Seagrasses and coastal protection: The role of *Halophila stipulacea* in sediment stability at the coast of St. Eustatius, Dutch Caribbean

MSc Thesis

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Preface

People have asked me jokingly at times: "You study seagrass? So what..., you count the leaves?", to which my answer was always an enthusiastic "Yes! That is exactly what I do". Naturally, there is a lot more to it and after spending over eight months studying and reading about seagrasses, their growth and their ecosystem functions, my interest in this topic has only become stronger. The role seagrasses play as ecosystem engineers is something I find fascinating, and I consider myself lucky to have been provided with the opportunity to study these species as part of my master's thesis research.

The Caribbean Netherlands Science Institute on St. Eustatius has supported me in this study, and I would like to give special thanks to Anna Maitz, my supervisor at CNSI, for granting me this opportunity, always helping me and being the best "boss"! Next, I am extremely grateful for the time my study mate, Tom van Ee, has sacrificed to always assist in the data collection. The help that colleagues Inês Freire and Kimani Kitson-Walters have given during this study is much appreciated. A last thanks goes to my supervisor at Utrecht University, Valérie Reijers, for her understanding, support, and feedback during this study.

To the friends I have made on Statia: may we cross paths again some day.

Francine van Hee
March 8th, 2022
Utrecht

Abstract

Seagrasses are increasingly being recognized for their potential in protecting the coastlines from flooding and erosion. As ecosystem engineers, seagrasses can attenuate waves as well as trap and stabilise sediment, causing the seabed to become more stable, which can contribute to coastal protection. Where many tropical countries lack the means to undertake traditional coastal protection measures, natural ecosystems, such as seagrass meadows, can provide cost-effective alternatives to protect coastal communities from natural hazards and improve their well-being, as ecosystem services are continuously provided. The Caribbean regions holds a large cover in seagrass relative to the coastlines, yet few studies have focused specifically on seagrass and sediment stability in this region. Over the last decades, native seagrass meadows have been degrading and the non-native *Halophila stipulacea*, originating from the Red Sea, has been spreading rapidly through the region relatively recently. A knowledge gap exists in whether this opportunistic species could provide essential ecosystem services, such as coastal protection, where native species have been lost. The extent to which seagrass species contribute to coastal protection services depends on the growth properties of these species as well as the environmental conditions. Therefore, a need remains to study sediment dynamics in seagrass meadows in different scenarios. The present study aims to increase the understanding of the role of *H. stipulacea* in sediment dynamics, specifying on the coast St. Eustatius, Dutch Caribbean.

First, current available knowledge on sediment stabilising properties of seagrass species in the wider Caribbean region was reviewed. Second, an experiment was set up at a study site with a depth of 18 m, in a monospecific *H. stipulacea* meadow, and in a sand patch within the meadow. In addition to measuring the growth properties of *H. stipulacea*, sediment stability was investigated by measuring changes in seabed level over time, as well as using sediment traps to calculate the sediment deposition rate. Data on meteorological conditions was retrieved to investigate correlations between the weather and sediment change.

Results showed that *H. stipulacea* at a depth of 18 m at the coast of St. Eustatius, grew a new shoot within 3.3 days, over twice as fast as measured for its native range. Average leaf length was 4 cm while eight shoots were observed per strand. Similar values were observed in its native range. Although the leaf length was smaller than most native seagrasses in the Caribbean, *H. stipulacea* showed a higher density, which likely contributed to the findings of this study. The sediment deposition rate was much lower in the *H. stipulacea* meadow than in the sand patch, which is probably the result of limited resuspension within the seagrass meadow. After 14 weeks, the sediment in the *H. stipulacea* meadow had eroded. This is believed to be the result of erosion of the surface sediment layer, a less stabilised layer of sediment that was potentially resuspended and carried away when the weather became more turbulent after months of calm conditions. The subsurface layer, however, is believed to be more stabilised by the root and rhizome system of *H. stipulacea*, which explains why smaller and relatively constant changes in sediment level were found after weather conditions had increased. The sediment level in the sand patch showed a larger variance over time, also varying much more spatially between erosion and accumulation.

This study showed that *H. stipulacea* seems to stabilise the subsurface sediment layer via its root and rhizome system, which is assumed to contribute to a more stable seabed. However, this result only became apparent after the erosion of the surface layer and might even disappear with more extreme weather conditions. This study urges for future research to investigate the sediment stabilising effect of *H. stipulacea* at shallower depths as well as over longer terms, as different results might be found for different seasons.

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1. Introduction

Seagrasses are marine flowering plants – adapted to live fully submerged in seawater – that occur in coastal habitats worldwide. As ecosystem engineers, seagrasses modify the local physical environment, and they are known for the ecosystem services they provide. The term 'ecosystem services' is defined here as the goods and services provided by the ecosystem that (in)directly benefit humans (de Groot, Wilson, & Boumans, 2002). For seagrass ecosystems, this includes habitat and nursery for commercially important fish species and their potential to sequester organic carbon in the sediment (Potouroglou, et al., 2017; McKenzie, et al., 2020; Miyajima & Hamaguchi, 2019). In addition, seagrass meadows are ecologically linked to adjacent ecosystems such as coral reefs, mangroves and salt marshes via, for example, trophic transfer (i.e., biomass/ energy exchange between levels in a food web), or by facilitating many other species, including epiphytes (Green & Short, 2003; Ondiviela, et al., 2014; Heck Jr., et al., 2008; van Tussenbroek, et al., 2014; MacRae & Esteban, 2007).

Marine and coastal ecosystems, including seagrass ecosystems, are increasingly recognized for their potential in protecting the coastlines from flooding or erosion (Ondiviela, et al., 2014). Rather than approaching coastal protection with traditional structures, such as seawalls and dikes, these ecosystems could potentially be used in combination, or serve as alternatives to man-made structures (Guannel, Arkema, Ruggiero, & Verutes, 2016; Ondiviela, et al., 2014). According to Ondiviela et al. (2014), combining intertidal coastal ecosystems with traditional coastal engineering measures seems a promising step towards reducing the increasing risk of flooding and erosion that comes with current climate change. For instance, vegetation acting as ecosystem engineers can attenuate waves, and trap and stabilise sediment, causing the seabed to become more stable and erosion-resistant, thereby stimulating the protection of the coastline (Borsje, et al., 2011; James, et al., 2020).

Studies have shown that seagrass meadows can contribute to coastal protection by attenuating waves, affecting current flow and stabilising the sediment (Ondiviela, et al., 2014; Potouroglou, et al., 2017; Christianen, et al., 2013; Fonseca & Cahalan, 1992; Gacia & Duarte, 2001; Bos, Bouma, de Kort, & van Katwijk, 2007; Bouma, et al., 2014). For example, Potouroglou et al. (2017) studied the extent that seagrass meadows contribute to sediment stability and deposition, in multiple settings and locations (Scotland, Kenya, Tanzania and Saudi Arabia), and compared their results to studies performed worldwide, mainly considering regions in Europe, the USA, Asia, and Australia. The study pointed out that meadows of different seagrass species and at varying settings can contribute to sediment stabilisation and sediment accumulation, raising the surface (Potouroglou, et al., 2017).

In Europe, traditional engineering measures for coastal protection are used and seagrass ecosystems provide a feasible opportunity to combine with and support engineering measures (Ondiviela, et al., 2014). Unfortunately, many tropical countries lack the means (i.e., finances and infrastructure) to undertake traditional engineering solutions to prevent coastal erosion (James, et al., 2019). Yet, these countries have a high dependency on the coastal zone for tourism and flood safety. In addition, beach erosion will increase with sea-level rise and increasing storm frequency and intensity. Hence, James et al. (2019) urges the need for cost-effective solutions. As established by McKenzie et al. (2020), the Caribbean region holds a large cover in seagrass relative to the coastlines (McKenzie, et al., 2020). These seagrass ecosystems could potentially provide a cost-effective solution, thereby protecting the coastal communities from natural hazards and improve their well-being, while continuing to provide other ecosystems services (Guannel, Arkema, Ruggiero, & Verutes, 2016). Notwithstanding, multiple studies point out that the value of coastal ecosystems for coastal protection is strongly site specific and varies as a function of hydrodynamic conditions and local geomorphology. For seagrass

ecosystems, their ability to provide coastal protection services relates to the environmental boundary conditions (e.g., water depth and hydrodynamics), the traits of the seagrass species (e.g., leaf length and shoot density) and seasonality in shoot density (Bouma, et al., 2014; Guannel, Arkema, Ruggiero, & Verutes, 2016; Viana, Zoysa, Willette, & Gillis, 2019; Johnson, Gulick, Bolten, & Bjorndal, 2019).

1.1 Seagrass in the Caribbean

To date, few studies have focused specifically on seagrass and sediment stability in the Caribbean region (James, et al., 2019). However, the Caribbean region has been recognized for the changes in its coastal habitats over the last decades. Native seagrass beds have been degrading, probably as a result of growing human populations and economies, rapid urbanization, tourism growth, and intensive grazing by megaherbivores (Viana, Zoysa, Willette, & Gillis, 2019; Christianen, et al., 2014). Degradation of these seagrass meadows can lead to reductions in coastal protection services (Viana, Zoysa, Willette, & Gillis, 2019; Bouma, et al., 2014). According to Bouma et al. (2014), it is exceedingly difficult to restore coastal vegetation that has been lost after the collapse of the ecosystem. Interestingly, a non-native seagrass species (*Halophila stipulacea*) has recently been spreading through the Caribbean region. This opportunistic species originating from the Red Sea is believed to have expanded to the Mediterranean after the opening of the Suez Canal in 1869 (Lipkin, 1975; Willette & Ambrose, 2009). Subsequently, it spread to the Caribbean region, likely via recreational vessels, where it was first observed in 2002 along the coastline of Grenada (Willette, et al., 2014; Ruiz & Ballantine, 2004).

Seeing the relatively recent appearance of *H. stipulacea* in the Caribbean, there is limited research available on the coastal protection services – and more specifically sediment stabilising properties – provided by this species in the Caribbean. In a review that explored how *H. stipulacea* could provide essential ecosystem services where native species had been lost, Viana et al. (2019) emphasized, that much is still unknown, and more baseline data is needed. This is in compliance with other studies that indicate the need to study sediment dynamics in seagrass meadows under different circumstances (James, et al., 2020; Potouroglou, et al., 2017; Johnson, Gulick, Bolten, & Bjorndal, 2019). Considering the extent to which seagrass species contribute to coastal protection services depends on the properties of the species, as well as the ecosystem characteristics and environmental conditions (Viana, Zoysa, Willette, & Gillis, 2019; James, et al., 2020), studying the occurrence of *H. stipulacea* in varying locations would be key in decreasing this knowledge gap. As a step towards increasing the understanding of the potential coastal protection services provided by *H. stipulacea* in its non-native range, the present study focuses on the island of St. Eustatius in the Dutch Caribbean, as currently no research on the sediment stabilising properties of this species in this location can be found.

1.2 Seagrass in St. Eustatius

The island of St. Eustatius, locally referred to as 'Statia', is in the north-eastern part of the Caribbean Sea (figure 1.1). The island covers an area of 21 km^2 and is part of the Caribbean Netherlands. It is surrounded by a near-shore island shelf of 25.3 km^2 with depths of 5 to 30 m. This area includes varying marine habitats, such as bare sand, coral reefs, and seagrass meadows (Debrot, et al., 2014).

Figure 1.1: Map of Caribbean indicating geographical location of Sint Eustatius (OnTheWorldMap, 2021).

The seagrass meadows around St. Eustatius have been changing over the past decades. A report published in 2007 stated that seagrass beds, mainly consisting of the native species *Thalassia testudinum* and *Syringodium filiforme*, were observed at depths of 10 to 35 m along the whole coastline (see appendix III, figure F for habitat map; MacRae & Esteban, 2007). The report mentions major declines were reported by fishermen and island residents, believed to be caused by hurricanes, boat anchors and disturbances in seawater dynamics. During a benthic habitat survey in 2012 (performed by Debrot et al., 2014), the non-native *Halophila stipulacea* was observed for the first time on St. Eustatius (Willette, et al., 2014). Debrot et al. (2014) presented a marine habitat map of the St. Eustatius shelf (see appendix III, figure G) and indicated a decline in seagrass cover (estimation of 124 ha). The meadows were now almost limited to the northern part of the island shelf. The seagrass amounted only 5 percent of the habitats studied, whereas the sand habitat had the largest contribution (almost 30%), potentially indicating bare sand areas remain where seagrass is lost. The main seagrass species was *H. stipulacea*, much less cover of *S. filiforme* was found (2%) and *T. testudinum* was not found at all. This decline corresponds to another study published in September 2013, that used multispectral imagery to determine the habitats around St. Eustatius, which reported that the seagrass habitat was mainly found in the north-western part of the island, and the species were mainly *H. stipulacea* and *H. decipiens* (Nieto, Mücher, Meesters, & Clevers, 2013). In the years following, fields of the opportunistic *H. stipulacea* became more extensive and colonized bare sand areas, as well as areas where the native species had previously been lost and unvegetated areas remained (Davies & Piontek, 2017). A thesis study conducted in 2020 verified the occurrence of *H. stipulacea* meadows in three locations around the island (see appendix III, figure H), including in Orange bay (van Weert & van Wijk, 2020).

These changes in seagrass distribution along the coast of St. Eustatius suggest parallel changes in the coastal protection services that are provided by the seagrass meadows. With the degradation of the native seagrass meadows that has been observed around St. Eustatius, one would expect their ecosystem services are also lost when no vegetation remains, considering for example, bare sand areas provide a less stable seabed and support less biodiversity (Waycott, et al., 2009). Slijkerman (2011) stated that it is unlikely for the native seagrasses to recolonize once they are lost. This raises the question as to whether the non-native *H. stipulacea*, which seems to be spreading rapidly around the coast of St. Eustatius, can provide similar ecosystem services, or at best provide a more fruitful habitat than non-vegetated areas. It is therefore important to 1) review existing knowledge on sediment stability in seagrass, specifically for *H. stipulacea*, not only around St. Eustatius but in the Wider Caribbean, and 2) study the extent to which *H. stipulacea* stabilises the sediment at St. Eustatius.

1.3 Objectives and Research Questions

The aim of this research is twofold: (i) review the current knowledge on sediment stabilising properties of seagrass species in the Wider Caribbean; (ii) investigate the effect of the rapid expansion of *Halophila stipulacea* on sediment stability at the coast of St. Eustatius. This includes identifying the growth properties of *H. stipulacea* in its native and non-native range.

Main question: To what extent can *Halophila stipulacea* provide coastal protection services (i.e., sediment stabilisation) at the coast of St. Eustatius, Dutch Caribbean?

Sub-questions:

1. What is currently known about the sediment stabilising properties of the non-native and native seagrass species (specifically, *Syringodium filiforme* and *Thalassia testudinum*) in the Wider Caribbean?

2. To what extent is sediment stability at the coast of St. Eustatius influenced by growth rate and biometrics (i.e., internode length, leaf length, and width) of *Halophila stipulacea*?

This report first proceeds with a literature review chapter that elaborates the current knowledge on sediment stabilising properties of the non-native and native seagrass species in the Wider Caribbean (chapter 2). Following is the methodology (chapter 3), which elaborates on the study area, research set-up and data analysis. In chapter 4, results of the present study are presented. The discussion (chapter 5) makes sense of the results by interpreting and comparing to literature, as well as discussing the potential influence on the wider ecosystem, reflecting on the limitations of the study and the relevance to practice. In the conclusions (chapter 6), answers are formulated to the defined research questions. Finally, recommendations (chapter 7) are given for future research.

2. Sediment stabilising properties of seagrass in the Wider Caribbean

In this chapter, a detailed assessment of the available literature is conducted, focusing on what is currently known about the sediment stabilising properties of the non-native and native seagrass species in the Wider Caribbean. This is essential to get an in-depth baseline of knowledge on seagrass linked to sediment stability. Hence, this chapter starts with a description of the seagrass species occurring in the Wider Caribbean. As the present study focuses on *Halophila stipulacea*, the growth properties for this species are described in detail, and compared to native seagrass species. The final section then reviews the available literature on sediment stabilising properties of seagrass to reflect on how the growth properties of *Halophila stipulacea* will likely affect seabed level dynamics.

2.1 Seagrass species and growth properties of *Halophila stipulacea*

Of the approximately 60 species of seagrass that occur worldwide, 10 species occur in the Caribbean region, one of which is the non-native *Halophila stipulacea*. The native seagrasses include: *Thalassia testudinum, Syringodium filiforme, Halodule wrightii, Halodule beaudettei, Halophila baillonii, Halophila decipiens, Halophila engelmanni, Halophila jognsonii* (east Florida only)*, and *Ruppia maritima*. The first three are the main occurring species in the Caribbean region. (Debrot, Henkens, & Verweij, 2018; Green & Short, 2003; Short, Carruthers, Dennison, & Waycott, 2007).

Growth properties of *Halophila stipulacea*

Almost four decades ago, Wahbeh (1984) published an article on the growth of *H. stipulacea* in the Jordanian Red Sea, its native range. At a depth of 10 m, the study found that the leaf growth rate decreased linearly with leaf size (also see figure 3.2 for a photo of *H. stipulacea*). At mean leaf length, the growth rate was 0.069 cm leaf^{-1} day^{-1}. A new leaf was produced in 8.1 days (mean), with a mean of eight leaves per strand. On average, a leaf detached from the strand 33 days after it stopped growing. A mean dry weight (DW) of 3.13 mg per 1 cm of leaf length was recorded. Next to this, a mean shoot density of 405 m^{-2} was found, as well as a maximum leaf length of 5.91 cm. In 2020, a study aimed to supplement the existing baseline of knowledge on growth rates and biomass production of *H. stipulacea*, which was also performed in the Jordanian Red Sea (Azcárate-García, Beca-Carretero, Villamayer, Stengel, & Winters, 2020). At a depth of 14 m, they found a leaf area growth rate of 0.88 cm^2 plant^{-1} day^{-1}. A new shoot was produced in 6.9 days and the mean leaf length was approximately 4 cm. They found an averaged aboveground (AB) biomass of 3.8 mg DW plant^{-1} day^{-1} and an averaged belowground (BG) biomass of 1.63 mg DW plant^{-1} day^{-1}. Next to this, an average rhizome internode length of 0.97 cm was recorded. Their study also revealed the following for the Red Sea and Mediterranean Sea: leaf lengths ranged from 1.22 to 8.43 cm, leaf growth rates from 0.01 to 0.62 cm leaf^{-1} day^{-1}, shoot formation values from 0.037 to 0.5 shoot day^{-1}, and AG/BG biomass ratios ranged from 0.27 to 2.70 (see Azcárate-García, Beca-Carretero, Villamayer, Stengel, & Winters, 2020).

In comparison (also see table 2.1), for *T. testudinum* (native to Caribbean) the average leaf length fluctuated between 12.6 to 26.4 cm, the average shoot density ranged from 784 to 1500 shoots m^{-2}, and the average above- and belowground dry biomass ranged from 194 to 420 g m^{-2} and 300 g to 4 kg m^{-2}, respectively (Fonseca & Fisher, 1986; James, et al., 2020; Johnson, Gulick, Bolten, & Bjorndal, 2019; Koch, 1999). For *H. wrightii*, the leaf length averaged between 14.9 and 19.8 cm, with a density of 1900 to 2870 shoots m^{-2}, and for *S. filiforme* the average length of the leaves was found to be 24 to 26 cm, with a density of 230 to 1350 shoots m^{-2} (Fonseca & Fisher, 1986).

Table 2.1: Summarizing table of growth properties of H. stipulacea (native range), T. testudinum, H. wrightii and S. filiforme.

Species	Most important traits			Source
	Leaf length (cm)	Shoot density (shoots m^{-2})	Aboveground biomass / production	
Halophila stipulacea	1.36 – 5.91 1.22 – 8.43	405 -	3.16 – 8.01 mg DW shoot^{-1} d^{-1} 2.9 – 4.8 mg DW plant^{-1} d^{-1}	Wahbeh, 1984 Azcárate-Garcia, et al., 2020
Thalassia testudinum	12.6 – 20.3 15.8 +- 1.5 26.4 +- 5.9 20 +- 2 4 +- 1 (clipped)	850 – 1500 776 – 786 784 +- 43 - -	- 259.4 +- 44.6 g DW m^{-2} - 420 +- 126 g DW m^{-2} 125 +- 17 g DW m^{-2} (clipped)	Fonseca & Fisher, 1986 Johnson et al., 2019 Koch, 1999 James et al. 2020 James et al. 2020
Halodule wrightii	14.9 – 19.8	1900 – 2870	-	Fonseca & Fisher, 1986
Syringodium filiforme	24 – 26	230 – 1350	-	Fonseca & Fisher, 1986

2.2 Sediment stabilising properties

In general, seagrasses contribute to coastal protection in multiple ways (also see figure 2.1). Firstly, the canopy (i.e., leaves) of the meadows attenuate waves and (tidal) currents before those reach the shore. The leaves sway back and forth and through friction between the leaves and the water, wave energy is reduced. Secondly, this attenuation also enhances sedimentation and reduces erosion and sediment resuspension. As the leaves bend over the sediment surface, the flow is deflected away from the seabed. Thirdly, the roots and rhizomes that extend outward horizontally further stabilise the sediment that was captured, protecting it from erosion. (James, et al., 2021; James, et al., 2020).
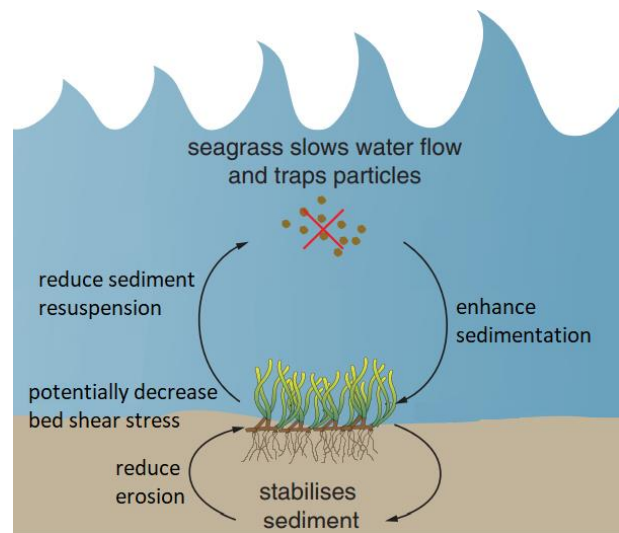

Figure 2.1: Schematic overview of sediment feedbacks in seagrass meadows, adapted from Maxwell et al. (2017).

Zooming in on the Caribbean, the literature found during this study on sediment stabilising properties in seagrass focused on *T. testudinum*, *S. filiforme* and *H. wrightii* (Fonseca & Fisher, 1986; Johnson, Gulick, Bolten, & Bjorndal, 2019; James, et al., 2019; James, et al., 2020; James, et al., 2021). Only one study included *H. stipulacea* (James, et al., 2020). A study that used flume experiments to compare canopy friction and sediment movement in three tropical seagrass species, found that *T. testudinum* reduced sediment erosion at the seabed to the greatest extent, whereas this was intermediate for *H. wrightii* and the lowest for *S. filiforme* (Fonseca & Fisher, 1986). They relate this to the shape and length of the leaves of each species. Where *T. testudinum* has long flexible strap-like leaves, *S. filiforme* has relatively inflexible and near-cylindrical leaves. These findings correspond to a different study on *T. testudinum* meadows at Saint Martin, which found that the strong and flexible leaves of this species bend low over the seabed and thus reduce drag forces at the bottom (James, et al., 2021). It should be noted that this result was found where unidirectional flow conditions occurred, and orbital forcing (swaying) may not show the same result although the difference in impact is probably limited (James, et al., 2021). Because of the property of the leaves, *T. testudinum* persisted after the category 5 hurricane Irma and very likely provided coastal protection services during the storm. This persistence

was likely also caused by the robust rhizomes and roots typically extending 10 to 40 cm into the sediment, which limited uprooting of the seagrass and kept the sediment surface relatively stable (James, et al., 2021; Fourqurean & Rutten, 2004). Fourqurean & Rutten (2004) found that after hurricane George in Florida Keys, *S. filiforme* was uprooted by 19%, whereas the stronger and deeper roots of *T. testudinum* caused this species to only lose 3% in cover (Fourqurean & Rutten, 2004). James et al. (2021) also notes that the wave attenuating effect of seagrass meadows is less in deeper waters, considering this effect depends on the relative height of the seagrass canopy to the depth of the water column.

These findings suggest that seagrass species having shorter leaves (e.g., *H. stipulacea; table 2.1*), as well as seagrasses in deeper water, may not contribute to coastal protection via wave attenuation. However, this does not imply that these species do not contribute to sediment stabilisation, as the rhizomes and roots play a key role in binding sediments (Short, Carruthers, Dennison, & Waycott, 2007). Because of this, seagrass species with low aboveground biomass may still provide important services in coastal protection (Ondiviela, et al., 2014). James et al. (2020) studied the sediment stabilisation ability of patch types of the native *T. testudinum* versus the non-native *H. stipulacea* in Lac Bay, Bonaire (< 6 m depth), by using field flumes to simulate flow regimes. They found that un-grazed patches of *T. testudinum* effectively stabilised the sediment, whereas this effect was reduced with shorter (grazed) canopies. Moreover, a study on the effects of grazing on erosion in a *T. testudinum* meadow in the Cayman Islands, found that the grazed meadows, having an average canopy height of 4 cm, did not directly result in increased sediment erosion (Johnson, Gulick, Bolten, & Bjorndal, 2019). These results correspond to another study that was performed in Indonesia, on whether low-biomass canopies of *Halodule uninervis* still reduced sediment erosion (Christianen, et al., 2013). They found no significant difference in the sediment stabilising ability between grazed and un-grazed meadows. Their results demonstrated that even very short-canopied meadows could still effectively stabilise the sediment, suggesting the belowground biomass (i.e., roots and rhizomes) of seagrass plays a key role in this coastal protection service (Christianen, et al., 2013). In addition, James et al. (2020) showed that within patches of *H. stipulacea*, finer grained sediment was accumulated. They speculate the reason might be because the denser meadows of this species are closer to the seabed (low canopy height), and thereby reduce bed shear stress in the canopy. The shear stress is a force acting on the seabed that initiates motion in sediment grains, as a result of velocity gradients in the above water column (Reidenbach & Thomas, 2018). A reduction in the bed shear stress leads to minimized sediment resuspension and an accumulation of finer grains. This corresponds to the finding that the sparse shoot density of *T. testudinum* has little influence on bed shear stress, and therefore the sediment grain size was not significantly different from that in bare sand patches. (James, et al., 2020).

These results from previous studies suggest that *H. stipulacea*, having short canopies, could still effectively stabilise the sediment compared to unvegetated areas. Where native seagrass meadows were previously lost, bare sand areas remained. Potentially, the introduction of *H. stipulacea* to these bare sand areas might result in sediment stabilisation. However, this remains under-investigated.

3. Methodology

This chapter describes the methodology used to investigate the role of *Halophila stipulacea* in sediment stabilisation. The first section elaborates on the study area, followed by the research set-up and lastly, the data analysis is explained.

3.1 Study area

This study was conducted at the dive site called Double Wreck (GPS 17.479867°, -62.994017°), located in Orange bay (figure 3.1). The site has an average depth of 18 m and is covered with a monospecific *Halophila stipulacea* meadow that contains multiple patches of bare sand, of which the shapes and sizes fluctuate over time. The meadow extends seaward to at least 50 m depth (A. Maitz, personal communication, March 21, 2022), as well as to shallower depths (avg. 6 m) toward the coast. A rough estimation of the meadow's edge along the coastline in front of the study site Double Wreck, was mapped out based on the personal observations (figure 3.1).
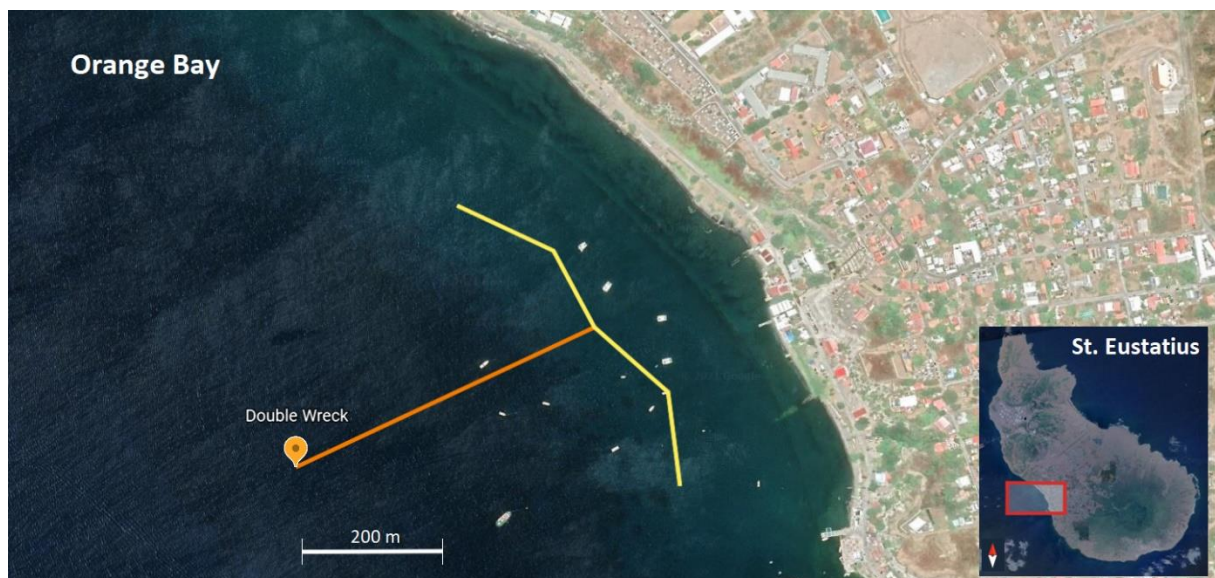

Figure 3.1: Map of Orange Bay, St. Eustatius, adapted from Google Earth (2021). Showing dive site 'Double Wreck'. The yellow line represents the rough estimate of the landward-edge of the seagrass meadow, based on personal observations.

3.2 Research set-up

To investigate to what extent *Halophila stipulacea* growth affects sediment stability at the coast of St. Eustatius, measurements were taken over a period of 15 weeks. Three types of measurements were taken, namely: growth properties of *H. stipulacea*, sediment trap dry weight, and sediment level, all of which are described in depth below.

Growth properties of *H. stipulacea*

In a time window of 49 days within the entire study period, growth properties of *H. stipulacea* were measured. On August 20th, 2021, a total of 200 zip-ties were attached to strands of *H. stipulacea* by SCUBA divers to set up the baseline from which subsequent growth of the seagrass was measured (i.e., marking technique). This was done as follows. A zip-tie was attached to the rhizome internode right behind the first fully grown apical and before the first shoot pair (figure 3.2). One of the leaves of the first shoot pair was cut in a 45 degrees angle as a marker of identifying the start of the measurements.

Figure 3.2: Photo of fragment of Halophila stipulacea. 1 = Apical; 2 = first shoot pair; 3 = rhizome internode. Red solid line indicates location of zip-tie. Red dotted line indicates diagonal cut at a leaf of the first shoot. Arrow marks direction of growth.

On a weekly basis, 15 fragments (a.k.a. strands) of the seagrass were collected by the same SCUBA divers. This was done by carefully uprooting the seagrass strand and cutting the internode between the zip-tie and the marked (cut) shoot pair, right before that shoot. The fragments were carefully placed in a transparent zip-lock bag and brought to the surface. The zip-lock bags, still containing seawater, were transported to the laboratory to measure the seagrass fragments manually on the same day. Last fragments were taken on October 8th (day 49).

For each fragment, the length and width of the apical leaves and shoot leaves were measured, as well as the length of the internodes (between shoots) and roots. This was all measured in order, starting at the apical. The biomass was separated into aboveground (leaves) and belowground (rhizome and roots) biomass and dried at 70°C for 24h, and subsequently weighed.

Sediment traps

The sediment traps used during this study were made from a PVC pipe with a diameter of 4 cm (opening area of 12.57 cm^2). The PVC pipe was cut into six pieces of 15 cm in length, which were subsequently sealed off at one side of the pipe. The traps were individually marked and then vertically attached to a rebar (see next section) just above the seabed using zip-ties, with the closed side facing down to allow the free-flowing sediment to be collected at the bottom in the trap. Three traps were placed within a seagrass meadow and three traps were placed in a sand patch.

After 7 weeks, SCUBA divers retrieved the content of the sediment traps by closing off the top before removing the trap from the rebars. The closed traps were then transported to the laboratory where they were stored in a cool place for a few hours until they were processed. The content was first sieved through a 710 µm steel sieve to remove any shells, biota, and other large material. The sediment was collected in a glass measuring cup and filled up with fresh water. After the content was settled to the bottom of the glass (24 hours was given to ensure all particles were settled), the water was syphoned out and the glass refilled with fresh water. This was done four times to make sure all excess salt was removed. Next, as much water as possible was removed from the glass without disturbing the sediment and the content was subsequently dried at 70°C until constant dry weight.

The traps were placed back onto the rebars for a second measurement at the end of the study period, which lasted another six weeks.

Sediment stability

Two locations in near vicinity to each other were chosen to set up the experiment, to eliminate differences in hydrodynamic conditions. The locations were: 1) inside the monospecific *H. stipulacea* meadow; and 2) in a patch of bare sand within the *H. stipulacea* meadow. At the start of the study, the size of the sand patch was approximately 18 m^2. In each location, three rebars were placed vertically in the seabed, with 30 cm above and 30 cm below the sediment (to ensure stability and eliminate swaying). The three rebars were placed with a distance of 2 m between them, shaping a triangle (figure 3.3). After placement of these 'triangles', three weeks time was given for the sediment to settle after some disturbance created during instalment of the rebars. Next, the marked sediment traps, as explained in the previous section, were placed on these rebars with zip-ties and therefore functioned as identification markers for the individual rebars.
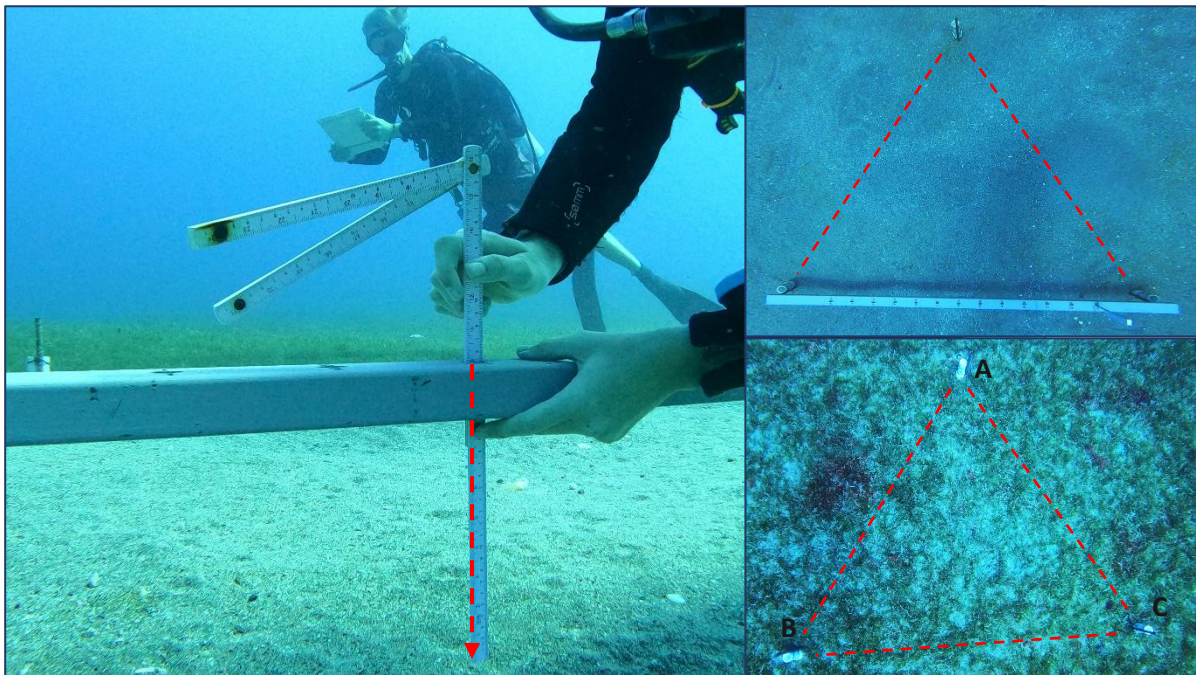

Figure 3.3: Triangle-shaped set up of rebars (right) and measurement using the folding ruler (left). See appendix II for more photos.

On a weekly basis, measurements were taken by SCUBA divers with the use of a large metal tube (rectangle) bar of 2.2 m in length (see appendix II for photos). This bar (hereafter referred to as 'Gizelle') contained a cut-in at the bottom part of both ends which allowed the divers to place it stably on top of two triangle-rebars at precise places each time. Gizelle contained 13 holes (individually marked slot 1 to 13) with an equal distance of 10 cm between each of them, leaving 30 cm between the ends of Gizelle and the first and 13th slot. The 30 cm was necessary to prevent any influence of the triangle-rebars on the measurements taken, as it was observed the sediment dipped right next to the rebars. The identification markers on the rebars allowed the divers to place Gizelle in the same direction and order every time. For example, the end of Gizelle with slot 1 was always placed at rebar A, with slot 13 being placed at rebar B (triangle-side 'A-B'). Next, triangle-side 'B-C' was measured by moving one end of Gizelle from rebar A to C, therefore leaving slot 13 closest to rebar B again. The last triangle-side (A-C) was measured after moving the end of Gizelle from B to A. This way, the same slot was always above the same place.

After placing Gizelle over a triangle-side, a folding ruler was placed in each individual slot to measure the distance from the top of Gizelle to the sediment surface (figure 3.3). These measurements were taken by the same SCUBA diver every week to maintain the same technique of placing the folding ruler every time. The second diver wrote down all measurements that were being recorded. During this

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process, the divers took care to not disturb the sediment. These measurements were obtained in the same manner in both the sand patch and the seagrass meadow.

Next, to determine the density (i.e., shoot count) of the *H. stipulacea* meadow at the seagrass-triangle, five density cuts were taken. A 25*25 cm quadrant was placed no more than 1 m away from a triangle-side, and a dive knife was used to cut the seagrass along the sides of the quadrant. The seagrass was carefully uprooted and put in a transparent zip-lock bag. These bags were transported to the laboratory, where measurements were taken on the same day. The content of a bag was first rinsed carefully with fresh water to remove any sediment and other non-seagrass material. Subsequently, all apical shoots, shoot pairs and scars per strand were counted, as well as the free-flowing green leaves. Next, the above- and belowground biomass was separated and dried at 70°C for 24h to retrieve dry weight.

Meteorological conditions
A HOBO Pendant Temperature/Light 64 k Logger (UA-00x) was used to measure a specific temperature (in °C) and light intensity (in lux) between August 20th and October 8th. The logger was mounted on a vertical rebar and placed in a monospecific *H. stipulacea* meadow 40 cm above the sediment. To give a general idea about the seawater temperature during the entire study period (August to December), seawater temperature at depth of the study site was read from the dive computers (Suunto Zoop Novo) during the dives.

Furthermore, data on wind and waves was retrieved from a marine weather buoy located at the dive site Hangover reef (GPS 17.464350°, -62.985617°), less than 2 km south of Double Wreck, from spotters.sofarocean.com (SPOT-1133). This buoy observed significant wave height, wave period, wave direction, wind speed and wind direction. The buoy also observed seawater temperatures, which were retrieved from aqualink.org (site 978).

2.3 Data analysis
For the analysis of the data, R software was used (R Core Team, 2020). Specific analyses per topic are described below.

Growth properties of *H. stipulacea*
The descriptive statistics for the weekly growth measurements were calculated, including mean shoot growth per day, mean number of shoots per strand, mean leaf, and rhizome internode length, mean above- and belowground (AG & BG respectively) dry weight biomass, and the increase rates for biomass.

From the density cuts, shoot count per square metre and average number of shoots per strand were calculated (including apical shoots and shoot pairs), as well as the above and belowground dry weight biomass per square metre.

Sediment traps
For each habitat, six data points of dry weight content (DW; in mg per sediment trap) were retrieved, three per collection period. The sediment deposition rate in gram DW per square metre per day could

be calculated subsequently. It should be noted that this also included sediment deposition after resuspension. To test a potential difference between the two collection periods, a paired t-test was used. Furthermore, to test a potential difference between the sand and seagrass habitat, a Welch two sample t-test was used, as the data was normally distributed (Shapiro-Wilk normality test; $p = 0.76$ and $p = 0.31$, respectively) but did not have equal variances (F test; $p < 0.05$).

Sediment stability

The data collected consisted of three samples per location (each triangle side is a sample). Per sample, the sediment level was measured in 13 slots. The weekly difference of the measurements relative to the previous week was calculated for each observation (week 1 – week 0, week 2 – week 1, etc.). These values were also denoted as positive numbers, where no distinction was made between erosion and accumulation. Week 0 refers to the first measurement and therefore represents a baseline of the seabed. No data was collected in week 4, therefore the difference in week 5 is relative to week 3. The difference in sediment level for each week relative to week 0 was also calculated.

Next, all observations were grouped per habitat (seagrass vs. sand) to confirm if there was a statistical difference. The Wilcoxon Rank-Sum test was used, as the data was not normally distributed (Shapiro-Wilk normality test; $p < 2.2^{-16}$).

Then, observations were grouped per week and per habitat. For each week, these were again tested for a statistical difference (Wilcoxon Rank-Sum test).

Finally, all observations of week 8 to week 14 were grouped per habitat, and the statistical difference between the habitats was tested using the Wilcoxon Rank-Sum test.

Using descriptive statistics, correlations were investigated between the sediment data and weather data (next section). In this process, plots were also made where deposition and erosion were separated.

Meteorological conditions

The descriptive statistics (mean + se) for the meteorological data were calculated and wind direction and speed were plotted in a frequency distribution. The significant wave height and wind speed were also plotted over time to investigate potential patterns that corresponded with the sediment data.

In investigating the correlation between weather and sediment change, week numbers were assigned to match the week numbers of the sediment measurements (table 3.1). This was done in such a way that the sediment measurements were taken at the end of each assigned week.

Table 3.1: Assigned week numbers

Date	Week
28 Aug – 3 Sept	0
4 Sept – 10 Sept	1
11 Sept – 17 Sept	2
18 Sept – 24 Sept	3
25 Sept – 1 Oct	4
2 Oct – 8 Oct	5
9 Oct – 15 Oct	6
16 Oct – 22 Oct	7
23 Oct – 29 Oct	8
30 Oct – 5 Nov	9
6 Nov – 12 Nov	10
13 Nov – 19 Nov	11
20 Nov – 26 Nov	12
27 Nov – 3 Dec	13
4 Dec – 10 Dec	14

4. Results

This chapter presents the results, which are further interpreted in the discussion. First, growth properties of *Halophila stipulacea* as measured during this study are presented. This is followed by a presentation of the results of the sediment trap measurements (section 4.2) and subsequently of the sediment measurements in the triangles (section 4.3). Lastly, the meteorological conditions during the study period are described.

4.1 Growth properties of *Halophila stipulacea*

Within 7 weeks of this study, mean shoot growth was 0.3 shoots day^{-1} (n=7, se=0.01). A new shoot was found to grow in 3.3 days and an average of 8.2 shoots strand^{-1} was found (n=105, se=0.57). The average leaf length during the period was 40.31 mm (n=1428, se=0.16), the mean rhizome internode length was found to be 10.45 mm (n=1066, se=0.16), and the mean root length was 42.73 mm (n=763, se=1.1).

The measured aboveground biomass dry weight (AG DW) showed a mean biomass per strand of 146.48 mg (n=7, se=30.45) and a belowground biomass dry weight (BG DW) of 110.41 mg (n=7, se=25.44). This translated back to a daily increase in biomass of 5.34 mg AG DW strand^{-1} day^{-1} (n=7, se=0.32) and 3.8 mg BG DW strand^{-1} day^{-1} (n=7, se=0.22).

From the separate shoot density measurements at the triangle, a shoot count of 9657.6 shoots m^{-2} (n=5, se=649.15) was found, with an average of 7.6 shoots strand^{-1} (n=464, se=0.15). Next to this, the above- and belowground biomass dry weights were 127.49 g m^{-2} (n=5, se=9.32) and 175.1 g m^{-2} (n=5, se=12.08), respectively.

4.2 Sediment deposition rate

A statistically significant difference (figure 4.1) was found for the dry weight content of the sediment traps between the sand and the seagrass habitat (Welch two sample t-test; $p < 0.01$). The average deposition rate over the entire period for the seagrass habitat was 4.49 g DW m^{-2} day^{-1} (n=6, se=1.18) and this was 100.09 g DW m^{-2} day^{-1} (n=6, se=13.80) for the sand habitat.

The dry weight content of the sediment traps did not significantly differ between the two collection periods (paired t-test; $p = 0.37$).
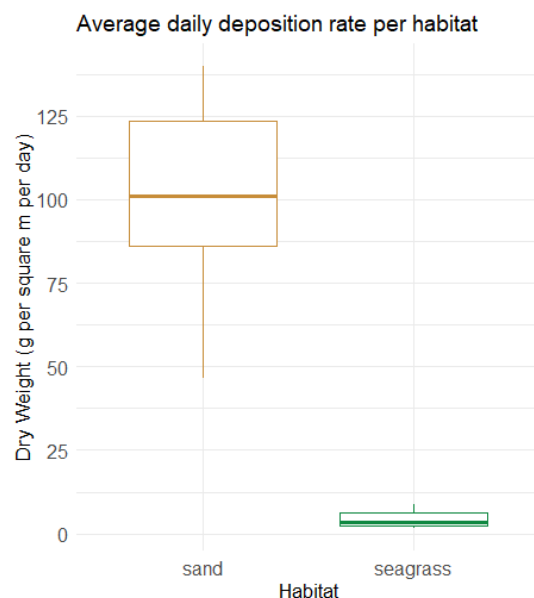

Figure 4.1: Box plot of the difference between sand and seagrass habitat in mean deposition rate (gram dry weight per square metre per day).

4.3 Sediment stability

The difference (or change) in sediment level relative to the previous week (figure 4.2), showed a weekly change averaged over the entire study period of 9.11 mm (n=507, se=0.46) for the sand habitat, and 8.25 mm (n=507, se=0.32) for the seagrass habitat. Over all the observations combined, no significant difference in the change in sediment was found between the sand and seagrass habitat (Wilcoxon Rank-Sum; p = 0.73). Testing the statistical difference between sand and seagrass habitat per week gives varying results. A significant difference was only found for weeks 2, 6, 7, 8, 12 and 13 (Wilcoxon Rank-Sum; p < 0.05).
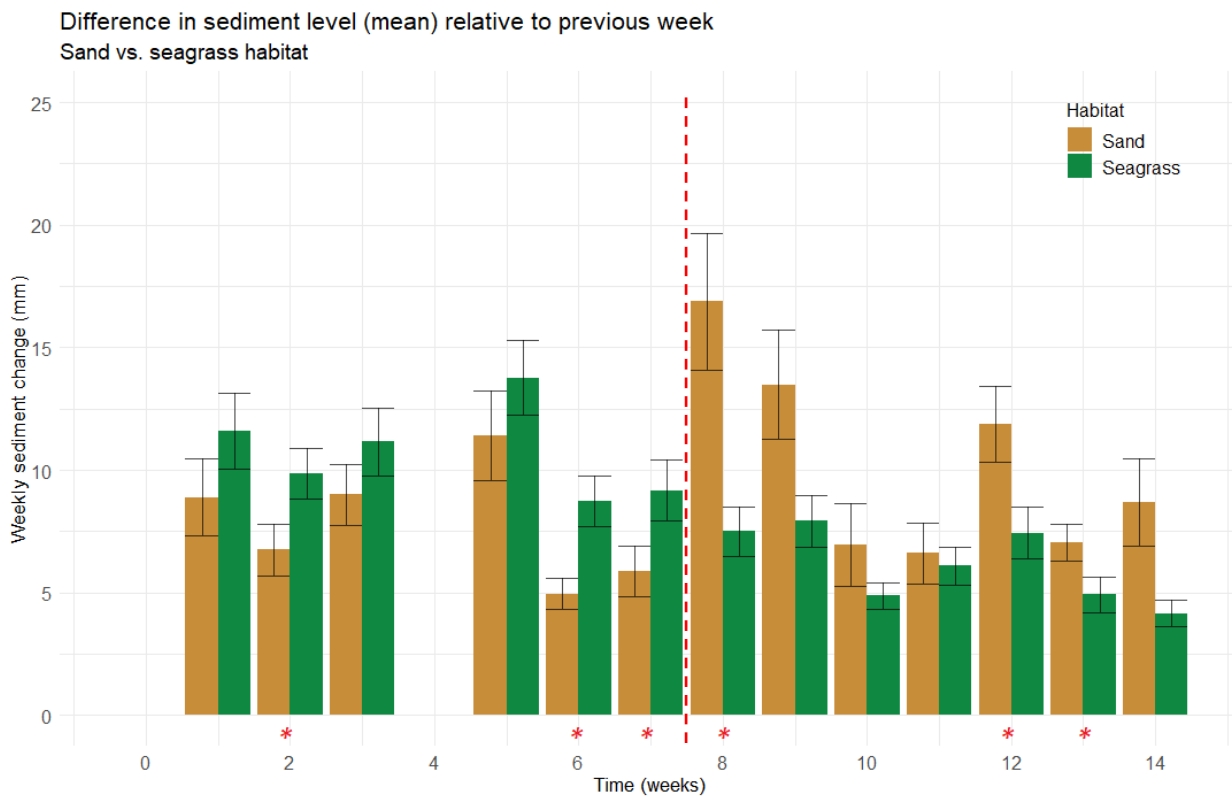

*Figure 4.2: Bar plot of weekly mean (n=13*3) difference in measured sediment level relative to previous week of data collection. Error bars indicate standard error. Note that no data was collected in week 4, thus the differences in week 5 are relative to week 3. Asterisks indicate significant difference between habitats for those weeks. Red dashed line emphasizes the sudden disturbance in the pattern.*

From figure 4.2, it seems that in the first couple of weeks (1 to 7), both habitats follow the same pattern in sediment change. After week 7, there seems to be a sudden disturbance in this pattern as the sand habitat shows a much higher change compared to the seagrass habitat. From this week onward, it appears the seagrass habitat has a more stable seabed than the sand habitat. Testing the statistical difference between the sand and seagrass habitat for weeks 8 to 14, indeed shows the sediment change was significantly greater in the sand habitat compared to the seagrass habitat (Wilcoxon Rank-Sum; p < 0.01).

Separating sediment accumulation and erosion over the sediment profile for each week (appendix I, figure A), shows that from week 5 and onward, the changes in seabed level in the seagrass habitat remained relatively constant, whereas the sand habitat experienced much more spatial variance in accumulation versus erosion. At the end of the entire study period, compared to the start, the seabed level in the seagrass habitat had decreased, whereas the sand habitat showed spatially both increases and decreases in sediment (appendix I, figure B). In plotting the difference in sediment level for each week relative to week 0, a clear pattern of erosion over time for the seagrass habitat is seen (appendix I, figure C).

4.4 Meteorological conditions

The water temperature at depth (18 m) at the study site (Double Wreck) changed from 29°C in August to 28°C in December. The HOBO logger measured a mean temperature of 29.51°C (n=2400, se=0.01) between August 20th and October 8th, 2021, and a mean light intensity (excluding night-time) of 2805.64 Lux (n=1212, se=80.74). These months are considered the warm season, with highest sea water temperatures (up to 30°C), which generally decreases to 26°C in January to March, as observed by the marine weather buoy.

The wind direction was most frequently from a south-eastern direction, with wind speeds (weekly mean) ranging from 2.01 to 4.87 m s^{-1}, and an average wind speed of 3.36 m s^{-1} (n=3644, se=0.00) over the entire study period (figure 4.3).

On average, waves came from a similar direction as the wind, namely a southern direction (mean=175.38 degrees; n=3644, se=0.69), which ranged from south-western to south-eastern.

The average significant wave height was 0.57 m (n=3644, se=0.00), but this showed variances over time (figure 4.4). The weather started to pick up after October 2nd (week 5), which resulted in higher significant wave heights as well as higher wind speeds on average.
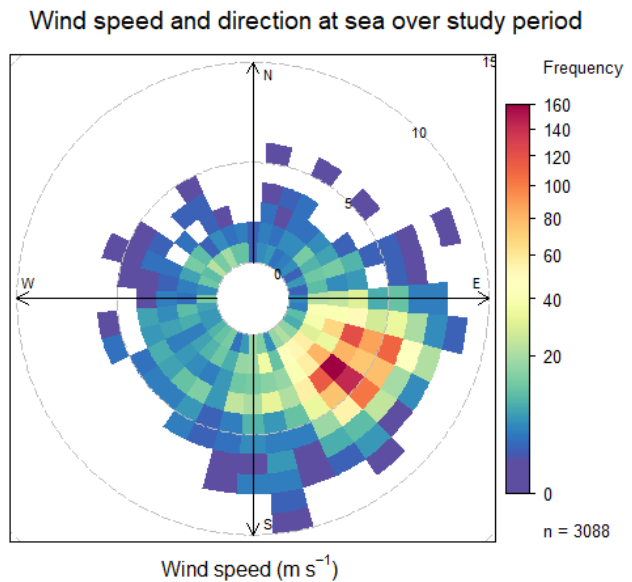

Figure 4.3: Frequency distribution (polarFreq) of wind data (n=3088) during the entire study period (August 28th to December 10th, 2021).
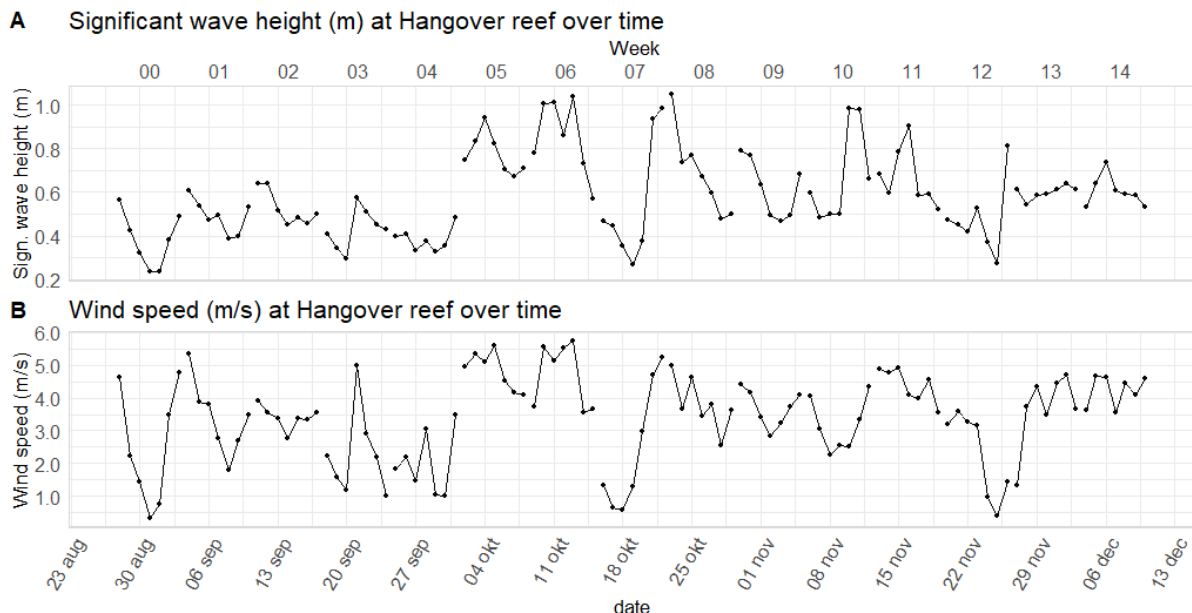

Figure 4.4: Daily means of the significant wave height (A) and the wind speed (B) over time. Lower x-axis = date. Intervals in the lines indicate weeks of the study period (upper x-axis).

5. Discussion

This study aimed to investigate whether the relatively recently expanding seagrass species *Halophila stipulacea* stabilised the sediment at the coast of St. Eustatius. No existing literature was found specifically for this species at St. Eustatius. For the wider Caribbean, sediment stability in *H. stipulacea* was only studied in Bonaire (James, et al., 2020). Measuring the sediment change as an indicator of stability in this study, was a means of determining the sediment stabilising properties of *H. stipulacea* at a depth of 18 m. This chapter first summarizes and discusses the results with reference to literature. This is followed by a section on the potential ecosystem change as a result of the expansion of *H. stipulacea*. Next, the limitations of the study are addressed, followed by a description of the relevance of this study to practice.

5.1 Interpretation of the results

Growth properties

Results showed that for *H. stipulacea* a new shoot was produced in 3.3 days, with a mean of about eight shoots per strand. While the latter corresponds to the findings for the Red Sea, the time it took for a new shoot to be produced was longer in the Red Sea, where it was measured to take 7 to 8 days (Wahbeh, 1984; Azcárate-García, Beca-Carretero, Villamayer, Stengel, & Winters, 2020). The leaf length (~4 cm) does correspond to the native range of *H. stipulacea*, as well as the rhizome internode length of about 1 cm. Interestingly, the shoot count per square metre was over 20 times higher in this study compared to the Red Sea. This means that *H. stipulacea* must be growing more crowded at the study site, which also results in denser meadows at St. Eustatius. This is likely a result of the fast growth of *H. stipulacea* at St. Eustatius. The fast growth also caused the sand patch to decrease in size by ~13% towards the end of the study, as the seagrass grew in it. Azcárate-García et al. (2020) speculates that growth conditions are probably more favourable in the Caribbean Sea as compared to the native conditions of *H. stipulacea*, which likely contributes to the rapid expansion of this species in the Caribbean. It is therefore probable that growth conditions for *H. stipulacea* are also more favourable at St. Eustatius than its native range.

Moreover, the shoot density of *H. stipulacea* was also higher in this study compared to shoot densities measured for Caribbean native species. Compared to *H. stipulacea*, the average shoot densities were 10 times, 12 times and 4 times lower for *T. testudinum*, *S. filiforme* and *H. wrightii*, respectively (table 2.1). Although the *H. stipulacea* meadow is very dense, the species has shorter leaves; 4 cm for *H. stipulacea* compared to ~18 cm for *T. testudinum*, ~25 cm for *S. filiforme* and ~17 cm for *H. wrightii*.

Sediment stability

Results showed that during this study, the sediment deposition rate was much lower for the seagrass habitat (*H. stipulacea* meadow) than for the sand habitat. This suggests a higher amount of sediment was available for resuspension in the bare sand patch compared to the *H. stipulacea* meadow. Furthermore, results showed that while fluctuations in seabed level were generally higher in the first period of data collection, this pattern changed in the second half. From week 8 to 14 of the study period, the sediment change was significantly higher in the sand habitat than in the *H. stipulacea* meadow, where the changes were more homogeneous. Next to this, comparing the sediment change (accumulation vs erosion) each week with the start of the study (week 0), showed a pattern of erosion in the seagrass habitat (appendix I, figure C), and the final sediment change in week 14 relative to week 0 was therefore negative (mean= −18.92, se= 1.63; appendix I, figure B). In contrast, the sand habitat

had fluctuated more temporally and spatially (accumulation as well as erosion), leading to a higher variance that is not reflected in the mean (mean= –2.36, se= 4.01; appendix I, figure B and C). The final decrease in seabed level in the *H. stipulacea* meadow corresponds to the low deposition rate in this habitat. Although in the seagrass habitat, it differed weekly whether sediment had accumulated or eroded relative to the previous week, erosion exceeded accumulation over the long term. This is an interesting result considering the literature generally discusses erosion is often reduced in other seagrass meadows (Fonseca, 1989; Potouroglou, et al., 2017; Ondiviela, et al., 2014; Koch, 1999).

In interpreting the results, first, the most apparent pattern that was recognized in the weekly sediment change was the temporal correlation with the weather (i.e., wave height and wind speed). Hydrodynamic conditions are a function of weather conditions, and although the influence decreases with depth, the weather could still play a role in sediment dynamics at the study site of 18 m deep (Brown, et al., 2001). The most obvious finding in this study was the peak in sediment change for the sand habitat after week 7, which seemed to correspond to rough weather conditions in the days prior to the observed peak. However, more interesting is the result of week 5. At that time, the weather had just picked up after the calm summer conditions that occurred in the previous months. A sudden increase in wave height can be seen and this most likely resulted in the peak in sediment change for the seagrass habitat, as well as the higher change in the sand patch. From that week onward, the seagrass habitat seemed to experience relatively constant sediment changes, whereas the sand habitat showed larger changes for the rest of the study period, indicating the sand habitat was highly unstable.

A possible explanation for the result in week 5 has to do with the surface sediment layer versus the subsurface layer. The less stabilised surface layer (upper 1 or 2 cm) generally experiences most influence from hydrodynamics, bioturbation, and microbial activity (Luna, Corinaldesi, Rastelli, & Danovaro, 2013). This can all play a role in sediment resuspension of this surface layer, whereas the subsurface layer is probably more stabilised. In this study, it seems reasonable that with the sudden increase in water movements, after months of calmer conditions, this surface layer was resuspended and carried away. The measured sediment change for that week in the seagrass habitat was in fact negative (mean = -13.36 mm; se = 1.61), meaning the sediment surface had mostly eroded (see appendix I, figure A, subplot T05). The subsurface layer was likely more stabilised by the root and rhizome system of the seagrass meadow. On average, the roots extended to 4 cm depth into the sediment, further that the assumed surface sediment layer, and the separate rhizomes formed layers in and over the sediment. Consequently, a higher bed shear stress would have been needed to resuspend this more compact subsurface sediment compared to the surface sediment that was carried away (Ward, Kemp, & Walter, 1984; Christianen, et al., 2013; James, et al., 2020). This is seen in the smaller weekly sediment changes after week 5 in the *H. stipulacea* meadow, which appears to remain relatively constant from that week onward. The sand habitat, on the other hand, experiences larger variations in seabed level earlier as compared to the seagrass habitat. There, it also seems to vary more spatially between sediment accumulation and erosion. This difference suggests *H. stipulacea* stabilises the subsurface sediment within the meadow.

Moreover, the erosion of the surface layer in week 5 corresponds to the finding in week 14, that showed the sediment level was lower compared to the start of the study. This erosion was, however, not observed for the sand habitat, something that is likely explained by the much lower sediment deposition rate in the *H. stipulacea* meadow as compared to the sand patch. The unvegetated patch seems to be influenced more by the weather and therefore experiences both erosion and accumulation, as well as more variation over time. This statement can further be supported by the larger objects, such as a brick and a conch shell (appendix II), that were observed at the sand habitat. In photos taken over the length of the study period, these objects became more uncovered with sand

over time. The brick, for example, was observed most uncovered on November 5th, right after the peak in sediment change for the sand habitat in week 9. This also corresponds to a peak in weather conditions, therefore suggesting the rougher weather conditions halfway into the study period did influence resuspension/ erosion of the sediment in the sand habitat.

In discussing the larger variations in sediment level for the sand habitat, it is important to consider the potential influence of the biota as well. In taking the measurements, it was obvious that the southern stingray (*Hypanus americanus*) influenced the level of the surface layer in the unvegetated areas (sand patches). Clear indents in the sand by the stingrays were observed, as well as seeing them laying inside the study area, between the triangle-rebars (appendix II). The movement of these animals (and other biota) could potentially have resulted in more resuspension of the sediment and a larger variance in sediment change in the sand habitat. These sting ray indents were not observed in the *H. stipulacea* meadow, which is probably due to the assumption that the sting rays cannot dig into the sediment within the dense structure of the seagrass meadow in the same manner as they do in a bare sand area. It is possible that the presence of *H. stipulacea* further stabilised the sediment indirectly by preventing bioturbation. It should be noted here that if grazing by megaherbivores occurs, this could still evoke erosion within the meadow (Christianen, et al., 2019; Christianen, et al., 2014; James, et al., 2020).

While the above discusses why the sand patch experienced larger variations in seabed level halfway into the study, *H. stipulacea* still experienced small variations as well. As described in chapter 2, the growth properties of seagrass species play a key role in their ability to reduce erosion and stabilise the sediment. With the aboveground canopy, tall-growing seagrass species can influence the hydrodynamic forces that play a role in sediment dynamics (Hansen & Reidenbach, 2012). However, this is also a function of depth (James, et al., 2021). Studies state that other seagrasses (e.g., *S. filiforme*, *T. testudinum*, *H. wrightii*, and *Z. marina*) are most effective in reducing flow (i.e., wave attenuation) at shallower depths, especially where the canopy occupies the entire or most of the water column, which generally results in the accumulation of sediment (Fonseca & Cahalan, 1992; Koch, 1999). At deeper depths however, such as the 18 m of this study site, sediment tends to accumulate as well as resuspend because wave attenuation is less efficient (Koch, 1999). For *H. stipulacea*, the leaves are noticeably short (mean of 4 cm in this study) as compared to several native Caribbean seagrass species (e.g., ~18 cm for *Thalassia testudinum*). These short leaves are less effective in attenuating waves. Notwithstanding, *H. stipulacea* does have a higher density (~9700 shoots m^{-2} in this study; vs. ~940 shoots m^{-2} for *T. testudinum*; Fonseca & Fisher, 1986). This translates into dense vertical rhizome systems which tend to reduce bottom shear stress within the meadow, thereby limiting resuspension, which increases sediment stability (James, et al., 2020; Gacia & Duarte, 2001). On top of that, James et al. (2020) found that finer-grained sediments were accumulated in a *H. stipulacea* meadow, compared to unvegetated areas. They state that resuspension must be lower in the *H. stipulacea* meadow, or these smaller grains would not have been able to settle to the seabed during normal physical conditions. Considering, firstly, that the dense rhizome system likely limits resuspension in the *H. stipulacea* meadow, and secondly, finer-grained particles are potentially accumulated, it would make sense that a lower sediment trap content (and thus sediment deposition rate) was found for the *H. stipulacea* meadow than for the sand patch.

5.2 Ecosystem change
It is obvious the rapid expansion of *Halophila stipulacea* has changed the pre-existing ecosystem. Where previous bare sand conditions occurred at the study site, there is now an extensive monospecific *H. stipulacea* meadow. The results of this study have shown that *H. stipulacea* contributes to sediment stabilisation and sediment deposition/ resuspension is limited within the

meadow. The seabed experiences net erosion throughout the study period, yet the seagrass habitat was demonstrated to be more stable both spatially and temporally. Potentially, this new habitat resulted in further ecosystem changes in the physical environment as well as in the biological community. At the study site, changes might occur not only within the seagrass meadow and its inhabiting biota, but possibly the neighbouring coral reefs as well.

For example, Posey (1988) examined the changes in benthic community as a result of the introduction of the seagrass *Zostera japonica* to a previously unvegetated area. The *Z. japonica* meadow stabilised the sediment which was favourable to near-surface organisms, sedentary polychaetes and bivalves, and an increase in species richness was observed relative to the unvegetated area. However, the study also found a decrease in the abundance of burrowing animals. Potentially, this shift in benthic community could further influence the stability of the seabed. Posey further suggests these changes in the benthic community indicate similar changes could be found in other seagrasses (Posey, 1988). For *H. stipulacea*, the shoot density contributes to sustaining diverse invertebrate and fish populations, and *H. stipulacea* seems a favourable habitat for large sessile filter feeders, such as sponges and bivalves (Viana, Zoysa, Willette, & Gillis, 2019). According to Willette & Ambrose (2012), the expansion of *H. stipulacea* to previously unvegetated areas may lead to an abundance in epibiota, which in turn would attract predatory fish species and therefore lead to higher trophic level changes (Willette & Ambrose, 2012). Their study, which compared associated fish and epibiota communities in *H. stipulacea* versus *S. filiforme*, found a higher abundance of epibiota, especially crustacea and amphipods, in the *H. stipulacea* meadows. A different study suggests trophic level changes following the introduction of *H. stipulacea* are very likely (Heck Jr., et al., 2008). For example, seagrass meadows provide a nursery habitat for juvenile reef fishes and invertebrates. With the introduction of *H. stipulacea* to unvegetated areas bordering coral reefs, a new nursery or foraging area for coral reef fish is created. This might lead to an increase in the abundance of seagrass and non-seagrass associated fish (Viana, Zoysa, Willette, & Gillis, 2019). The growth of seagrass near coral reefs might also increase the number of algivorous fish (e.g., parrotfish, surgeonfish and butterflyfish), which is beneficial to the neighbouring coral reefs as these fish graze on light-competing algae (Gillis, et al., 2014). Additionally, a multitude of reef fish, both herbivory (e.g., parrotfish) and predatory (e.g., grunts, squirrelfish, and moray eels), forage daily on seagrasses, small invertebrates and fish in adjacent seagrass meadows (Heck Jr., et al., 2008). This trophic energy linkage between the coral reef and seagrass meadow contributes to high fish biomass on the reef (Heck Jr., et al., 2008). Furthermore, the limited resuspension of sediment within the *H. stipulacea* meadows, can also be beneficial to coral reefs as it leads to clear water in which light penetration is increased, leading to increased coral reef productivity (Gillis, et al., 2014; Viana, Zoysa, Willette, & Gillis, 2019). On top of that, the high uptake rates of nutrients in *H. stipulacea* also contributes to improved water quality for coral reefs (Viana, Zoysa, Willette, & Gillis, 2019).

5.3 Limitations of the study
Where more recommendations for future studies are given in chapter 7, it is important to address here a few limitations of the study. The design of this study and method of data collection could have resulted in some unwanted changes in sediment dynamics that could have masked / increased the effect sizes found. Firstly, due to practical constraints, measurements could only be taken in a single location of both habitat types. Increasing the sample size could show whether the observed effects are site-specific or apply to all different habitats. Secondly, it was not possible to include a set-up at a shallower depth than 18 m. Sampling along a depth gradient would be interesting to see if the sediment stabilising effect of *H. stipulacea* shows different results at different depth levels. Thirdly, the

sediment traps were only emptied twice, halfway and at the end of the study. A more continuous sampling design would have allowed to analyse more temporal trends in sediment fluctuations and a more accurate relation to observed changes in wind speed and wave height. In addition, the weather data used in the analysis was retrieved from a buoy located approximately 2 km away, in the same latitude of the study site. The location of the weather buoy might have been more sheltered by the island volcano compared to the study site Double Wreck. Although significant wave height and wind speed still seemed to correlate with sediment changes in the sand habitat, it cannot be excluded conditions might have been slightly different at the study site.

Furthermore, according to Koch (1999), other seagrass meadows (e.g., *Thalassia testudinum*) generally remain relatively constant in sediment level over time, under non-extreme conditions, indicating there must be some sort of equilibrium over time between erosion and deposition. Interestingly, the results in this study showed erosion exceeded deposition of sediment in the end. Even if deposition and erosion would equal each other out in the long term in *H. stipulacea* meadows as well, this is not observed over the time span of this study. For this reason, it would be interesting to conduct this study over a longer term, especially considering all seasons. Lastly, it is good to point out that during this study, the influence by biota could not be excluded. However, the aim in this study was focused on the contribution of *Halophila stipulacea* to sediment stability at St. Eustatius, which thus includes the influence of the biota that inhabits the area.

5.4 Relevance to practice

This study aimed to investigate the sediment stabilising properties of *Halophila stipulacea* at 18 m depth at St. Eustatius. The results of this study increase current knowledge on the spread of this non-native species throughout the Caribbean and increase the understanding of the potential coastal protection services provided by this rapidly expanding species. As mentioned in the introduction, there remains a need to study sediment dynamics in seagrass meadows under different circumstances, meaning investigating varying species and under varying environmental variables. This study was the first to focus on sediment dynamics in *H. stipulacea* at the coast of St. Eustatius. The information can be used by managers and organisations aiming to use seagrass meadows in their coastal protection plans and can be important for those trying to restore ecosystem services that had been lost with the disappearance of native seagrasses in the Caribbean.

6. Conclusions

This chapter provides an answer to the question: "To what extent can *Halophila stipulacea* provide coastal protection services (i.e., sediment stabilisation) at the coast of St. Eustatius, Dutch Caribbean?". Where the first sub-question, being "What is currently known about the sediment stabilising properties of the non-native and native seagrass species (specifically, *Syringodium filiforme* and *Thalassia testudinum*) in the Wider Caribbean?", is answered in chapter 2, a conclusion is given for the second sub-question in this chapter.

To what extent is sediment stability at the coast of St. Eustatius influenced by growth rate and biometrics (i.e., internode length, leaf length, and width) of *Halophila stipulacea*?

The non-native *H. stipulacea* appears to be stabilising the sediment layer below the surface via its root and rhizome system. This became apparent when the surface layer was resuspended and carried away during increased weather conditions. The sediment surface remained lower for the rest of the study period, which likely also relates to the low sediment deposition rate. This in turn is believed to be the result of limited resuspension in the *H. stipulacea* meadow as well as potentially smaller grain-sizes of that sediment. Notwithstanding, smaller changes in sediment still remained, potentially the result of less optimal growth properties compared to, for example, taller growing seagrass species with deeper root systems.

To conclude, the extent to which *H. stipulacea* can provide coastal protection services (i.e., sediment stabilisation) at the coast of St. Eustatius, seems limited at a depth of 18 m. Although a stabilising function became apparent in the subsurface layer, the final result was erosion and should be taken into account when considering *H. stipulacea* for coastal protection purposes. The subsequent change in benthic community as a result of the introduction of *H. stipulacea*, compared to the previously bare sand ecosystem, and its potential influence on sediment stability should also be considered.

7. Recommendations

Based on the findings in this study, recommendations for future research are given in this chapter.

Turnover and uprooting

During this study, a small variation in sediment change was still observed in the seagrass habitat. Although the causes for this variation remain uncertain, it would be interesting for future research to focus on the turnover of *H. stipulacea* leaves and strands. According to Potouroglou et al. (2017), the accumulation and resuspension of sediments within other seagrass meadows also depends on the development stage and the health of the seagrass strands. This raises the question as to whether the dying of individual *H. stipulacea* strands and subsequent decomposition or uprooting, would release the sediments that had previously been captured and bound by those strands. More importantly, whether this would be a significant factor in the sediment dynamics within *H. stipulacea* meadows.

Next to this, the literature states *H. stipulacea* is more susceptible to uprooting during severe storms and hurricanes compared to the native Caribbean seagrass species (James, et al., 2020). Individual *H. stipulacea* strands are able to survive for a few days in the water column before settling again, which is thought to have contributed to its rapid expansion through the Caribbean (Willette, et al., 2020; Smulders, Vonk, Engel, & Christianen, 2017; James, et al., 2020). When areas of *H. stipulacea* are uprooted after a storm, this leaves a bare seabed that is more vulnerable to erosion, at least for some period of time (James, et al., 2020). It might be interesting to study how such storm events and uprooting affect the seabed and its local ecosystem, perhaps considering the succession after these events.

Benthic community changes

Multiple studies have found benthic community changes after the introduction of seagrasses to areas that were previously unvegetated (Viana, Zoysa, Willette, & Gillis, 2019; Willette & Ambrose, 2012; Gillis, et al., 2014). It would therefore be interesting to investigate these changes for *H. stipulacea* meadows at St. Eustatius, neighbouring coral reefs as well as further away, including whether benthic fauna contributes further to sediment stabilisation versus resuspension.

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Appendices

Appendix I: Additional figures of results

Sedimentation versus erosion for each week (T01-T14) relative to previous week
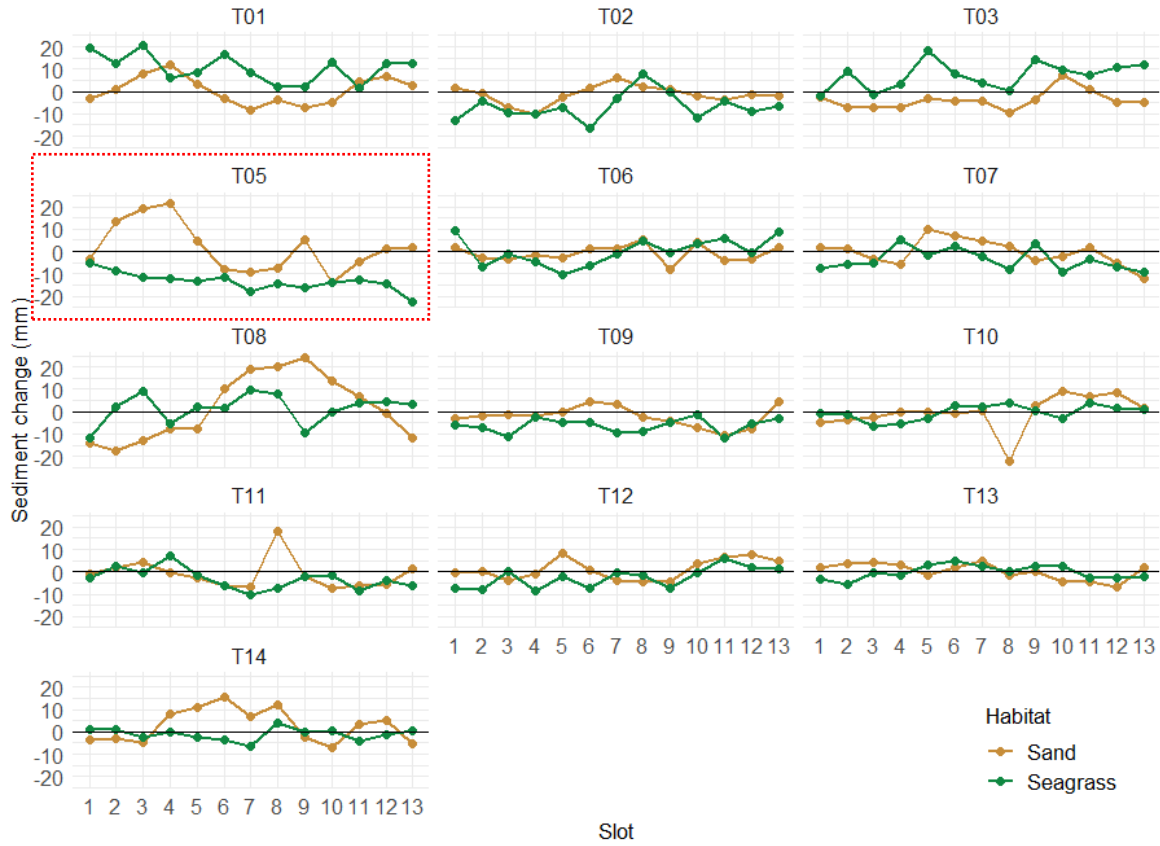mean sediment change over the sediment profile (slots 1-13)

Figure A: Mean sediment accumulation (positive) and erosion (negative) over the sediment profiles (slot 1-13) for each week (T01 to T14), relative to previous week. Emphasize is placed on week 5 (red dotted rectangle).

Sediment change after 14 weeks
accumulation vs. erosion per habitat

Figure B: Mean sediment accumulation (positive) and erosion (negative) over the sediment profile (slots) after 14 weeks relative to week 0. Error bars indicate standard error. Dashed line represents mean over the sediment profile.

Figure C: Sediment accumulation (positive) versus erosion (negative) for each week relative to week 0. Error bars indicate standard error.

Appendix II: Photos of set-up and observations

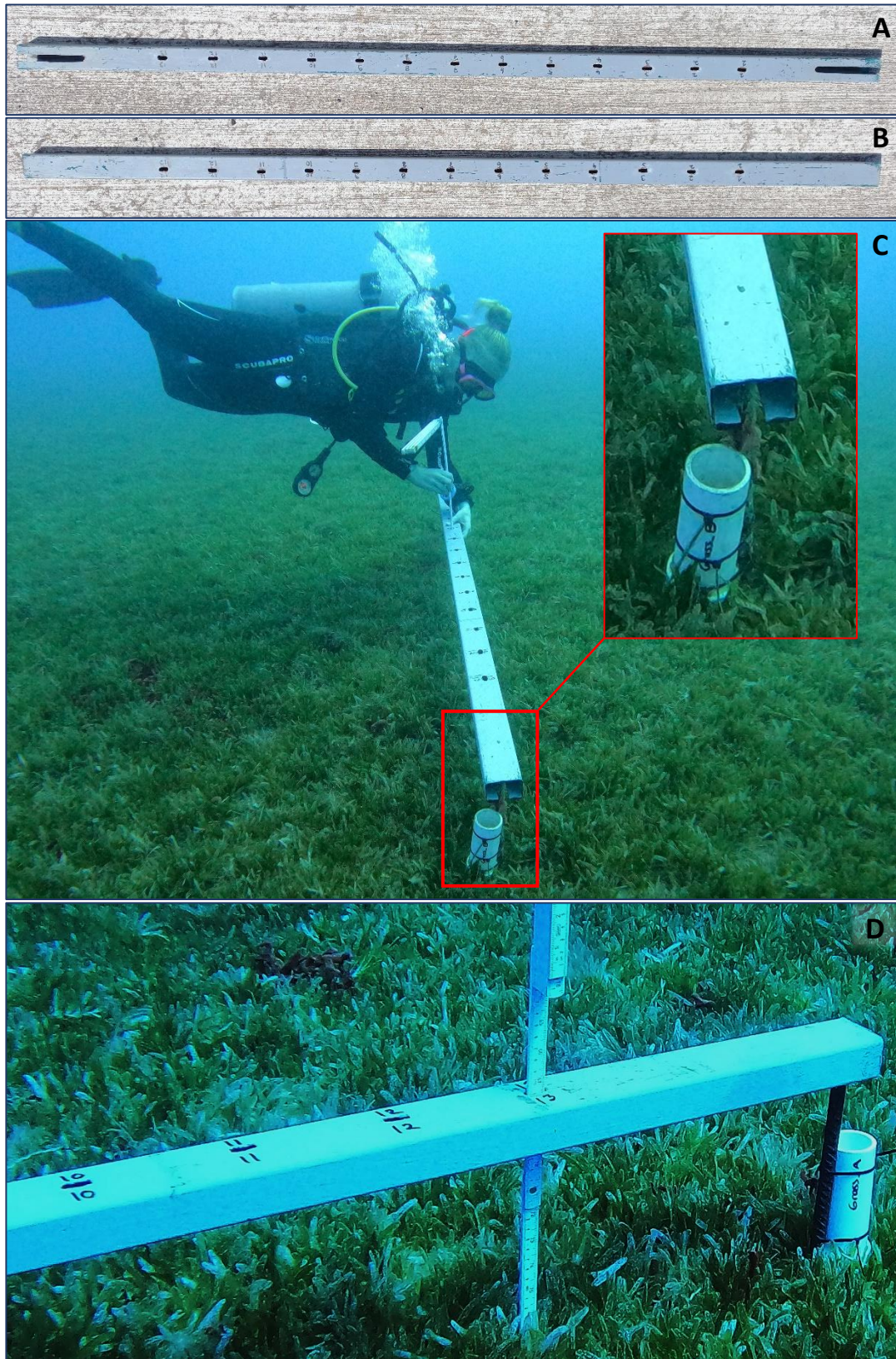**Measuring bar Gizelle and placement in the field**

Figure D: Photos of Gizelle and its placement on the set-up. A = Bottom of Gizelle; B = Top of Gizelle; C = Fit of Gizelle onto rebar via the cut-in on the bottom; D = Folding ruler through numbered hole (slot) in Gizelle.
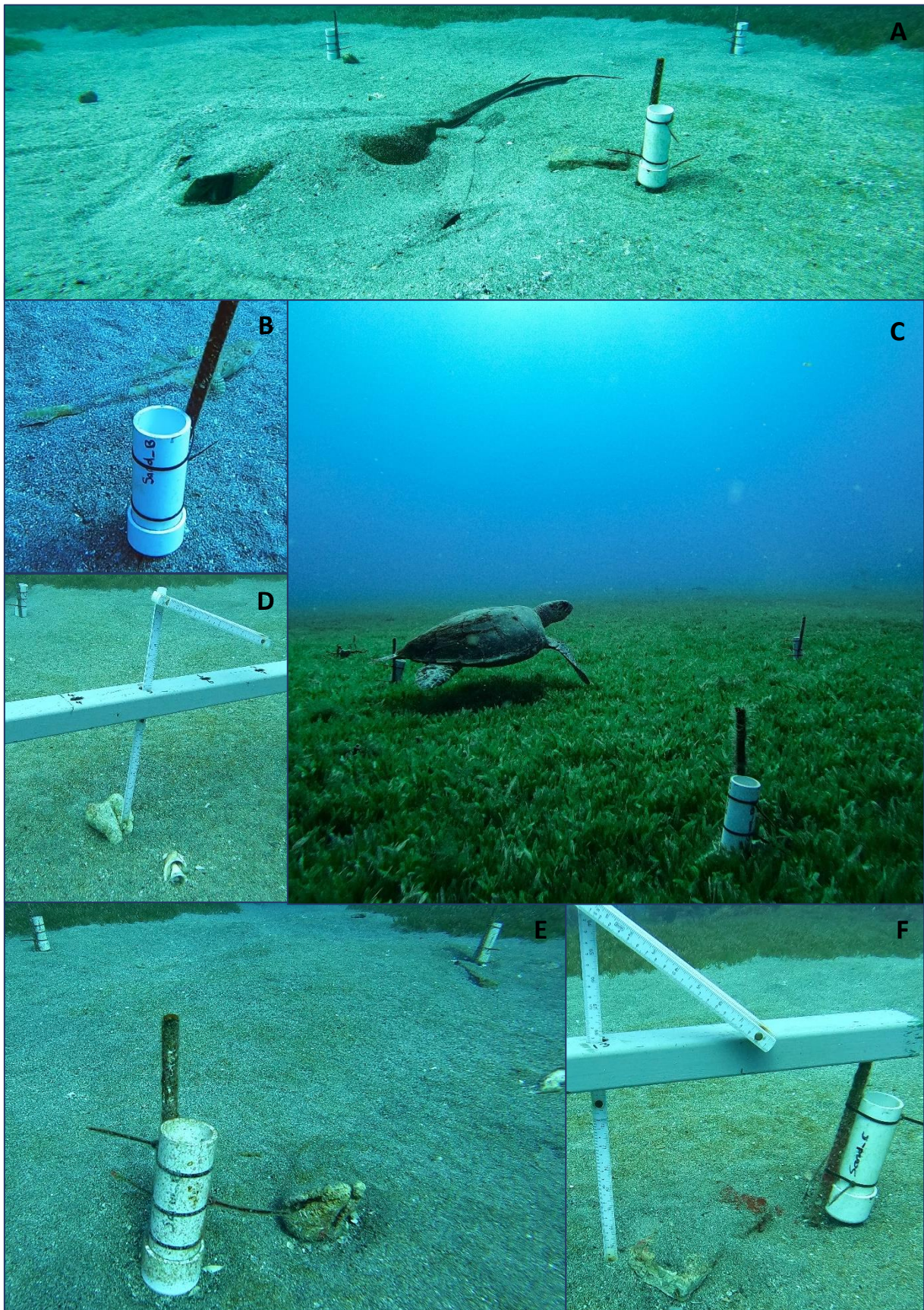
Observations in/around the triangle

Figure E: Observations of biota or objects in/around the rebar triangles. A = Stingray; B = Fish behind the sediment trap; C = Turtle at seagrass triangle; D = Shell along one triangle side; E = Conch shell near one sediment trap; F = Brick in front of sediment trap, which has been there during the entire study period.
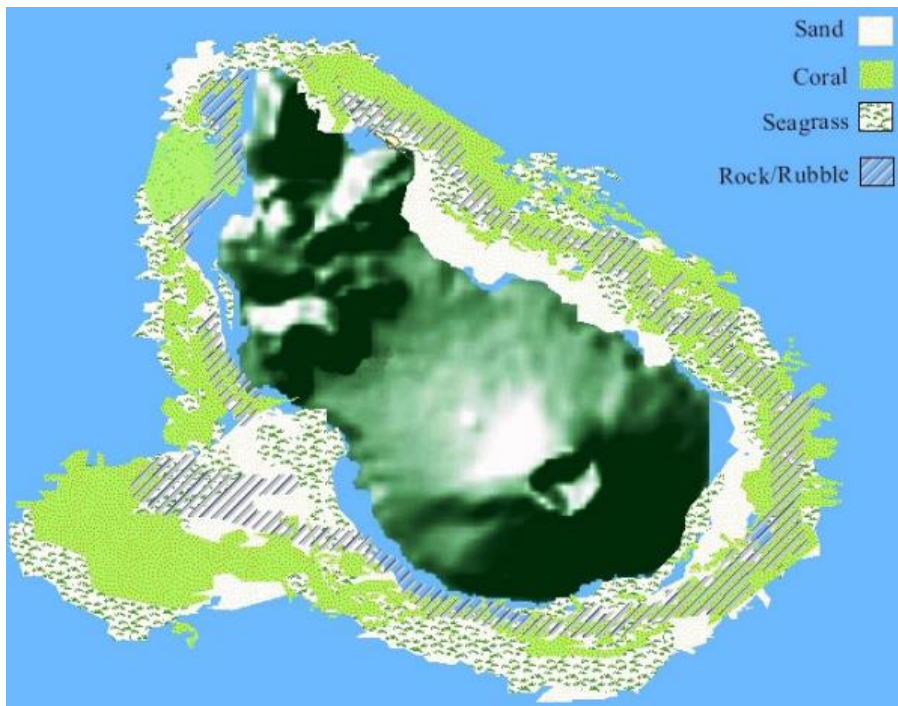
Appendix III: Marine habitat maps

Figure F: Distribution of marine habitats around St. Eustatius as presented by MacRae & Esteban (2007).
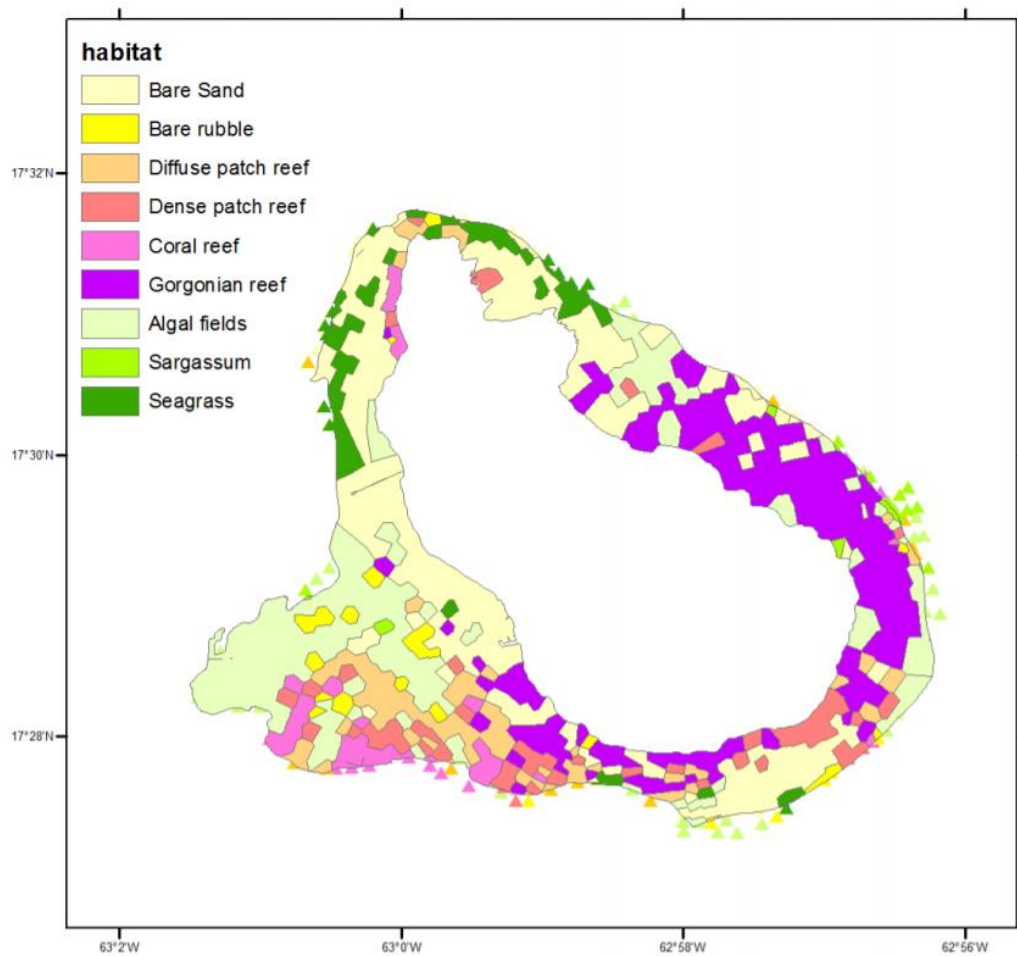

Figure G: Marine habitat map of St. Eustatius in 2014, as presented by Debrot, et al (2014).
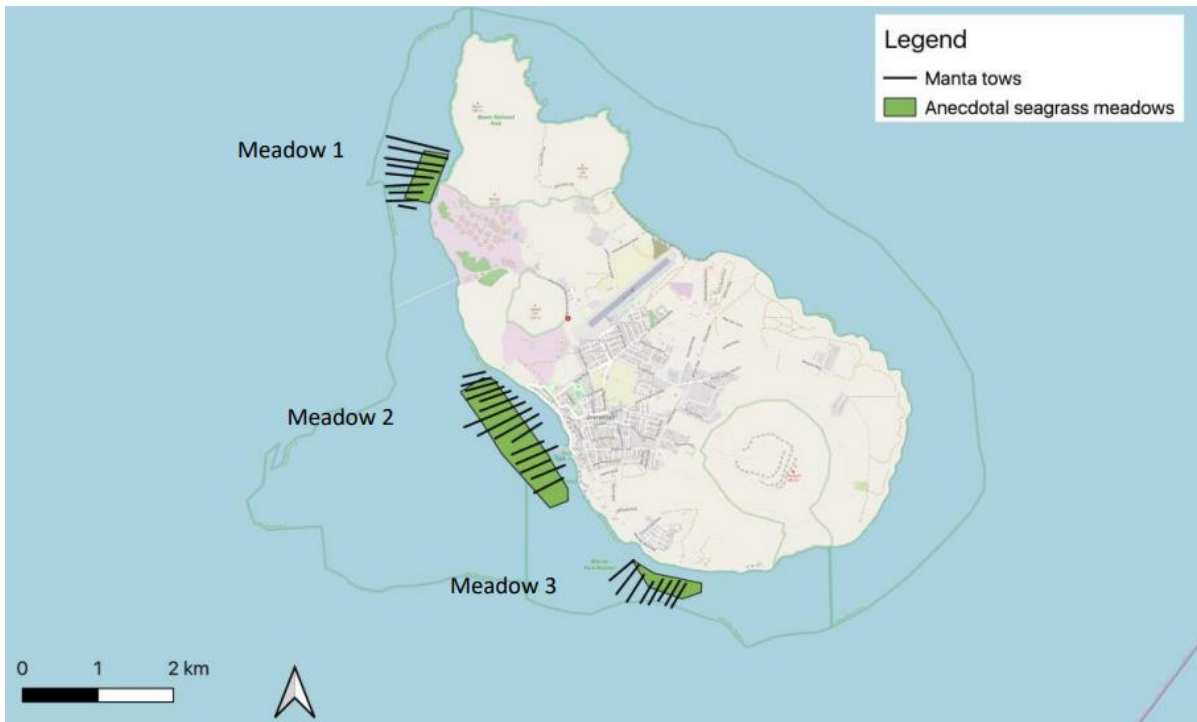
Figure H: Anecdotal seagrass meadows that were verified in 2020 by van Weert & van Wijk (2020).