that *H. stipulacea* first settled on the leeward coast and does co-occur with *T. testudinum* elsewhere. We argue that windward locations with oceanographic parameters similar to Dominica's northeast may be a refuge for some native seagrass species and a future source of seeds, while native leeward meadows will remain highly invasible (Capers et al. 2007) and alter in size, composition, and appearance.

Changes in Dominica's coastal marine environments including seagrass beds and their species composition currently outpace the efforts to investigate their ecological implications. Concrete national seagrass conservation measures are not in place, and given the expanse of *H. stipulacea*'s dispersal, its island-wide eradication, if considered, is unrealistic. However, a reduction of anthropogenic scarring (e.g., anchoring) on the remaining *S. filiforme* strongholds is feasible and may allow the species to vegetatively re-expand in the event that *H. stipulacea* looses ground. A possible future settlement of *H. stipulacea* on the comparatively small (>1.5 h a) northeastern meadows could also be mitigated with modest resources. Yet so far, there has only been anecdotal evaluation of the the potential benefits and losses of this angiosperm invasion (see Davis et al. 2011). The prospectives of harvesting this species and eco-political benefits of a potentially increased carbon sequestration are discussed in political circles, while fishermen claim a reduced near-shore catch to coincide with the emergence of *H. stipulacea* carpets.

On a regional scale, prevailing surface currents and storm paths are plausible vectors of *H. stipulacea*'s swift latitudinal dispersal (Willette et al. 2014) because most Lesser Antillean islands are separated by less than 100 km. Fragments of *Halophila johnsonii* are viable for one week and successfully resettle and root in aquaria (Hall et al. 2006). Similar attributes in *H. stipulacea*, as indicated by the observed colonization of blowouts, may further expedite its dispersal across the wider Caribbean via ballast-water tanks of cargo and cruise ships. Commerce (e.g., processed goods), infrastructure (e.g., building materials), electric power (e.g., fossil fuels), and the availability of fresh water (e.g., fuels for desalination plants) in the Antilles today depend almost exclusively on supply ships with multiple ports of call linked to global shipping routes. At the expense of native seagrasses, the introduction of *H. stipulacea* has resulted in a regional invasion whose mitigation appears improbable and whose ecological consequences remain to be witnessed.

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Literature Cited

Acunto, S., F. Maltagliati, F. Rindi, F. Rossi, F. Cinelli, and C. Lardicci. 1997. Indagine su una prateria di Halophila stipulacea (Forssk.) Aschers. (Hydrochorotaceae) dell'Isloa di Vulcano. Pp. 51–60, *In* Piccazzo (Ed.) Atti 12º Congresso della'Associazione Italiana di Oceanologia e Limnologoa (AIOL), Isola di Vulcano, 1996, Genova, Italy.

Alongi, G., M. Cormaci, and F. Pizzuto. 1992. La macroflora epifita di *Halophila stipulacea* (Forssk.) Aschers dele porto Catania. Proceedings of the 23rd Congress of the Italian Society of Marine Biology (SIBM), Biologia Marina, Supplemento Notizario Societa Italiana di Biologia Marina 1:287–288.

Ascherson, P. 1906. Die geographische Verbreitung der Seegräser. Pp. 389–413, *In* , G. von Neumayer (Ed.). Anleitungen zu wissenschaftlichen Beobachtungen auf Reisen. Jänecke, M., Verlagsbuchhandlung, Hannover, dritte Auflage, Germany. 880 pp.

Bax, N., A. Williamson, M. Aguero, E. Gonzales, and W. Greeves. 2003. Marine invasive alien species: A threat to global biodiversity. Marine Policy 27:313–323.

Beer, S., and Y. Waisel. 1981. Effects of light and pressure on photosynthesis in two seagrasses. Aquatic Botany 13:331–337.

Biliotti, C.N., and N. Abdelahad. 1990. *Halophila stipulacea* (Forssk.) Aschers. (Hydrocharitaceae): Espèce nouvelle pour L'Italie. Posidonia Newsletter 3:23–26.

Boudouresque, C.F., and M. Verlaque. 2002. Biological pollution in the Mediterranean Sea: Invasive versus introduced macrophytes. Marine Pollution Bulletin 44:32–38.

Byrnes, J.E., P.L. Reynolds, and J.J. Stachowicz. 2007. Invasions and extinctions reshape coastal marine food webs. PloS ONE 2:295.

Capers, R.S., R. Selsky, G.J. Bugbee, and J.C. White. 2007. Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. Ecology 88:3135–3143.

Cecherelli, G., L. Piazzi, and F. Cinelli. 2000. Response of the non-indigenous *Caulerpa racemosa* (Forsskål) J. Agardh to the native seagrass *Posidonia oceanica* (L.) Delile: Effect of density of shoots and orientation of edges of meadows. Journal of Experimental Marine Biology 243:227–240.

Davis, M.A., M.K. Chew, R.J. Hobbs, A.E. Lugo, J.J. Ewel, G.J. Vermeij, J.H. Brown, M.L. Rosenzweig, M.R. Gardener, S.P. Carroll, K. Thompson, S.T.A. Pickett, S.C. Stromberg, P.L. Terdici, K.N. Suding, E.H. Ehrenfelf, J.P. Grime, J. Mascaro, and J.P. Briggs. 2011. Don't judge species on their origins. Nature 474:153–154.

Dawes, C.J., and J.M. Lawrence. 1980. Seasonal changes in the proximate constituents of the seagrasses *Thalassia testudinum, Halodule wrightii*, and *Syringodium filiforme*. Aquatic Botany 8:371–380.

Debrot, A.O., A. Hylkema, W. Vogelaar, H.W.G. Meesters, M.S. Engel, R. de León, W.F. Prud'homme van Reine, and I. Nagelkerken. 2012. Baseline survey of Lac Bay benthic and fish communities, Bonaire. Institute for Marine Resource Ecosystem Studies Report C129/12.

Direcion de l'environment, de l'amenagement et du logement (DEAL) - Guadelpoupe et Martinique. 2011. Diagnostique sur l'invasion biologique aux Antilles Française. Pointe de Jaham, Martinique, Vol. 2. 143 pp.

Delaney, D.G., C.D. Sperling, C.S. Adams, and B. Leung. 2008. Marine invasivespecies: Validation of citizen science and implications for national monitoring networks. Biological Invasions 10:117–128.

den Hartog, C. 1970. The seagrasses of the World. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeeling Natuurkunde. Amsterdam, The Netherlands. No. 59. 275 pp.

den Hartog, C. 1972. Range extensions of *Halophila stipulacea* (Hydrochoritaceae) in the Mediterranean. Blumea 20:154.

Duarte, C.M., and C.L. Chiscano. 1999. Seagrass biomass and production: A reassessment. Aquatic Botany 65:159–174.

Duarte, C.M., M. Merino, N.S.R. Agawin, J. Uri, M.D. Fortes, M. Gallegos, N. Marbá, and M.A. Henning. 1998. Root production and belowground seagrass biomass. Marine Ecology Progress Series 171:97–108.

Forsskål, P. 1775. Flora Aegypto: Arabic sive descriptiones plantaru, quas per aegyptum inferiorem et arabicam felicem. Moeller, Copenhagen, Denmark. 219 pp.

Fritsch, C. 1895. Über die Auffindung einer marinen Hydrochoritacea im Mittelmeer. Verhandlungen der Zoologisch-Botanischen Gesellschaft, Wien 45:104–106.

Gallegos, M.E., M. Merino, A. Rodriguez, N. Marba, and C.A. Duarte. 1994. Growth patterns and demography of pioneering seagrass *Halodule wrightii* and *Syringodium filiforme.* Marine Ecology Progress Series 109:99–104.

Gambi, M.C., F. Barbieri, and C.M. Bianchi. 2009. New record of the alien seagrass *Halophila stpiulacea* (Hydrochoritaceae) in the western Mediterranean: A clue to changing Mediterranean Sea biogeography. Marine Biodiversity Records doi:101017/s175526720900058X.

Gibson, R.N., R.J.A. Atkinson, and J.D.M. Gordon. 2005. Globalization in marine ecosystems: The story of non-indigenous marine species across European seas. Oceanography and Marine Biology: An Annual Review 43:419–453.

Hall, L.M., M.D. Hanisak, and R.W. Virnstein. 2006. Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. Marine Ecology Progress Series 310:109–117.

Kernion, F. 2012. Première actions de mis en place d'un réseau d'observation des herbiers de l'Outre-mer. Master, Siences de la mer et du littoral. Inst. Universitaire Européen de la Mer, Plouzané, France. 136 pp.

Klein, J., and M. Verlaque. 2008. The *Caulerpa racemosa* invasion: A critical review. Marine Pollution Bulletin 56:205–225.

Lipkin, Y. 1975a. *Halophila stipulacea,* a review of a successful immigration. Aquatic Botany 1:203–215.

Lipkin, Y. 1975b. *Halophila stipulacea* in Cyprus and Rhodes, 1967–1970. Aquatic Botany 1:309–318.

Mège, S. 2013. Etude de l'espace *Halophila stipulacea*. INFRECOR. La feuille marine 1:9.

Ostenfeld, C.H. 1914. On the geographical distribution of the seagrasses. Proceedings of the Royal Society of Victoria 27:179–191.

Ostenfeld, C.H. 1926. Meeresgräser. I. Marine Hydrocharitaceae. Pp. 35–38, *In* E. Henning and H. Winkler (Eds.). Die Pflanzenareale. Gustav Fischer, Jena, Germany.

Pangallo, R.A., and S.S. Bell. 1988. Dynamics of aboveground and belowground structure of the seagrasss *Halodule whrightii.* Marine Ecology Progress Series 43:297–301.

Piazzi, L., G. Ceccherelli, and F. Cinelli. 2001. Threat to macroalgal diversity: Effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. Marine Ecology Progress Series 210:149–159.

Procaccini, G., S. Acunto, O. Famà, and F. Maltagliati. 1999. Structural, morphological, and genetic variability in *Halophila stipulacea* (Hydrocharitaceae) populations of the Western Mediterranean. Marine Biology135:181–189.

Ricciardi, A., W.W.M. Steiner, R.N. Mack, and D. Simberloff. 2000. Toward a global information system for invasive species. BioScience 50:239–244.

Ruiz, H., and D.L. Ballentine. 2004. Occurrence of the seagrass *Halophila stipulacea* in the tropical Western Atlantic. Bulletin of Marine Science 75:131–134.

Schwarz, A.M., and F. Hellblom. 2002. The photosynthetic light response of *Halophila stipulacea* growing along a depth gradient in the Gulf of Aqaba, the Red Sea. Aquatic Botany 74:263–272.

Sghaier, Y.R., R. Zakhama-Sraieb, I. Benamer, and F. Charfi-Cheikhrouha. 2011. Occurrence of the seagrass *Halophila stipulacea* (Hydocharitaceae) in the southern Mediterranean Sea. Botanica Marina 54(6):575–582.

Sharon, Y., G. Dishon, and S. Beer. 2011. The effects of UV radiation on chloroplast clumping and photosynthesis in the seagrass *Halophila stipulacea* growth under high-PAR conditions. Journal of Marine Biology doi:10.1155/2011/483428.

Steiner, S.C.C., and D.A. Willette. 2009. The distribution and size of benthic marine habitats in Dominica, Lesser Antilles. Appendix: Benthic cover of habitat types by region. Institute for Tropical Marine Ecology Research Report Number 13. Available online at http://www.itme.org/reports/ITME_DATA%20Appx20%Steiner%20&%20 Willette%2009.pdf. Accessed December 2014.

Steiner, S.C.C., and D.A. Willette. 2010. Distribution and size of benthic marine habitats in Dominica, Lesser Antilles. Revista de Biologia Tropical 58:589–602.

Steiner, S.C.C., and D.A. Willette. 2014. Supplemental material to: The invasive seagrass *Halophila stipulacea* (Hydrocharitaceae, Angiospermae) and its impact on the benthic landscape of Dominica, Lesser Antillles. Institute for Tropical Marine Ecology Research Report Number 13. Available online at http://www.itme.org/reports/ITME_DATA_ SUP_2013Steiner_Willette.pdf. Accessed December 2014.

Steiner, S.C.C., K.J. Macfarlane, L.M. Price, and D.A. Willette. 2010. Distribution of seagrasses in Dominica, Lesser Antilles. Revista de Biologia Tropical 58(3):89–98.

Valera-Álvarez, E., F. Rindi, L. Cavas, E.A. Serrao, C.M. Duarte, and N. Marbá. 2011. Molecular identification of *Halophila stipulacea* from Turkey. Cahier de Biologie Marine 52:227–232.

Van der Velte, C., and C. den Hartog. 1992. Continuing range extension of *Halophila stipulacea* (Forssk.) Aschers. (Hydrocharitaceae) in the Mediterranean—now found at Kefallinia and Ithaki (Ionian Sea). Acta Botanica Neerlandica 41:345–348.

Van Tussenbroek, B. 1994. Spatial and seasonal variability in biomass and leaf morphology of the manatee grass *Syringodium filiforme* in a tropical coral reef lagoon, Mexico. Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 21:15–22.

Vedie, F. 2013. Dynamique de population de l'espece invasive *Halophila stipulacea* en Martinique. INFRECOR, La feuille marine 1:6–7.

Willette, D.A. 2010. The description of Caribbean seagrass communities in Dominica, West Indies, and their response to anthropogenic and natural disturbances. Ph. D. Dissertation. University of California, Los Angeles, CA, USA.

Willette, D.A., and R.F. Ambrose. 2009. The distribution and expansion of the invasive seagrass *Halophila stipulacea* in Dominica, with a preliminary from St. Lucia. Aquatic Botany 9:137–142.

Willette, D.A., and R.F. Ambrose. 2012. Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass *Syringodium filiforme,* and associated fish and epibiota communities in the Eastern Caribbean. Aquatic Botany 103:74–82.

Willette, D.M., J. Chalifour, A.O.D. Debrot, M.S. Engel, J. Miller, H.A. Oxenford, F.T. Short, S.C.C. Steiner, and F. Védie. 2014. Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the Eastern Caribbean. Aquatic Botany 112:98–102.

Williams, S.L. 1987. Comparison between the seagrasses *Syringodium filiforme* and *Thalassia tesudinum* in a Caribbean Lagoon. Marine Ecology Progress Series 35:91–98.

Williams, S.L. 2007. Introduced species in seagrass ecosystems: Status and concerns. Journal of Experimental Marine Biology and Ecology 350:89–110.