

THE INVASIVE SEAGRASS *HALOPHILA STIPULACEA*
(HYDROCHARITACEAE, ANGIOSPERMAE) AND ITS IMPACT
ON THE BENTHIC LANDSCAPE OF DOMINICA,
LESSER ANTILLES.

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The invasive seagrass *Halophila stipulacea* (Hydrocharitaceae, Angiospermae) and its impact on the benthic landscape of Dominica, Lesser Antilles.

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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, reduced the depth range of *Halodule wrightii* by 9 m, and possibly extirpated *Halophila decipiens*. 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 estimate 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*.

Key words: Seagrass, invasive species, landscape, Dominica

Introduction

Biological invasions in marine environments, have caused the displacement of native species as well as structural changes in their habitats (Boudouresque and Verlaque 2002, Piazzini et al. 2001, Williams 2007). Subsequent alterations in biodiversity and food-webs were among the ecological consequences with socioeconomic ramifications (Bax et al. 2003, Byrnes et al. 2007, Klein and Verlaque 2008). Despite the heightened international awareness on the topic (Delaney et al. 2008, Ricciardi et al. 2000), the incidence of accidental and intentional alien species introductions continues to rise with the growing volume of global trade (Gibson et al. 2005), and an effective control or eradication of invasives has become increasingly difficult. In most cases the vulnerability of a region, habitat, or species to the invasion by an alien species only becomes evident after a successful invasion. Understanding this vulnerability may facilitate a proactive control of introduced species. To do so, the dynamics from the point

where an alien species survives and reproduces or spreads vegetatively in its new habitat, to where it out-competes native species, needs to be elucidated. This requires an early detection of the alien and baseline information on the distribution of native species within well-defined areas. Here we present a case study of this approach based on seagrasses from Dominica, an island with a narrow euphotic benthos.

The distribution and benthic cover of Dominica's seagrasses were initially assessed in 2007 by Steiner and Willette (2010), during the only island-wide mapping of sublittoral habitats to date, and included the identification of the alien Hydrocharitaceae *Halophila stipulacea* Ascherson, 1867, by Willette (Willette and Ambrose 2009). *Syringodium filiforme* (Keuzig 1860) and *Halodule wrightii* Ascherson, 1868, in the family Cymodoceaceae, and the Hydrocharitaceae *Thalassia testudinum* Bank ex König, 1805, and *Halophila decipiens* Ostenfeld, 1902, were the native species. Seagrasses were limited to the western sublittoral (leeward) and to sheltered bays along the northeast (windward). Due to the island's young volcanic topography with a narrow and steep shelf, seagrasses mostly grew within 300 meters from shore. In their spatial extension and three-dimensional structure above and below the sediments, seagrasses were Dominica's largest organism-built marine habitat, the benthic cover of which was dominated by *S. filiforme* (Steiner and Willette 2010).

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 1867, Ostenfeld 1914, 1926, den Hartog 1970), and has spread to the eastern Mediterranean Sea via the Suez Canal, which opened in 1869. Lipkin (1975a, 1975b) thoroughly reviewed the history of its Mediterranean dispersal from the first plant fragments collected in Rhodes by Johann Nemetz in 1894 and later identified as *H. stipulacea* by Fritsch (1895), to the reports of living plants and meadows along Aegean islands in 1924 and 1926, Crete in 1955, Egypt in 1958, Lebanon in 1966, Cyprus between 1967 and 1970, and Malta in 1970 (den Hartog 1972). Over a decade later, new Mediterranean records of *H. stipulacea* came from the Tyrrhenian Sea (Acunto et al. 1997, Procaccini et al. 1999, Gambi et al. 2009), the Ionian coasts of Sicily (Bilotti and Abdelahad 1990, Alongi et al. 1992) and Greece (Van der Velte and den Hartog 1992), and most recently from Turkey (Valera-Álvarez et al. 2011), Tunisia and Libya (Sghaier et al. 2011).

To date, no stepping-stone locations of *H. stipulacea* were reported between the Central Mediterranean and the Lesser Antilles, where it was first identified in Grenada in 2002 (Ruiz and Ballentine 2004). Dominica was the second Antillean island where this species was identified, and in 2007 its distribution was limited to patches, on the west coast between Prince Rupert's Bay and Lamothe (first site of identification), and in the vicinity of Canefield (Fig.1 and 2a). In 2008, Willette identified the species in St. Lucia (Willette and Ambrose 2009) and demonstrated its rapid lateral expansion and ability to supplant *S. filiforme* in field experiments in Dominica (Willette and Ambrose 2009, 2012). Incited by the aggressive and opportunistic nature of *H. stipulacea*, Steiner et al. (2010) studied the depth range and horizontal distribution of native seagrasses in 2008, observed distinct western and northeastern seagrass landscapes.

West coast seagrasses inhabited most sandy environments north of Roseau, in 4 to at least 24 m depth with a negligible spatial overlap among the species (Steiner et al. 2010). *Syringodium filiforme* formed mono-specific or pure meadows, and isolated patches along its shallow distribution limit. Its meadows, which reached shoot densities that covered close to 80 % of the benthos (Willette 2010), shaped the contour of the seafloor in depths of 5-12 m like no other west coast seagrass. Multiple rhizome layers deposited over time, stabilized accumulating sediments and built mounds parallel to the coastline. A sharp, 20-40 cm step-down separated the shallow boundary in such *S. filiforme* meadows from their sandy shoreward surroundings (Steiner et al. 2010). A smoother step-down was common in depths 12 m, from where the benthic cover of *S. filiforme* decreased with depth, ending abruptly at 18 m or less. 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 and *H. stipulacea* were restricted to the west. *Halophila decipiens* grew below 4 m depth. In the absence of *H. stipulacea* it grew in pure patches and vast meadows, and with a consistently low benthic cover (<10 %), yet never intermixed with *S. filiforme*. It was common along and below the deep boundaries of *S. filiforme* meadows. *Halophila stipulacea* was spreading in Prince Rupert's and Pringle's bays and had rooted at eight additional locations (Steiner et al. 2010), partially within *H. decipiens* stands. 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*.

Northeastern seagrass meadows were exclusively established on the back reef flats (0.5 m depth) of fringing reefs, and were dominated by mixed stands of *T. testudinum* and *S. filiforme*. *Thalassia testudinum*, which was limited to the windward side of Dominica, 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.

Meanwhile, new sightings *Halophila stipulacea* have been reported from Bonaire and Curaçao, and across the Lesser Antillean archipelago from the Grenadines, St. Vincent, Martinique, Guadeloupe, St. Eustatius, St. Maarten, and St. John (Deal 2011, Debrot et al. 2012, Kerninon 2012, Mège 2013, Védie 2013, Willette et al. 2014). By late 2012 *Halophila stipulacea* grew throughout the Dominica's west coast, occupying sandy areas previously devoid of seagrasses or dominated by *H. decipiens*, and had infiltrated *S. filiforme* beds (pers. obs. S. Steiner).

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) structurally changed the meadow landscape and (c) augmented Dominica's benthic seagrass cover, and whether or not factors limiting the success of *H. stipulacea* on the island were discernable and corroborated by recent sightings of *H. stipulacea* in the Lesser Antilles.

Materials and methods

The benthic habitat maps by Steiner and Willette (2010) are based on *in situ* surveys from 2007, covering 1815ha along 90% of Dominica 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 sixteen of the previously studied meadows, and examined seagrasses at eight 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 sixteen reexamined sites, transects 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; which-ever 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, height and benthic cover of leaf shoots) and their central sections (species composition, height and benthic cover of shoots, signs of endofauna, epiphytes, sessile and vagile fauna). We noted 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 m² 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 m² quadrat subdivided into four 0.25 m² 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 1m² quadrat with one hundred square subdivisions of 100 cm². 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 m² 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; identifying the organisms to the lowest taxonomic level when possible. Depth was recorded at each plot.

To further ascertain *H. stipulacea*'s expansion in Dominica, we executed eight 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 depth at Grande Savane, Salisbury, Mero, and the northern Sourfrière Bay, and received complementary reports on Grande Savane and Anse Bateaux from A. Madisetti.

In order to compare *H. stipulacea*'s distribution, abundance and its possible displacement of native species, to the information gathered between 2007 and 2008 for the entire west coast, fishermen and divers were interviewed and shown photographs of all reported seagrasses, as well as fresh specimens. 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 provided information on the depth range. Brief exploratory snorkels 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 from 2009

(http://www.itme.org/reports/ITME_DATA%20Appx%20Steiner%20&%20Willette%2009.pdf).

For each of the sixteen reexamined sites we also expressed change in seagrass species distribution as the per cent 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 are thus dominantly *S. filiforme* along the western coast, and *T. testudinum* and *S. filiforme* along the northeast coast.

Results

The distribution *H. stipulacea* ballooned from isolated patches in 2008 to a 55 km swath along the west coast (62 km) with few discontinuities in four-and-a-half years (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 leave-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, 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* (Table 2). No specimens of *H. decipiens* were found and its former growing areas were covered by *H. stipulacea*. *Halodule wrightii*'s 2008 depth range (2-15 m) and distribution was reduced to 2-4 m depth in sandy areas at not occupied by *H. stipulacea*.

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, where bands of pure *S. filiforme* 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 of 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 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 m² 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, Layout, Jimmit, Mahaut, Canefield, and Pt. Michel where *H. stipulacea* had replaced most or all of the native meadows. Remnants of *S. filiforme* meadows at Mahaut and Jimmit, contributed up to 5 % and 20 % 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, Layout and Pt. Michel. At Layout (Fig. 5) the only previously known pure meadow of *H. decipiens* had disappeared and *H. stipulacea* was in its place. Similarly, *S. filiforme* beds at Prince Rupert's Bay, and Mero Bay, 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 this and the previous scenario, *S. filiforme* was no longer present below 13 m depth anywhere in Dominica.

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 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* and the echinoid *Meoma ventricosa*, as well as fishes such as mullids and the burrow-building malacanthid *Malacanthus plumeri*.

The architecture of seagrass meadows, successfully invaded by *H. stipulacea*, had changed. What used to be vast areas of *S. filiforme* with a mean shoot height of 20 cm and a mean benthic cover under 45 % in 2008, was covered by densely packed *H. stipulacea* leaves with a mean height of 4 cm in 2013. Open spaces between seagrass shoots and under the seagrass canopy, were drastically reduced. This 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 (Supplemental Table A in http://www.itme.org/reports/ITME_DATA_SUP_2013Steiner_Willette.pdf). The taxa with

the highest numbers of species were Chlorophyta (6), Echinodermata (10) and Osteichthyes (19). Compared to the 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% and 32% of the echinoderms and 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 and to densities up to 32 pods per m² in pure stands of *S. filiforme*.

Northeast Coast

No changes were noted in the seagrass species composition of northeastern seagrasses. As in 2008, meadows at Calibishie and Anse Soldat were formed by the 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 tidal channels and blowouts. The occurrence of algae and invertebrates associated to the seagrasses at Calibishie and Anse Soldat was nearly identical to 2008.

In the marginal and isolated seagrasses pockets 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 at a depth of 3 m. Along the southwestern margin of Hodges Reef, we observed the first and so far only monospecific 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 m² with a circum-marginal 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, which is the most turbulent site, *T. testudinum* was the only seagrass species present. Small patches (< 20 m² 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*, *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 (*Penicillus lamourouxii*, *Caulerpa cupressoides*, *C. serrulata*, *Ventricaria ventricosa*, 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 & Waisel 1981, Schwarz & Hellblom 2002). Barren sandy areas favored the spread of *H. stipulacea*. In 2008, with the exception of Prince Rupert's Bay, *H. stipulacea* had expanded along and below the deep distribution limit of *S. filiforme*, occasionally supplanting *H. decipiens*. We suggest that *H. stipulacea* infiltrated west coast *S. filiforme* meadows on their deep margins where the benthic seagrass cover was consistently low (<5%) (Steiner et al. 2010). *Halophila decipiens* was supplanted in this process. So far, the *S. filiforme* strong-holds withstood the replacement by *H. stipulacea*. However, storms may have further accelerated the expansion of *H. stipulacea* by creating new open spaces, at last up to 15 m depth, which is within the depth range where native strong-holds developed.

Due to the absence of wave-energy dissipating features as a wide shallow shelf, barrier reefs or fringing lagoon reefs, storm-induced swells are a chronic disturbance shaping Dominica's seagrass meadows. Seagrasses are commonly uprooted to depths up to 8 m during storms, and buried by redeposited sediments up to depths of 15 m. During the four-and-a-half years considered, fourteen tropical depressions and storms, including three hurricanes passed within 500 km of the island. None were direct hits, yet all caused turbulent coastal waters (pers. obs., pers. comm. A. Magloire). Waves driven by outer wind bands of Hurricane Omar (450 km NW of Dominica) were the most destructive (Steiner et al. 2010). Slow moving high-pressure systems to the west of Dominica, which are not recorded as storms, also lead to pressure-gradient-driven westerly winds with destructive surges along the west coast (pers. obs.). In 2013 *H. stipulacea* had colonized most open areas crated by storms. Blowouts colonized by *H. stipulacea*, and located within pure *S. filiforme* strong-holds, indicate that negatively buoyant clumps (Willette and Ambrose 2012) of this alien species can take root.

Contrasting *H. stipulacea*'s swiftly gained dominance along the west coast, is its continued absence in the northeast. What hindered *H. stipulacea* to colonize the windward seagrasses? 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 (pers. obs.), during the retrieval of anchors, fish traps, or the dragging of seine nets (Willette and Ambrose 2012, Dominican fishermen pers. comm.). The shallow limit of *H. stipulacea*'s depth range along the west coast results from its poor rooting ability under the given near-shore turbulence regimes. 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 0.5 meters and expand into back reefs that are far less agitated than western shores. The absence of *H. stipulacea* in the northeast is hence not an effect of turbulence.

Furthermore, the species' ability of clumping chloroplasts, and thus protecting most of its chloroplast from high irradiance (Sharon et al. 2011), speaks against UV radiation as possible limiting factor under high-PAR conditions. Structurally, the compact rhizome layers and height benthic cover of shoot in northern seagrasses beds may have prevented *H. stipulacea* to settle (see Cecherelli et al. 2000). *Thalassia testudinum* has the deepest live rhizome layers of the native species (den Hartog 1970, Duarte & Chiscano 1999) and in combination with the intermixed *S. filiforme*, possibly limits the availability of suitable settlement spaces. Alternatively, Dominica's rough windward seas and the prevailing easterly surface currents barred *H. stipulacea* from the northeast so far. Introductions of *H. stipulacea* fragments tangled in fishing gear would be possible but fishing on or above seagrass meadows has traditionally only been carried out on the west coast. There is no regular boat traffic between western and northern landing sites, and the boats are small without ballast tanks that could hold seagrass fragments. However, fishing boats from the northeast periodically transport agricultural goods across the 50 km Dominica Passage to Guadeloupe, where *H. stipulacea* has recently been sighted (supplemental Table B in www.itme.org/data/2014 Steiner and Willette).

The pliable leaves of *Halodule wrightii* are the narrowest (0.5-1mm) among Dominica's native seagrasses species. Coupled with their belowground structural complexity that is achieved by a single plant with many intermingled unidirectional rhizomes (Harnett 1983) observed by Pangallo and Bell (1988), they are evidently well adapted to the island's marginal seagrass habitats in shallow turbulent sandy environments. Consequently, *H. wrightii* has so far grown with little inter-species seagrass competition. However, in the recent direct spatial competition with *H. stipulacea* along the west coast, the species has lost 9 m of its local depth range.

If the remaining strong-holds of *S. filiforme* on the west coast keep their ground over time, other ecological limitations in *H. stipulacea*'s expansion related to structural or chemical thresholds by *S. filiforme* stands may become apparent. In addition, seasonal fluctuations in the biomass of roots, rhizomes and leaves of *S. filiforme* (Dawes & Lawrence 1980, Gallegos 1994, Van Tussenbroek 1994) need to also be considered as possible settlement windows for *H. stipulacea*. Investigations on 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). Seagrass conservation mechanisms in Dominica, which are not in place, would need to reduce or eliminate anthropogenic scarring of the last consolidated *S. filiforme* strongholds from which the species can vegetatively expand and reseed, in the event that *H. stipulacea* succumbs to massive mortality.

Given the aforementioned natural variables (storm disturbances), annual expansion rates of *H. stipulacea* in Dominica are likely highly variable and indiscernible based our observation points from 2008 and 2013. However, by overlaying *H. stipulacea*'s current distribution onto our habitat maps from 2008, we estimated the seagrass cover to have increased from approximately 316 ha in 2008 to at least 773 ha in 2013 and driven by the a

minimum gain of 649 ha of *H. stipulacea* and a minimum loss of 150 ha of *S. filiforme*. It is therefore plausible that the first settlement of *H. stipulacea* in Dominica was only a few years before its initial sighting in 2007.

Although Steiner et al. (2010) mentioned the possibility of *H. stipulacea* surpassing the distribution and benthic cover of *H. decipiens*, the defenselessness of *H. decipiens* and the scope of *H. stipulacea*'s invasive nature in Dominica are staggering. In sum, the west coast sandy environments up to 30 m have undergone a phase shift from intermittent open areas and seagrass meadows consisting of three species with minor spatial overlap, to a monospecific low-canopy carpet of *H. stipulacea*, remnants of two native species and a notably reduced diversity and abundance of cohabiting macroalgae,

It remains to be investigated how the changing seagrass landscape further influences marine biodiversity, as well as symbioses, foodwebs, and the biological oxygen demand of biodegrading bacterial communities. While Dominica's fishermen claim a reduced near shore catch to coincide with the appearance of *H. stipulacea* carpets, decision makers discuss prospectives of harvesting this species and the eco-political benefits of a potentially increased CO₂ sequestration.

The way in which such topics will be evaluated (see Davis et al. 2011), will define ecological and economic benefits and losses of this marine angiosperm invasion. What is already clear is that Dominica's seagrasses are subject to chronic storm-induced fluctuations in the expanses of native meadows (Steiner et al. 2010). In addition, landscape changes have recently been effected by the opportunistic and out-competing *H. stipulacea*. The mere assessment of basic biotic and abiotic features of seagrass meadows is therefore a resource-intensive undertaking and the eradication of *H. stipulacea*, if considered, is unrealistic at this scale. Conservation measures must omit the premise of static seagrass boundaries and species composition. In Dominica coastal marine environments and their species composition are changing at a pace exceeding public and political reaction time and most research and dissemination processes.

How, where and when *H. stipulacea* first took hold in the Caribbean, remains unanswered. Ruiz and Ballentine (2004) observed a single 300 m² patch of this species in Grenada in 2002. It is likely that the species had an earlier-than-reported presence in the eastern Caribbean and that it had spread to other islands before its sighting in Dominica in 2007 (Willette and Ambrose 2009). Ballast water tanks in ships are a possible vector for its introduction that explains the geographic distribution-gap of *H. stipulacea* between the central Mediterranean and the Caribbean. Fragments of *Halophila johnsonii* are known to be viable for approximately one week in aquaria, and they successfully resettle and root in mesocosms (Hall et al. 2006). Similar attributes in *H. stipulacea* could facilitate its dispersal between islands. Across the Eastern Caribbean, 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) depend heavily on supply ships with multiple ports of call, coming from the Americas. Furthermore several islands have oil depots and refineries, supplied by transoceanic tankers with global shipping routes, and cruise ship tourism is common in the region. *Halophila stipulacea* may easily have had multiple "starting points"

by 2002, with surface currents and hurricanes complementing the colonization of “downstream” shores.

The comparison of oceanographic settings from the Lesser Antilles where *H. stipulacea* has established (Supplemental Table B in http://www.itme.org/reports/ITME_DATA_SUP_2013Steiner_Willette.pdf) shows the species’ “preference” for leeward or shelters areas, as we observed in Dominica. Results from island-wide seagrass surveys that cover multiple disturbance regimes in neighboring Guadeloupe (Mège 2013) and Martinique, (Vedie 2013) support this pattern in that *H. stipulacea* settled on the leeward coast first from where it expanded. We argue that windward locations in the region, with similar parameters to Dominica’s northeast, may be the future source of seeds and a refuge for some of the native seagrass species, while native leeward meadows will be highly invasible (Capers et al. 2007) and change drastically under *H. stipulacea*. Consequently and in view of the latitudinal expansion of *H. stipulacea* (Willette et al. 2014), we expect significant alterations in the community structure and biodiversity of seagrass meadows throughout the Caribbean within the next decade, and the possible demise of *H. decipiens* in the region.

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Index of Tables and Figures

Table 1 a) Location and transect features of quantitatively surveyed sites.	15
Table1 b) Location and belt transect features of qualitatively surveyed sites.	15
Table 2 a) Seagrass species composition of meadows in 2008 and 2013.	16
Table b) Seagrass species composition of meadows and patches, based on habitat maps 2007, observations between 1999 and 2009, and from 2013.	16
Fig. 1 Location of survey sites (2013) in Dominica	17
Fig. 2 Distribution of native seagrasses and <i>H. stipulacea</i>	18
Fig. 3 Change of distribution of <i>H. stipulacea</i> versus native seagrass species along transects.	19
Fig. 4 Seagrass profile at Layou; seagrass composition in 2008 and 2013.	19
Fig. 5 Seagrass profile at Bioche; seagrass composition in 2008 and 2013.	20
Figs. 6a, 6b Expanse and composition of seagrass meadows in 2008 and 20013 at Mero.	20

Table 1 a) Location and transect features of quantitatively surveyed sites. Transect lengths and maximum depths are given for the years 2008 and 2013, respectively. Starting points are located in the intertidal. **b)** Location and belt transect features of qualitatively surveyed sites. Headings for the 24 sites are in reference to the 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).

a)	Site name	Transect				
		Starting point		Heading	Length (m) 2008 / 2013	Max. depth (m) 2008 / 2013
1	Toucar	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°25'08.93" N	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°15'34.55" N	61°22'39.37" W	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

b)	Site name	Transect				
		Starting point		Heading	Length · width (m)	Depth range (m)
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

Table 2 a) Seagrass species composition of meadows in 2008 and 2013. The spatial dominance of species is expressed as the extent (meters) of pure stands along each transect. In 2008 *Halodule wrightii* (HWR), *Halophila decipiens* (HDE) and *H. stipulacea* (HST) were the marginal species. In 2013 *Syringodium filiforme* (SFI) was occasionally intermixed¹ and in isolated pure stands² 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. **b)** Seagrass species composition of meadows and patches, based on habitat maps 2007, observations between 1999 and 2009, and from 2013.

a)	Site name	Principal seagrasses and their meadow's width in m		Marginal, intermixed ¹ and pure stands ² in decreasing benthic cover	
		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
b)					
	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

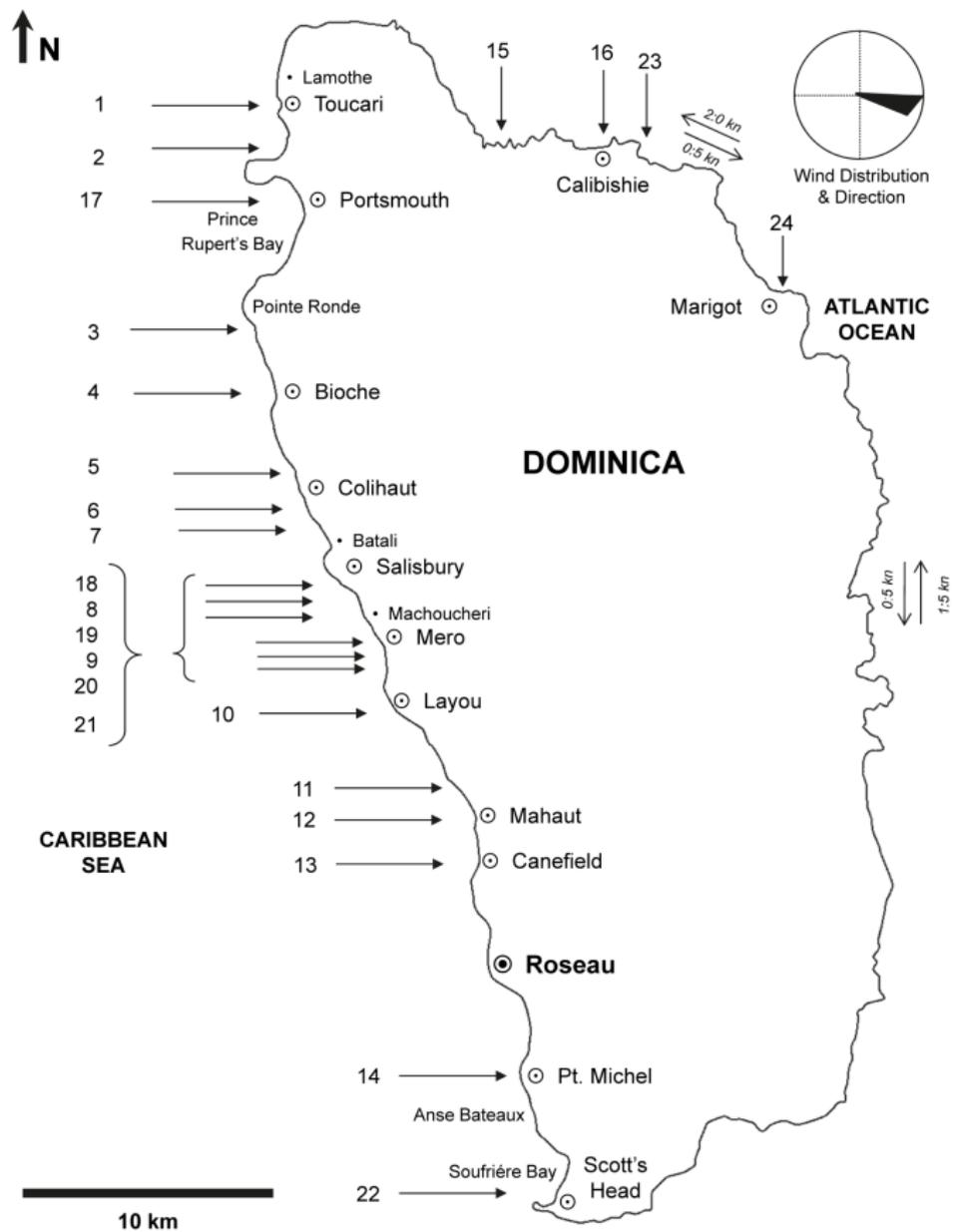


Fig. 1 Location of survey sites (2013) in Dominica. Site numbers as in Table 1. Sites 1-16 were previously surveyed by Steiner et al. (2010), site 17 was monitored by Willette from 2007 to 2009 (unpublished information), sites 18 - 24 were monitored by Steiner from 2000 - 2009 (unpublished information).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

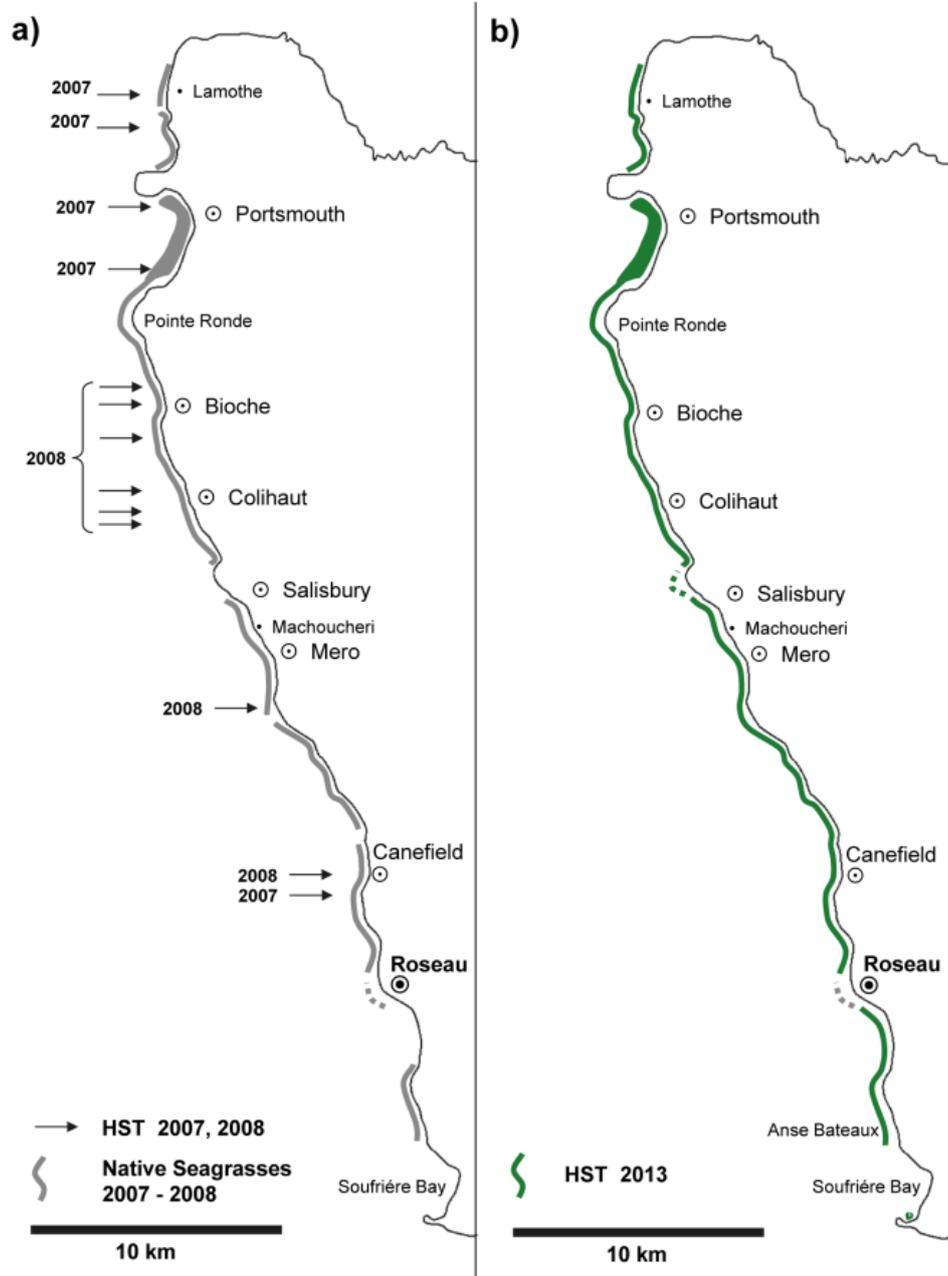


Fig. 2 a) Distribution of native seagrasses (solid lines) and *H. stipulacea* (arrows) in late 2007 and 2008. **b)** Distribution of *H. stipulacea* in March 2013. The solid distribution line is not to scale in terms of width. Dotted distribution line indicates the known interruption of seagrasses by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

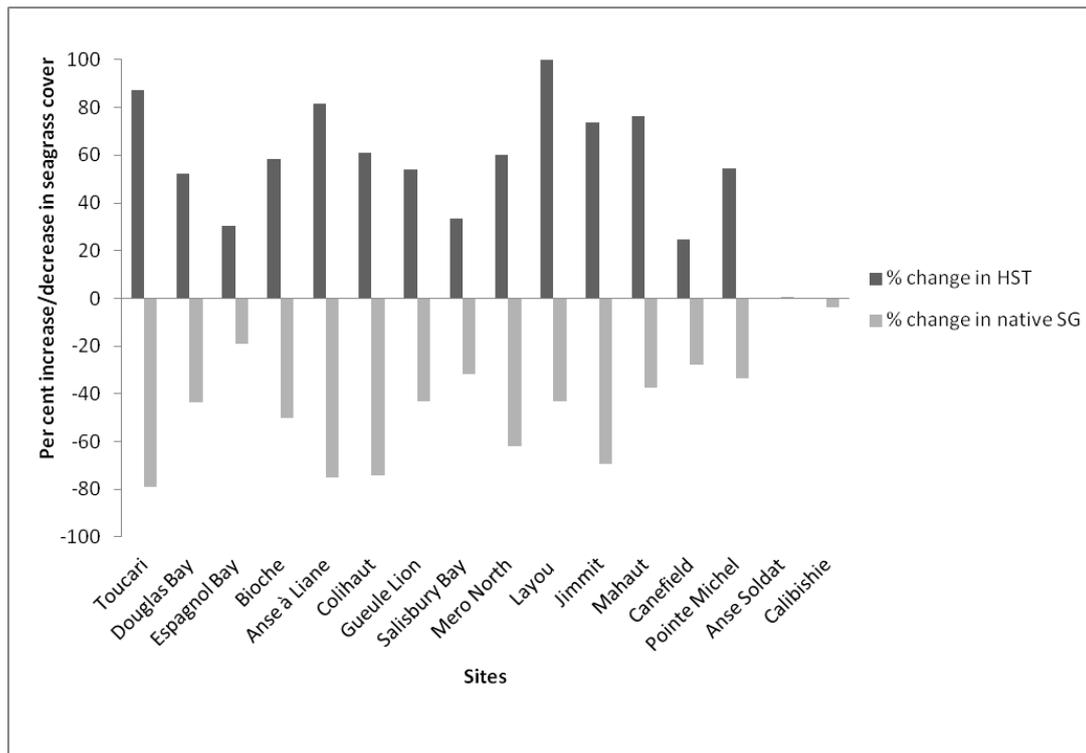


Fig. 3 Change of distribution of *H. stipulacea* versus native seagrass species along transects. Native species were primarily *S. filiforme* on the west coast, and *T. testudinum* and *S. filiforme* along the northeast coast.

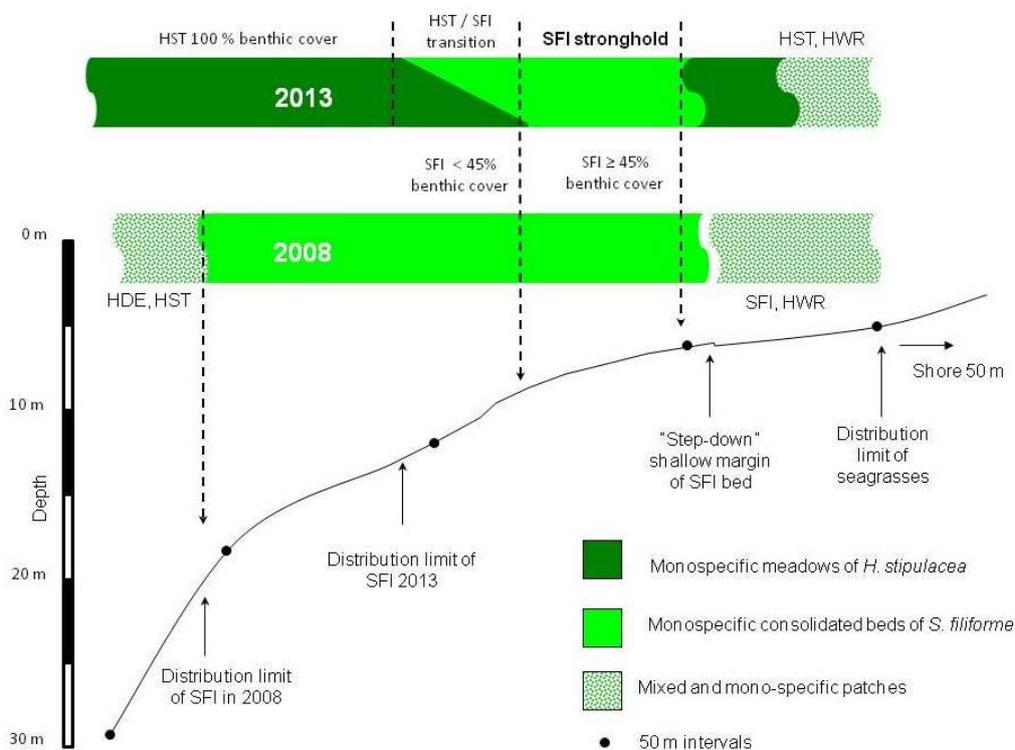


Fig. 4 Seagrass profile at Layou; seagrass composition in 2008 and 2013. The invasive *Halophila stipulacea* replaced all native seagrasses.

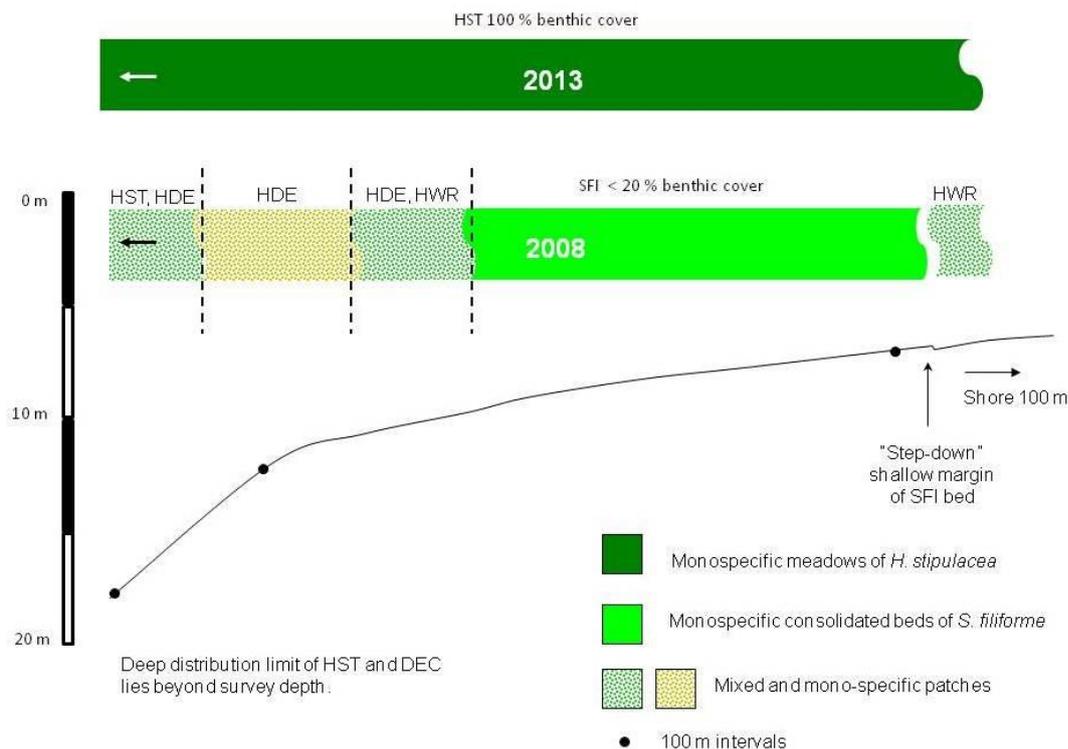
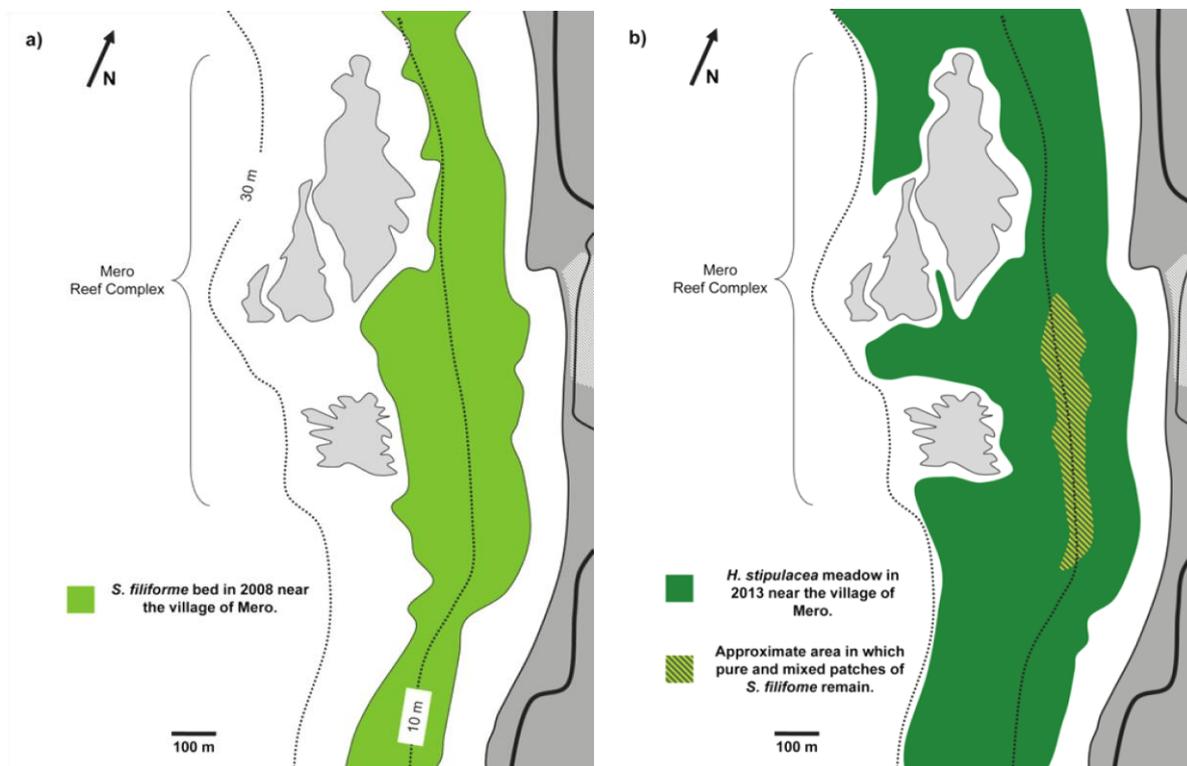


Fig. 5 Seagrass profile at Bioche; seagrass composition in 2008 and 2013. The *S. filiforme* (SFI) stronghold is located within shallow third of the 2008 seagrass bed. *Halodule wrightii*, *Halophila decipiens* and *H. stipulacea* are abbreviated as HWR, HDE and HST.



Figs. 6a, 6b Expanse and composition of seagrass meadows in 2008 and 20013 at Mero.